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Climatic and management determinants of large herbivore production in semiarid grassland☆

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A B S T R A C T

Knowledge of climatic and management influences on large herbivore production (LHP, kg ha^{-1}) is needed for low productivity, semiarid grasslands to address potential consequences of both increasing climate variability and the need to increase animal protein for human consumption. Here, we evaluate the influence of climatic variability and herbivore density on LHP in semiarid grassland using a unique long-term (80 years: 1939–2018) grazing study with three grazing intensities based on forage utilization (light, moderate and heavy). Seasonal variation in precipitation, but not temperature, was the primary influence on LHP. Winter (October-March) and spring (April-June), but not summer (July-September), precipitation during the current year positively influenced LHP across the 3 grazing intensities, whereas prior growing season (prior April-September) precipitation was consistently a negative influence. Although spring precipitation was the most influential seasonal weather variable for LHP, the effect of winter precipitation closely followed under all three grazing intensities, suggesting that non-growing season precipitation is essential for soil water storage to initiate production of sufficient high-quality forage in the subsequent grazing season, resulting in a positive feedback on LHP. A key finding from our analysis was that the effect of summer precipitation is smaller than the combined effects of winter and spring precipitation. As such, much of the variation in LHP can be predicted by seasonal weather parameters that are known early in the growing season. The magnitude of seasonal precipitation effects on LHP was greatest for heavy grazing; consequently LHP with heavy grazing is more reliant on primary production produced in the current year to increase LHP as forage quantity is more limiting than forage quality. Moreover, stability of LHP across years (range: 7.5 to 34.6 kg ha^{-1}) was less with heavy grazing, which results in "boom-bust" economics that threaten sustainability of operations. Management adaptations to mitigate climatic variability, therefore, will be most necessary and advantageous when land managers employ heavy grazing intensities. Despite the substantial interannual variability in precipitation that characterizes semiarid grasslands, our results show that proactive flexibility by land managers in adjusting grazing management decisions to seasonal precipitation amounts forecasted for the winter and spring seasons would reduce enterprise risk and improve confidence in decision-making, profitability, production efficiency and environmental sustainability from semiarid grasslands.

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1. Introduction

Understanding climatic and management determinants on large herbivore production (LHP, kg ha^{-1}) in semiarid grasslands is important for examining potential consequences of increasing climate variability (e.g., Janzen, 2009; IPCC, 2012; Conant et al., 2018), as well as meeting the need to increase animal protein for an increasing global population (FAO, 2011). Yet, long-term (> 20 years) data sets from which relationships can be derived regarding climatic and management influences on LHP are sparse (Briske et al., 2011) despite the fact that semi-arid grasslands constitute 28 % of the world's grassland ecosystems (White et al., 2000). The paucity of studies addressing both climatic and management determinants on LHP has limited modeling efforts that could enhance strategic planning and reduce risk (e.g., Andales et al., 2005, 2006; Derner et al., 2012, but see Boone and Wang, 2007), and has restricted broader interpretative ability for grasslands around the world within the context of climate change and sustainability (Craine et al., 2009; Nardone et al., 2010; Henry et al., 2012; Moore and Ghahramani, 2013; Derner et al., 2018).

Effects of precipitation on primary production have been well investigated in semiarid grasslands (Lauenroth and Sala, 1992; Milchunas et al., 1994; O'Connor et al., 2001; Khumalo and Holecheck, 2005; Derner and Hart, 2007; Smart et al., 2007; Bai et al., 2008; Derner et al., 2008a; Ma et al., 2010; Sala et al., 2012), in mesic grasslands (Craine et al., 2010a, 2012), and across precipitation gradients (Yang et al., 2008; Hsu et al., 2012, Petrie et al., 2018). Moreover, manipulations of precipitation amount and timing on primary production (Fay et al., 2008, 2011, Heisler-White et al., 2008, 2009, Evans et al., 2011; Thomey et al., 2011; Cherwin and Knapp, 2012; Byrne et al., 2013) have provided additional valuable insight to effects of rainfall event size and frequency, and drought impacts on primary production. Variability in annual primary production of semiarid grasslands is mostly explained by seasonal precipitation in the current year (e.g., Milchunas et al., 1994; Derner and Hart, 2007; Derner et al., 2008a) as well as prior year precipitation (Lauenroth and Sala, 1992; Oesterheld et al., 2001; Ma et al., 2010; Sala et al., 2012), as fluctuations of primary production are buffered if wet, more productive years alternate with dry, less productive years, and they are amplified if wet or dry sequences of several years occur (Oesterheld et al., 2001). Management effects on primary production demonstrate that increased grazing intensity reduces production (Milchunas et al., 1994; Derner and Hart, 2007; Briske et al., 2011). Evaluation of both climatic and management effects on primary production, however, is limited to Irisarri et al. (2016) and the global review of Milchunas and Lauenroth (1993). Furthermore, the linkage between primary production and LHP is unclear as LHP may or may not follow primary production due to factors such as forage quality and timing of production in association with animal demand.

Seasonal (e.g., winter, spring and summer) precipitation positively affected LHP in semiarid grasslands with moderate productivity > 1400 kg ha^{-1} (Derner et al., 2008b; Reeves et al., 2013a, b, 2014), which cover 51 % of the Great Plains (Augustine et al., 2019), and in mesic grasslands with high productivity, > 4000 kg ha^{-1} (e.g., Craine et al., 2009, 2013). Spring temperatures also influenced LHP in semiarid grasslands with moderate productivity > 1400 kg ha^{-1}, with cooler temperatures beneficial (MacNeil and Vermeire, 2012; Reeves et al., 2013a, 2013b, 2014). Moreover, forage quality for ruminants declines with increasing temperatures and decreasing precipitation, with predictions for ruminants to experience greater nutritional stress with future climates (Craine et al., 2010b; Augustine et al., 2018). For low productivity (< 1000 kg ha^{-1}), semiarid grasslands, however, the linkage of climatic determinants on LHP has been little studied despite the fact that such low productivity grasslands cover 26 % of the Great Plains (Augustine et al., 2019). Conversely, a substantial body of literature has examined management effects on LHP. For example, LHP increases until limitations in forage availability due to management reduce intake and/or increases energy output in foraging activity, resulting in decreased productivity (Bement, 1969; Hart et al., 1988; Manley et al., 1997; McCollum et al., 1999; Derner et al., 2008b; Briske et al., 2011). Interactions between climatic and management determinants, though, have received less attention (but see Irisarri et al., 2019).

The influence of environmental conditions on LHP have been qualitatively reviewed (Ames, 1980), and modeling efforts have addressed both direct and indirect effects of climate change on LHP (e.g., Hanson et al., 1993; Andales et al., 2005; Mader et al., 2009; Ritten et al., 2010; Torell et al., 2010; Bastian et al., 2018). Yet, these models are limited by the inadequate data regarding direct, quantitative influences of climate and management on LHP. Providing increased capacity through inclusion of data to these models and associated decision support systems (e.g., Great Plains Framework for Agricultural Resource Management, GPFARM, Shaffer et al., 2000), would enhance decision making for land managers (Derner et al., 2012). For example, applications on mobile devices for land managers that integrate predictions of climatic and management determinants on LHP with forecasted seasonal precipitation and temperature available online (e.g., forecasts from National Weather Service Climate Prediction Center of the National Atmospheric and Oceanic Administration [NOAA], http://www.nws.noaa.gov/predictions.php) would optimize utility of decision support tools (Derner et al., 2012; Derner and Augustine, 2016; Peck et al., 2019).

Here, we evaluate how both climate and management influence LHP using a long-term (80 years: 1939–2018) record of yearling weight gains in a semiarid grassland under three grazing intensities: light, moderate and heavy (see methods). We used this unique, long-term data set to test two hypotheses: (1) spring (April-June) and summer (July-September) precipitation are the primary climatic determinants for LHP in semiarid, shortgrass steppe, with limited influence of winter (prior October to current March) and prior growing season (prior April to prior September) precipitation, or temperature, and (2) LHP from different grazing management intensities is differentially influenced by climatic determinants with LHP more sensitive to climatic determinants under heavy compared to moderate or light grazing.

2. Materials and methods

2.1. Site description

The USDA-Agricultural Research Service Central Plains Experimental Range (CPER), which is a Long-Term Agroecosystem Research network site (LTAR, https://ltar.ars.usda.gov/), is located in north-central Colorado, USA (40°49′ N, 107°46′ W). Mean annual precipitation (1939–2018) is 340 mm (Table 1), with 40 % of this occurring from April through June, and 35 % from July through September. Mean annual aboveground net primary productivity (ANPP ± 1 standard deviation) is 960 ± 280 kg ha^{-1} (Petrie et al., 2018). Major soils on the study pastures were Ascalon fine sandy loam (fine-loamy mixed mesic Aridic Argiustoll), Renohill fine sandy loam (fine montmorillonitic mesic Ustollic Haplargid), Nunn loam, and clay loam (fine, montmorillonitic mesic Aridic Argiustoll). The main ecological site is Loamy Plains (Site ID: R067BY002CO, https://esis.sc.egov.usda.gov/). The perennial C_4, shortgrass blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag ex Griffiths) is the dominant species and increases as grazing intensity increases, as does the perennial C_4 shortgrass buffalograss (*B. dactyloides* [Nutt.] J.T. Columbus). Conversely, the perennial C_3 midheight grasses western wheatgrass (*Pascopyrum smithii [Rydb] A. Love*) and needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth ssp. *comata*) decrease with increasing grazing intensity (Hart and Ashby, 1998). Needleleaf sedge (*Carex duriuscula* C.A. Mey) is another important perennial C_3 graminoid. Scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.) is the primary forb and plains pricklypear (*Opuntia polyacantha* Haw) is frequent.

Table 1
Summary of model averaged estimates by grazing intensity (light, moderate and heavy) for large herbivore production, LHP (kg ha^{-1}). Sample sizes (n) reported in grazing intensity column headings represent the number of models averaged (i.e. number of models with Δ AICc $\leq$ 2). Precipitation values (P) are on mm scale; average temperatures (T) are on °C scale. Standard errors are unconditional standard errors that incorporate uncertainty both in model selection and the parameter estimate. Non-standardized and standardized values are shown; non-standardized parameters were used for predictions in Fig. 1. Blank cells within table indicate that those parameters were not part of the models with Δ AICc $\leq$ 2.

	Light (n = 3)				Moderate (n = 5)				Heavy (n = 4)			
	Non-standardized		Standardized		Non-standardized		Standardized		Non-standardized		Standardized	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	3.2984	2.3531			6.3230	6.5831			14.2849	8.4884		
Entry wt	0.0367	0.0082	0.2623	0.0584	0.0373	0.0105	0.2665	0.0751	0.0309	0.0155	0.2204	0.1104
Summer P	0.0042	0.0064	0.0380	0.0577								
Spring P	0.0138	0.0055	0.1403	0.0563	0.0149	0.0271	0.2172	0.0760	0.0400	0.0114	0.4068	0.1156
Spring T					−0.6004	0.5647	−0.0952	0.0784	−0.9103	0.5130	−0.2020	0.1138
Winter P	0.0116	0.0122	0.0573	0.0603	0.0332	0.0151	0.1642	0.0747	0.0623	0.0219	0.3085	0.1086
Prior growing season P	−0.0076	0.0039	−0.1118	0.0565	−0.0079	0.0048	−0.1160	0.0701	−0.0155	0.0071	−0.2276	0.1041

2.2. Experiment description

The study began in 1939 on three 129.5 ha pastures. Of these 3 pastures, one each was stocked annually at a low, moderate, and heavy stocking rate as follows. From 1939 through 1964, annual stocking rates were set to achieve an average annual apparent utilization (peak standing forage biomass minus end-of-grazing-season residual forage biomass) of 20 % (light), 40 % (moderate) and 60 % (heavy). From 1965–2018, grazing treatments were imposed to leave 500 kg ha^{-1} (light), 335 kg ha^{-1} (moderate), and 225 kg ha^{-1} (heavy) of ungrazed herbage at the end of the grazing season (Hart and Ashby, 1998). These values correspond with the threshold level of residual herbage requiring the provision of emergency feed (225 kg ha^{-1}, heavy), the amount of residual herbage deemed optimal for sustained animal production (335 kg ha^{-1}, moderate), and the amount of residual herbage where underutilization of available forage results in similar economic returns as the heavy grazing treatment (500 kg ha^{-1}, light; Bement, 1969). Using average forage production values reported by Milchunas et al. (1994) on this study from 1939 to 1990, apparent utilization in the three treatments increased for the 1965–2018 period; the heavy treatment increased to 65 % (average production of 570 kg ha^{-1}, residue of 225 kg ha^{-1}), moderate to 51 % (average production of 680 kg ha^{-1}, residue of 335 kg ha^{-1}) and light intensity to 29 % (average production of 710 kg ha^{-1}, residue of 500 kg ha^{-1}).

British breed yearlings were used throughout the study. The grazing season typically began in May and ended in October but was shorter in some years when adaptive management was employed for removal of cattle prior to the end of the grazing season when threshold triggers of desired use (1939–1964) or residual forage values (1965–2018) were met (Appendix A). Yearlings were weighed prior to and following the grazing season, after being held overnight without feed or water. Large herbivore production (kg ha^{-1}) was calculated by multiplying animal weight gain (kg/head) by the number of yearlings in the respective intensity treatment and dividing the product by the pasture area. Livestock data from years 1954, 1955, 1957, 1962-64, 1969, and 1982 were not used as the cattle were rotated among treatments across months in those years rather than remaining on the same treatment for the entire grazing season (1957, 1962–1964, 1969) or were not stocked in each grazing intensity treatment (1954,1955, 1982) (Appendix A).

2.3. Statistical analyses

The influence of seasonal variation in precipitation and temperature on LHP at each grazing intensity was evaluated using model averaging methodology (Burnham and Anderson, 2002). The fitting and averaging of multiple competing models accounts for model uncertainty and selection procedure bias, thereby preventing selection of a poor model (Wang et al., 2009). Model averaging tends to produce models with excellent predictive abilities, which can often be more accurate than "best-model" strategies (Burnham and Anderson, 2004). For reviews of model averaging, see Burnham and Anderson (2004) and Wang et al. (2009). To minimize spurious effects and over-fitting of the data, our selected model structure was based on parsimony and *a priori* hypotheses (Anderson et al., 2001). The selected model structure was also chosen to maximize utility for decision support tools (Derner et al., 2012), as it aggregated climatic data into three-month periods to parallel the three-month weather forecasts available from the National Atmospheric and Oceanic Administration (NOAA) (http://www.nws.noaa.gov/predictions.php). We aggregated current-season weather data into three-month periods because this length of precipitation period was shown by Derner et al. (2008b) to be a better predictor of LHP than individual months in a nearby northern mixed-grass prairie. We considered models with up to eight possible weather variables (Reeves et al., 2013a,b, 2014). Predictors were total precipitation (mm) and average temperature (°C; average of mid-point between maximum and minimum daily temperatures) for spring (April – June) and summer (July – September) of the current grazing season, precipitation x temperature interaction terms for spring and summer of the current grazing season, precipitation during the prior winter (October – March), and precipitation during the prior growing season (prior April – prior Sept). Given that initial weight of cattle at the start of the grazing season increased over the seven-decade time period (Appendix B), we accounted for these changes by including average weights at the start of each grazing season (entry weight) in the LHP models following Reeves et al. (2013a,b, 2014).

Models were selected to best correspond to the goals of the study (i.e., to maximize utility of results for inclusion in decision support tools) rather than to provide the best fit or most intricate ecological model possible. For each model, we calculated AICc, Δ AICc (relative to the model with the lowest AICc), and the model's Akaike weight relative to the overall model set. Given that models with ΔAICc of 0–2 represent those with substantial empirical support (Burnham and Anderson, 2002), we applied model averaging to the subset of models with ΔAICc $\leq$ 2 to calculate final model parameter (coefficient) estimates and standard errors for model parameter for each grazing intensity. For each parameter estimate we calculated the unconditional standard error, which incorporates uncertainty both in model selection and in the parameter estimate conditioned on each model, following Burnham and Anderson (2002, pg. 162). We present both standardized and non-standardized model parameter estimates. Standardized estimates permit direct comparisons of time period and temperature and precipitation (as temperature (°C) and precipitation (mm) values are on different scales), whereas the non-standardized coefficients have utility for use in models for predictive purposes (i.e., inclusion in decision support tools), as well as to compare results to other similar long-term datasets (Reeves et al., 2013a, b, 2014). All statistical tests were conducted using R statistical software (R Development Core Team, 2019).

3. Results

3.1. Entry weights of yearlings

Entry weights increased from approximately 175 kg hd^{-1} in the early 1940s to near 250 kg hd^{-1} by the mid-1980s, with sharp increases during the latter years of that decade (Appendix B). Entry weights have averaged 285 kg hd^{-1} over the last decade. As noted above, due to the increase in entry weights over the course of this study, we included entry weight as a covariate in all models.

3.2. Seasonal precipitation and temperatures

Considerable variability occurred across the seven decades for the seasonal precipitation and temperature variables (Appendix A). Current summer (July-September) precipitation ranged ten-fold from 27.7 mm (1943) to 292.1 mm (1997), and average summer temperature ranged from 15.9 °C (1986) to 21.2 °C (1980). The lowest amount for current spring (April-June) precipitation was 53.6 mm (2006), whereas 348.2 mm (1967) was the maximum value, a 6.5-fold range. For average temperature during the spring, values ranged from 8.6 °C (1983) to 15.4 °C (1990). Winter (prior October to current March) precipitation was lowest in 1966 with 8.6 mm and highest in 1980 with 146.8 mm. In 1940, prior grazing season (prior April to prior September) precipitation was the lowest (87.6 mm), and in 2000 it was the highest (512.6 mm).

3.3. Large herbivore production

3.3.1. Light grazing

Under light grazing, LHP increased with increasing precipitation in winter and spring of the current-year and decreased with increasing precipitation in the prior year (Table 1, Fig. 2). LHP was not sensitive to summer or spring temperature and summer precipitation. The largest effect sizes on LHP were from spring and prior growing season precipitation, followed by winter precipitation.

3.3.2. Moderate grazing

As with light grazing, spring and winter precipitation positively influenced LHP, and prior growing season precipitation had a negative relationship (Table 1, Fig. 2). Moreover, neither summer precipitation nor summer temperature influenced LHP, while increasing spring temperature had a negative relationship. The weather variable with the largest effect on LHP was spring precipitation, followed by winter precipitation, prior growing season precipitation and spring temperature. The magnitude of seasonal precipitation effect sizes on LHP was higher for moderate than light grazing in terms of effects of precipitation in winter (187 % greater) and spring (55 % greater), whereas the effect of prior growing season precipitation on LHP was similar between moderate and light grazing.

3.3.3. Heavy grazing

Similar to the light and moderate grazing intensities, seasonal variation in precipitation during the winter and spring of the current year positively influenced LHP, and prior growing season precipitation negatively influenced LHP (Table 1, Fig. 2). Consistent with moderate grazing, spring precipitation had the largest effect size for LHP, followed by winter, prior growing precipitation and spring temperature (Table 1).

Comparing heavy to moderate grazing, the magnitude of seasonal precipitation effect sizes on LHP was higher with heavy grazing for spring (47 % greater), winter (88 % greater) and prior growing season (96 % greater) precipitation, whereas the lack of effect of summer precipitation on LHP was similar between heavy and moderate grazing. A 122 % increase in the effect size of spring temperature indicated LHP under heavy grazing was sensitive to increasing spring temperature. For comparisons of heavy to light grazing, the magnitude of seasonal precipitation effect sizes on LHP were much higher than observed for the heavy vs. moderate comparisons. Effect sizes for winter (438 % greater), spring (190 % greater), and prior growing season (104 % greater) precipitation were all higher with heavy compared to light grazing indicating that sensitivity of LHP to seasonal precipitation is greatest with heavy grazing. The range of LHP increased from 16.1 kg ha^{-1} (range: 3.6–19.7) and 23.8 kg ha^{-1} (range: 4.2–28.0) under light grazing and moderate grazing intensity, respectively, to 27.1 kg ha^{-1} (range: 7.5–34.6) under heavy grazing intensity; indicating greater instability of LHP with heavy grazing.

4. Discussion

Interannual variation in seasonal precipitation, but not temperature, was the primary determinant of large herbivore production (LHP) in semiarid grassland. Current year (winter and spring) seasonal precipitation levels were positive influences on LHP for all three grazing management treatments. This partially supports our hypothesis that spring (April-June) and summer (July-September) precipitation would be the primary climatic determinants for LHP. Although we had hypothesized that winter (prior October to current March) would have limited influence on LHP, winter precipitation consistently influenced LHP with increasing magnitude across our grazing intensity gradient. We infer from this finding that non-growing season precipitation is essential for soil water storage to initiate production of sufficient high quality forage for animals coming out a season where forage quality and quantity are lowest, and in a grassland where cool-season forage is low compared to dominant warm-season species (Milchunas et al., 1994), including a diversity of cool-season forbs (Eck et al., 1975) in the subsequent grazing season, resulting in a positive feedback on LHP. A key finding from our analysis was that even though summer precipitation accounts for 35 % of the total annual precipitation and can be very difficult to predict due to monsoonal influences, the influence of summer precipitation on LHP is minimal relative to spring and winter precipitation. As such, much of the variation in LHP can be predicted by seasonal weather parameters that are known early in the growing season.

Prior research demonstrated that spring precipitation is important in controlling primary production (Milchunas et al., 1994; Derner et al., 2008a) and that prior year conditions can have legacy effects on current-year primary production (Lauenroth and Sala, 1992; Oesterheld et al., 2001; Petrie et al., 2018). However, these studies did not identify the role of fall-winter precipitation or evaluate the relative effects of each season on LHP. Our results show that livestock producers can predict a substantial amount of variation in annual LHP from seasonal weather conditions that are known to them early in the growing season as well incorporating forecasted seasonal precipitation available online (e.g., forecasts from National Weather Service Climate Prediction Center of the National Atmospheric and Oceanic Administration [NOAA], http://www.nws.noaa.gov/predictions.php) in a decision support framework (e.g., Derner et al., 2012; Peck et al., 2019). Moreover, our finding that summer precipitation (Jul – Sep) had a weak influence on LHP across our three grazing management treatments agrees with work in the Northern Great Plains (Reeves et al., 2014). Collectively, results of these LHP studies suggests end of summer seasonal precipitation forecasts have minimal utility for yearling beef steer production management. We surmise the low quality- forage available in late summer is adequate to meet basic nutritional maintenance requirements, but not sufficient to promote growth (*see* Bohman, 1955).

Sensitivity of LHP to seasonal climatic variability increased with increasing grazing intensity as evidenced by greater effect sizes for the

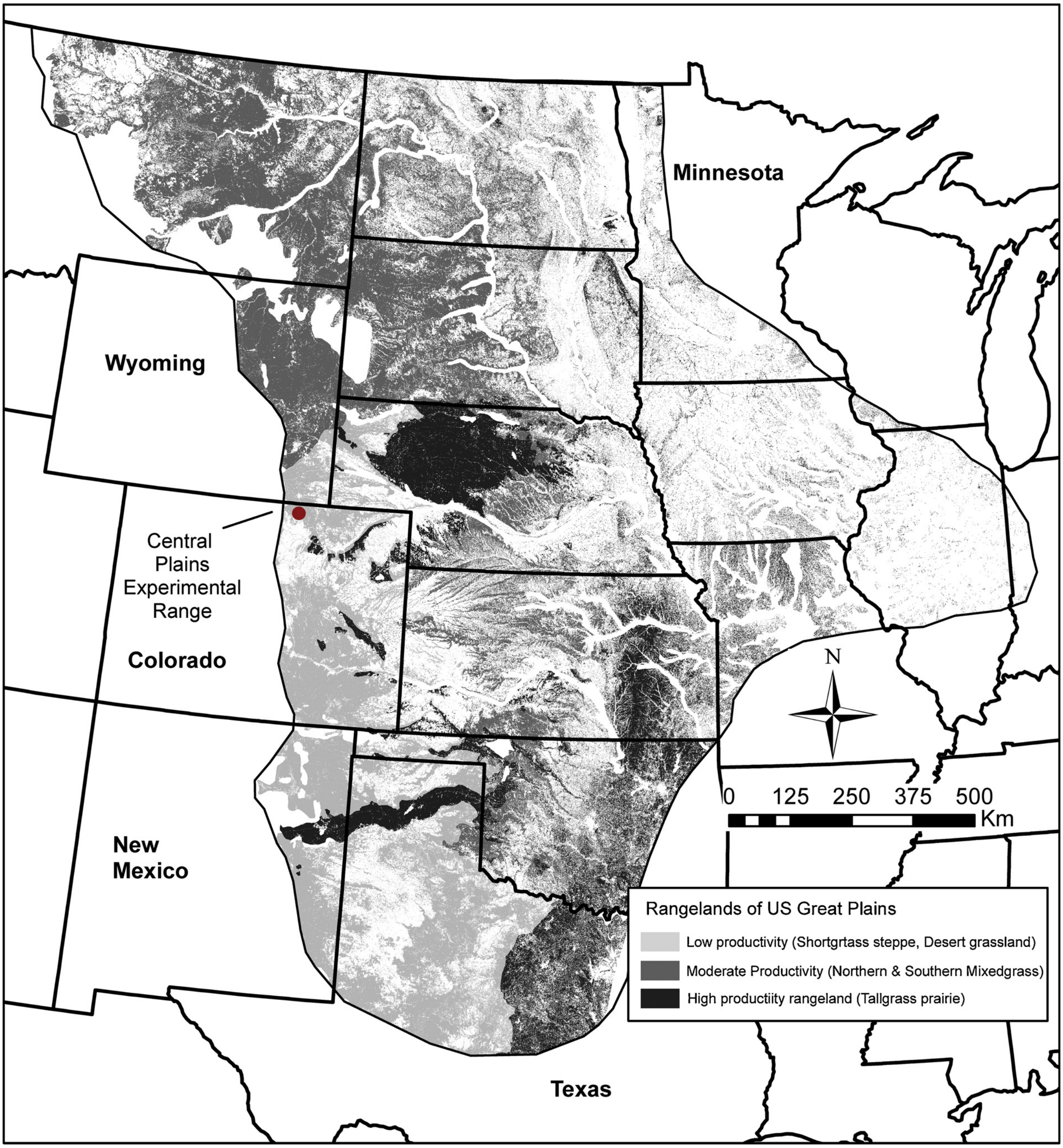

Fig. 1. Map of the United States Great Plains showing the geographic areas of the high, moderate, and low forage productivity including the location of the Central Plains Experimental Range, Nunn, Colorado, USA. Map modified from Augustine et al., (*in press*).

seasonal precipitation values with heavy compared to moderate and light grazing. This supports our hypothesis that LHP from different grazing management treatments would be differentially influenced by climatic determinants. Management adaptations to mitigate climatic variability, therefore, will be most necessary and advantageous for producers employing heavy grazing intensities. Alternatively, the lower sensitivity of LHP to seasonal precipitation with light grazing intensities infers higher risk avoidance approaches to management, and therefore a greater resiliency, with an increasingly variable climate. Heavy grazing reduces carryover residual forage to minimum levels (225 kg ha^{-1}) to begin the following grazing season which exacerbates the reliance of LHP on current growing season primary production. Therefore, dependence on winter and spring precipitation increases for conditions conducive for vegetation growth. Grazers in the heavy grazing management intensity are consequently more reliant on primary production produced in the current year to increase LHP as forage quantity is more limiting than forage quality (Milchunas et al., 1995). Moreover, this reduces the stability of LHP across years, leading to widely variable production (7.5 to 34.6 kg ha^{-1}; Appendix A) over the seven decades. As such, this variability is problematic for managing enterprise risk by land managers and results in “boom-bust” LHP and associated economics that threaten sustainability of operations (Irisarri et al., 2019; Peck et al., 2019). Conversely, the lower utilization and higher residual forage carryover from prior year in the light grazing intensity provides a buffer to this inherent variability in primary production (Lauenroth and Sala, 1992; Milchunas et al., 1994).

Our results agree with previously established positive influences of winter and spring seasonal precipitation on LHP in northern mixed-grass prairie (Derner et al., 2008b; Reeves et al., 2013a,b, 2014). In addition, our results of negative influences of prior growing season

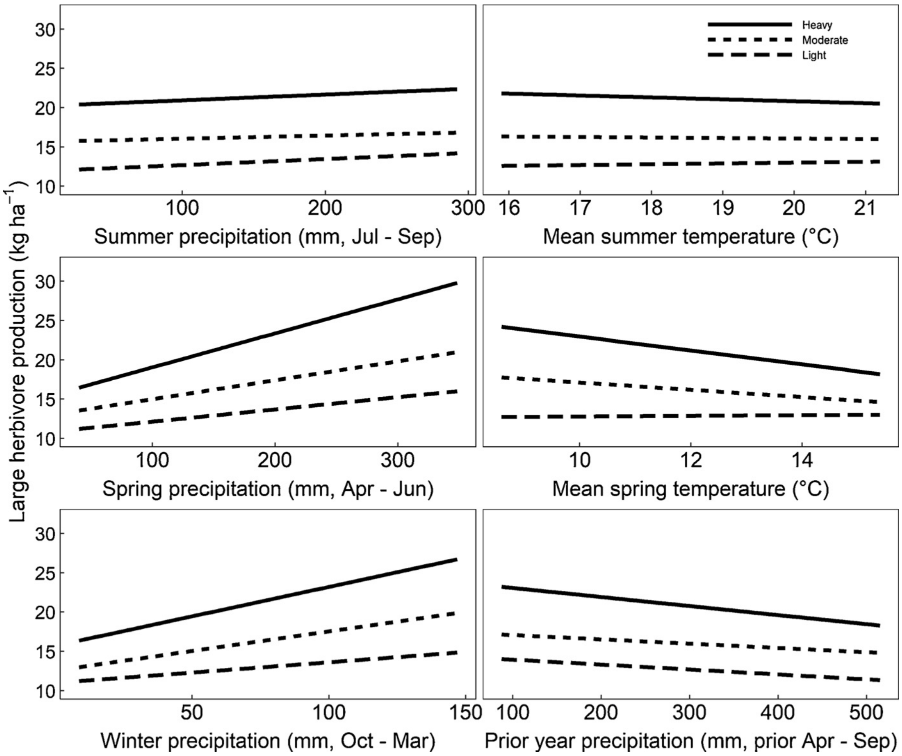

Fig. 2. Predicted Large Herbivore Production (LHP, kg ha^{-1}) under light, moderate and heavy grazing intensities as a function of six weather parameters. In each panel, the range of values over which predictions are shown on the y-axis represents the minimum and maximum values recorded over the seven decade study period. See Table 1 for model parameters and standard errors for each grazing intensity.

precipitation on LHP agree with prior findings by Reeves et al. (2013a) with yearlings in northern mixed-grass prairie. These findings provide clear empirical support for the idea that low-quality forage consisting of remaining plant material from the prior growing season has an important negative legacy effect on grazers in semiarid grasslands (Vavra et al., 1973).

There is a large base of literature for climatic determinants on primary production in semiarid grasslands (e.g., Lauenroth and Sala, 1992; Milchunas et al., 1994; O'Connor et al., 2001; Khumalo and Holecheck, 2005; Derner and Hart, 2007; Smart et al., 2007; Bai et al., 2008; Derner et al., 2008a; Ma et al., 2010). Current cool-season (Milchunas et al., 1994; Derner et al., 2008a) and prior year precipitation (Lauenroth and Sala, 1992; Oesterheld et al., 2001; Sala et al., 2012; Petrie et al., 2018) are determinants of primary production for semiarid grasslands. The strong influence of precipitation variability in multiple seasons on primary (Lauenroth and Sala, 1992; Oesterheld et al., 2001; Sala et al., 2012) and secondary production (Vavra et al., 1973; Reeves et al., 2013a, this study) in semiarid grasslands suggests that cumulative patterns of soil water infiltration and storage from precipitation events of varying sizes during each season (Sala and Lauenroth, 1982) merit additional attention for efforts to forecast livestock production based on current conditions and near-term weather forecasts. Such efforts would also benefit from improved fundamental understanding of linkages among characteristics of seasonal precipitation events, soil moisture storage, primary productivity, and secondary production. To our knowledge, this study and Reeves et al. (2013a,b, 2014) are the first to evaluate the role of winter precipitation on secondary production in rangeland systems. Each study showed significant effects of winter precipitation on LHP; thus, our finding was not unique to our study site but does suggest this phenomenon may more common than originally expected.

Our result that yearling entry weight increased over the seven decades agrees with previously established trends in livestock production elsewhere in the Great Plains, which have been attributed to genetic selection for larger cow size (Galyean et al., 2011; Reeves et al., 2013a). Although larger size implies individuals will yield more beef at the end of the grazing season (Galyean et al., 2011), this desired outcome is not always realized in variable production environments such as rangelands where high year-to-year variability in forage production is common. For example, Scasta et al. (2015) demonstrated weight gain efficiency of small yearlings outperformed moderate and large yearlings in semi-arid rangelands in southeastern Wyoming during the 2012 drought. Thus, this trend of increasing yearling entry weight likely has negative implications for future LHP and rangeland management because grazing lands are forecasted to experience higher variability in forage production due to a higher frequency of drought (Derner et al., 2018).

Similar relationships, but differential levels of importance and effect sizes, regarding the influence of climatic determinants on LHP for the three grazing management intensities has clear implications for land managers in semiarid grasslands. For example, land managers could make grazing management decisions by April 1 for the current grazing season with knowledge of the winter (prior October to March 31) and predicted spring (April-June) precipitation amounts from available web resources such as the Climate Prediction Center (http://www.cpc.ncep.noaa.gov/). Because winter precipitation was the second-most robust predictor variable for both moderate and heavy grazing, which constitute the majority of management on grasslands in the North American Great Plains (Dunn et al., 2010), land managers could reduce risk associated with LHP, provide increased confidence in decision-making for ranchers, and increase profitability compared to waiting for the beginning of the grazing season to make stocking rate adjustments. Second, incorporation of these relationships between seasonal precipitation and LHP into decision support systems would enhance strategic planning (between years) and reduce risk in highly variable environments to improve sustainability (Derner et al., 2012; Peck et al., 2019). Coupling the observed relationships for LHP and seasonal precipitation with downscaled climatic predictions in decision support systems would facilitate contingency planning associated with precipitation variability. This would lead to improvements in production capacity, production efficiencies and environmental sustainability from semiarid grasslands.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.106761.

References

Ames, D., 1980. Thermal environment affects production efficiency of livestock. BioSci. 30, 457–460.
Andales, A.A., Derner, J.D., Bartling, P.N.S., Ahuja, L.R., Dunn, G.H., Hart, R.H., Hanson, J.D., 2005. Evaluation of GPFARM for simulation of forage production and cow-calf weights. Rangel. Ecol. Manag. 58, 247–255.
Andales, A.A., Derner, J.D., Ahuja, L.R., Hart, R.H., 2006. Strategic and tactical prediction of forage production in northern mixed-grass prairie. Rangel. Ecol. Manag. 59, 576–584.
Anderson, D.R., Burnham, K.P., Gould, W.R., Cherry, S., 2001. Concerns about finding effects that are actually spurious. Wildl. Soc. Bull. 29, 311–316.
Augustine, D.J., Blumenthal, D.M., Springer, T.L., LeCain, D.R., Gunter, S.A., Derner, J.D., 2018. Elevated CO_2 induces substantial and persistent declines in forage quality irrespective of warming in mixedgrass prairie. Ecol. Appl. 28, 721–735.
Augustine, D.J., Davidson, A., Dickinson, K., Van Pelt, W., 2019. 2020. Thinking like a grassland: challenges and opportunities for biodiversity conservation in the Great Plains of North America. Rangel. Ecol. Manag. 73 in press.
Bai, Y., Wu, J., Xing, Q., Pan, Q., Huang, J., Yang, D., Han, X., 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecol. 89, 2140–2153.
Bastian, C.T., Ritten, J.P., Derner, J.D., 2018. Ranch profitability given increased precipitation variability and flexible stocking. J. Am. Soc. Farm Managers Rural Appraisers 81, 122–139.
Bement, R.E., 1969. A stocking-rate guide for beef production on blue-grama range. J. Range Manag. 22, 83–86.
Bohman, V.R., 1955. Compensatory growth of beef cattle: the effect of hay maturity. J. Anim. Sci. 14, 249–255. https://doi.org/10.2527/jas1955.141249x.
Boone, R.B., Wang, G., 2007. Cattle dynamics in African grazing systems under variable climates. J. Arid Environ. 70, 495–513.
Briske, D.D., Derner, J.D., Milchunas, D.G., Tate, K.W., 2011. An evidence-based assessment of prescribed grazing practices. In: Briske, D.D. (Ed.), Conservation Benefits of Rangeland Practices: Assessment, Recommendations, and Knowledge Gaps. United States Department of Agriculture, Natural Resources Conservation Service, pp. 21–74.
Burnham, K.P., Anderson, D.R., 2004. Multimodal inference – understanding AIC and BIC in model selection. Sociol. Methodol. Res. 33, 261–304.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer, New York, NY, USA, pp. 488.
Byrne, K.M., Lauenroth, W.K., Adler, P.B., 2013. Contrasting effects of precipitation manipulations on production in two sites within the central grassland region, USA. Ecosystem 16, 1039–1051.
Cherwin, K., Knapp, A., 2012. Unexpected patterns of sensitivity to drought in three semi-arid grasslands. Oecologia 169, 845–852.
Conant, R.T., Kluck, D., Anderson, M., Badger, A., Boustead, B.M., Derner, J., Farris, L., Hayes, M., Livneh, B., McNeeley, S., Peck, D., Shulski, M., Small, V., 2018. Northern Great Plains. In: In: Reidmiller, D.R., Avery, C.W., Easterling, D.R., Kunkel, K.E., Lewis, K.L.M., Maycock, T.K., Stewart, B.C. (Eds.), Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment Vol. II U.S. Global Change Research Program, Washington, DC. https://doi.org/10.7930/NCA4.2018. CH22.
Craine, J.M., Towne, E.G., Joern, A., Hamilton, R.G., 2009. Consequences of climate variability for the performance of bison on tallgrass prairie. Glob. Change Biol. 15, 772–779. https://doi.org/10.1111/j.1365-2486.2008.01769.x.
Craine, J.M., Towne, E.G., Nippert, J.B., 2010a. Climate controls on grass culm production over a quarter century in a tallgrass prairie. Ecology 91, 2132–2140.
Craine, J.M., Elmore, A.J., Olson, K.C., Tolleson, D., 2010b. Climate change and cattle nutritional stress. Glob. Change Biol. 16, 2901–2911.
Craine, J.M., Nippert, J.B., Elmore, A.J., Skibbe, A.M., Hutchinson, S.L., Brunsell, N.A., 2012. Timing of climate variability and grassland productivity. PNAS 109, 3401–3405.
Craine, J.M., Towne, E.G., Tolleson, D., Nippert, J.B., 2013. Precipitation timing and grazer performance in tallgrass prairie. Oikos 122, 191–198.
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.
Derner, J.D., Hess, B.W., Olson, R.A., Schuman, G.E., 2008a. Functional group and species responses to precipitation in three semi-arid rangeland ecosystems. Arid Land Res. Manag. 22, 81–92.
Derner, J.D., Hart, R.H., Smith, M.A., Waggoner Jr., J.W., 2008b. Long-term cattle gain responses to stocking rate and grazing systems in northern mixed-grass prairie. Livest. Sci. 117, 60–69.
Derner, J.D., Augustine, D.J., Ascough II, J.C., Ahuja, L.R., 2012. Opportunities for increasing utility of models for rangeland management. Rangel. Ecol. Manag. 65, 623–631.
Derner, J.D., Augustine, D.J., 2016. Adaptive management for drought on rangelands. Rangel 38, 211–215.
Derner, J.D., Briske, D., Reeves, M., Brown-Brandl, T., Meehan, M., Blumenthal, D., Travis, W., Augustine, D.J., Wilmer, H., Scasta, D., Hencrickson, J., Volesky, J., Edwards, L., Peck, D., 2018. Vulnerability of grazing and confined livestock in the Northern Great Plains to projected mid and late-twenty-first century climate. Clim. Change 146, 19–32.
Dunn, B.H., Smart, A.J., Gates, R.N., Johnston, P.S., Beutler, M.K., Diersen, M.A., Janssen, L.L., 2010. Long-term production and profitability from grazing cattle in the Northern Mixed Grass Prairie. Rangel. Ecol. Manag. 63, 233–242.
Eck, H.V., McCully, W.G., Stubendieck, J., 1975. Response of shortgrass plains vegetation to clipping, precipitation, and soil water. J. Range Manag. 28, 194–197.
Evans, S.E., Byrne, K.M., Lauenroth, W.K., Burke, I.C., 2011. Defining the limit to resistance in a drought-tolerant grassland: long-term severe drought significantly reduces the dominant species and increases ruderals. J. Ecol. 99, 1500–1507.
FAO (Food and Agriculture Organization of the United Nations), 2011. The State of the World's Land and Water Resources for Food and Agriculture. Rome, Italy.
Fay, P.A., Kaufman, D.M., Nippert, J.B., Carlisle, J.D., Harper, C.W., 2008. Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. Glob. Change Biol. 14, 1600–1608.
Fay, P.A., Blair, J.M., Smith, M.D., Nippert, J.B., Carlisle, J.D., Knapp, A.K., 2011. Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. Biogeoscience 8, 3053–3068.
Galyean, M.L., Ponce, C., Schutz, J., 2011. The future of beef production in North America. Anim. Front. 1, 29–36.
Hanson, J.D., Baker, B.B., Bourdon, R.M., 1993. Comparison of the effects of different climate change scenarios on rangeland livestock production. Agric. Syst. 41, 487–502.
Hart, R.H., Ashby, M.M., 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. J. Range Manag. 51, 392–398.
Hart, R.H., Samuel, M.J., Test, P.S., Smith, M.A., 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. J. Range Manag. 41, 282–286.
Heisler-White, J.L., Knapp, A.K., Kelly, E.F., 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158, 129–140.
Heisler-White, J.L., Blair, J.M., Kelly, E.F., Harmoney, K., Knapp, A.K., 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Glob. Change Biol. 15 (12), 2894–2904.
Henry, B., Charmley, E., Eckard, R., Gaughan, J.B., Hegarty, R., 2012. Livestock production in a changing climate: adaptation and mitigation research in Australia. Crop Pasture Sci. 63, 191–202.
Hsu, J.S., Powell, J., Adler, P.B., 2012. Sensitivity of mean annual primary production to precipitation. Glob. Change Biol. 18, 2246–2255.
IPCC (Intergovernmental Panel on Climate Change), 2012. In: Field, C.B., Barros, V., Stocker, T.F., Qin, D., Kokken, D.J., Ebi, K.L., Mastrandrea, M.D., Mach, K.J., Plattner, G.K., Allen, S.K., Tignor, M., Midgley, P.M. (Eds.), Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. Cambridge University Press, Cambridge, pp. 582.
Irisarri, J.G., Derner, J.D., Porensky, L.M., Augustine, D.J., Reeves, J.L., Mueller, K.E., 2016. Grazing intensity differentially regulates ANPP response to precipitation in North American semiarid grasslands. Ecol. Appl. 26, 1370–1380.
Irisarri, J.G., Derner, J.D., Ritten, J.P., Peck, D.E., 2019. Beef production and net revenue variability from grazing systems on semiarid grasslands of North America. Livest. Sci. 220, 93–99.
Janzen, H.H., 2009. Long-term ecological sites: musings on the future, as seen (dimly) from the past. Glob. Change Biol https://doil.org/10.111/j/1365-2486.2009.01971.x.
Khumalo, G., Holecheck, J., 2005. Relationships between Chihuahuan desert perennial grass production and precipitation. Rangel. Ecol. Manag. 58, 239–246.
Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. Ecol. Appl. 2, 397–403.
Ma, W., Liu, Z., Wang, Z., Wang, W., Liang, C., Tang, Y., He, J., Fang, J., 2010. Climate change alters interannual variation of grassland aboveground productivity: evidence from a 22-year measurement series in the Inner Mongolian grassland. J. Plant Res.

123 (4), 509–517.
MacNeil, M.D., Vermeire, L.T., 2012. Effect of weather patterns on preweaning growth of beef calves in the Northern Great Plains. Agric. Syst. 3, 929–935.
Mader, T.L., Frank, K.L., Harrington, J.A., Hahn, G.L., Nienaber, J.A., 2009. Potential climate change effects on warm-season livestock production in the Great Plains. Clim. Change 97, 529–541.
Manley, W.A., Hart, R.H., Samuel, M.J., Smith, M.A., Waggoner Jr., J.W., Manley, J.T., 1997. Vegetation, cattle, and economic responses to grazing strategies and pressures. J. Range Manag. 50, 638–646.
McCollum, F.T., Gillen, L., Karges, B.R., Hodges, M.E., 1999. Stocker cattle response to grazing management in tallgrass prairie. J. Range Manag. 52, 120–126.
Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Monogr. 63, 327–366.
Milchunas, D.G., Forwood, J.R., Lauenroth, W.K., 1994. Productivity of long-term grazing treatments in response to seasonal precipitation. J. Range Manag. 47, 133–139.
Milchunas, D.G., Varnamkhasti, A.S., Lauenroth, W.K., Goetz, H., 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. Oecologia 101, 366–374.
Moore, A.D., Ghahramani, A., 2013. Climate change and broadacre livestock production across southern Australia. 1. Impacts of climate change on pasture and livestock productivity, and on sustainable levels of profitability. Glob. Change Biol. 19, 1440–1455.
Nardone, A., Ronchi, B., Lacetera, N., Ranieri, M.S., Bernabucci, U., 2010. Effects of climate changes on animal production and sustainability of livestock systems. Livest. Sci. 130, 57–69.
O'Connor, T.G., Haines, L.M., Snyman, H.A., 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. J. Ecol. 89, 850–860.
Oesterheld, M., Loreti, J., Semmartin, M., Sala, O.E., 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. J. Veg. Sci. 12, 137–142.
Peck, D., Derner, J., Parton, W., Hartman, M., Fuchs, B., 2019. Flexible stocking with Grass-Cast: a new grassland productivity forecast to translate climate outlooks for ranchers. West. Econ. Forum 17, 24–39.
Petrie, M.D., Peters, D.P.C., Yao, J., Blair, J.M., Burruss, N.D., Collins, S.L., Derner, J.D., Gherardi, L.A., Hendrickson, R., Sala, O.E., Starks, P.J., Steiner, J.L., 2018. Regional grassland productivity responses to precipitation during multiyear above- and below-average rainfall periods. Glob. Change Biol. 24, 1935–1951.
R Development Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Reeves, J.L., Derner, J.D., Sanderson, M.A., Petersen, M.K., Vermeire, L.T., Hendrickson, J.R., Kronberg, S.L., 2013a. Temperature and precipitation affect steer weight gains differentially by stocking rate in northern mixed-grass prairie. Rangel. Ecol. Manag. 66, 438–444.
Reeves, J.L., Derner, J.D., Sanderson, M.A., Petersen, M.K., Vermeire, L.T., Hendrickson, J.R., Kronberg, S.L., 2013b. Seasonal temperature and precipitation effects on cow-calf production in northern mixed-grass prairie. Livest. Sci. 155, 355–363.
Reeves, J.L., Derner, J.D., Sanderson, M.A., Hendrickson, J.R., Kronberg, S.L., Petersen, M.K., Vermeire, L.T., 2014. Seasonal weather influences on yearling beef steer production in C_3-dominated Northern Great Plains rangeland. Agric. Ecosyst. Environ. 183, 110–117.
Ritten, J.P., Frasier, W.M., Bastian, C.T., Gray, S.T., 2010. Optimal rangeland stocking decisions under stochastic and climate-impacted weather. Am. J. Agric. Econ. 92, 1242–1255.
Sala, O.E., Lauenroth, W.K., 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia 53, 301–304.
Sala, O.E., Gherardi, L.A., Reichmann, L., Jobbagy, E., Peters, D., 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. Philos. Trans. Biol. Sci. 367, 3135–3144.
Scasta, J.D., Henderson, L., Smith, T., 2015. Drought effect on weaning weight and efficiency relative to cow size in semiarid rangeland. J. Anim. Sci. 93, 5829–5839.
Shaffer, M.J., Bartling, P.N.S., Ascough II, J.C., 2000. Object-oriented simulation of integrated whole farms: GPFARM framework. Comput. Electron. Agric. 28, 29–49.
Smart, A.J., Dunn, B.H., Johnson, P.S., Xu, L., Gates, R.N., 2007. Using weather data to explain herbage yield on three Great Plains plant communities. Rangel. Ecol. Manag. 60, 146–153.
Thomey, M.L., Collins, S.L., Vargas, R., Johnson, J.E., Brown, R.F., Natvig, D.O., Friggens, M.T., 2011. Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. Glob. Change Biol. 17, 1505–1515.
Torell, L.A., Murugan, S., Ramirez, O.A., 2010. Economics of flexible versus conservative stocking rates to manage climate variability risk. R. Ecol. Manag. 63, 415–425.
Vavra, M., Rice, R.W., Bement, R.E., 1973. Chemical composition of the diet, intake and gain of yearling cattle on different grazing intensities. J. Anim. Sci. 36, 411–414.
Wang, H., Zhang, X., Zou, G., 2009. Frequentist model averaging estimation: a review. J. Syst. Sci. Complex. 2009, 732–748.
White, R.P., Murray, S., Rohweder, M., Prince, S.D., Thompson, K.M., 2000. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. World Resources Institute, Washington, DC, USA, pp. 81.
Yang, Y., Fang, J., Ma, W., Wang, W., 2008. Relationship between variability in aboveground net primary production and precipitation in global grasslands. Geophys. Res. Lett. 35 (23). https://doi.org/10.1029/2008GL035408.