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Effects of moderate drought on forage quality and quantity lasted for 3 years post drought and were exacerbated by heavy grazing

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Abstract

Growing season droughts can have major impacts on grassland vegetation and are predicted to become increasingly frequent in temperate rangelands due to climate change. To sustain livestock production systems, we need to understand what grazing management strategies will best support long-term ecosystem and livelihood sustainability in the face of increasing drought. Little is known about how droughts interact with grazing management to affect forage quality and quantity. In two North American grasslands where grazing by domestic livestock is the primary land-use, we assessed the separate and combined effects of experimental rainfall reductions and grazing management strategies on forage quality and quantity over five years. During a 2-yr experimental rainfall reduction period, rainfall reductions decreased both forage quality and quantity at one site. At a second site, heavy grazing during the first year of experimental drought reduced forage biomass and digestibility during the second year. In the first year after experimental rainfall reduction treatments ended, plots that formerly received large rainfall reductions displayed strong legacy effects. These plots had 26% to 57% less digestible forage biomass but greater forage quality than controls. Experimental treatments did not induce long-term changes in forage quantity at either site, but reductions in forage quality persisted up to three years after droughts ended. Our results highlight the resilience of North American Great Plains grasslands to both drought and grazing, but also suggest that these disturbances can have additive and long-term effects on forage nutritive value. Legacy effects of droughts on forage quality and quantity may impact ruminant nutrition for 1-3 years following a drought, and heavy grazing during drought may strengthen the effects of drought on livestock nutrition.

Introduction

The ecosystem services provided by natural grasslands can be disrupted by drought (Smith et al. 2024), and growing season droughts are predicted to become more frequent due to climate change (Knapp et al. 2023). Global change experiments routinely measure effects of simulated droughts on the biomass and community composition of natural grasslands (Smith et al. 2024). Drought-induced changes to grassland vegetation can affect wild and domesticated ungulate ruminants via shifts in both the quantity and quality of forage. For example, drought-

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induced reductions in forage biomass can negatively impact ruminant performance, and that effect can be exacerbated by concurrent reductions in forage quality (White et al. 2014). Conversely, droughts could maintain or increase forage quality despite drought-induced reductions in forage biomass, leading to weaker bottom-up effects on animal performance (Grant et al. 2014).

Bottom-up drought effects may be further influenced by interactions between drought and land management (e.g. grazing regimes) (White et al. 2014, Deléglise et al. 2015). Due to logistical hurdles, drought manipulation experiments rarely include manipulations of large ruminant grazers. More research is therefore needed to understand when, where and how grazing and drought interact to shape ruminant nutrition. For example, heavy grazing during drought could lead to reductions in aboveground production potential or shifts in plant species composition (e.g., Deléglise et al. 2015), both of which may result in altered forage quantity and quality. Most studies of forage quality and drought do not track recovery for multiple years after the disturbance event, so the legacy effects of drought on forage quality are also poorly understood (White et al. 2014, Deléglise et al. 2015). Legacies of prior year conditions are known to be strong drivers of grassland productivity (Sala et al. 2012), but less work has explored the role of legacy effects on forage quality. To fill these knowledge gaps, we tested the separate and combined effects of rainfall reduction and grazing treatments on forage (grass and forb) availability and nutritive value in grasslands of the northern Great Plains of North America.

Methods

The study was conducted at two field sites in the west-central semi-arid prairies of North America (EPA Level II ecoregion 9.3; Omernik 1987). One site was in eastern Montana (MT) at the Fort Keogh Livestock and Range Research Laboratory (46°20'N, 105°59'W). The other site was at a private cattle ranch (43°18'N, 105°03'W) in the Thunder Basin region of northeastern Wyoming (WY). Mean annual precipitation and temperature are 320 mm and 7.8°C at the MT site and 320 mm and 6°C at the WY site. Most precipitation falls during the growing season (April – October). Floristically, both sites are in a broad ecotone between shrublands of the North American Deserts, and grasslands of the Great Plains. Plant communities commonly include a sparse overstory of *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young (Wyoming big sagebrush) and an understory characteristic of northern mixed-grass prairie (Frost et al. 2023).

We manipulated grazing and rainfall reduction in a full factorial (3×5) with a split plot. Main plots (paddocks) were arranged in a randomized complete block design with three blocks per site. Grazing treatments were randomly assigned to three paddocks per block, and the fourth paddock was used to supply water. Grazing treatments were designed around multi-year, regionally relevant drought management strategies. Paddocks assigned to the “heavy” treatment experienced heavy grazing (70% biomass removal) during the drought period (2019-2020) and moderate grazing (50% biomass removal) during the post-drought period (2021-2023). The “stable” treatment received a consistent, moderate grazing intensity (50% biomass removal) across all years. A third “destock” treatment was also included but results are not presented here. Grazing treatments were implemented in early July in WY and early August in MT. Fort Keogh Livestock and Range Research Lab’s Institutional Animal Care and Use Committee determined our use of animals was consistent with standard livestock management. Within each paddock, we established six plots (2 × 2 m). Four plots were randomly assigned to rainfall reduction treatments and two were randomly designated as control plots. Rainfall reduction treatments (-25%, -50%, -75%, and -99%) were applied with rain-out shelters (3 × 4 m) positioned over plots from April – October in 2019-2020. Rain-out shelters were removed during grazing treatments. Ambient precipitation in MT was near average in 2019 and 2020, below average in 2021, and slightly below average in 2022 and 2023. In WY, precipitation was above average in 2019, below average in 2020 and 2022, and near average in 2021 and 2023.

To sample forage, we clipped one or two 10 x 50 cm quadrats within each 2 x 2 m plot in May, June, and July for 5-yr (2019-2023). Sampling areas were excluded from grazing during the current sampling year. Forage samples

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were a composite of living and dead herbaceous material and excluded cactus, woody vegetation, and litter. Forage material was oven dried (60°C, 48 hr), weighed to obtain forage biomass estimates (g × m^{-2}), and ground to pass through a 2-mm screen. From the composite sample, 0.25g subsamples were added to filterbags (F57, Ankom Technology Corp., Fairport, NY, USA) and used for in-vitro organic matter (OM) digestibility analysis via an ANKOM DaisyII incubator (Daisy Incubator; Ankom Technology Corp., Fairport, NY, USA; ANKOM 2017a). Separate subsamples were used for neutral detergent fiber analysis (ANKOM 2017b). In addition, we calculated digestible forage biomass (g × m^{-2}). Species composition data are presented in Frost et al. (2023) and Bloodworth et al. (in review).

For each response variable we ran separate linear mixed models by year and site, since treatment applications and associated hypotheses differed among years, and sites experienced different weather patterns over the course of the experiment. In each model, fixed effects included percent rainfall reduction (continuous), grazing treatment (categorical), month (categorical), and all possible interactions. To account for spatial and temporal non-independence, we included random intercepts for block, paddock nested within block, and plot nested within paddock and block, and we utilized a compound symmetry covariance structure. For each model, we also included May 2019 data from each plot as a fixed effect covariate to account for baseline differences among plots. Whenever two- or three-way interactions with month were significant, we ran separate models by month. We ran models in R 4.2.1 using the nlme package (Pinheiro and Bates 2000).

Results

In Montana, experimental rainfall reduction treatments were associated with lower forage quality and quantity during the first two years. Plots experiencing the most rainfall reduction had 4.1% more fiber content than control plots (Fig. 1; main effect of rainfall reduction 2019 $P = 0.002$; 2020 $P = 0.07$). The quantity of digestible forage declined by up to 27.0% with rainfall reduction in 2019 (Fig. 1; $P = 0.001$). In 2020, digestible forage biomass declined by 46.0-53.5% with rainfall reduction in June and July, but not May (Fig. 1; rainfall reduction*month $P = 0.003$). In 2021, a natural drought year in Montana when we did not impose experimental rainfall reduction treatments, forage quality tended to be higher and forage quantity was lower in plots that had formerly been subject to experimental rainfall reductions, compared to control plots. Forage fiber content was 4.9% lower in plots with the most former rainfall reduction, compared to control plots (Fig. 1; $P < 0.0001$). In May 2021, forage digestibility was 7.4% higher in plots with the most former rainfall reduction, compared to control plots (Fig. 1; rainfall reduction*month $P = 0.008$). Even in the presence of a strong natural drought in 2021, former rainfall reduction treatments were associated with up to 57.2% lower biomass of digestible forage (Fig. 1; $P < 0.0001$). Grazing treatments did not influence forage results in Montana.

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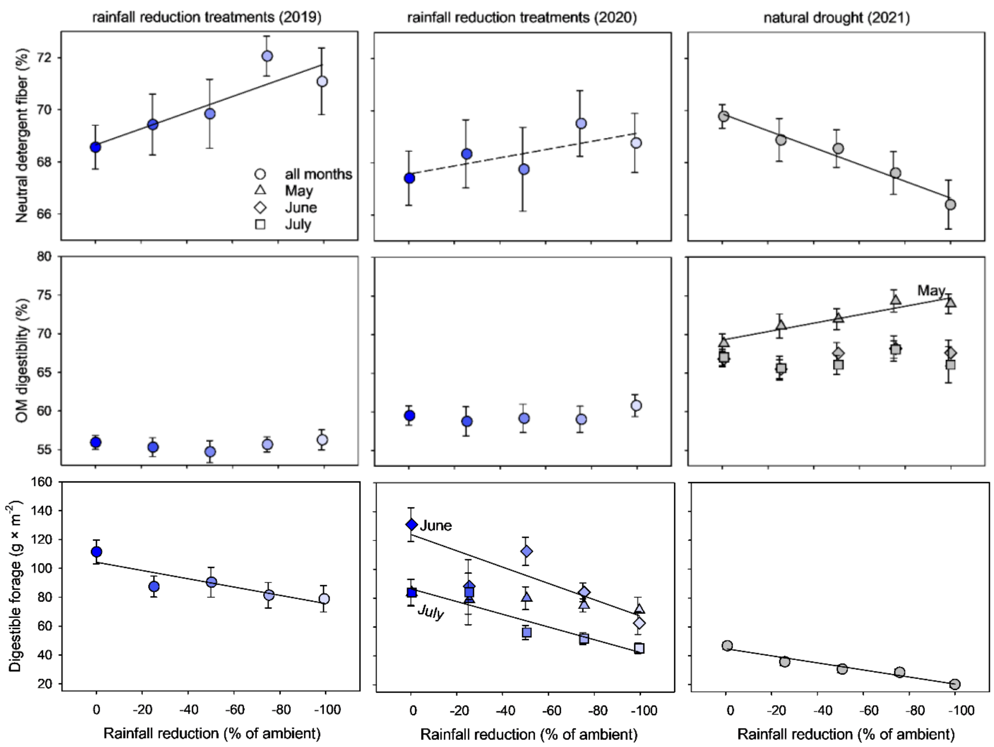

Fig. 1. Effect of rainfall reduction treatments (2019-2020) and a natural drought (2021) on average (±1 SE) forage nutritive value and biomass in Montana. Solid lines indicate significant effects of rainfall reduction ($P \leq 0.05$), and dashed lines indicate marginal significance ($0.05 < P \leq 0.10$)

In Wyoming, our treatments were mostly unrelated to forage quality or quantity during 2019-2020. In 2020, however, digestibility declined with rainfall reduction, but only in the heavy grazing treatment (P = 0.02). In 2020, forage biomass was also 27.7% lower in the heavy grazing treatment than stable grazing treatment ($P = 0.04$). During the first post-drought year (2021), forage fiber content was greater with former rainfall reduction in May, but decreased with former rainfall reduction by July (rainfall reduction*month P = 0.007). Plots that had formerly received the most rainfall reduction also had 26.2% less digestible forage (P = 0.0001).

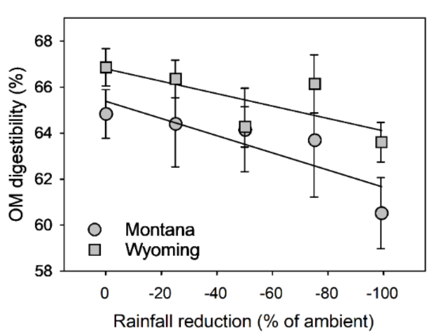

Fig. 2. Legacy effects of 2019-2020 rainfall reduction treatments on 2023 average (±1 SE) organic matter digestibility. Solid lines indicate significant main effects of rainfall reduction (P≤ 0.05)

Several effects of experimental rainfall reduction treatments persisted into 2022 and 2023. In Montana, forage fiber content patterns in 2022 matched those of 2021. Fiber content declined with former rainfall reduction ($P = 0.007$), such that plots which received the most rainfall reduction in 2019-2020 had 3.1% lower fiber content in 2022. At both sites, experimental rainfall reductions in 2019-2020 were associated with lower forage digestibility in 2023 (Fig. 2; MT $P = 0.009$; WY $P = 0.01$). Plots receiving the most rainfall reduction had 4.1-6.7% lower digestibility.

Discussion

Over a 5-yr timespan, we observed strong effects of experimental rainfall reductions and grazing management on both forage quality and quantity in two North American rangelands. Despite major differences in plant communities and weather patterns, responses were surprisingly consistent across our two sites. During experimental droughts, we observed neutral to negative effects of rainfall reductions on forage quality and quantity, as well as some evidence that heavy grazing further reduced forage quality and quantity. After experimental droughts ended, we observed short-term, strongly negative legacy effects on forage quantity. The magnitude of these effects matched or exceeded those observed in other systems (e.g., Oesterheld et al. 2001). We also observed some short-term positive legacy effects on forage quality, which were likely driven by shifts in soil nutrient availability (i.e. higher nutrient concentrations in formerly droughted plots), phenology, and species composition (Frost et al. 2023). From a ruminant nutrition perspective, the strong negative short-term legacy effects we observed on forage quantity may override any short-term positive effects on forage quality.

Grazing and drought shifted plant species composition towards less nutritious species in our study (Frost et al. 2023, Bloodworth et al. in review), leading to the potential for longer-term legacies after extreme disturbance events. Moreover, in perennial dominated systems, multi-year plant resource allocation patterns may lead to complex long-term legacies (Vermeire et al. 2024). We indeed saw evidence that experimental rainfall reductions led to reductions in forage quality at both sites in 2023, a full three years after experimental droughts ceased. Given the already low quality of forage in extensive rangelands, additional reductions could be detrimental to livestock weight gains or necessitate additional supplementation. Our findings emphasize that although northern Great Plains grasslands are resilient to both grazing and drought, these disturbances can have additive and lasting effects on a critical forage resource.

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