Rangeland Ecology & Management 73 (2020) 796–810

Contents lists available at ScienceDirect

Rangeland Ecology & Management

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

Adaptive, Multipaddock Rotational Grazing Management: A Ranch-Scale Assessment of Effects on Vegetation and Livestock Performance in Semiarid Rangeland☆

David J. Augustine[a,1,*], Justin D. Derner[b,2], María E. Fernández-Giménez[c,3], Lauren M. Porensky[d,4], Hailey Wilmer[e,5], David D. Briske[f,6], the CARM Stakeholder Group[7]

[a] US Department of Agriculture (USDA)–Agricultural Research Services (ARS) Plains Area Rangeland Resources and Systems Research Unit, Fort Collins, CO 80526, USA
[b] USDA-ARS Plains Area Rangeland Resources and Systems Research Unit, Cheyenne, WY 82001, USA
[c] Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523-1472, USA
[d] USDA-ARS Plains Area Rangeland Resources and Systems Research Unit, Fort Collins, CO 80526, USA
[e] USDA Northern Plains Climate Hub, Fort Collins, CO 80526, USA
[f] Department of Ecology and Conservation Biology, Texas A&M University, MS2120 TAMU, College Station, TX 77843-2120, USA

ARTICLE INFO

Article history:
Received 24 January 2020
Revised 13 July 2020
Accepted 27 July 2020

Key Words:
cattle weight gain
collaborative adaptive rangeland management
ecosystem services
grazing management
plant-herbivore interactions
rotational grazing management
shortgrass steppe
stocking density

ABSTRACT

A comprehensive understanding of multipaddock, rotational grazing management on rangelands has been slow to develop, and the contribution of adaptive management (Briske et al. 2011) and sufficient scale (Teague and Barnes 2017) have been identified as key omissions. We designed an experiment to compare responses of vegetation and cattle in an adaptively managed, multipaddock, rotational system with that of a season-long, continuous system at scales comparable with those of a working ranch. We hypothesized that 1) year-long rest periods in the adaptively managed, rotational pastures would increase the density and productivity of perennial C_3 graminoids compared with continuously grazed pastures and 2) adaptive management, supported with detailed monitoring data, would result in similar cattle performance in the rotational as in the continuously grazed pastures. However, we found little supporting evidence for grazing management effects on C_3 graminoid abundance or production under either above-average or below-average precipitation conditions during the 5-yr experiment. Furthermore, adaptive rotational grazing resulted in a 12–16% reduction in total cattle weight gain relative to continuous grazing each year. Our work shows that the implementation of adaptive management by a stakeholder group provided with detailed vegetation and animal monitoring data was unable to fully mitigate the adverse consequences of high stock density on animal weight gain. Under adaptive rotational grazing, C_3 perennial grass productivity and stocking rate both increased following above-average precipitation. But when adaptive rotational management was directly compared with continuous grazing with the same increase in stocking rate, continuous grazing achieved similar vegetation outcomes with greater cattle weight gains. We suggest that managers in semiarid rangelands strive to maintain cattle at stock densities low enough to allow for maximal cattle growth rates, while still providing spatiotemporal variability in grazing distribution to enhance rangeland heterogeneity and long-term sustainability of forage production.

☆ Research was funded by the US Dept of Agriculture–Agricultural Research Service, by USDA-AFRI awards 2012-38415-20328 and 2015-67019-23009, the Colorado Agricultural Experiment Station project COLO0698, and the Center for Collaborative Conservation at Colorado State University. The USDA-ARS, Plains Area, is an equal opportunity/affirmative action employer, and all agency services are available without discrimination. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

* Correspondence: David Augustine, Ecologist, USDA-ARS Plains Area Rangeland Resources and Systems Research Unit, 1701 Center Ave, Fort Collins, CO, USA 80526. Tel.: 970-492-7125.

E-mail address: David.Augustine@usda.gov (D.J. Augustine).

[1] Ecologist.
[2] Research Leader and Supervisory Research Rangeland Management Specialist.
[3] Professor.
[4] Ecologist.
[5] Fellow.
[6] T.M. O'Connor and Regents Professor.
[7] Stakeholder contributors Rachel Murph (Natural Resource Conservation Service), Kim Obele and Stephanie Magnuson (USDA-Forest Service), Matt Pollart (Colorado State Land Board), Terri Schulz (The Nature Conservancy), Ted Toombs (Environmental Defense Fund), Seth Gallagher and Angela Dwyer (Bird Conservancy of the Rockies), Casey Matney and Annie Overlin (Colorado State University Extension), and the Crow Valley Livestock Cooperative, Inc. (Steve Anderson, Leonard Ball, Dana Bowman, Andy Lawrence, and Jeff Wahlert).

https://doi.org/10.1016/j.rama.2020.07.005
1550-7424/Published by Elsevier Inc. on behalf of The Society for Range Management.

Introduction

Semiarid rangelands of the North American Great Plains simultaneously support livestock production and an array of other ecosystem services, such as wildlife habitat and carbon storage. Enhancing decision making by managers of these rangelands requires understanding the ecological processes that regulate the provision of ecosystem services. Interactive effects of climate/weather, soils/ecological sites and grazing management on forage production, livestock weight gain, and wildlife habitat are complex and poorly understood (Boyd and Svejcar 2009; Briske et al. 2011a). While decisions on how to move livestock in space and time (e.g., via rotational grazing management) are central to livestock management, few studies have examined the effects of such movements in heterogeneous and spatially extensive landscapes (Briske et al. 2008; Hawkins et al. 2017; Teague and Barnes 2017). Livestock distribution on the landscape is typically managed via fencing and water infrastructure, which can be costly (Knight et al. 2011), yet experimental studies addressing the ecological and economic benefits of such management remain rare. Despite decades of small-scale experimental research in homogenous plant communities, substantial uncertainty exists regarding the degree to which adaptive movements of cattle in space and time contribute to achieving desired vegetation and livestock outcomes at scales relevant to livestock producers (Briske et al. 2008, 2011b; Teague and Barnes 2017).

Controlled experiments in small paddocks consistently find that rotational grazing in the absence of adaptive management does not enhance vegetation or animal performance, as compared with continuous, season-long grazing (reviewed by Briske et al. 2008; Hawkins 2017). Experiments that disentangle stocking rate (animals present over a defined period of time, typically expressed on an annual basis per hectare) from stocking density (animal units per hectare at a given point in time) consistently show a strong effect of overall stocking rate on vegetation and livestock outcomes (e.g., Pinchak et al. 1990; Holechek et al. 1999; O'Reagain et al. 2014; Thomas et al. 2015; Porensky et al. 2016; Veblen et al. 2016). Yet some social and biophysical scientists working at the scale of ranching enterprises indicate that ecological and economic benefits arise from various forms of rotational grazing management (*sensu* adaptive, multipaddock, Teague et al. 2013; Teague and Barnes 2017). Recent efforts to determine adaptive, multipaddock, rotational grazing outcomes at scales of ranches are limited in terms of experimental controls, replication, and control over stocking rates and have produced mixed results. In a large-scale study in a South African grassland, Venter et al. (2019a, 2019b) did not find any benefits to vegetation or livestock production arising from rotational versus season-long grazing regimes. In North American tallgrass prairie, Teague et al. (2011) found evidence that adaptive, multipaddock grazing at ranch scales enhanced soil organic matter, soil water-holding capacity, and vegetation composition of tallgrass species relative to long-term continuous grazing, but they did not evaluate livestock production responses. A synthesis of research in northern Australian rangelands concluded that complex, multipaddock, rotational grazing systems were not appropriate for the region, but that moderate stocking rates and management strategies that provide for periodic growing-season rest from grazing were essential to maintaining pasture condition (O'Reagain et al. 2014). A critical knowledge gap regarding the potential benefits of multipaddock grazing is whether *adaptive* management, involving livestock movement in response to weather, forage dynamics, and ecological site variation, is a major contributor to the provisioning of desired ecosystem services at ranch scales (Briske et al. 2011; Teague and Barnes 2017). Here, we report on a grazing management experiment that incorporates study design recommendations discussed by Teague and Barnes (2017) to examine the effects of adaptive, multipaddock, rotational grazing management on vegetation and livestock production in a semiarid rangeland.

A central premise of multipaddock grazing is the short but intensive grazing periods, interspersed with long periods of grazing deferment, will enhance vegetation composition (Teague and Barnes 2017). This is important for shortgrass steppe rangelands that support a combination of grass functional types. The combination of warm growing seasons and limited precipitation, which primarily occurs during the summer, facilitates dominance of grazing- and drought-tolerant C_4 shortgrasses (*Bouteloua gracilis* and *B. dactyloides;* Milchunas et al. 1994; Lauenroth et al. 1999; Irrisari et al. 2016). In contrast, the subdominant perennial C_3 graminoids are reliant on spring precipitation (Milchunas et al. 1994), capable of producing more biomass in years with high precipitation (Irrisari et al. 2016), and are more sensitive to effects of grazing (Eneboe et al. 2002; Augustine et al. 2011). Perennial C3 graminoids are essential to livestock operations in the shortgrass steppe based on their contribution to forage production in spring and fall (USDA-NRCS 2007a, 2007b; Derner and Hart 2010).

Another key consideration for ranching operations is how adaptive rotational grazing management affects livestock production. Because higher stocking densities are typically used, this can lead to declines in the quality of forage consumed and total forage intake rate, resulting in reduced cattle weight gain (e.g., McCollum and Gillen 1998; McCollum et al. 1999; Briske et al. 2008). Given that investment in the fencing and water infrastructure necessary to implement rotational grazing can be costly (Knight et al. 2011; Windh et al. 2019), evaluating effects of adaptive, rotational grazing management on cattle weight gains is needed to assess potential consequences for ranching enterprise profitability.

We designed a ranch-scale (2 600-ha) experiment to evaluate the responses of vegetation and cattle performance to 1) adaptive, multipaddock, rotational grazing and 2) season-long, continuous grazing, where the latter is traditionally used in this ecosystem (Traditional Rangeland Management, TRM; Bement 1969). Decisions regarding annual stocking rate and the sequence and timing of cattle movements among pastures for the adaptive, multipaddock grazing were made by an 11-member stakeholder group seeking to achieve a suite of vegetation, livestock, and wildlife and objectives (see Wilmer et al. 2018); this experimental treatment is hereafter referred to as Collaborative Adaptive Rangeland Management (CARM). For CARM, ten 130-ha pastures were grazed by a single herd of steers managed using adaptive, rotational grazing that incorporated planned year-long rest in 20% of the pastures. For TRM, 10 paired, 130-ha pastures experienced season-long, continuous grazing by herds of yearling steers at one-tenth the stocking density of the single CARM herd. Overall stocking rates for both treatments were identical. We hypothesized that 1) year-long rest from grazing in the CARM treatment would increase the abundance and productivity of perennial C_3 graminoids compared with TRM pastures and 2) adaptive, rotational grazing management with CARM would compensate for negative effects of high stock densities to yield similar livestock performance as in TRM.

Methods

Study Area and Experimental Design

Research was conducted at the Central Plains Experimental Range (CPER) approximately 12 km northeast of Nunn, Colorado (40°50′N, 104°43′W), which is a Long-Term Agroecosystem Research (LTAR) site (Speigal et al. 2018). Long-term mean annual precipitation on the CPER is 340 mm, of which > 80% occurs during the growing season of April through September (Lauenroth and Milchunas 1992). Topography is flat to gently rolling; soils range

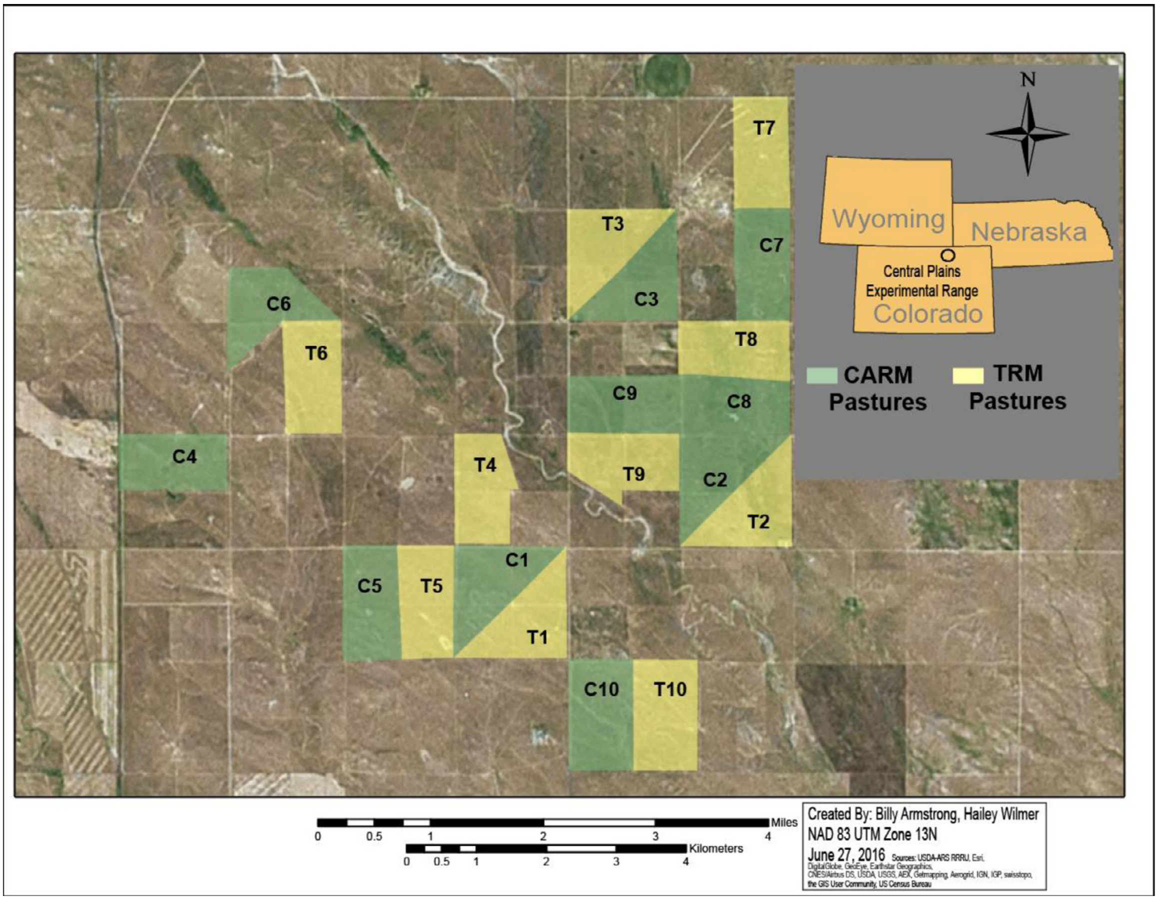

Fig. 1. Map depicting location of the Central Plains Experimental Range in northeastern Colorado (inset) and the 10 pairs of pastures (each ~130 ha) used to compare the effects of Collaborative Adaptive Rangeland Management (CARM) versus Traditional Rangeland Management (TRM) on vegetation responses and livestock performance.

from fine sandy loams on upland plains to alkaline salt flats bordering a large drainage running north-south in the eastern portion of the site. Two C_4 shortgrass species—blue grama *(Bouteloua gracilis)* and buffalograss *(B. dactyloides)*—comprise over 70% of aboveground net primary productivity at the CPER (Lauenroth and Sala 1992). C_3 perennial grasses (*Pascopyrum smithii, Hesperostipa comata,* and *Elymus elymoides*), C_4 bunchgrasses *(Aristida longiseta, Sporobolus cryptandrus),* plains pricklypear cactus *(Opuntia polyacantha),* subshrubs *(Gutierrezia sarothrae, Eriogonum effusum, Artemisia frigida),* and saltbush *(Atriplex canescens)* are less abundant but generate taller structure on the landscape (Augustine and Derner 2015).

Twenty 130-ha pastures were paired into 10 blocks, each containing two pastures similar in terms of soil and plant characteristics; topographical patterns as measured by a topographical wetness index (TWI, a remotely sensed index of water flow on a landscape; Beven and Kirkby 1979); and prior management history of season-long grazing at moderate stocking rates. One pasture in each pair was randomly assigned to the TRM treatment. Each TRM pasture was grazed throughout the growing season (mid-May to early October) by a single herd of yearling steers. The other pasture in each pair was assigned to the CARM treatment (Fernandez-Giménez et al. 2019; Fig. 1). Average ranch/farm size in Colorado is 345 ha (853 acres; USDA NASS 2012), and a recent survey of ranches in the adjacent portion of Wyoming found ranching operations employing rotational grazing typically have 5–10 pastures (Kachergis et al. 2013). Even assuming that ranches in our study region are double the state average would result in pasture sizes of 69 ha (assuming 10 pastures per ranch) to 138 ha (assuming 5 pastures per ranch). Pastures of 130 ha are common on privately owned rangeland adjacent to CPER, but we acknowledge that some ranches in our study region employ season-long grazing in pastures substantially larger than 130 ha. Critical to our experiment, previous studies have shown that pastures of 130 ha are sufficiently large to allow cattle to exhibit uneven foraging distribution in response to topography, distance to water, and spatial variation in plant composition in this ecosystem (Senft et al. 1985; Gersie et al. 2019).

Each TRM pasture was grazed (i.e., none were rested) by a herd of yearling steers that occupied each pasture separately, whereas the CARM pastures were grazed by a single 10-fold larger herd of steers managed with an adaptive, rotational grazing system, with 20% of the pastures planned for year-long rest each year (Fernández-Giménez et al. 2019). Details of the cattle management strategy applied to the CARM pastures were decided by the 11-member stakeholder group, which used stocking rate adjustments, grazing rotations, and season-long rest as adaptive management tools designed to help achieve specific goals and objectives (Wilmer et al. 2018). Stakeholders decided on the stocking rate, grazing sequence, and which pastures to rest each grazing season and developed a suite of criteria used to rotate cattle in response to real-time conditions of the pastures during the growing season. This stakeholder group included four ranchers, three representatives from nonprofit conservation organizations, and four land managers from federal and state agencies, who collectively made decisions based on consensus or supermajority

(Wilmer et al. 2018). The stakeholder decision-making process was intended to produce repeatable, evidence-based decisions that were explicitly tied to management objectives and incorporated local and professional knowledge, as well as experimentally derived monitoring data (Fernández-Giménez et al. 2019). Collaborative processes like this could potentially apply to management of public lands grazing allotments where management goals include multiple ecosystem services. However, we note that an adaptive grazing management approach could also be implemented by one manager in a noncollaborative manner that does not require frequent meetings and discussions.

Each year of the study, the same total number of steers grazed in the CARM and TRM pastures. The stocking rate was initially set at 214 yearlings in 2014 based on the recommended moderate stocking rate for the soil and plant communities present in the study area (equivalent to 0.61 animal unit months (AUM) ha^{-1}; USDA-NRCS 2007a, 2007b, 2007c). In subsequent years, the stakeholder group adjusted the stocking rate in April, before the 15 May grazing start date, depending on past vegetation conditions and seasonal weather forecasts. Stakeholders increased the stocking rate to 0.64, 0.67, 0.70, and 0.81 AUM ha^{-1} in 2015, 2016, 2017, and 2018, respectively (equivalent to a total of 224, 234, 244, and 280 steers). The TRM stocking rate was also adjusted each study year to match the CARM stocking rate, such that pastures in the two treatments differed only in the adaptively managed spatiotemporal pattern of cattle grazing. On the basis of our annual measurements of forage production in grazing cages in all pastures, combined with the assumption that yearling steers consume 2.6% of their body weight daily at an average weight of 364 kg (800 lb), we estimate that cattle at these stocking rates would have grazed an average of 23% and 17% of forage produced in the wet yr of 2014 and 2015, 27% of forage in the average yr of 2017, and 35% and 47% of forage in the dry yr of 2016 and 2018, respectively. Pretreatment vegetation and cattle performance data were collected in 2013, when all 20 pastures received the TRM treatment. Due to a severe drought in 2012, all pastures were stocked at 70% of the normal moderate rate during the 2013 grazing season.

Management of the CARM pastures during 2014–2018 resulted in the application of two contrasting grazing intensities to pastures, consisting of either 1) pulsed grazing by the large cattle herd (at 10 times greater stocking density than TRM pastures, which we hereafter refer to as pulse grazing), or 2) year-long lack of grazing (referred to hereafter as rest). Which CARM pastures experienced pulse grazing and which were rested from grazing varied across years and depended on an adaptive grazing management plan developed by the stakeholders, as well as on-the-ground, weather-dependent conditions (i.e., forage biomass and cattle behavior) measured weekly during the grazing season. On the basis of weather and vegetation conditions experienced during our study, we applied year-long rest to three, six, three, one, and one of the CARM pastures during 2014–2018, respectively, with the remaining pastures being pulse grazed (see Fig. 1; Appendix A). The larger number of rested pastures in 2015 was a result of above-average forage production in both 2014 and 2015, which allowed the CARM cattle herd to meet its forage requirements by grazing only four pastures over the growing season. By the end of the second yr of treatments, 9 of the 10 CARM pastures had been rested for an entire growing season at least once. The timing of rotations among pastures each year was determined by rotation criteria codeveloped by stakeholders and scientists (Appendix B). In the first yr, cattle were moved when a threshold was met in vegetation biomass, cattle behavior, or a maximum number of grazing days set for each pasture based on multiple management objectives. In the second yr (2015), the maximum days threshold was removed to allow the rotation to be based primarily on vegetation thresholds. However, due to exceptional precipitation and forage production in 2015, long grazing periods (in most cases > 40 d) were required to reduce vegetation to target thresholds. Based on forage production values, stocking rate, and rotation pattern employed in 2015, we estimate that cattle grazed 13%, 31%, 47%, and 48% of forage production in grazed pastures (again assuming steers consume 2.6% of body weight daily), while the remaining six pastures were rested. By contrast, we estimate cattle grazed approximately 12–23% of forage across all 10 TRM pastures in 2015. Due to stakeholders' concerns regarding the effect of long graze periods on cattle performance, the maximum days threshold was reinstated in 2016 and used in all years thereafter (see Appendix B). In addition, the maximum days criterion was reduced in 2017 and 2018 to test whether more rapid rotations, particularly earlier in the growing season, would enhance weight gain by cattle. The cattle behavior threshold was measured by CPER staff who checked and observed cattle 3 d/wk to note patterns of herd size and distribution and whether any cattle displayed signs of attempting to leave the pasture. Staff also estimated forage biomass weekly on the basis of visual obstruction readings (Robel 1970, as modified by Augustine and Derner 2015) to assess whether minimum forage biomass criteria were met. Beginning in 2015, we also planned to move cattle to the final pasture in the sequence on a date that would allow them to spend 7−14 d in the last-grazed pasture, in order to avoid rotating the cattle into the last pasture for a lesser number of days (see Appendix B).

In addition to adaptively varying the sequence of grazed pastures annually, stakeholders had the option to implement prescribed burns in locations and conditions where they could potentially help achieve stakeholder-defined objectives for vegetation, livestock production, and wildlife habitat (Wilmer et al. 2018). Stakeholders chose to implement 32-ha patch burns during the nongrowing season in some years. They hypothesized that removal of a portion of the residual grass in particular pastures could enhance preferential grazing in these patch-burned areas with higher forage quality early in the next growing season (Augustine and Derner 2014) while also creating habitat for certain grassland birds (Augustine and Derner 2012). Any time that stakeholders decided to implement a patch burn in a given pasture within the CARM treatment, we also implemented a patch burn of the same size and on the same soil types in the paired TRM pasture. This was done to allow for implementation of adaptive management by the stakeholders while maintaining control pastures that only differed in the adaptively managed spatiotemporal pattern of cattle grazing. Patch burns were implemented in the autumn (October or November) in blocks 1 and 9 in 2014, block 6 in 2016, and block 10 in 2017.

To evaluate vegetation responses, we accounted for variation within and among pastures in soil types using maps of "ecological sites" derived from the national soil survey (SSURGO), where an ecological site represents a distinctive kind of land with specific soil and climate processes and properties that determine the land's ability to support certain plant species and amounts of vegetation (Duniway et al. 2010). Our study pastures encompassed three types of ecological sites: loamy plains, sandy plains, and salt flats (USDA-NRCS 2007a, 2007b, 2007c). On the CPER, the loamy plains ecological site is dominated by C_4 shortgrasses (USDA-NRCS 2007a) and is the most prevalent but least productive ecological site. The sandy plains ecological site is characterized by increased codominance by C_3 perennial midgrasses and scattered shrubs (USDA-NRCS 2007b) and is moderately prevalent and productive. The salt flats ecological site is characterized by the dominance of C_4 saltgrasses (*Sporobolus airoides, Distichlis spicata;* USDA-NRCS 2007c) and is the least prevalent but most productive ecological site. Within the experimental pastures, four blocks were entirely on the loamy plains ecological site, one block was entirely on the sandy plains ecological site, two blocks were on a mosaic of loamy and sandy plains, and three blocks contained a mosaic of loamy and sandy plains plus an additional lowland portion of the pasture dominated by salt flats.

Vegetation Measurements

Pastures were stratified by ecological site and topography (based on classes of the topographic wetness index derived from a digital elevation model obtained from the National Ecological Observatory Network) and monitoring plots were established within paired strata for the two pastures in each experimental block. We established four pairs of plots in the seven experimental blocks containing loamy and/or sandy plains ecological sites and six pairs of plots in three blocks that additionally contained the salt flat ecological site. Each plot contained a systematic grid of four 25-m transects oriented north-south and spaced 106 m apart, where we measured vegetation. Vegetation measurements occurred during 1–20 June each year, corresponding to the time period when C_3 grasses are approaching peak biomass and producing inflorescences, while C_4 grasses are still in a vegetative growth stage. Along each transect, we measured the density of the two most abundant C_3 grasses, *P. smithii* and *H. comata*, within 0.25-m^2 circular quadrats placed at 3-m intervals (8 quadrats per transect; 32 per plot). For *P. smithii,* a rhizomatous grass, we counted the density of individual tillers. For *H. comata,* a bunchgrass, we counted the density of individual bunches.

We measured aboveground net primary production (ANPP) of plant functional groups (C_4 perennial grasses, C_3 perennial graminoids, annual grasses, forbs, and subshrubs) at peak biomass in August (as recommended by Milchunas and Lauenroth 1992), with harvests occurring in a 0.18-m^2 rectangular quadrat centered within 1×1 m moveable grazing cages. In each plot, we placed two cages, each along transects one and four (four cages per plot). Cages were moved annually in April, before the grazing season, to a new random location within 10 m of the associated permanently marked transect where we measured vegetation cover and composition.

Measurements in 2013 occurred before implementation of the CARM treatment, and measurements of plant density in 2014 occurred only 3 weeks after beginning the treatment, at which time grazing could not yet have directly influenced plant density. Measurements of ANPP in 2014 occurred inside grazing cages placed before the 2014 grazing season and hence could not have been influenced by the grazing treatment in 2014. Therefore, in all vegetation analyses, we use 2013 and 2014 as pretreatment measurements.

All cattle in the experiment were yearling steers of mixed European breeds. Each year, we stratified the animals assigned to each treatment according to herd source. We weighed steers individually at the beginning of the grazing season (mid-May), stratified steers by weight, and randomly assigned them to TRM and CARM treatments. We individually weighed steers again at the end (early October) of each grazing season. We used shrunk weights (Derner et al. 2016) to determine seasonal gains (kg steer^{-1}) and average daily gain (kg steer^{-1} day^{-1}), calculated as seasonal gain divided by number of grazing days.

Data Analysis

Vegetation responses to the CARM versus TRM treatment were analyzed using linear mixed models in SAS (SAS version 9.4, SAS Institute Inc., Cary, NC), which treated block as a random effect, accounted for repeated measures at each plot over time, and evaluated potential interactions among grazing treatment, ecological site, and year. In all models, we also included pretreatment vegetation measurements (the average of 2013 and 2014) in each plot as a covariate, and we used the Kenward-Roger method to compute the denominator degrees of freedom. Cattle weight gain data from treatment yr (2014−2018) were analyzed using a linear mixed model in JMP (JMP, Version 12. SAS Institute Inc.). To account for autocorrelation among animals in the same herd, we included herd nested within year as a random factor (10 herds per year for TRM, one herd per year for CARM). Because new yearling steers were used each year, we did not have any repeated measurements on the same animals. We included 2013 weight gain data as a covariate to account for preexisting variation in gain potential among pastures. Data were transformed or variance-weighted when necessary to meet model assumptions. In cases where we detected a potentially important interaction term ($P < 0.10$), we evaluated contrasts between treatments for each ecological site, year, or ecological site/year combination (depending on the interaction) and then considered these contrasts significant at the $P < 0.05$ level.

In addition to examining experiment-wide changes in plant densities and ANPP, we conducted focal analyses of the pastures that were rested within the CARM treatment each year. We sought to examine the hypothesized mechanism that pastures receiving year-long rest from grazing would experience an increase in the abundance and productivity of C_3 perennial graminoids in the growing season following the year of rest, when compared with paired pastures receiving TRM. For plant density, we calculated the difference in *P. smithii* tiller density measured in June of the year following rest minus the density in June of the year of rest, in each of the CARM pastures rested in a given year. We calculated the same value for each paired TRM pasture and then compared the magnitude of change between the two pastures using a paired *t*-test. Because these analyses did not account for within-pasture variation in ecological sites, and the small number of plots located on the salt flat ecological site contained substantially greater densities of *P. smithii* than the other two ecological sites and were not rested in all years, we excluded plots on salt flats from the analyses (resulting in $N = 4$ plots on loamy and/or sandy plains ecological sites per pasture in all comparisons). We also did not include *H. comata* density in the rested pasture analysis because this species was more patchily distributed across the experiment and did not always occur in pastures that were rested each year. We calculated the change in ANPP of C_3 perennial graminoids as the difference in production within cages in the year following rest (when plants within cages in rested pastures were growing for their second full growing season without grazing) minus production within cages in the year of rest. We compared the change in C_3 perennial ANPP in each rested pasture to its paired TRM pasture using a paired *t*-test ($N =$ four per comparison). These analyses yielded 13 paired comparisons of rested versus TRM pastures over the study period. In addition to the pasture-level comparisons, we analyzed mean differences across all 13 pairs in terms of both *P. smithii* density and C_3 perennial ANPP using a paired *t*-test ($N = 13$).

Finally, we conducted focal analyses of whether 14 plots affected by four different pairs of patch burns exhibited any difference in C3 and C4 perennial grass production the year after the burn was grazed by either the CARM herd (which grazed on the patch burns for 13, 21, 41, and 44 d, respectively) versus the year after season-long grazing on the patch burn by a TRM herd. Two pairs of burns were implemented in the fall of 2014, one pair in the fall of 2016, and one pair in the fall of 2017. We analyzed ANPP on the burns using a linear mixed model of production for each functional group with plot pair included as a random effect.

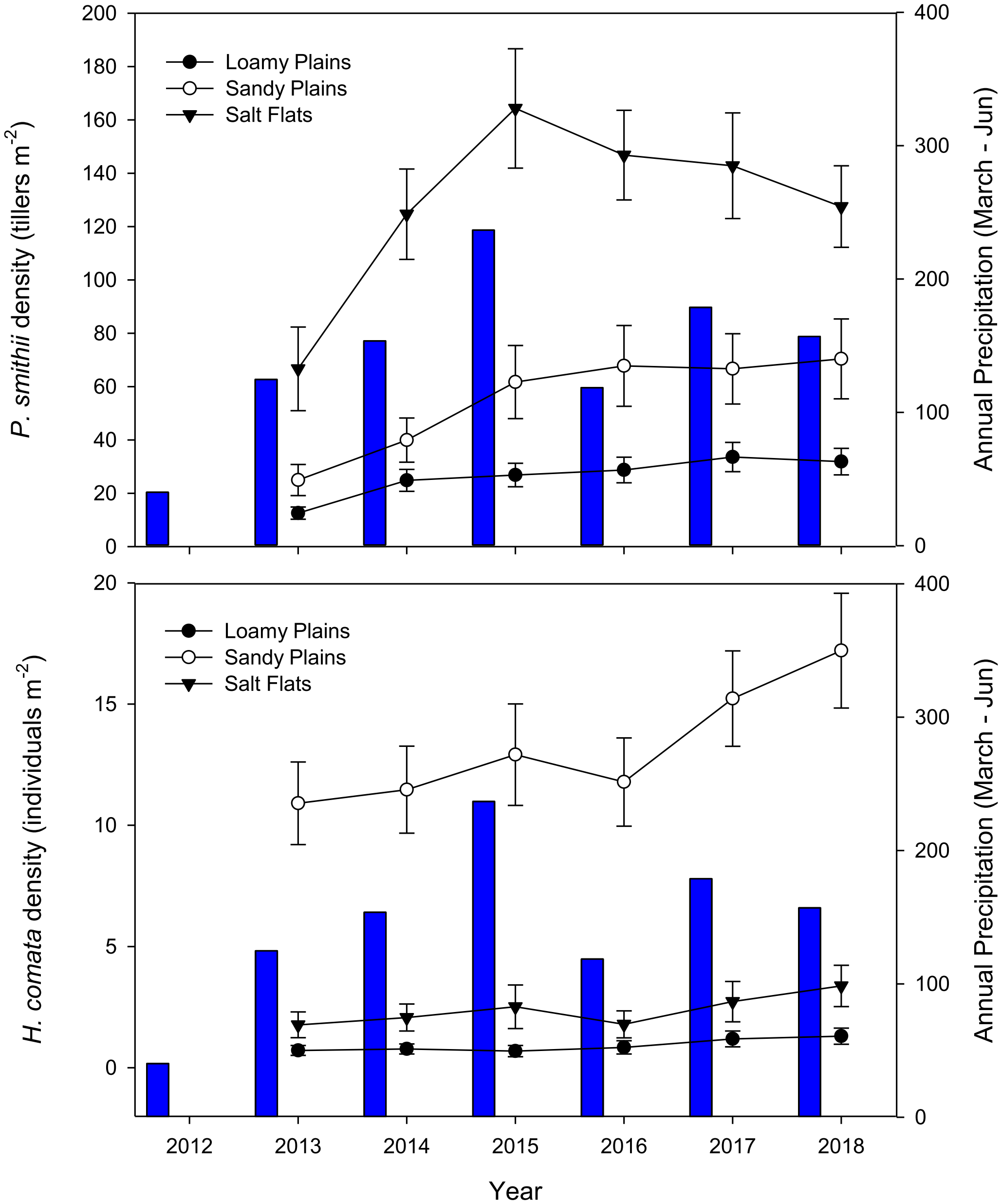

Fig. 2. Temporal trends in abundance of two C_3 perennial midgrasses on three different ecological sites, averaged across both grazing treatments in the shortgrass steppe of northeastern Colorado. *Blue bars* show variation in precipitation during March–June each year and plant density measurements occurred in mid-June each year. Error bars show ± 1 standard of error.

Results

C_3 Midgrass Densities

Densities of both C_3 midgrass species (*P. smithii* tillers and *H. comata* individuals) were low experiment wide on all ecological sites in the first pretreatment yr (2013), which followed an extreme drought in 2012 (Fig. 2). *P. smithii* density increased substantially in 2014 and again in 2015 in both grazing treatments in response to above-average precipitation and then remained stable thereafter (see Fig. 2a). *H. comata* density increased steadily from 2013 to 2018, with the exception of a decline between 2015 and 2016, which reflected low precipitation early in 2016 (see Fig. 2b). In all years, densities of *P. smithii* were ~fivefold greater on the salt flat ecological site and ~twofold greater on the sandy plains ecological site as compared with the loamy plains ecological site (see Fig. 2a). In contrast, *H. comata* occurred at low densities on loamy plains and salt flats and was sevenfold to ninefold more abundant on sandy plains (see Fig. 2b).

The linear mixed model of post-treatment *P. smithii* densities (2015–2018) showed no significant 3-way interaction among grazing treatment, ecological site and year, and no significant treatment × ecological site interaction (Table 1). We did find a potential interaction between treatment and year (see Table 1), leading us to examine contrasts between treatments over time. Tests for treatment effects in each of the 4 yr revealed no significant treatment-related differences during 2015−2017 ($P = 0.57$, 0.23, and 0.47, respectively) and that *P. smithii* density was reduced by 19% in CARM relative to the TRM treatment in 2018 ($P = 0.044$, Fig. 3a).

As with *P. smithii,* post-treatment *H. comata* densities showed no significant 3-way interaction among grazing treatment, ecological site and year, and no treatment × ecological site interaction (see

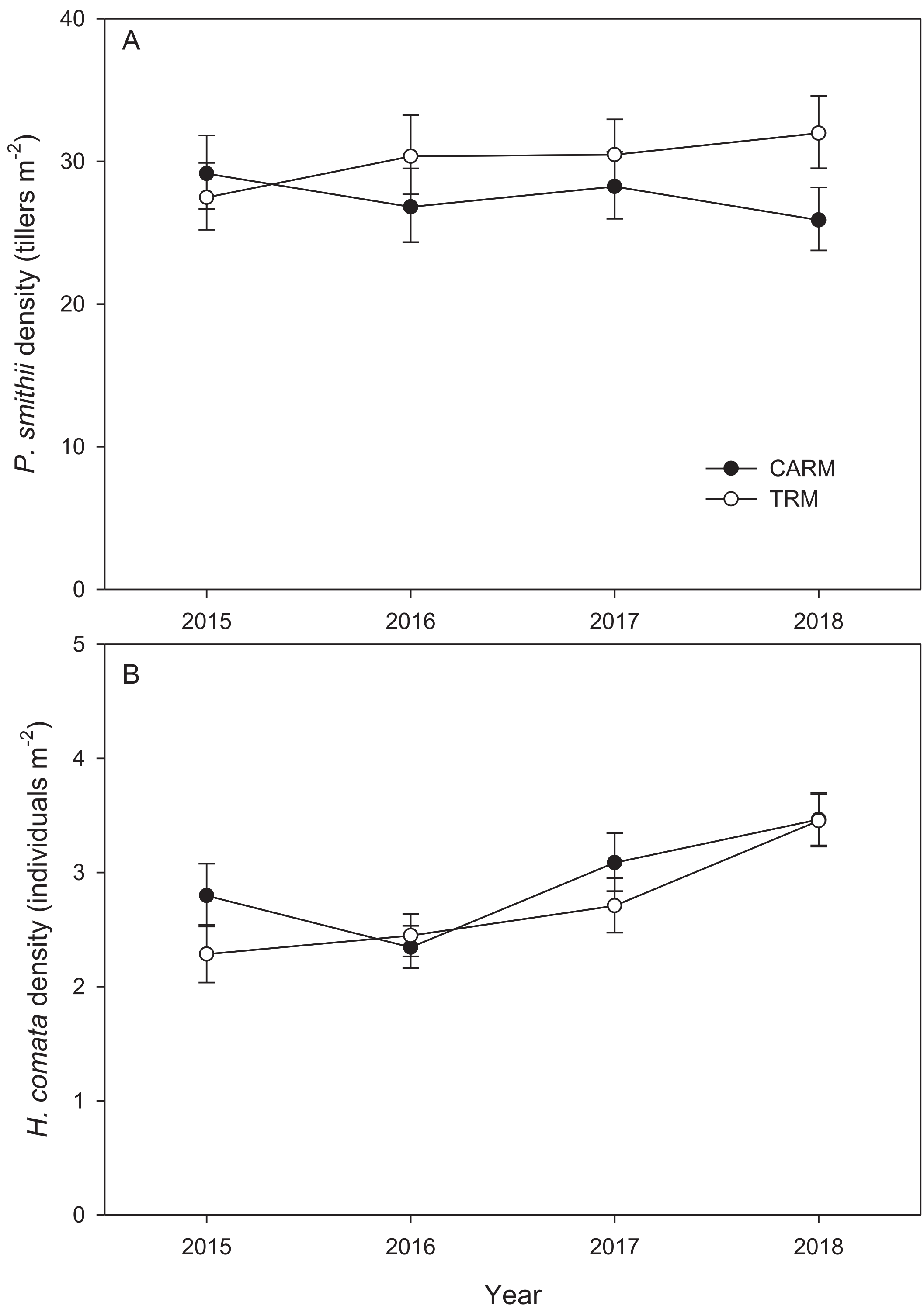

Fig. 3. Effect of cattle grazing management treatments (Collaborative Adaptive Rangeland Management, CARM vs. Traditional Rangeland Management, TRM) on the density of two perennial C_3 midgrasses, *Pascopyrum smithii* (A) and *Hesperostipa comata* (B) in the shortgrass steppe of northeastern Colorado. Means shown are back-transformed, least-square means from a linear mixed model of plant densities that included pretreatment densities as a covariate. Error bars show mean ± 1 standard error. Analyses of the contrasts between grazing treatments for each year showed no significant differences in any year for either species ($P > 0.15$ for each contrast).

Table 1). We did find a significant interaction between treatment and year and therefore examined contrasts between the two treatments over time. *H. comata* density was 18% lower in TRM relative to the CARM treatment in 2015 ($P = 0.05$) and did not differ between treatments during 2016–2018 ($P = 0.69$, 0.17, and 0.96, respectively; see Fig. 3b).

Comparisons of changes in *P. smithii* density in rested pastures of the CARM treatment did not identify any significant increases in *P. smithii* density in any year or pasture, relative to the respective paired TRM pastures ($P > 0.05$, Fig. 4). We also did not find any cases where resting a pasture resulted in a significantly greater increase or smaller decrease in C_3 perennial ANPP compared with

Table 1
Results of linear mixed models examining the response of densities of two C_3 midgrasses (*H. comata* and *P. smithii*) and productivity of four plant functional groups in response to Collaborative Adaptive Rangeland Management versus traditional grazing management, year, and ecological site in the shortgrass steppe of northeastern Colorado. All models also included pretreatment values of the response variable (mean of 2013 and 2014) as a highly significant ($P < 0.001$) covariate. DF (N, D) refers to the degrees of freedom in the numerator and denominator of the *F*-test for statistical significance. Values in boldface indicate statistically significant interaction terms.

Response variable	C_3 perennial grass density (#·m^{-2})				Herbaceous production (kg·ha^{-1})							
	P. smithii		*H. comata*		C_3 perennial graminoids		C_4 perennial grasses		C_3 annual grass		Forbs	
	DF (N, D)	*P*	DF (N, D)	*P*	DF (N, D)	*P*	DF (N, D)	*P*	DF (N, D)	*P*	DF (N, D)	*P*
Treatment	1, 53.5	0.276	1, 82.7	0.328	1, 62.9	0.102	1, 70.2	0.0005	1,86.8	0.318	1, 99.3	0.858
Yr	3, 15	0.943	3, 26.2	0.0001	3, 27.1	0.022	3, 17.2	0.0009	3, 25.2	< 0.0001	3, 17.8	< 0.0001
Ecosite	2, 49.5	0.037	2, 96.2	0.94	2, 53.9	0.0007	2, 54.6	< 0.0001	2, 51.6	0.001	2, 119	0.0719
Ecosite x yr	6, 114	0.042	6, 151	0.245	6, 124	0.125	6, 140	0.004	6, 88.1	0.001	6, 139	0.127
Treatment x yr	3, 175	**0.077**	3, 166	**0.016**	3, 149	0.312	3, 178	0.71	3, 181	0.219	3, 177	0.485
Treatment x ecosite	2, 51.1	0.158	2, 83.3	0.893	2, 61.5	**0.020**	2, 69.3	**0.001**	2, 87.6	0.414	2, 101	0.248
Treatment x yr x ecosite	6, 179	0.507	6, 180	0.131	6, 169	0.339	6, 193	**< 0.001**	6, 199	**0.005**	6, 193	0.797
Pretreatment covariate	1, 91.9	< 0.0001	1, 102	< 0.0001	1, 111	< 0.0001	1, 101	< 0.0001	1, 109	< 0.0001	1, 119	< 0.0001

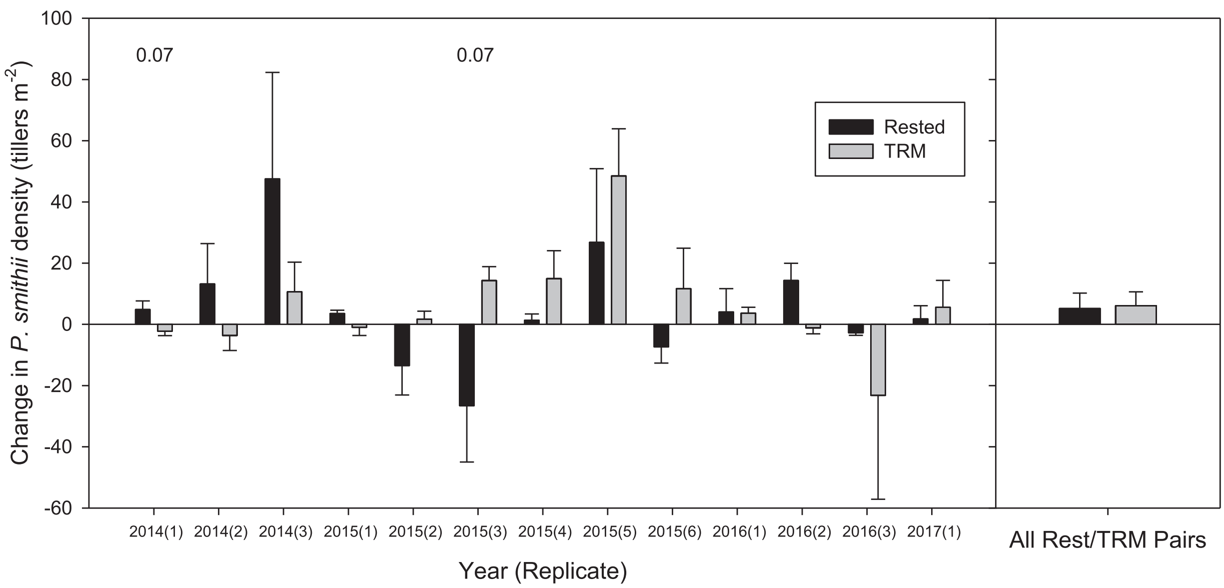

Fig. 4. Comparisons of changes in *Pascopyrum smithii* density in pastures that received year-long rest from grazing (Rested) versus paired pastures that received the traditional rangeland management (TRM) treatment consisting of season-long grazing in the shortgrass steppe of northeastern Colorado. Pairs of bars in the main panel show individual comparisons of paired Rested versus TRM pastures, based on 3, 6, 3, and 1 pasture(s) rested in 2014, 2015, 2016, and 2017, respectively; error bars show 1 standard of error (SE) based on within-pasture variation among monitoring plots, and values above each comparison show the *P* value for the paired *t*-test based on within-pasture variation. Bars on the far right show the mean change in *Pascopyrum smithii* density for each treatment, averaged across all 13 Rested versus TRM comparison replicates over space and time, with 1 SE based on among-pasture variation.

TRM pastures. Averaging across all paired comparisons of rested versus TRM pastures, we found no evidence that year-long rest increased *P. smithii* density relative to TRM (see Fig. 4).

Aboveground Plant Production

ANPP of C_3 perennial graminoids was relatively low in 2013 (following the drought of 2012), increased substantially during 2014 and 2015 in response to above-average precipitation, and then declined to moderate levels during 2016–2018 (Fig. 5a). Perennial C_3 graminoid production was similar on the sandy plains and salt flats ecological sites and substantially lower on the loamy plains ecological site (see Fig. 5a). Aboveground production of C_4 perennial grasses, which is more dependent on midsummer precipitation, was less affected by variation in precipitation during 2012–2015 (see Fig. 5b). However, C_4 grass production declined substantially in 2016, which reflects both an increase in C_3 midgrasses during the wet period of 2014–2015 and lower midsummer precipitation in 2016. C_4 grass production returned to moderate levels during 2017–2018 (see Fig. 5b). C_4 production was greatest on salt flats, intermediate on loamy plains, and lowest on sandy plains.

Although production of both C_3 and C_4 perennial graminoids responded to precipitation variation, we found that effects of grazing treatment were weak and largely constrained to the salt flat ecological site (see Table 1). For C_3 perennial graminoids, treatment effects did not vary by ecological site or year and we found no significant main effect of grazing treatment, but we found a significant treatment × ecosite interaction ($P = 0.02$; see Table 1; Fig. 6). Tests for the effect of grazing treatment within each of the three ecological sites (averaged across all years, given the lack of a three-way treatment × ecological site × year interaction; see Table 1) revealed no detectable effect of grazing treatment on either loamy plains ($P = 0.75$; see Fig. 5a) or sandy plains ($P = 0.37$; see Fig. 6b), but CARM reduced C_3 production by 37% relative to TRM on the salt flats ecological site ($P = 0.007$; see Fig. 6c).

For C_4 grass production, we found a significant ecological site × grazing treatment × year interaction (see Table 1), indicating complex variation in the treatment effects. Contrasts by ecological

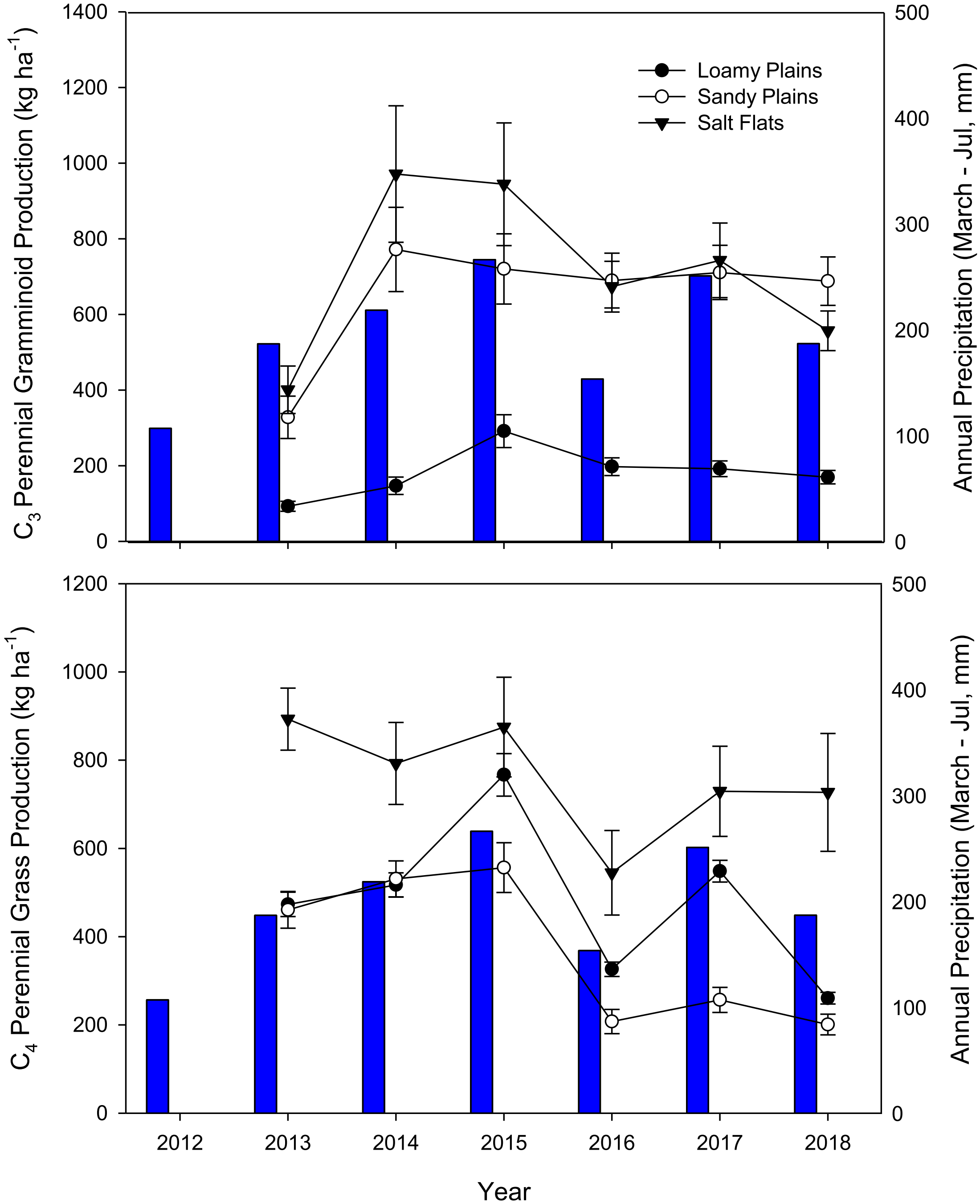

Fig. 5. Temporal trends in aboveground production of C_3 perennial graminoids (A, grasses and sedges and B, C_4 perennial grasses on three different ecological sites, averaged across both CARM and TRM grazing treatments in the shortgrass steppe of northeastern Colorado during 2013–2018. *Blue bars* show variation in precipitation during March–July each year, and production measurements occurred in early August each year.

site and year revealed that in 2015 only, CARM produced more C_4 grass biomass on loamy plains while TRM produced more C_4 grass biomass on sandy plains. On salt flats, TRM pastures produced 18–34% more C_4 grass biomass than CARM pastures in 3 out of 4 yr (2015, 2016, and 2018; Fig. 7).

Annual grasses consisted almost exclusively of the C_3 species, *Vulpia octoflora,* which is avoided by cattle and interferes with their ability to graze shortgrasses. ANPP of C_3 annual grasses varied substantially among years, with high production in 2016 and 2018, and little to no production in other years. Analyses of treatment effects by year and ecological site (due to a significant treatment × year × ecosite interaction; see Table 1) showed that the only grazing treatment effect in years of annual grass abundance was on the sandy plains ecosite in 2018 (40.2 vs. 19.3 kg ha^{-1} in CARM vs. TRM, respectively). Forb production also varied widely among years in response to variation in the timing and amount of precipitation but was unaffected by grazing treatment (see Table 1).

We did not find any cases where resting a pasture resulted in a significantly greater increase or smaller decrease in C_3 perennial ANPP relative to TRM (see Fig. 7; $P > 0.1$ for all pasture-level comparisons). Averaging across plots to generate paired pasture comparisons, we found no evidence that year-long rest increased C_3 perennial ANPP relative to TRM (Fig. 8; $P = 0.15$). Finally, we found

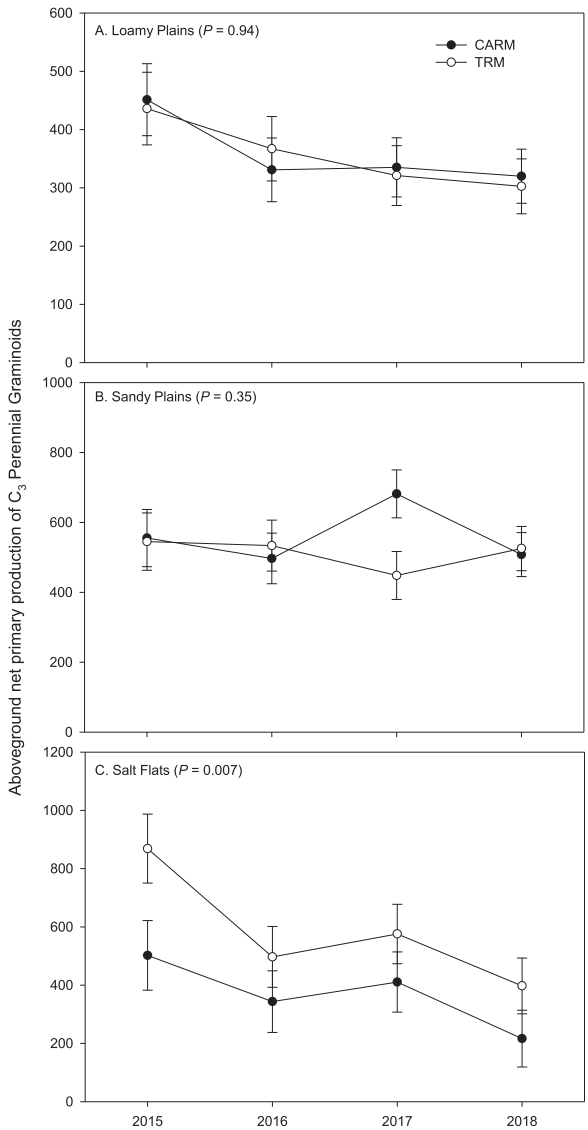

Fig. 6. Effect of cattle grazing management treatments (Collaborative Adaptive Rangeland Management, CARM vs. Traditional Rangeland Management, TRM) on aboveground net primary production of C_3 perennial graminoids in the shortgrass steppe of northeastern Colorado. Means shown are back-transformed, least-square means from a linear mixed model of aboveground net primary production (ANPP). Error bars show + 1 standard error. The effect of grazing treatment varied among ecological sites, with a significant reduction in C3 perennial ANPP in CARM relative to TRM on the Salt Flats ecological site, but not on either the Loamy or Sandy Plains ecological sites.

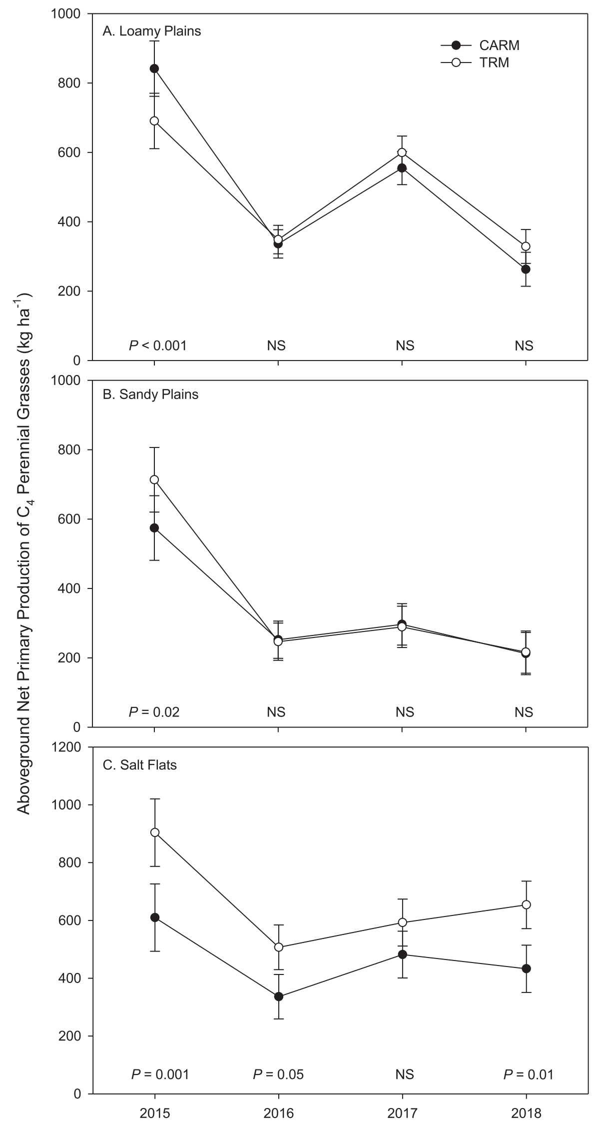

Fig. 7. Effect of cattle grazing management treatments (Collaborative Adaptive Rangeland Management, CARM vs. Traditional Rangeland Management, TRM) on aboveground net primary production by C4 perennial grasses during 2015–2018 in the shortgrass steppe of northeastern Colorado. Means shown are back-transformed, least-square means from a linear mixed model of ANPP. Error bars show + 1 standard error. The effect of grazing treatment varied by ecological site and year, with a significant increase in C4 perennial ANPP in CARM relative to TRM on the loamy plains in 2015 (but not 2016–2018), a significant reduction in C4 perennial ANPP in CARM relative to TRM on the Sandy Plains in 2015 (but not 2016–2018), and a significant reduction in C4 perennial ANPP in CARM relative to TRM on Salt Flats in 2015, 2016, and 2018.

no difference between aboveground production on patch-burned plots grazed by CARM versus TRM herds for either C_3 grasses (434 vs. 430 g m^{-2} in CARM vs. TRM; $F_{1,6.59} = 0.01$, $P = 0.98$) or C_4 grasses (516 vs. 524 g m^{-2} in CARM vs. TRM; $F_{1,6.18} = 0.01$, $P = 0.95$).

Cattle Weight Gains

Cattle weight gains were strongly affected by year ($F_{4,33}$= 5.56, $P = 0.002$) and grazing treatment ($F_{1,33}$= 16.2, $P = 0.0003$) during the treatment yr (2014–2018). Averaged across years, daily weight gains for cattle in CARM were 14.1% lower than gains for cattle in TRM (Fig. 9). Cattle gains were 16.2% lower in CARM relative to TRM in 2015, when cattle were slowly rotated among only 4 of 10 CARM pastures and 11.7–13.8% lower in CARM relative to TRM in 2017 and 2018 when cattle were more rapidly rotated among 9 of 10 CARM pastures. The magnitude of the grazing treatment effect did not vary significantly among years ($F_{4,33} = 0.06$, $P = 0.99$).

Discussion

We implemented adaptive, multipaddock rotational grazing management in semiarid, shortgrass rangeland in which we accounted for many of the spatial and temporal shortcomings of prior rotational grazing experiments. Key aspects of our experimental design included varying the timing and length of graze periods among pastures each year, incorporating phenological and compositional variation among pastures in forage production into planning movements of cattle, and using both forage biomass estimates and cattle behavior to determine the timing

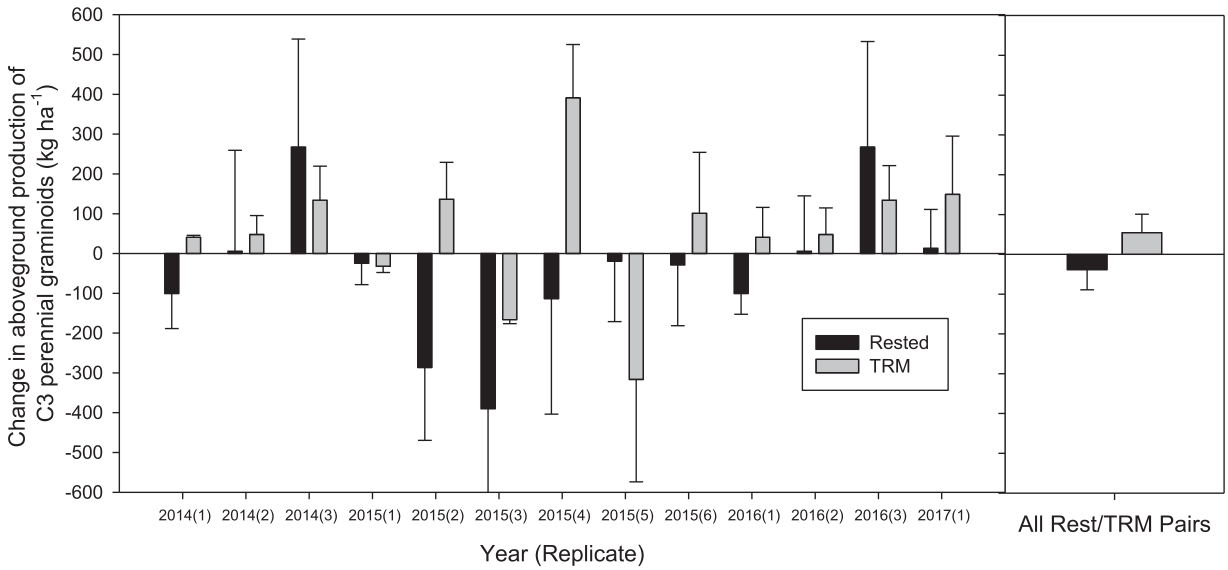

Fig. 8. Comparisons of changes in aboveground net primary production of C3 perennial graminoids (kg ha^{-1}) in pastures that received year-long rest from grazing (Rested) versus paired pastures that received the traditional rangeland management (TRM) treatment consisting of season-long grazing in the shortgrass steppe of northeastern Colorado. The main panel shows individual comparisons of paired Rested versus TRM pastures, based on 3, 6, 3, and 1 pasture(s) rested in 2014, 2015, 2016, and 2017, respectively; error bars show 1 standard of error based on within-pasture variation among monitoring plots. The pair of bars on the far right shows the mean change aboveground net primary production of C3 perennial graminoids for each treatment, averaged across all 13 Rested versus TRM comparison replicates, with 1 SE based on among-pasture variation. No comparisons were statistically significant at the $P < 0.1$ level.

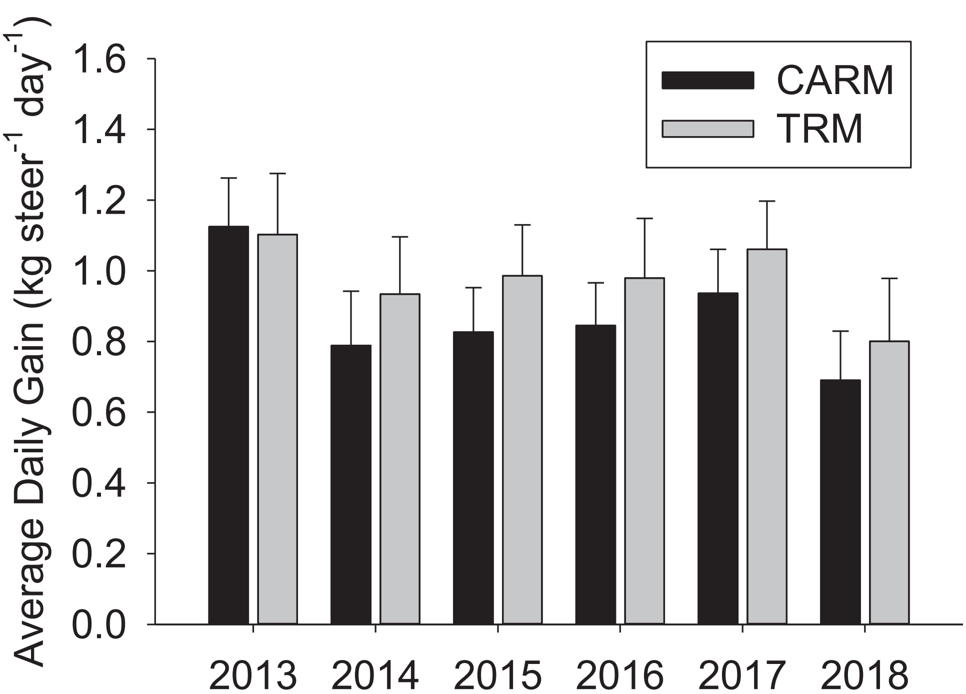

Fig. 9. Effect of cattle grazing management treatments (Collaborative Adaptive Rangeland Management, CARM vs. Traditional Rangeland Management, TRM) on average daily livestock weight gains (kg $steer^{-1}$ day^{-1}). Error bars show 1 standard deviation.

of cattle rotation among pastures. Approximately 10–60% of the total area remained ungrazed each year in the CARM treatment, while the remaining area was grazed at an increased stock density for varying portions of the growing season. Adaptive, multipaddock rotational grazing management did not enhance vegetation productivity or the density of perennial C_3 grasses, but it did markedly reduce livestock performance.

A fundamental tenet of adaptive, multipaddock grazing is that long rest periods are vital for the enhancement of vegetation conditions. However, our results do not support this assumption, despite repeated tests over multiple years that included both above-average and below-average precipitation (see Figs. 1, 4). Instead, when comparing the full set of adaptively managed, rotationally grazed pastures with a paired set of traditionally managed pastures over a 5-yr period, we found that adaptive rotation did not enhance, and even decreased, the abundance (see Fig. 3) and productivity (see Figs. 6 and 7) of perennial graminoids. On the dominant ecological sites, we found no effects of grazing treatment on production of C_3 perennial graminoids and only minor effects on the production of C_4 perennial grasses. The response of C_4

grasses in the second yr of the experiment was inversely affected by grazing treatment on different ecological sites; production was greater in TRM on the sandy plains ecosite and greater in CARM on the loamy plains ecological site. Neither of these responses persisted through the remainder of the experiment. On the relatively less abundant salt flat ecological site, we found notable reductions in both C_3 and C_4 perennial graminoid production in CARM relative to TRM. These results demonstrate that the intensity and pattern of defoliation imposed by season-long grazing at the stocking rates implemented in this experiment are not suppressing C_3 graminoid productivity in a manner that can be reversed by a year of rest from grazing or by a combination of year-long rest interspersed with years when vegetation is pulse-grazed by cattle at high stock density for only a portion of the growing season. Finally, we also found that in the patch-burned portions of study pastures, subsequent grazing on the burn by the CARM versus a TRM herd did not differentially affect either C_3 or C_4 perennial grass productivity. Burns in the CARM treatment were intensively grazed early in the growing season (for an average of 30 d in May and/or June) but then had the remainder of the growing season to regrow, whereas burns in the TRM treatment were less intensively grazed for the entirety of the growing season. All of these results are consistent with numerous previous studies showing that shortgrass steppe plant communities are highly resistant to short-term effects of grazing and fire treatments (reviewed by Milchunas et al. 2008).

The initial stocking rate for both CARM and TRM was set at a moderate level based on historical stocking rate experiments conducted at our study site (Bement 1969; Hart and Ashby 1998). The stocking rate was increased adaptively over the course of the study by a group of ranchers and natural resource professionals in response to prior weather conditions, vegetation monitoring results, and seasonal weather forecasts, to a level ~10%, 15%, and 30% above the initial moderate rate in yr 3, 4, and 5 of the experiment. Even with these incremental increases in stocking rate, our results show that continuous, season-long grazing did not impose detrimental effects on C_3 perennial graminoids relative to the adaptive, rotational grazing treatment. Adaptive rotational grazing did not increase total forage production or shift the composition of forage production toward C_3 perennials, relative to season-long grazing, over temporal scales of 1−4 yr. This outcome suggests that the cumulative defoliation intensities imposed on C_3 graminoids on the dominant ecological sites over multiple years is similar in both grazing treatments, even though the temporal pattern of utilization varies. Although studies have shown that defoliation of an individual tiller or group of tillers of *P. smithii* negatively affects total productivity of the plant in the short term (Everson 1966; Eneboe et al. 2002; Augustine et al. 2011), we hypothesize that a large proportion of the tillers in any given pasture remain undefoliated in a given year, such that a negative effect of moderate stocking was not detected under either grazing treatment. Furthermore, even those CARM pastures grazed early in the rotational sequence in a given year (and hence experiencing greater tiller defoliation rates than in the paired TRM pasture) would have significant time after rotation of the cattle for defoliated tillers to regrow and recover, which could explain the lack of detectable effect on production in the subsequent year.

Important caveats to our findings are that larger vegetation responses could still potentially occur with longer-term implementation of adaptive, rotational grazing and that our study period did not encompass a severe drought. Further research into the effects of year-long grazing exclusion and pulse grazing during and/or following severe drought is still needed. In addition, the study pastures were not considered degraded at the beginning of the study. It is possible that the outcomes of adaptive, rotational grazing management may vary on the basis of moisture availability and initial pasture condition (Hawkins et al. 2017).

Although CARM did not enhance C_3 perennial graminoid production or density, it is important to note that CARM altered vegetation structure in a manner that significantly affected densities of certain grassland bird species (Davis et al. 2020), which highlights the complexity of managing for multiple objectives. For pastures on the loamy plains ecological site, year-long rest enhanced the abundance of grasshopper sparrows *(Ammodramus savannarum)* in the subsequent breeding season, while pulse grazing enhanced the abundance of horned larks *(Eremophila alpestris)*, relative to the TRM treatment (Davis et al. 2020). These findings match expectations based on habitat associations of these two species (with grasshopper sparrows nesting in taller, more dense midgrass cover and horned larks nesting in sparse, shortgrass cover) and illustrate how multipaddock adaptive rotational grazing can enhance habitat for two species using opposing vegetation structure (Davis et al. 2020). However, for the thick-billed longspur (*Rhynchophanes mccownii*), which is a species of conservation concern across the western Great Plains states, resting pastures consistently suppressed their abundance, while pulse grazing did not enhance their abundance (Davis et al. 2020), leading to uncertainty in whether CARM can sustain habitat for this species over the long term without focusing grazing in certain areas for the context-specific needs of the species. Given these tradeoffs in management for different bird species via CARM versus TRM, a key question for livestock producers seeking to achieve multiple ecological outcomes on rangelands is how their grazing management affects livestock production and associated economics of their operation.

Reduced animal weight gains have been consistently documented in numerous grazing experiments comparing multipaddock rotational grazing with continuous grazing at similar stocking rates (Briske et al. 2008). Our findings corroborate this response because individual animal weight gains were lower (12–16%) in the CARM than TRM treatment in each year of the experiment. We acknowledge that the rotational herd in the CARM treatment was not replicated within a given year, which is a limitation of our experimental design. However, our pretreatment measures of cattle weight gain were replicated across the 10 blocks within the experiment and demonstrated equivalent weight gains when both sets of pastures were managed with season-long grazing. Furthermore, the CARM herd (composed of different animals each year) gained significantly less weight than the TRM herds in each of the 5 yr of the experimental treatment, regardless of the precise pattern and rate of rotation used. Reduced weight gains will decrease profits for livestock producers, as these losses are further magnified by the greater infrastructure costs (fence and water development) of CARM, which may not be offset by labor savings (Windh et al. 2019).

Reduced animal weight gain in rotational grazing systems appears to be a consequence of the reduction in quality of forage consumed by cattle at high stock densities (McCollum et al. 1998, 1999). Cattle were grazed at stock densities of ~0.6–0.8 AU ha^{-1}, equivalent to ~600–775 kg steer biomass ha^{-1} in CARM, which was 10 × greater than in TRM. These densities are lower than in some high-intensity, short-duration grazing systems where stock densities can exceed 15 000-kg cattle biomass ha^{-1} (Venter et al. 2018). We suggest that 1) the reduced selectivity of animals foraging at high stock densities and 2) cattle moving into pastures that contain standing dead vegetation from prior rest periods could both be contributing to reduced diet quality of steers in the CARM treatment. The 16% reduction in animal weight gain in CARM relative to TRM in the first yr of the grazing treatment, when standing dead vegetation distribution was equivalent across both sets of pastures, further suggests that reduced cattle foraging selectivity at increased stocking density may be particularly important as a mechanism driving reduced weight gain. The negative effect of

CARM on grass production in the salt flat ecological site is also consistent with the inference that cattle in CARM forage less selectively than those in TRM. TRM herds often avoid areas dominated by salt grasses (Gersie et al. 2019), but the high stock density of the CARM herd may have reduced selectivity and increased utilization of this relatively unpalatable forage resource, leading to negative consequences for both weight gains and vegetation production.

Management Implications

Our understanding of how adaptive, multipasture rotational grazing management approaches can achieve multiple desired ecosystem services on rangelands has advanced slowly, as long-term studies conducted at the scale of ranching operations are difficult to implement (Hawkins et al. 2017; Teague and Barnes 2017). Recent assessments of the long-term consequences of rotational grazing systems in Australia and Africa found neutral or negative effects on vegetation and livestock production (Badgery, 2017; Venter et al. 2018). Our results corroborate these conclusions by demonstrating that individual animal gain decreases with high stock densities and that periodic rest does not necessarily increase plant production or improve species composition. This experiment is among the first to demonstrate that the implementation of adaptive, rotational grazing management by decision makers provided with detailed vegetation and animal monitoring data was unable to overcome the adverse consequences of high stock density on animal weight gain.

Our experimental design provides further insight into the inconsistency observed between the negative results of experimental grazing research and the positive outcomes of rotational grazing observed by some producers and scientists. In our study, the outcomes of CARM appeared to be positive in the absence of direct comparisons to paired TRM pastures. These outcomes included increasing C_3 graminoid production during the first 2 yr following CARM implementation, the persistence of the plant community in a desired condition throughout the experiment, and the ability of stakeholders to increase stocking rate over time. However, when these outcomes were directly compared with those of TRM in an experimental framework, it became evident that similar vegetation outcomes were achieved with greater cattle weight gains with TRM than with CARM. A key challenge for rangeland researchers and managers is to move beyond implementation of "best management practices" to recognize how weather variability, landscape heterogeneity, and adaptive management interact to influence specific management outcomes. We suggest that managers in semiarid rangelands seeking to achieve multiple ecosystem services with adaptive, multipaddock grazing need to carefully consider the influence of stocking density on livestock weight gains and economic returns, while still providing spatiotemporal variability in grazing distribution, long-term sustainability of forage production, and the provision of multiple ecosystem services.

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.

Acknowledgments

We thank the many dedicated technical personnel who were essential to implementing this experiment, especially Melissa Johnston, Nick Dufek, Jeff Thomas, Jake Thomas, Craig Lawrence, Tami Jorns, David Smith, Matt Mortenson, Pam Freeman, Averi Reynolds, and many summer seasonal students working with USDA-ARS. We thank Emily Kachergis for her contributions initiating this study and the editors and anonymous reviewers who provided valuable suggestions to improve the manuscript. We thank the Crow Valley Livestock Cooperative, Inc. for providing the cattle. This research was a contribution from the Long-Term Agroecosystem Research (LTAR) network.

Appendix A. Records of the order in which cattle rotated through Collaborative Adaptive Rangeland Management pastures during 2014–2018. Cells with "R" indicate years in which a pasture was rested from grazing. The grazing season began on approximately 15 May and ended approximately 1 October each year

Block	Ecological sites	2014		2015		2016		2017		2018	
		Order	D grazed	Order	D grazed	Order	D grazed	Order	D grazed	Order	D grazed
1	Loamy	7	22	R		5	25	6	21	5	13
2	Loamy	R		3	44	R		2	19	R	
3	Loamy	R		4	44	R		4	8	6	16
4	Loamy, Sandy	6	22	R		4	28	5	20	4	21
5	Loamy, Sandy	R		R		3	25	7	6	3	20
6	Sandy	4	21	1	12	6	14	1	21	2	15
7	Sandy, Loamy	5	15	R		1	25	9	10	7	14
8	Sandy, Saltflat	2	14	R		2	23	R		1	13
9	Loamy, Sandy, Saltflat	3	18	R		7	11	2	22	8	14
10	Loamy, Sandy, Saltflat	1	26	2	41	R		8	15	9	15

Appendix B. List of criteria approved by the stakeholder group each year that were used to guide the timing of cattle movements from one pasture to the next during each year of Collaborative Adaptive Rangeland Management implementation. Minimum vegetation biomass is expressed in lb/acre because stakeholders were more familiar with estimation in these units

Criteria used for cattle rotation	2014	2015	2016	2017	2018
Minimum vegetation biomass	Yes	Yes	Yes	Yes	Yes
Cattle behavior	Yes	Yes	Yes	Yes	Yes
Maximum days in pasture	Yes	No	Yes	Yes	Yes
Days in last pasture	No	Yes	Yes	Yes	Yes
Definition of criteria:					
Minimum forage biomass criteria (lb/ac) for average or wet yr:					
Loamy Pastures	300	300	450	450	450
Mixed Pastures	400	400	500	500	500
Sandy Pastures	450	450	550	550	550
Minimum forage biomass criteria for drought years (lb/ac; not used in any yr):					
Loamy Pastures	300	300	300	300	300
Mixed Pastures	400	400	400	400	400
Sandy Pastures	450	450	450	450	450
Maximum days in pasture	Varying based on ecological sites	Not Used	24	21	14 early; 21 mid-late season
Minimum days in last pasture		7	10	10	10

References

Augustine, D.J., Derner, J.D., 2012. Disturbance regimes and mountain plover habitat in shortgrass steppe: large herbivore grazing does not substitute for prairie dog grazing or fire. Journal of Wildlife Management 76, 721–728.

Augustine, D.J., Derner, J.D., 2014. Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. Journal of Applied Ecology 51, 242–250.

Augustine, D.J., Derner, J.D., 2015. Patch-burn grazing management, vegetation heterogeneity, and avian responses in a semi-arid grassland. Journal of Wildlife Management 79, 927–936.

Augustine, D.J., Dijkstra, F.A., Hamilton III, E.W., Morgan, J.A., 2011. Rhizosphere interactions, carbon allocation, and nitrogen acquisition of two perennial North American grasses in response to defoliation and elevated atmospheric CO_2. Oecologia 165, 755–770.

Badgery, W.B., 2017. Longer rest periods for intensive rotational grazing limit diet quality of sheep without enhancing environmental benefits. African Journal of Range and Forage Science 34, 99–109.

Bement, R., 1969. A stocking-rate guide for beef production on blue-grama range. Journal of Range Management 22, 83–86.

Beven, K., Kirkby, M., 1979. A physically based, variable contributing area model of basin hydrology. Hydrological Sciences Bulletin 24, 43–68.

Boyd, C.S., Svejcar, T.J., 2009. Managing complex problems in rangeland ecosystems. Rangeland Ecology & Management 62, 491–499.

Briske, D.D., Derner, J.D., Brown, J.R., Fuhlendorf, S.D., Teague, W.R., Havstad, K.M., Gillen, R.L., Ash, A.J., Willms, W.D., 2008. Rotational grazing on rangelands: reconciliation of perception and experimental evidence. Rangeland Ecology & Management 61, 3–17.

Briske, D.D., Derner, J.D., Milchunas, D.G., Tate, K.W., 2011a. An evidence-based assessment of prescribed grazing practices. In: Briske, D.D. (Ed.), Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. USDA-NRCS, Washington, DC, USA, pp. 21–74.

Briske, D.D., Sayre, N.F., Huntsinger, L., Fernández-Giménez, M.E., Budd, B., Derner, J.D., 2011b. Origin, persistence, and resolution of the rotational grazing debate: integrating human dimensions into rangeland research. Rangeland Ecology & Management 64, 325–334.

Davis, K.P., Augustine, D.J., Monroe, A.P., Derner, J.D., Aldridge, C.L., 2020. Adaptive rangeland management benefits grassland birds utilizing opposing vegetation structure in the shortgrass steppe. Ecological Applications 30 (1), e02020.

Derner, J.D., Hart, R.H., 2010. Livestock responses to complementary forages in shortgrass steppe. Great Plains Research 20, 223–238.

Derner, J.D., Reeves, J.L., Mortenson, M.C., West, M., Gonzalo Irisarri, J., Durante, M., 2016. Estimating overnight weight loss of corralled yearling steers in semiarid rangeland. Rangelands 38, 101–104.

Eneboe, E., Sowell, B., Heitschmidt, R., Karl, M., Haferkamp, M., 2002. Drought and grazing IV: blue grama and western wheatgrass. Journal of Range Management 55, 73–79.

Everson, A.C., 1966. Effects of frequent clipping at different stubble heights on western wheatgrass (*Agropyron smithii*, Rydb.). Agronomy Journal 58, 33–35.

Fernández-Giménez, M.E., Augustine, D.J., Porensky, L.M., Wilmer, H., Derner, J.D., Briske, D.D., Stewart, M.O., 2019. Complexity fosters learning in collaborative adaptive management. Ecology and Society 24 (2), 29.

Gersie, S.P., Augustine, D.J., Derner, J.D., 2019. Cattle grazing distribution in shortgrass steppe: influences of topography and saline soils. Rangeland Ecology & Management 72, 602–614.

Hart, R., Ashby, M., 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. Journal of Range Management 51, 392–398.

Hawkins, H.-J., Short, A., Kirkman, K.P., 2017. Does Holistic Planned Grazing™ work on native rangelands. African Journal of Range & Forage Science 34, 59–63.

Holechek, J.L., Gomez, H., Molinar, F., Galt, D., 1999. Grazing studies: what we've learned. Rangelands 21, 12–16.

Irisarri, J.G.N., 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. Ecological Applications 26, 1370–1380.

Kachergis, E., Derner, J., Roche, L., Tate, K., Lubell, M., Mealor, R., Magagna, J., 2013. Characterizing Wyoming ranching operations: natural resource goals, management practices and information sources. Natural Resources 4, 45–54.

Knight, K.B., Toombs, T.P., Derner, J.D., 2011. Cross-fencing on private US rangelands: financial costs and producer risks. Rangelands 33, 41–44.

Lauenroth, W., Milchunas, D., 1992. Short-grass steppe. In: Coupland, R. (Ed.), Ecosystems of the world 8A: natural grasslands. Elsevier, New York, NY, USA, pp. 183–226.

Lauenroth, W.K., Burke, I.C., Gutmann, M.P., 1999. The structure and function of ecosystems in the central North American grassland region. Great Plains Research 9, 223–260.

Lauenroth, W.K., Sala, O.E., 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2, 397–403.

McCollum III, F.T., Gillen, R.L., 1998. Grazing management affects nutrient intake by steers grazing tallgrass prairie. Journal of Range Management 51, 69–72.

McCollum III, F.T., Gillen, R.L., Karges, B.R., Hodges, M.E., 1999. Stocker cattle response to grazing management in tallgrass prairie. Journal of Range Management 52, 120–126.

Milchunas, D., Forwood, J., Lauenroth, W., 1994. Productivity of long-term grazing treatments in response to seasonal precipitation. Journal of Range Management 47, 133–139.

O'Reagain, P., Scanlan, J., Hunt, L., Cowley, R., Walsh, D., 2014. Sustainable grazing management for temporal and spatial variability in north Australian rangelands—a synthesis of the latest evidence and recommendations. Rangeland Journal 36, 223–232.

Pinchak, W.E., Canon, S.K., Heitschmidt, R.K., Dowher, S.L., 1990. Effect of long-term, year-long grazing at moderate and heavy rates of stocking on diet selection and forage intake dynamics. Journal of Range Management 43, 304–309.

Porensky, L.M., Mueller, K.E., Augustine, D.J., Derner, J.D., 2016. Thresholds and gradients in a semi-arid grassland: long-term grazing treatments induce slow, continuous and reversible vegetation change. Journal of Applied Ecology 53, 1013–1022.

Senft, R., Rittenhouse, L., Woodmansee, R., 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. Journal of Range Management 38, 82–87.

Spiegal, S., Bestelmeyer, B.T., Archer, D.W., Augustine, D.J., Boughton, E.H., Boughton, R.K., Cavigelli, M.A., Clark, P.E., Derner, J.D., Duncan, E.W., Hapeman, C.J., Harmel, R.D., Heilman, P., Holly, M.A., Huggins, D.R., King, K., Kleinman, P.J.A., Liebig, M.A., Locke, M.A., McCarty, G.W., Millar, N., Mirsky, S.B., Moorman, T.B., Pierson, F.B., Rigby, J.R., Robertson, G.P., Steiner, J.L., Strickland, T.C., Swain, H.M., Wienhold, B.J., Wulfhorst, J.D., Yost, M.A., Walthall, C.L., 2018. Evaluating strategies for sustainable intensification of US agriculture through the Long-Term Agroecosystem Research network. Environmental Research Letters 13.

Teague, R., Barnes, M., 2017. Grazing management that regenerates ecosystem function and grazingland livelihoods. African Journal of Range & Forage Science 34, 77–86.

Teague, R., Provenza, F., Kreuter, U., Steffens, T., Barnes, M., 2013. Multi-paddock grazing on rangelands: why the perceptual dichotomy between research results and rancher experience. Journal of Environmental Management 128, 699–717.

Teague, W.R., Dowhower, S.L., Baker, S.A., Haile, N., DeLaune, P.B., Conover, D.M., 2011. Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. Agriculture, Ecosystems & Environment 141, 310–322.

Thomas, M.G., Mohamed, A.H., Sawalhah, M.N., Holechek, J.L., Bailey, D.W., Hawkes, J.M., Luna-Nevarez, P., Molinar, F., Khumalo, G., 2015. Long-term forage and cow-calf performance and economic considerations of two stocking levels on Chihuahuan desert rangeland. Rangeland Ecology & Management 68, 158–165.

USDA. 2007a. Ecological site description for Loamy Plains (R067BY002CO). Available at: https://edit.jornada.nmsu.edu/catalogs/esd/067B/R067BY002CO. Accessed 8/11/2020.

USDA. 2007b. Ecological site description for Salt Flat (R067BY033CO). Available at: https://edit.jornada.nmsu.edu/catalogs/esd/067B/R067BY033CO. Accessed 8/11/2020.

USDA. 2007c. Ecological site description for Sandy Plains (R067BY024CO). Available at: https://edit.jornada.nmsu.edu/catalogs/esd/067B/R067BY024CO. Accessed 8/11/2020.

USDA National Agricultural Statistics Service (NASS) Colorado Field Office. 2012. Colorado Agricultural Statistics. Available at: www.nass.usda.gov/co. Accessed …

Veblen, K.E., Porensky, L.M., Riginos, C., Young, T.P., 2016. Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. Ecological Applications 26, 1610–1623.

Venter, Z.S., Cramer, M.D., Hawkins, H.J., 2019. Rotational grazing management has little effect on remotely-sensed vegetation characteristics across farm fence-line contrasts. Agriculture, Ecosystems and Environment 282, 40–48.

Venter, Z.S., Hawkins, H.J., Cramer, M.D., 2019. Cattle don't care: animal behaviour is similar regardless of grazing management in grasslands. Agriculture, Ecosystems & Environment 272, 175–187.

Wilmer, H., Derner, J.D., Fernández-Giménez, M.E., Briske, D.D., Augustine, D.J., Porensky, L.M., 2018. Collaborative adaptive rangeland management fosters management-science partnerships. Rangeland Ecology & Management 71, 646–657.

Windh, J., Ritten, J., Derner, J.D., Paisley, S., Lee, B., 2019. Economic cost analysis of continuous-season-long versus rotational grazing systems. Western Economics Forum 17, 62–72.