Long-term growing season aridity and grazing seasonality effects on perennial grass biomass in a Chihuahuan Desert rangeland

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ABSTRACT

Growing season aridity and livestock grazing seasonality can influence primary productivity of perennial grasses in dryland systems. For this study, we used a long-term dataset (1967–2004) to investigate the independent and joint effects of growing season aridity and season of grazing (yearlong continuous, fall, winter/spring, or summer season grazing) on the mean annual primary productivity of the perennial grasses *Bouteloua eriopoda* (black grama), *Aristida* spp. (threeawn), and *Sporobolus* spp. (dropseed) in a southwestern United States Chihuahuan Desert rangeland system. Over the 37-year study period, total perennial grass biomass decreased as aridity increased, but the extent of this relationship depended upon season of grazing and specific grass taxon. Aridity-related decreases in total perennial grass biomass were most severe in the summer grazing treatment. Our findings indicate that over time, summer and fall grazing can potentially exacerbate the negative effects of increasing aridity on perennial grass biomass. As arid and semi-arid rangelands globally face increasing aridity associated with a changing climate, land managers can modulate the season of grazing, dependent on dominant taxa present, to minimize these effects. Our study and those from other arid land locations indicate continuous grazing at light to conservative intensities can better sustain key perennial grasses than strategies involving concentrated seasons of grazing. However, growing season aridity levels must also be taken into consideration.

1. Introduction

Drylands make up over 40% of the terrestrial land surface area, and support over half the world's livestock and the livelihoods of roughly three billion people (IPCC. Mirzabaev et al., 2019; Hoover et al., 2020). Perennial grass biomass, in addition to other forms of photosynthetic primary production, is a critical ecosystem service across these lands that is threatened by a diversity of global changes. Increasing aridity (i. e., hotter and drier conditions) associated with climate change is of particular concern because it poses a threat to multiple ecosystem level changes, including the long-term quality and quantity of primary productivity (Huang et al., 2020). Increasing aridity exacerbates water scarcity, reduces continuous vegetative cover, decreases the availability

of livestock and wildlife forage, and can accelerate the encroachment of invasive woody plant species (Havstad et al., 2018). Losses of primary productivity also can have critical implications for environmental quality and human wellbeing (Holechek et al., 2020; Peters et al., 2012), including socioeconomic relationships derived from livestock production. In this context, knowledge of how temporal variation in aridity alters the composition and biomass of plant communities is essential for mitigating impacts of climate change in dryland environments upon which communities worldwide depend.

Livestock grazing is an extensive land use across arid and semi-arid systems. Alongside their influence on ecosystem services, grazing practices can also have a major influence on rates of abiotic (e.g., fire) disturbance intervals, biological invasions, and, ultimately, the species

composition in vascular plant communities (Brown and McDonald, 1995; Condon and Pyke, 2018; Filazzola et al., 2020). Thus, effective grazing management is an essential component of sustainable livestock production to ensure ecosystem services that meet and augment human needs while minimizing or, ideally, halting land degradation (Cowie et al., 2011). In this context, the timing and season of grazing that is implemented is a critical consideration. Seasonal rotational grazing involves rotating a livestock herd through different pastures throughout the seasons of the year (Beck et al., 2007). Alternatively, continuous grazing allows a herd to access a large pasture or landscape throughout the calendar year (Holechek et al., 1999). Many empirical studies have evaluated the ecological effects of seasonal rotational vs. continuous grazing practices in drylands, but results are highly nuanced (e.g., Briske et al., 2008). Importantly, there is considerable opportunity to understand how temporal variation in aridity influences the ecological outcomes of grazing by season (Beck et al., 2007).

In addition to identifying the influence of livestock grazing in drylands, understanding the relationship between grazing and vegetation structure and function is an area of active focus. Perennial grasses are an ecologically and economically important vegetation class influenced by aridity and season of grazing in drylands. Perennial grasses provision primary productivity with high forage value for livestock and wildlife (Vavra, 2005), resist biological invasions by annual plant species (Maestas et al., 2022), and help maintain ecosystem function (Pan et al., 2016). Thus, perennial grasses are a crucial component of healthy, productive rangelands in dryland systems (Whitford et al., 1998). Primary productivity by perennial grasses across scales follows the amount and timing of precipitation across years (Beck et al., 2007; McIntosh et al., 2019) and is also sensitive to the intensity and season of grazing (Valentine, 1967). Additionally, perennial grasses differ greatly at the species level in their annual and seasonal palatability to livestock, drought tolerance, lifespan, and reproductive capacity (Valentine, 1970).

Investigations examining how aridity and season of grazing independently and jointly influence perennial grass annual primary production, particularly over long time series, can provide valuable insight into drivers of change, which can in turn inform management actions. This knowledge is important because arid and semi-arid rangelands face increasing pressure to meet the demands of a growing human population (Hoover et al., 2020), while aridification jeopardizes their capability to meet this demand. In this context, long-term datasets that capture year-to-year variation in aridity across a variety of grazing systems are highly valuable.

We used a 37-year dataset to examine how variability in growing season aridity and season of grazing independently and jointly influenced primary productivity of perennial grasses in the northern Chihuahuan Desert. Specifically, we asked: 1) How does growing season aridity and season of grazing influence perennial grass biomass across a 37-year time series? 2) Do growing season aridity and season of grazing jointly influence perennial grass biomass, and if so, 3) how does this relationship vary by perennial grass taxa? We predicted that increasing aridity (i.e., hotter and drier conditions) during the growing season corresponds to decreasing mean annual biomass of perennial grasses, but that the strength of aridity-biomass relationships also depends upon the season of grazing and grass taxa.

2. Materials and methods

2.1. Site description

This study was conducted at the Chihuahuan Desert Rangeland Research Center (CDRRC) between 1967 and 2002, and 2004 (data were not collected in 2003) with the original study design and field data collection led and maintained by Dr. Reldon Beck. The CDRRC is owned and operated by New Mexico State University and is in the northern region of the Chihuahuan Desert (Fig. 1). Encompassing 26,671 ha, the CDRRC is situated in the Jornada del Muerto plain between the San Andres mountains to the east and the Rio Grande to the west and is approximately 37 km north of Las Cruces, New Mexico, U.S.A. (32° 32′30″ N, 106° 52′30″ W) in Doña Ana County (mean elevation: 1325 m)

Fig. 1. Map of research site (black star) within Chihuahuan Desert (Adapted from McIntosh et al., 2019).

(Gibbens et al., 2005). Study pastures were located on soils of the Wink Harrisburg association (Coarse-loamy, mixed, superactive, thermic Typic Haplocalcids and Coarse-loamy, mixed, superactive, thermic Typic Petrocalcids, respectively), which is characterized by a mixture of shallow sandy, sandy, and deep sand ecological sites (Soil classification based on the USDA Keys to Soil Taxonomy; Soil Survey Staff, 2022). Wink Harrisburg soils feature approximately 0.13 cm*cm^{-1} of available water capacity, ~0.25% organic matter, and 70.5%, 16.5%, 13% sand, silt, and clay, respectively (Soil Survey Staff, 2022). They generally extend ~50–100 cm deep before they meet a water-restrictive indurated petrocalcic horizon (colloquially "caliche").

2.2. Climate and aridity

The Northern Chihuahuan Desert is classified as an arid to semi-arid region (Peters et al., 2012) with an annual mean temperature during the 37 years of the study from 1967 to 2004 of 11.93 °C and annual mean maximum temperature of 21.10 °C. (Wooton et al., 2022). Annual temperature reached its maximum (30.74 °C) in June and its annual minimum (-7.2 °C) in December (Wooton et al., 2022). The mean precipitation observed on the CDRRC over the timeframe of the study was 254 mm yr^{-1} (Schroeder et al., 2022). Monsoon driven events bring about 65% of the annual precipitation in the summer and fall months from July through October (Peters et al., 2014).

The aridity indicator used for this study was the De Martonne Aridity Index, which presents aridity as a function of mean annual precipitation and mean annual temperature (Equation (1)). When presented, high De Martonne aridity (I_{DM}) scores indicate cooler and wetter conditions, and lower aridity scores indicate hotter and drier conditions. Thus, high I_{DM} scores demonstrate low aridity, and low I_{DM} scores high aridity.

$$I_{DM} = \frac{\text{mean Annual Precipitation (mm)}}{\text{mean Annual Temperature } °C + 10} \qquad 1$$

Growing season aridity (Growing Season I_{DM}) was calculated using data from five rain gauges located in the yearlong grazing treatment (Schroeder et al., 2022) and temperature data collected from the nearby Jornada Experimental Range headquarters (~17 km east of the study area; Wooton et al., 2022) from 1967 to 2004. We analyzed the De Martonne Aridity Index for the mean monthly precipitation (mm) and temperature (°C) over the four months of June, July, August, and September (Equation (2)). For a given year, the Growing Season Aridity Index was calculated by taking the mean monthly precipitation (June through September, divided by four) and dividing by the mean monthly temperature (June through September, divided by four) plus 10. Similar to the annual De Martonne Aridity Index, when presented, high Growing Season De Martonne aridity (GS I_{DM}) scores indicate cooler and wetter growing seasons, and lower aridity scores indicate hotter and drier conditions. Thus, high GS I_{DM} scores demonstrate low growing season aridity, and low GS I_{DM} scores high growing season aridity.

Fig. 2. Map of study pastures, dominant ecological sites, long-term transect locations, and livestock watering troughs at Chihuahuan Desert Rangeland Research Center study site. Fencelines within respective pastures (black lines with lower weight) are the locations of grazing exclosures where other studies or sensitive infrastructure were located. Altered Grasslands typically have less abundant forage production, and historic grass has typically been replaced by less grazing-tolerant species' (Steele et al., 2012).

grazing which predates the establishment of the research center. For this study, cattle were rotated through four pastures in 1967–2004 (Beck et al., 2007) depending on four assigned seasonality treatments: 1) a yearlong grazing pasture (1267 ha), 2) a winter/spring grazing pasture (508 ha), 3) a fall grazing pasture (670 ha), and 4) a summer grazing pasture (494 ha; Fig. 2). The yearlong pasture was grazed continuously every year. The summer pasture was grazed from June to the middle of September. The fall pasture was grazed from the middle of September to the end of December. The winter/spring pasture was grazed from January to late June (Fig. 2). To keep stocking rates similar across the grazing season treatments, the number of cows in a pasture for a 3-month grazing season was 4-fold greater than the number of cows in the yearlong pasture.

Cattle of all ages used in the study from 1967 to 1971 were Hereford; Brangus cattle herds of all ages were used from 1972 to 1992 (Beck et al., 2007). A mixed herd (different breeds) was used from 1992 through 2004, and no cattle grazed the pastures in 1995 and 1996 due to drought and poor forage conditions. At the beginning of the study, stocking rates were established at a conservative rate which was equal to or less than 30% black grama utilization and 45% dropseed utilization (Beck et al., 2007). Herd sizes, maintained within each individual pasture, were monitored to adjust to changing conditions. Stocking rate increased in the 1980's when perennial biomass increased due to increased rainfall.

$$\text{Growing Season } I_{DM} = \frac{\frac{1}{4}\sum_{i=1}^{4} \textit{June} - \textit{September mean monthly precip (mm)}}{\left(\frac{1}{4}\sum_{i=1}^{4} \textit{June} - \textit{September mean monthly Temperature (}°C\textit{)}\right) + 10} \qquad 2$$

2.3. Grazing season treatments

The CDRRC has been used for grazing research for nearly a century (established in 1927) and the study pastures have a long history of
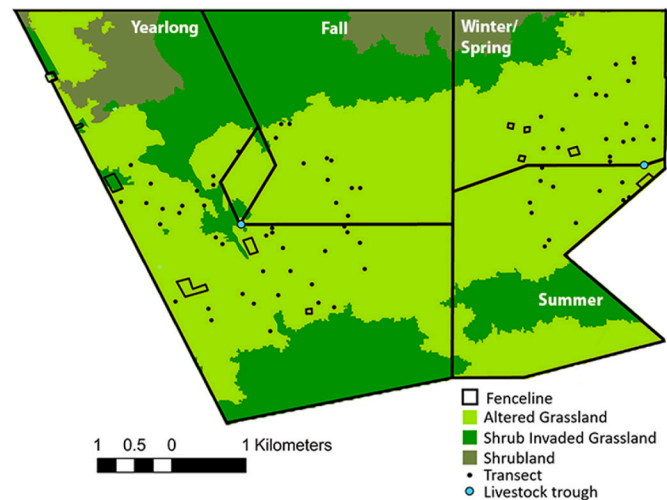
Each pasture was grazed conservatively to attempt to meet similar utilization rates on the dominant perennial grasses for the respective year and stocking density was standardized across pastures to account for pasture size differences (Beck et al., 2007). If the number of cattle in any pasture was adjusted, due to forage limitations or other phenomenon (e. g. sick cows needing to be removed), the number of cattle was also

adjusted in the other pastures to maintain a standard number of animal units (Beck et al., 2007). Cattle stocking rates were based on previous year's perennial grass biomass and maintaining a bull-cow ratio.

2.4. Dominant vegetation and perennial grass types

The target perennial grasses we focused on were the historically dominant vegetation within our study area (Gibbens and Beck, 1987) and this functional group can comprise over 85% of cattle diets depending on season and year in the Chihuahuan Desert (Beck et al., 2007), and therefore provide important ecosystem services in the form of native range forage for the Southwestern region of the U.S. (Beck et al., 2007; Havstad et al., 2018). Our three target perennial grass taxa make up > 90% of all perennial grasses on the CDRRC upland pastures: black grama (*Bouteloua eriopoda* [Torr.] Torr.); dropseed (*Sporobolus* spp.); and threeawns (*Aristida* spp.). For the purpose of this study, dropseeds could not be reliably identified at the species level because the primary species (*S. flexuosus* [Thurb. Ex Vasey] Rydb*., S. cryptandrus* [Torr.] A. Gray, and *S. contractus* Hitchc.) are difficult to differentiate without full inflorescences present. Similarly, threeawns could not be reliably identified at the species level because the species measured at

these field sites (*A. purpurea* Nutt., *A. pansa* Woot. & Standl. *A. havardii* Vasey) are difficult to differentiate without inflorescences present.

Other perennial grass species present in the study area but not included in the analyses were *Setaria leucopila* [Scribn. & Merr] K. Schum., *Enneapogon desvauxii* Desv. ex P. Beauv*., Muhlenbergia porteri* Scribn. ex Beal*, Dasyochloa pulchella* [Kunth] Willd. ex Rydb., and *Eragrostis lehmanniana* Nees*.* Primary shrub species included: *Prosopis glandulosa* Torr*., Larrea tridentata* [DC.] Coville*, Atriplex canescens* [Pursh] Nutt*., Ephedra trifurca* Torr. ex S. Watson, and *Yucca elata* [Engelm.] Engelm. Primary forb species included: *Croton pottsii* [Klotzsch] Müll. Arg*., Solanum elaeagnifolium* Cav*., Senna bauhinioides* [A. Gray] Irwin & Barneby, and *Hoffmannseggia glauca* [Ortega] Eifert.

2.5. Experimental Design and monitoring

In each pasture (or grazing season treatment), the west end of an individual transect was randomly located and then laid out due east from the starting point. The original study included 220 total transects (Beck et al., 2007), however for this study, a total of 78, 61m (200 ft) permanent transects were established and scaled to the size of the pasture: 35 transects in the yearlong pasture, 20 transects in the
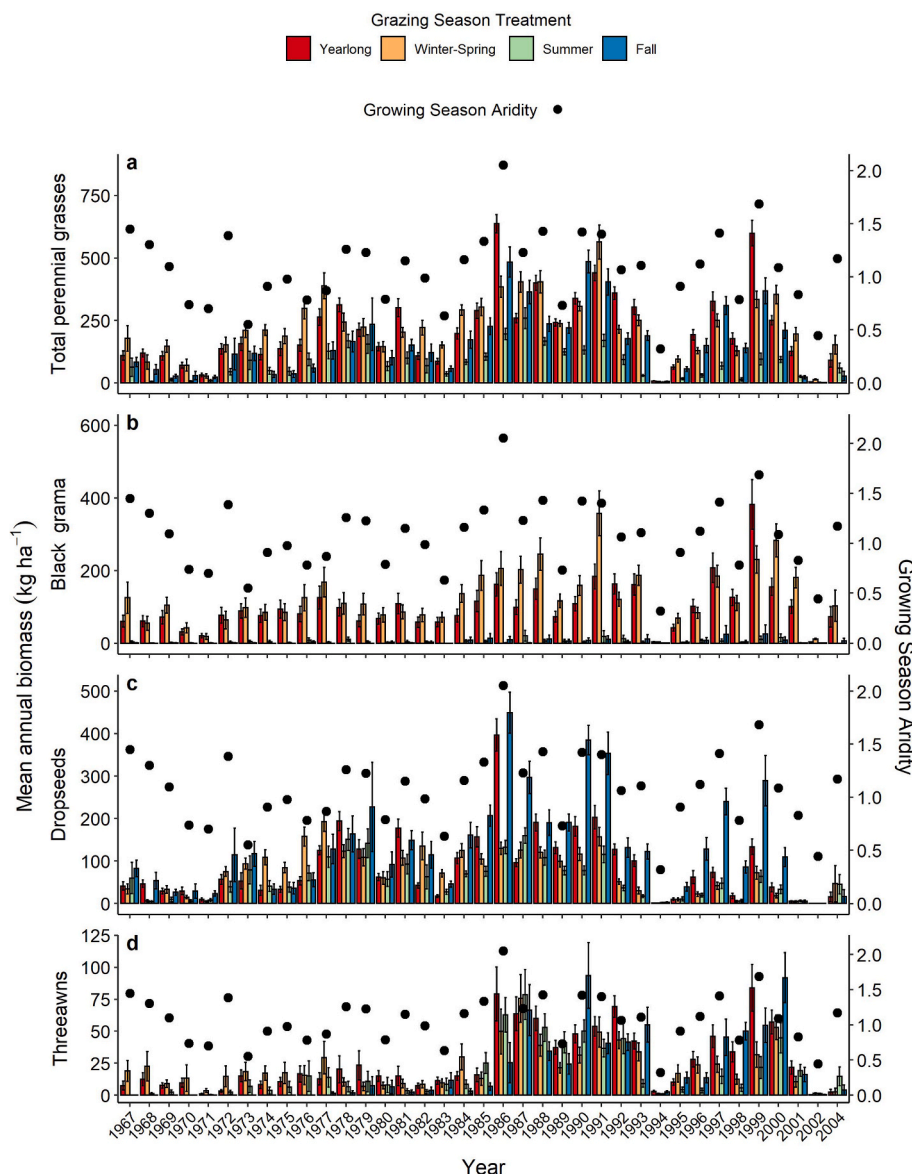

Fig. 3. (panels a–d). Bars represent four grazing season treatments (yearlong, winter/spring, summer, fall) mean annual biomass (kg ha^{-1}) of a) total perennial grasses combined, b) black grama (*Bouteloua eriopoda*), c) dropseed (*Sporobolus* spp.), and d) threeawn (*Aristida* spp.) and the corresponding growing season aridity scores (De Martonne index) for the 37-year study period. Error bars represent one standard error above and below the mean. Dots above each year represent De Martonne growing season aridity scores (lower numbers denote higher aridity levels).

winter/spring pasture, 12 transects in the summer pasture, and 11 transects in the fall pasture (Fig. 2). The yearlong and fall pastures shared a fenceline water source (32°34′46.3″N 106°55′19.1″W) as did the winter/spring and summer pastures (32°35′11.8″N 106°52′23.0″W; Fig. 2). To reduce the confounding influence of distance from water, we focused only on transects within 1609.34 m (1 mile; the point at which livestock grazing use begins to diminish; Holechek, 1988) of drinkers thus reducing transect totals from 220 to 78 in total. For comparison purposes across vegetation and soil characteristics, the four pastures, and associated transects, fell within similar predetermined ecological sites and states (e.g., Burkett et al., 2021) which fell on the landscape where the dominant vegetation and associated edaphic characteristics were similar (e.g., altered grasslands)(Fig. 2). Aboveground perennial grass biomass (kg/ha) was measured annually at the end of each growing season in mid-September through mid-October 1967 to 2002 and 2004. To directly measure current year's biomass, our three target species (black grama, threeawns, and dropseed that were taller than 2 cm) were clipped from five 0.3-m^2 plots distributed every 12 m along each transect (Beck et al., 2007). To account for previous year's impact of sampling, the plots were moved 1 m in either direction from year to year (McIntosh et al., 2019). The clipped biomass was separated to include only the particular year's growth and was then dried for 72 h at 66 °C (Beck et al., 2007; Khumalo and Holechek, 2005). After the biomass samples had been dried, they were weighed and averaged at the transect level. Accordingly, our biomass measurements are reported as kilograms of dry matter (DM) per hectare (kg DM*ha^{-1}). Following these protocols for the duration of the 37-year study, vegetation baseline conditions at the start of the monitoring period, as well as their variability over time were able to be assessed for total perennial grass biomass (Fig. 3 a) and our individual grass taxa (Fig. 3 b-d).

2.6. Statistical analyses

Analyses were conducted using the program R v4.1.2 (R Core Team, 2021). To evaluate the independent and joint effects of growing season aridity and seasons of grazing on perennial grass biomass, we fit linear models with total perennial grass biomass (all taxa combined), black grama biomass, dropseed biomass, or threeawn biomass (kg ha^{-1}, square-root transformed and averaged for each year at the grazing season treatment level) as the response variable, growing season aridity (i.e. GS I$_{DM}$) as a covariate; and season of grazing as a fixed effect, with an interaction between growing season aridity and season of grazing.
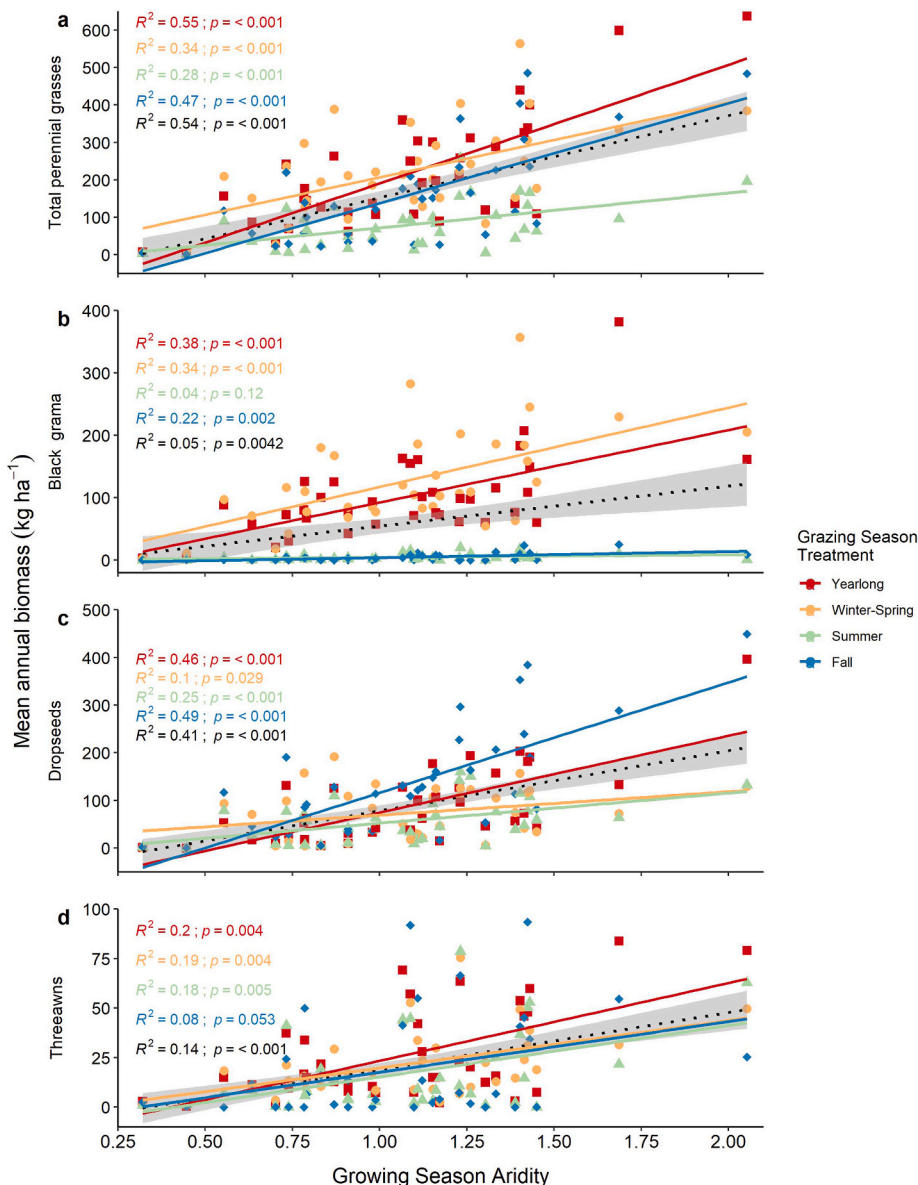

Fig. 4. (panels a-d). Linear models of Mean Annual Biomass (kg ha^{-1}) of total perennial grasses. Linear model results (R^2, and *p*-val) are those of biomass data that had been square-root transformed, whilst the scatter plots are of untransformed data, with the R^2 being the adjusted R^2 values. The bottom-most R^2 value (in black) for each linear model is of the overall model (black dotted line with SE intervals). Black grama (*Bouteloua eriopoda*), dropseeds (*Sporobolus* spp.), and threeawn (*Arisitida* spp.) top to bottom, respectively, as a function of Growing Season De Martonne's Aridity (lower values are hotter and drier, higher values are cooler and wetter) across the four grazing season treatments as a covariate from 1967 through 2002 and 2004 on the Chihuahuan Desert Rangeland Research Center (CDRRC).

Grazing season treatment biomass data were averaged by year and were square-root transformed to achieve the assumption of homoscedasticity of variance between grazing treatment groups, based on Box-Cox log-likelihood plots. Square-root transformations met this assumption for three of the four biomass variables (except black grama). Despite the homoscedasticity of variance assumption for black grama not being met, due to its continuously low biomass values in certain grazing treatments, we felt confident moving forward with the model, as the data were collected on transects on the same ecological site and state (Fig. 2; ergo similar vegetation potential, all else equal) as the rest of the sample units in the other grazing season treatments.

To further evaluate the independent effects of season of grazing on perennial grass biomass across the growing season aridity values, we used a non-parametric Permutational Analysis of Variance procedure on the untransformed biomass data. A non-parametric permutational approach was used because of an unbalanced sampling design (11–35 transects per pasture), Shapiro-Wilk and Anderson-Darling tests revealed that the data were not normally distributed, and Levene's test of homogeneity revealed the data distributions of the untransformed data across the different grazing season treatments were heteroscedastic. Data transformations (square-root and log) did not sufficiently improve the normality nor homoscedasticity of all response variables of the data. Square-root transformations did help improve normality of total perennial grass biomass and homogeneity of three of the four response variables, however, for consistency, we opted for running the same models for all response variables. Our permutational ANOVA utilized 5000 iterations to compare the biomass of total perennial grass, black grama, dropseed, and threeawn, and across the four different grazing season treatments pairwise differences between seasons of grazing using a false-discovery rate (FDR) correction (Mangiafico, 2021). An alpha of 0.05 was used to denote statistical significance throughout.

3. Results

3.1. Growing season aridity and perennial grass biomass

We found substantial interannual variability in growing season aridity and perennial grass biomass during our study period across the grazing season treatments (Fig. 4). From 1967 to 2004, growing season aridity scores across the CDRRC ranged from 0.32 to 2.05, with an average of $1.07 \pm 0.03SE$ (all variability values hereafter will be ± 1 standard error unless otherwise noted). Across the four grazing season treatments over the 37 years of the study, mean perennial grass biomass ranged from 0.9 to 683 kg ha^{-1} per year, with an average of 166.9 (± 23.6) kg ha^{-1} per year (Fig. 4a). Mean black grama biomass ranged from 0 to 381.7 kg ha^{-1} per year, with an average of 59 (± 14.2) kg ha^{-1} per year (Fig. 4b). Mean dropseed biomass ranged from 0 to 449.1 kg ha^{-1} per year, with an average of 86.9 (± 16.2) kg ha^{-1} per year (Fig. 4c). Mean threeawn biomass ranged from 0 to 93.5 kg ha^{-1} per year, with an average of 21 (± 6) kg ha^{-1} per year (Fig. 4d).

3.2. Effects of growing season aridity and season of grazing on perennial grass biomass

Growing season aridity and season of grazing independently and synergistically influenced total perennial grass biomass (Table 1, Fig. 4). Across grazing season treatments, increasing aridity (i.e., lower Growing Season I_{DM} scores) corresponded with decreasing total perennial grass biomass (Figs. 3a and 4a). Growing season aridity was the strongest predictor of total perennial grass biomass (F = 43.71, $p < 0.01$) and there was weak evidence that the interaction of growing season aridity and season of grazing influences total biomass between the grazing season treatments (F = 2.31, $p = 0.0787$) (Table 1). The interaction of grazing and aridity is significant in the summer grazing treatment, reducing the slope of total perennial grass biomass (t = −2.257, $p = 0.0256$) compared to the yearlong grazing treatment (Fig. 4a).

Not all grass taxa responded equally to the independent and joint effects of growing season aridity and season of grazing (Table 1, Fig. 4). For black grama, there was a significant interaction of growing season aridity and season of grazing (F = 11.04, p < 0.01) that reduced the slopes of black grama biomass increase in the summer (t = −3.709, $p <$ 0.001) and fall (t = −3.434, $p < 0.001$) grazing treatments, compared to the yearlong treatment (Fig. 4b). Growing season aridity was the strongest predictor of black grama biomass (F = 32.35, $p < 0.01$) overall. For dropseeds (Fig. 4c), there was also a significant interaction of growing season aridity and season of grazing (F = 3.59, $p = 0.015$), that reduced the slope of dropseed biomass increase in the winter/spring season (t = −2.10, $p = 0.037$), compared to the yearlong season. Growing season aridity was the strongest predictor of dropseed biomass (F = 29.38, $p < 0.01$) overall. For threeawns (Fig. 4d), the interaction of growing season aridity and season of grazing was not significant (F = 0.13, $p = 0.945$). Growing season aridity significantly influenced threeawn biomass (F = 8.297, $p < 0.01$), but not season of grazing nor their interaction (F < 1.085, $p > 0.05$ for both).

3.3. Effects of grazing season treatment on perennial grass biomass by taxa

Independent of aridity, season of grazing had nuanced effects on perennial grass biomass (Figs. 3 and 5). Across the 37 years of the study, the summer grazed pasture had lower total mean annual perennial grass biomass (78.4 ± 10.2 kg ha^{-1}) than the yearlong (212.5 ± 24.2 kg ha^{-1}, $p < 0.01$), winter/spring (220.4 ± 19.9 kg ha^{-1}, $p < 0.01$), or fall (156.3 ± 21.7 kg ha^{-1}, $p < 0.01$) pastures (Fig. 5a). For black grama (Fig. 5b), regardless of growing season aridity score, the summer and fall grazed pastures produced significantly less biomass (4.7 ± 1 kg ha^{-1} each) than the yearlong (100.6 ± 11.1 kg ha^{-1}) and winter/spring (126.2 ± 12.5 kg ha^{-1}) grazed pastures ($p < 0.05$). For dropseeds (Fig. 5c), the fall-grazed pasture produced more (132.2 ± 18.4 kg ha^{-1}) than the summer (56.7 ± 7.4 kg ha^{-1}, $p < 0.01$) or winter/spring grazed (72.7 ± 8.8 kg ha^{-1}, $p = 0.02$) pastures, but dropseed biomass in the yearlong pasture (85.8 ± 13.3 kg ha^{-1}) did not differ from other pastures ($p > 0.05$). Threeawn mean annual biomass (Fig. 5d) did not differ significantly across any of the grazing season treatments.
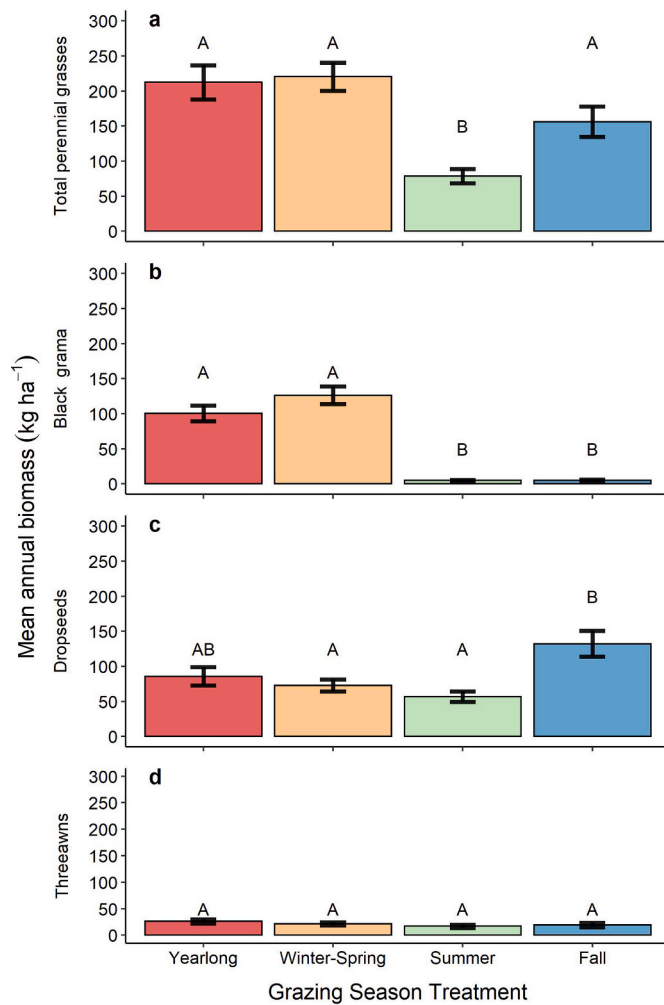
Table 1
Linear regression statistics (Type III Sums of Squares) of square-root transformed mean annual biomass data as predicted by growing season Aridity, Grazing Season Treatment, and the interaction thereof from 1967 to 2002 and 2004 on the CDRRC.

Source of Variance	Df	Total perennial grasses		Black grama		Dropseed		Threeawn	
		F-Val	ProbF	F-Val	ProbF	F-Val	ProbF	F-Val	ProbF
Growing season aridity	1	43.71	**< 0.0001**	32.35	**< 0.0001**	29.38	**< 0.0001**	8.29	**0.0046**
Grazing season	3	1.93	0.127	2.21	0.0896	1.48	0.222	0.25	0.864
Growing season aridity* Grazing season	3	2.31	0.0787	11.04	**< 0.0001**	3.59	**0.015**	0.13	0.945
Residuals	140								

Fig. 5. (panels a-d). Barplots of Mean Annual Biomass (kg ha^{-1}) of total perennial grasses, black grama (*Bouteloua eriopoda>*), dropseeds (*Sporobolus* spp.), and threawns (*Arisitida* spp.) top to bottom, respectively, across the four grazing season treatments from 1967 to 2002 and 2004 across the Chihuahuan Desert Rangeland Research Center (CDRRC). Error bars represent standard error and letters indicate significant differences ($p < 0.05$) between grazing season treatment (pasture) for the respective species' mean biomass, determined by pairwise permutation tests with a False Discovery Rate (FDR) correction.

4. Discussion

Our long-term study examined how growing season aridity using a De Martonne Index (Growing Season I$_{DM}$) and grazing season treatments influenced perennial grass biomass. This study demonstrated that growing season aridity and season of grazing jointly influence perennial grass biomass across dominant grass taxa at the pasture-scale. Aridity alone had some of the most pronounced effects on perennial grass biomass, however the season of grazing also had a strong influence, especially on the two most historically prevalent taxa (black grama and dropseeds). The strength of these relationships, within and across growing season aridity and grazing season treatments, varied depending on the grass taxon (Fig. 4).

4.1. Growing season aridity and perennial grass biomass

Across grazing treatments and years, growing season aridity had pronounced effects on total perennial grass biomass, and on focal taxa. Low aridity (i.e., higher Growing Season I$_{DM}$ scores) corresponded to increased perennial grass biomass per year, whereas high aridity (i.e., lower Growing Season I$_{DM}$ scores) corresponded to low grass biomass per year. This affirms our original prediction that hotter, drier growing conditions would decrease perennial grass biomass, and vice versa. Growing Season I$_{DM}$ most strongly affected total perennial grass biomass of all three dominant perennial grasses combined, and the specific taxa responses indicated that dropseeds more readily responded to changes in growing season aridity than did black grama, and threawns. It is well documented that inter-annual variability in seasonal precipitation amount and timing has marked negative effects on Chihuahuan Desert perennial forage biomass (McIntosh et al., 2019; Nelson, 1934; Paulsen and Ares, 1962; Peters et al., 2014; Valentine, 1970; and sources therein). Likewise, intra-annual variability can affect perennial grass biomass: each of the key forage taxa in this study can respond uniquely to pulse rain events and temperature extremes within and outside of the standard growing season (typically July–September). For example, black grama has been documented to respond positively to cool late summer temperatures and increased rainfall events (Paulsen and Ares, 1962), but may not respond to warm, wet springs as positively as dropseed (Beck et al., 2007; Gibbens, 1991).

Dropseeds were found to be the most responsive of the three focal taxa to increases in Growing Season I$_{DM}$ scores, as they readily regenerate from both large seed banks and caespitose buds during above-average monsoons (Coffin and Lauenroth, 1989). Whereas black grama is primarily reliant on vegetative reproduction (through stolons) and may take longer to respond to increases in moisture (Thomey et al., 2014), threawn biomass was found to have generally the lowest amount of variability explained by Growing Season I$_{DM}$ scores (R^2 = 0.14), likely because of their tendency to grow in mid-late spring, which falls outside of the standard growing season (Beck et al., 2007). Additionally, threawns were a relatively minor component of the plant community for the first 19 years of the study (1967–1985) and then increased across the CDRRC following the highest Growing Season I$_{DM}$ year (i.e., low aridity) during the study (1986, Growing Season I$_{DM}$ = 2.05) to become more prevalent in the plant community during the last 18 years of the study (1986–2004). Our results agree, generally, with a 6-y Chihuahuan Desert field experiment, where Gherardi and Sala (2015) reported an 81% reduction in perennial grass biomass as precipitation variability increased and that grass recovery was more greatly hampered by dry years than helped by wet years. Likewise, Gremer et al. (2015) found a similar negative trend among perennial grass cover in the Chihuahuan and Sonoran deserts, and the Colorado Plateau, as the variability in available soil water increased (e.g. dry days; Thomey et al., 2014).

Our results also agree with McIntosh et al. (2019) who reported a temperature by precipitation interaction effect on perennial grass biomass on one of our study pastures (yearlong treatment) between 1967 and 2018. McIntosh et al. (2019) found that as mean maximum ambient temperature (May through September) increased and cumulative precipitation (December through September) decreased, perennial grass biomass declined. Our results, like theirs, have strong implications for predicted and observed climate change trends in the Chihuahuan Desert; hotter and drier (more arid) conditions exacerbate reductions in forage biomass, which will impact livestock and wildlife carrying capacity (Havstad et al., 2018). Growing Season Aridity indices of 0.75 and lower occurred in 6 of 37 years (16%), resulting in 5 years of 100 kg ha^{-1} total perennial grass forage biomass or less. When forage production and biomass falls below the 100 kg ha^{-1} threshold, ranching becomes financially unviable in these ecosystems (Holechek, 1996). Already, the 2000–2021 period has been identified as one of the hottest and worst drought periods in the Chihuahuan Desert during the past 1200 years, and is expected to worsen, still, into the coming century (Stahle, 2020; Williams et al., 2022) thus amplifying the need to identify best management practices across these landscapes.

4.2. Season of grazing and perennial grass biomass

Total perennial grass biomass as measured after the summer growing season was lower in the summer grazing treatment compared to the yearlong, fall, and winter/spring grazing treatments. This was primarily created by marked lower black grama biomass in the summer grazing treatments compared to others (Figs. 4b and 5b). The fall grazing treatment also demonstrated lower black grama biomass (Fig. 5b) that was comparable to the summer grazing treatment (Figs. 4b and 5b). Despite this lower black grama biomass in the fall grazing treatment, the difference in total perennial grass biomass was offset by the high dropseed biomass in that pasture, which shared a similar response to Growing Season I_{DM} values as the yearlong grazing treatment (Fig. 4c). Considering black grama is an important perennial grass forage species in the northern Chihuahuan desert due to high palatability for cattle and wild ungulates (Nelson, 1934), our results strongly imply that summer and fall grazing treatments could have continued detrimental effects on black grama biomass. While starting with initially low values, black grama regeneration was observed in these pastures during the years of highest Growing Season I_{DM}, but did not persist in following years (Figs. 3b and 4b). These results agree with several other studies in arid and semi-arid rangelands showing that season-long grazing of conservatively stocked pastures can result in advantageous vegetation, livestock, and financial performance compared to those in seasonal/rotation schemes or implementing higher stocking rates (Beck et al., 2007; Holechek et al., 1999; Holechek and Galt, 2000). These findings imply that producers should carefully consider grazing system and growing season aridity when determining management schemes (Hudson et al., 2021).

Black grama is most palatable during its late summer/early fall growing season, therefore, it is expected that cattle will converge on this species during those periods. Our results are consistent with cattle behavior studies that suggest when cattle stocking rates are held constant, but confined to season, grazing preferences dictate how much of certain plants are consumed, and when (Beck et al., 2007). This might imply that cows in the summer and fall grazing pastures converged on growing black grama, whereas in the spring pasture may have foraged on a mixture of grasses, shrubs, and early-season forbs, and in the yearlong pasture, likely diversified their diets per month or season. This hypothesis is consistent with diet studies by Herbel and Nelson (1966) and Rosiere et al. (1975) who reported perennial grasses constituted up to 72 and 45% of cow and steer diets, respectively, and that grasses comprised the greatest percentage of cattle diets in the summer and fall in the Chihuahuan Desert. On the other hand, Hakkila et al. (1987), reported that black grama only constituted 2% of Hereford x Brangus cow diets and Becerra et al. (1998) suggested that several beef breeds consumed 32% more grass in winter than summer. Notably, cows in all of those studies were exposed to yearlong grazing conditions, so diet composition was likely unaffected by cattle numbers nor constrained to particular seasons. Earlier work by Paulsen and Ares (1962) and Valentine (1967) suggested grazing black grama grasslands only during the November to February winter/spring season, as grazing during the growing season led to reduced biomass and loss of basal cover. Similarly, Valentine (1970), Nelson (1934), and Khumalo et al. (2007) all suggested light-conservative use of black grama to maximize yields (hence the stocking rate of this study).

4.3. Growing season aridity and season of grazing joint responses by perennial grass type

Our results revealed weak evidence of a growing season aridity and season of grazing interaction that influenced total perennial grass biomass. This interaction was found to be significantly different in the summer grazing treatment, which had a significantly lower slope than the yearlong grazing treatment. The yearlong pasture had the strongest relationship between total perennial grass biomass and growing season

aridity ($R^2 = 0.55$). The fall grazing treatment and growing season aridity relationship was the next strongest ($R^2 = 0.47$), followed by winter/spring ($R^2 = 0.34$), and then the summer grazing treatments having the weakest relationship ($R^2 = 0.28$) with growing season aridity and perennial grass biomass. This phenomenon could suggest a disequilibrium effect (Derry and Boone, 2010), wherein both abiotic and biotic factors and Chihuahuan Desert perennial grass biomass are only moderately coupled. This idea is supported by the observed positive effects of Growing Season I_{DM} on mean annual biomass across all grazing treatments, implying that abiotic factors (precipitation and temperature; traditionally referred to as 'non-equilibrium') have an overriding effect on perennial grass biomass when stocking rates are held constant at a conservative level. However, concentrated summer and fall seasonal use by cattle (traditionally referred to as 'equilibrium') may reduce forage biomass (particularly that of black grama) in a manner comparable to heavier stocking rates.

The interaction effect of growing season aridity and season of grazing was most pronounced for black grama biomass, indicating that black grama synergistically responds to abiotic and biotic processes. Black grama biomass became decoupled from increases in Growing Season I_{DM} values ($R^2 = 0.04$, $p > 0.05$) in the summer grazing treatments and had a significantly reduced slope than the yearlong and winter/spring grazing treatments, suggesting that it was unable to recruit into the summer grazing treatment. Black grama biomass in the fall grazing treatment also was shown to have a significantly lower slope than the yearlong and winter/spring grazing treatments, but was able to better respond to increases in Growing Season I_{DM} than the summer grazing treatment ($R^2 = 0.22$).

Dropseed biomass was also found to respond to the interaction of growing season aridity and season of grazing. The Growing Season aridity by grazing treatment interaction was strong for dropseeds, with the winter/spring grazing treatment having a weaker relationship than the yearlong and fall grazing treatments. This is likely due to the prevalence of black grama in the winter/spring grazing treatment and lack of in the summer grazing treatment, and the large presence of dropseeds in the fall pasture compared to others. In the yearlong and fall grazing treatments, dropseed biomass responded well to increases in Growing Season I_{DM}, whereas in the summer and winter/spring grazing treatments, the response of dropseeds to Growing Season I_{DM} was lower ($R^2 = 0.25$ and $R^2 = 0.10$, respectively). Compared to stoloniferous black grama, dropseeds (~22% relative cover) have shorter lifespans, and they grow either from seed or below-ground basal buds in response to above average rainfall events (Gibbens, 1991), meaning they may be more decoupled from grazing effects than black grama.

Threeawns followed a different pattern than either black grama or dropseed in response to season of grazing pressures. Potential reasons for this could be physiological differences among threeawns that could drive threeawn response, or lack thereof, to the aridity measurements. A potential reason for the grazing treatments not yielding a strong relationship, or pressure could be the low palatability of threeawns where they have a lighter grazing pressure than the other grass taxa irrespective of grazing treatments. Finally, for the above mentioned reasons community composition and the influence that may have on threeawn abundance during the two halves of the study (Fig. 3d), could explain their weak relationship with both aridity and season of grazing.

5. Conclusions

Our results suggest that grazing yearlong with conservative stocking rates yields similar total perennial grass biomass to both winter/spring and fall grazing treatments when stocking rates are higher, but also maintains a tighter relationship with growing season aridity. This implies that yearlong conservative grazing in this system may reduce livestock reliance on delicate forage species by allowing fewer animals more access to an ever-changing forage supply (see McIntosh et al., 2022 for discussion on behavioral plasticity among rangeland cattle). Though

being conservatively grazed, we have seen similar effects of summer and fall grazing pastures to those of heavily grazed lands. Our results caution against such high-intensity systems, as confinement may lead to overuse of critical forage resources. As climate change is projected to intensify into the coming century, southwestern U.S. grazing capacity will likely continue to decrease (McIntosh et al., 2019), which, coupled with unfitting seasonal use (especially summer grazing of black grama grasslands) could exacerbate this process. In the face of a changing climate, yearlong grazing has the potential to help protect from further degradation of arid and semi-arid landscapes.

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CRediT authorship contribution statement

Sophia N. Lasché: Conceptualization, Data curation, Methodology, Writing – original draft, Writing – review & editing. **Ryan W.R. Schroeder:** Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Matthew M. McIntosh:** Conceptualization, Writing – original draft, Writing – review & editing. **Jacob E. Lucero:** Writing – original draft, Writing – review & editing. **Sheri A. Spiegel:** Funding acquisition, Writing – original draft, Writing – review & editing. **Micah P. Funk:** Writing – original draft, Writing – review & editing. **Reldon F. Beck:** Conceptualization, Funding acquisition, Project administration, Writing – original draft, Writing – review & editing. **Jerry L. Holechek:** Conceptualization, Project administration, Writing – original draft, Writing – review & editing. **Akasha M. Faist:** Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

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.

Data availability

The data for this study has been published and can be found at: https://portal-s.edirepository.org/nis/metadataviewer?packageid=knb-lter-jrn.200046001.3.

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