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# Collaborative Adaptive Rangeland Management, Multipaddock Rotational Grazing, and the Story of the Regrazed Grass Plant[☆,☆☆]

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ABSTRACT

Frequent, severe defoliation reduces grass production and can alter plant species composition in grasslands. Multipaddock rotational grazing has been proposed as a grazing strategy that may reduce the frequency and intensity of defoliation on palatable grass plants without altering stocking rates. Previous studies evaluated this hypothesis using small, homogeneous paddocks and nonadaptive rotation schedules and found small and inconsistent differences between continuous and rotational grazing systems. Using a stakeholder-driven collaborative adaptive management (CAM) framework, we conducted the first ranch-scale experimental investigation into tiller defoliation patterns in the context of adaptive multipaddock rotational grazing. We monitored tiller defoliation frequency and intensity in 10 paired 130-ha pastures assigned to either a collaborative adaptive multipaddock rotational grazing treatment (CARM, one livestock herd) or a season-long continuous grazing treatment (traditional rangeland management [TRM]; 10 separate herds) in shortgrass steppe. Consistent with previous studies, we observed that frequencies of grazing and regrazing on a palatable, cool-season grass (western wheatgrass, *Pascopyrum smithii*) were much more sensitive to stocking rate than grazing system. Under moderate stocking rates used in both CARM and TRM treatments, roughly two-thirds of western wheatgrass tillers remained ungrazed annually, regardless of grazing system. Thus, season-long rest is present in season-long continuous and rotational grazing systems. Frequencies of tiller regrazing were low (5–15%) and similar between CARM and TRM treatments. Although defoliation patterns were similar between treatments at the whole-ranch scale, CARM enhanced spatial and temporal heterogeneity in defoliation frequencies among individual pastures. Pastures grazed earlier in the season or for longer experienced more defoliation. Managers im-

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plementing adaptive, multipaddock rotational grazing could use this heightened and predictable variability to strategically manage impacts of grazing on western wheatgrass at the individual pasture scale. The CAM model enabled our team to identify and directly address key stakeholder hypotheses and resulted in coproduction of management-relevant research.

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## Introduction

Rangeland scientists have been measuring patterns of defoliation at the scale of individual grass plants for decades to better understand how grazing management affects the frequency, intensity, and uniformity of vegetation use. This body of research has produced knowledge about how grazing affects grass physiology and growth. In particular, both controlled clipping studies and grazing studies have found that as defoliation intensity or frequency increases, plant biomass and production tend to decline, though the magnitude of this decline varies among species (e.g., Branson 1956; Buwai and Trlica 1977; Eneboe et al. 2002; Bork et al. 2017; Broadbent et al. 2018). Some grasses have a high capacity for compensatory growth after herbivory, but negative effects of defoliation eventually become apparent as grazing intensity increases (McNaughton 1983). Negative effects of defoliation are especially severe for palatable species known to decline in abundance under heavy grazing, such as western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve) in the North American Great Plains (Milchunas et al. 2008; Porensky et al. 2016; Porensky et al. 2017). For this species, defoliation, and particularly multiple defoliations of an individual tiller, lead to reduced aboveground biomass production (Everson 1966; Buwai and Trlica 1977; Lauenroth et al. 1985; Eneboe et al. 2002), as well as increased allocation to shoots relative to roots (Branson 1956; Painter and Detling 1981; Polley and Detling 1989; Augustine et al. 2011).

Given the importance of defoliation as a driver of grass production and species composition, considerable attention has been focused on how to limit defoliation frequency and intensity while still allowing grazing animals to use forage from palatable species. Marking tillers and documenting their defoliation by grazing animals is challenging and tedious, and therefore only a few studies have addressed this question rigorously, mostly in the context of highly controlled experiments in small paddocks (e.g., Morris 1969; Hart and Balla 1982; Gillen et al. 1990; Derner et al. 1994; Cullan et al. 1999). These studies uniformly concluded that as stocking rate—the number of animals per unit land per unit time—increased, the occurrence of grazing and regrazing also increased (Morris 1969; Briske and Stuth 1982; Hart and Balla 1982; Gillen et al. 1990; Jensen et al. 1990; Hart et al. 1993; Derner et al. 1994; Volesky 1994; O'Reagain and Grau 1995; Cullan et al. 1999). Importantly, stocking rate was manipulated in two different ways across this group of studies: by changing either the number of animals that grazed a given area for a set amount of time or the amount of time that a set number of animals grazed a given area. In both cases, as stocking rate increased, the proportion of tillers defoliated and rates of regrazing increased.

Grazing managers often implement rotational grazing using multiple paddocks (Roche et al. 2015) to reduce repeated defoliation of palatable grass plants, when compared with season-long continuous grazing (Briske et al. 2011; Teague et al. 2013). Studies exploring the effects of rotational grazing on tiller defoliation have produced mixed results, often due to study designs that confound differences in grazing system with differences in stocking rates (Briske et al. 2011). For studies that did compare continuous (or lower stock density) and rotational (or higher stock density) grazing systems using similar stocking rates, results were also mixed. For example, the percentage of tillers grazed more than once was either similar (Pierson and Scarnecchia 1987; Hart et al. 1993; Volesky 1994), higher (Gammon and Roberts 1978; Gillen et al. 1990; Senock et al. 1993), or lower (Gammon and Roberts 1978, different species; Derner et al. 1994) in rotational than continuous treatments. Many of these studies concluded that the effects of stocking rate far outweighed the effects of grazing system and that regrazing was relatively rare at moderate stocking rates regardless of grazing system (e.g., Gammon and Roberts 1978; Hart et al. 1993; Derner et al. 1994).

Two limitations of previous rotational grazing studies are their limited spatial extent (small paddocks) and the use of fixed grazing schedules that ignored the human dimensions of adaptive decision making associated with multipaddock rotational grazing. Relationships between grazing systems and vegetation outcomes may operate differently in the context of adaptive management decision making at broad scales, where managers are often dealing with spatial and temporal variation in plant phenology, weather, plant community composition, and objectives (Briske et al. 2011; Hawkins 2017; Hawkins et al. 2017; Teague and Barnes 2017). To address these limitations, we investigated tiller defoliation dynamics of western wheatgrass within the Collaborative Adaptive Rangeland Management experiment, located in the shortgrass steppe of eastern Colorado (Wilmer et al. 2018; Fernández-Giménez et al. 2019; Augustine et al. 2020). This experiment is a ranch-scale (2 600-ha) study evaluating responses of vegetation, cattle, and wildlife to 1) collaborative adaptive multipaddock rotational grazing (hereafter CARM) and 2) season-long, continuous grazing traditionally used in these grasslands (hereafter traditional rangeland management [TRM], Bement 1969). For CARM, decisions regarding objectives, annual stocking rate, and the sequence and timing of cattle movements among pastures are made by an 11-member stakeholder group composed of ranchers, land management agency professionals, and conservation organization representatives.

The CARM stakeholder group uses a collaborative adaptive management (CAM) framework (Wilmer et al. 2018; Fernández-Giménez et al. 2019) designed to engage managers from different backgrounds in research to enhance its relevance and credibility to diverse stakeholders (Scarlett 2013; Fernández-Giménez et al. 2019). One of the stakeholder-defined objectives within the CARM treatment is increased production of cool-season ($C_3$) perennial grasses, a functional group dominated by western wheatgrass that provides important forage for cattle both early and late in the growing season, provides tall-structured habitat for grassland birds, and increases the system's capacity for enhanced forage production in wet years (Irisarri et al. 2016; Davis et al. 2019; Wilmer et al. 2019). The stakeholder group anticipated that CAM of a multipaddock rotational grazing system would help them achieve this objective.

Using worksheets and structured discussions, researchers queried stakeholders about why they expected CARM to alter vegetation and cattle outcomes, including production of cool-season perennial grasses. Through this process, it became clear that stakeholders expected that by reducing the amount of time cattle grazed in each paddock, rotational grazing would decrease the occurrence of repeated defoliation of individual palatable plants within the growing season. They expected that decreased defoliation of individual plants, in turn, would increase production of palatable cool-season species. To test this stakeholder-driven hypothesis, which has long been proposed as a mechanism through which rotational grazing should benefit individual plants, we measured defoliation dynamics for western wheatgrass, the primary palatable cool-season grass in this ecosystem. To our knowledge, this is the first ranch-scale experimental investigation into tiller defoliation patterns in the context of adaptive multipaddock rotational grazing. Focusing on the effects of adaptive rotational grazing on frequency, intensity, and uniformity of defoliation, we asked:

1) Did grazing treatment (CARM vs. TRM) affect the proportion of western wheatgrass tillers that were grazed, the average number of times a given tiller was grazed, or the average season-long change in tiller length?
2) Did grazing treatment affect tiller defoliation patterns among pastures?
3) Within the CARM grazing treatment using adaptive multipaddock rotation grazing, how did pasture-scale stocking rate and timing of grazing affect tiller defoliation?
4) Did the number of times a tiller was grazed affect its average, season-long change in length or regrowth capacity?

## Methods

### *Study site*

The study took place at the US Department of Agriculture–Agricultural Research Service Central Plains Experimental Range (CPER), a Long-Term Agroecosystem Research (LTAR) network site (https://ltar.ars.usda.gov), located in north-central Colorado (40°49′N, 107°46′W). Long-term mean annual precipitation on the CPER is 340 mm, with > 80% occurring during the growing season of April through September (Lauenroth and Milchunas 1992). Precipitation in 2017 was slightly above average throughout the season (water year precipitation = 377 mm), while in 2018 the site experienced a wet spring followed by a dry summer (water year precipitation = 264 mm). Mean annual air temperature is 8.4°C, ranging from −2.6°C in December to 21.2°C in July. Topography is flat to gently rolling; soils range 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 warm-season ($C_4$) shortgrass species—blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths) and buffalograss (*B. dactyloides* [Nutt.] J.T. Columbus)—comprise over one-third of aboveground net primary productivity (ANPP) at the CPER. Cool-season ($C_3$) perennial grasses (western wheatgrass, needle and thread [*Hesperostipa comata* {Trin. & Rupr.} Barkworth] and squirreltail [*Elymus elymoides* {Raf.} Swezey]) comprise approximately 41% of ANPP and 25% of foliar cover in moderately grazed pastures, and average densities of western wheatgrass are 12.6 tillers per $m^2$. Warm-season bunchgrasses (purple threeawn [*Aristida purpurea* Nutt.] and sand dropseed [*Sporobolus cryptandrus* {Torr.} A. Gray]), plains pricklypear cactus (*Opuntia polyacantha* Haw.), subshrubs (broom snakeweed [*Gutierrezia sarothrae* {Pursh} Britton & Rusby], spreading buckwheat [*Eriogonum effusum* Nutt.], and prairie sagewort [*Artemisia frigida* Willd.]), and fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.) are less abundant but generate a taller structure on the landscape (Augustine and Derner 2015). Cool-season annual grasses consist almost entirely of 6-wk fescue (*Vulpia octoflora* [Walter] Rydb.).

### *Experimental design*

To create the CARM experiment, twenty 130-ha pastures were paired into 10 blocks where each block contained two pastures similar in terms of soil and plant characteristics, topographic 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 (Fernández-Giménez et al. 2019; Augustine et al. 2020). One pasture in each pair was randomly assigned to the TRM treatment, and the other pasture was assigned to the CARM treatment (Appendix A). The 10 CARM pastures were grazed by a single, large herd of yearling steers managed by the stakeholder group using CARM, which incorporated planned year-long rest in 20% of the pastures. Season-long rest is not common in traditionally managed operations, and the stakeholders included rested pastures in their management plan with the goal of creating “grassbanks” to enhance drought resilience and allow for vegetation recovery within the aspirational CARM treatment. Each of the 10 paired TRM pastures was grazed continuously, season long (mid-May to early October) by a single herd of yearling steers at one-tenth the stocking density used in CARM. CARM and TRM thus shared the same ranch-scale stocking rate but differed in terms of stock density and pasture-level stocking rate and CAM of the spatiotemporal distribution of cattle within the growing season, including the use of season-long rest (Fernández-Giménez et al. 2019; Augustine et al. 2020).

Within each year, the same total number of yearling steers of mixed European breeds grazed in the CARM and TRM treatments. The stocking rate for both grazing treatments 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). In subsequent years, the stakeholder group adjusted the stocking rate in April, before the mid-May grazing start date, depending on past vegetation conditions and seasonal weather forecasts. Stakeholders set the stocking rate to 0.70 and 0.81 AUM $ha^{-1}$ in 2017 and 2018, respectively (equivalent to a total of 244 and 280 steers). The stakeholders chose to increase stocking rate between 2017 and 2018 due to ample residual forage availability carried over from 2017, combined with favorable weather forecasts for 2018. The TRM stocking rate was also adjusted each year to match the CARM stocking rate.

Details of the adaptive grazing management strategy applied to the CARM pastures were decided by the 11-member stakeholder group. The group developed an initial grazing management plan in 2013 and subsequently met three or more times annually during 2014–2018 to review results from prior grazing seasons and make decisions on stocking rate, grazing sequence, and which pastures to rest in the subsequent grazing season (Table 1**;** Wilmer et al. 2018). Although the stakeholders' objective was to rest two pastures every year, weather and vegetation conditions in 2017 and 2018 resulted in year-long rest being applied to only one of the CARM pastures in each of these years (see Table 1). Within CARM, rested pastures are not conceptualized as “extra” pastures available for other uses; the stakeholders are still leasing these pastures and intentionally reserving them to create grassbanks for drought resilience. Thus, although *pasture-scale* stocking rates are higher within grazed pastures in CARM (and also vary substantially among grazed pastures in CARM), the *ranch-scale* stocking rate remains the same between the two systems.

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 (Wilmer et al. 2018; Augustine et al. 2020). Stakeholders chose to implement 32-ha patch burns in some years. When stakeholders decided to implement a patch burn in a given CARM pasture, we also implemented a patch burn of the same size and on the same soil types in the paired TRM pasture. Patch burns were implemented in the

**Table 1**
Pasture rotations, stocking rates (animal unit days, AUD ha$^{-1}$), and monitoring details for 2017 and 2018 within the Collaborative Adaptive Rangeland Management (CARM) treatment. All pastures are 130 ha, and each steer was treated as 0.7 animal units.

| Yr | Block | Pasture | Rotation order | Date in | AUD ha$^{-1}$ | Days grazed | No. of steers | Unburned transects | Burned transects |
|---|---|---|---|---|---|---|---|---|---|
| 2017 | 6 | Snowfence | 1 | 5/11/17 | 27.6 | 21 | 244 | 3 | 3 (burned fall 2016) |
| 2017 | 9 | Headquarters | 2 | 6/1/17 | 28.9 | 22 | 244 | 3 | |
| 2017 | 2 | Nighthawk | 3 | 6/23/17 | 25.0 | 19 | 244 | 3 | |
| 2017 | 3 | Highway | 4 | 7/12/17 | 10.5 | 8 | 244 | 3 | |
| 2017 | 4 | Crossroads | 5 | 7/20/17 | 26.3 | 20 | 244 | 3 | |
| 2017 | 1 | Hilltank | 6 | 8/9/17 | 27.6 | 21 | 244 | 3 | |
| 2017 | 5 | South | 7 | 8/30/17 | 7.9 | 6 | 244 | 3 | |
| 2017 | 10 | Saltflat | 8 | 9/5/17 | 19.7 | 15 | 244 | 3 | |
| 2017 | 7 | Ridgeline | 9 | 9/20/17 | 13.1 | 10 | 244 | 3 | |
| 2017 | 8 | Elm | Rested | | 0.0 | 0 | 0 | 3 | |
| 2018 | 8 | Elm | 1 | 5/11/18 | 19.6 | 13 | 280 | 3 | 2 (burned fall 2017) |
| 2018 | 6 | Snowfence | 2 | 5/24/18 | 22.6 | 15 | 280 | 3 | 1 (burned fall 2016) |
| 2018 | 5 | South | 3 | 6/8/18 | 30.2 | 20 | 280 | 3 | |
| 2018 | 4 | Crossroads | 4 | 6/28/18 | 31.7 | 21 | 280 | 3 | |
| 2018 | 1 | Hilltank | 5 | 7/19/18 | 19.6 | 13 | 280 | 3 | |
| 2018 | 2 | Nighthawk | 6 | 8/1/18 | 24.1 | 16 | 280 | 3 | |
| 2018 | 7 | Ridgeline | 7 | 8/17/18 | 21.1 | 14 | 280 | 3 | |
| 2018 | 9 | Headquarters | 8 | 8/31/18 | 21.1 | 14 | 280 | 3 | |
| 2018 | 10 | Saltflat | 9 | 9/14/18 | 22.6 | 15 | 280 | 3 | |
| 2018 | 3 | Highway | Rested | | 0 | 0 | 0 | 3 | |

autumn (October or November) in one block in 2016 and one block in 2017 (see Table 1). Thus, pastures in the two treatments differed only in the *adaptively managed spatiotemporal pattern of cattle grazing* within the growing season; interannual stocking rate adjustments and application of other vegetation treatments were held constant between the two treatments. This reflects reality, in that ranching operations employing continuous season-long grazing (TRM) are able to be adaptive when it comes to interannual stocking rate adjustments and vegetation treatments but are not able to adaptively manage cattle distributions in space and time within a given growing season.

To enhance the inference space of the CARM results, data were also collected in two 130-ha pastures that were part of a long-term grazing intensity study (Klipple and Costello 1960; Hart and Ashby 1998; Porensky et al. 2017). One pasture had been grazed at a heavy stocking rate (targeted for 60% utilization of peak growing season biomass) and the other at a light stocking rate (targeted for 20% utilization) every yr since 1939 (Irisarri et al. 2016). Stocking rates for these pastures were 0.82 AUM ha$^{-1}$ in 2017 (30 yearlings) and 0.88 AUM ha$^{-1}$ in 2018 (35 yearlings) for the heavy pasture and 0.40 AUM ha$^{-1}$ in 2017 (15 yearlings) and 0.45 AUM ha$^{-1}$ in 2018 (17 yearlings) for the light pasture. Both pastures were managed using season-long continuous grazing from mid-May to early October, and grazing animals were mixed European breed yearlings.

### *Data collection*

We established four pairs of monitoring plots on loamy and/or sandy plains ecological sites within each pair of pastures, where each pair of plots was on the same ecological site (USDA NRCS 2007a, 2007b) and same topographic position. Plots were distributed across the two ecological sites in proportion to the extent of that ecological site within the pasture (e.g., for a pair of pastures where each contained ~50% loamy and sandy plains ecological sites, two plots in each pasture were on loamy and two on sandy plains). Annual monitoring of these plots over the first 5 yr of the experiment showed no evidence that the CARM treatment enhanced western wheatgrass tiller densities more than the TRM treatment (Augustine et al. 2020).

For the current study of tiller defoliation rates, we used the monitoring data from 2013 to 2015 (Augustine et al. 2020) to identify which three of the four long-term monitoring plots supported the highest density of western wheatgrass. Within each of these three plots per pasture, we then established a new 30-m long transect parallel to and 20 m away from whichever one of the four long-term monitoring transects in that plot supported the highest density of western wheatgrass. This approach enabled us to establish the tiller defoliation transects in locations where western wheatgrass was sufficiently abundant to monitor defoliation rates, while also ensuring they occurred on similar soil types and topographic positions within each of the 10 pairs of CARM/TRM pastures.

To account for the potential influence of prescribed fire on tiller defoliation patterns, we added tiller defoliation transects in burned areas for both CARM and paired TRM pastures. In 2017, we monitored three transects in the burned area and three in the unburned area for pastures that were burned the previous fall; in 2018, we reduced sampling to two transects in the burned area and also continued to monitor one additional transect in pastures burned in fall 2016 (see Table 1). We did not statistically analyze the effects of patch-burning on defoliation rates, since only two burns (one in CARM and one in TRM) were conducted in each year of the experiment. However, mean values are presented in Appendix B.

For the long-term light and heavy grazing intensity pastures, we split each pasture into thirds along its north-south axis. Within each third (north, central, or south), we randomly selected a location for the tiller defoliation transect. If the randomly selected location did not have sufficient western wheatgrass, we moved the transect to the closest available location with sufficient density of the target species.

Along each 30-m tiller defoliation transect, we used plastic twist-ties to mark 30 western wheatgrass tillers (ramets). At each meter along the transect, we marked the closest available tiller, being careful not to bias our selection based on tiller size. We maintained a minimum distance of 30 cm between marked tillers. Marking occurred before the start of the grazing season each year, and different tillers were monitored in each year.

Marked tillers were sampled repeatedly throughout each growing season. Sampling frequency corresponded to stocking density within each pasture. Tillers in TRM and the light and heavy grazing intensity pastures (which contained herds of 15–35 animals) were monitored every other week. Tillers in CARM pastures were monitored twice per week while the large herd (244 or 280 animals) was in the pasture and were monitored approximately once

**Figure 1.** Examples of how tillers of western wheatgrass *(Pascopyrum smithii)* at the Central Plains Experimental Range in northeastern Colorado were individually marked using twist ties placed at ground level. Both photos show how grazed tiller tips were marked with white paint in order to distinguish regrazing from initial grazing. Twist tie colors differed between years but were standardized across treatments.

per month when cattle were not grazing in the pasture (to capture wild ungulate or rabbit grazing events).

At each sampling date, the total aboveground length of each tiller was measured by straightening the tiller against the edge of a ruler. Evidence of grazing was recorded for each tiller, and grazed tiller tips were marked with white paint (Fig. 1). If the white paint was still present at the next sampling date, the tiller had not been regrazed. Newly grazed or regrazed tillers were clearly distinguished by evidence of grazed tips that were not painted white. Western wheatgrass has an early-season phenology, so many tillers senesced during the season. We continued to monitor these tillers until the end of the grazing season to capture any grazing events on dormant biomass. In early fall, many western wheatgrass plants produced new tillers that emerged < 1 cm from marked, senesced tillers. Once these new tillers appeared, they were also monitored (separately from senesced tillers) in order to capture any potential resurgence of grazing on new fall growth.

### *Data analysis*

We analyzed data using linear mixed models. To examine potential differences in response patterns between a wet yr (2017) and a dry yr (2018), each year was analyzed separately. For pasture-scale analyses, tiller-level data were averaged at the transect level (three per pasture) before analysis. Response variables included the proportion of tillers on a given transect that were grazed, average number of times a tiller was grazed per transect, average length of the tillers at the beginning and end of the grazing season, and average season-long change in length. Grazing treatment (CARM vs. TRM) was included as a fixed effect, while random factors included block (pasture pair) and pasture nested within block. Most tillers were monitored for the entire grazing season, but some tillers were lost or grew only in the fall, and these were monitored for less time. Because tillers monitored longer had the potential to experience more grazing and regrazing, duration of monitoring was included as an additional random factor for all analyses except start-of-season length. The unreplicated heavy and light grazing treatments (one pasture per treatment) were not included in statistical analyses, but we report the findings in results and figures to provide additional context for CARM and TRM results.

To determine the importance of pasture-scale stocking rate and timing of grazing as drivers of defoliation patterns within the adaptive multipaddock rotational system, we examined models for the nine grazed CARM pastures in each year. Pasture ID was included as a random factor, and fixed factors included pasture entry date and pasture-scale stocking rate (animal unit days [AUDs]). Response variables included the proportion of tillers on a given transect that experienced grazing and the average number of times a tiller was grazed per transect; we did not analyze impacts on tiller lengths because available biomass (correlated with grass height) was one trigger that drove cattle rotation decisions for CARM pastures (Wilmer et al. 2018).

We also conducted several analyses at the tiller scale. For these tests we used similar models, but data were not averaged by transect. Instead, transect nested within pasture and block was added as another random effect. To assess impacts of grazing and regrazing on aboveground resources (e.g., photosynthetic capacity), we asked if the number of times a tiller was grazed affected its season-long change in length. To assess regrowth capacity, we asked how much regrowth tillers produced after having been grazed once and whether this regrowth capacity differed by treatment. We ran this analysis for both all grazed tillers, to evaluate regrowth capacity at the season-long scale, and tillers grazed before June 15, which we predicted would have more time and resources available for potential regrowth.

All analyses were conducted in JMP version 12 (SAS Institute Inc., Cary, NC, 1989–2007). Data were transformed or variance-weighted when necessary to meet model assumptions. All results were considered significant at $P < 0.05$ and are reported as means ± 1 standard error.

## Results

### *Treatment effects on tiller defoliation*

In 2017, a relatively wet yr, approximately 40% of tillers were grazed in both CARM and TRM treatments (both moderately stocked) and the proportion of tillers grazed did not differ between treatments ($F_{1,9} = 0.85$, $P = 0.4$). In the lightly and heavily grazed pastures, 24% and 66% of the marked western wheatgrass tillers were grazed in 2017, respectively (Fig. 2a). In 2018, when a dry summer followed a wet spring, approximately 25% of tillers were grazed in CARM and TRM treatments, and the proportion again did

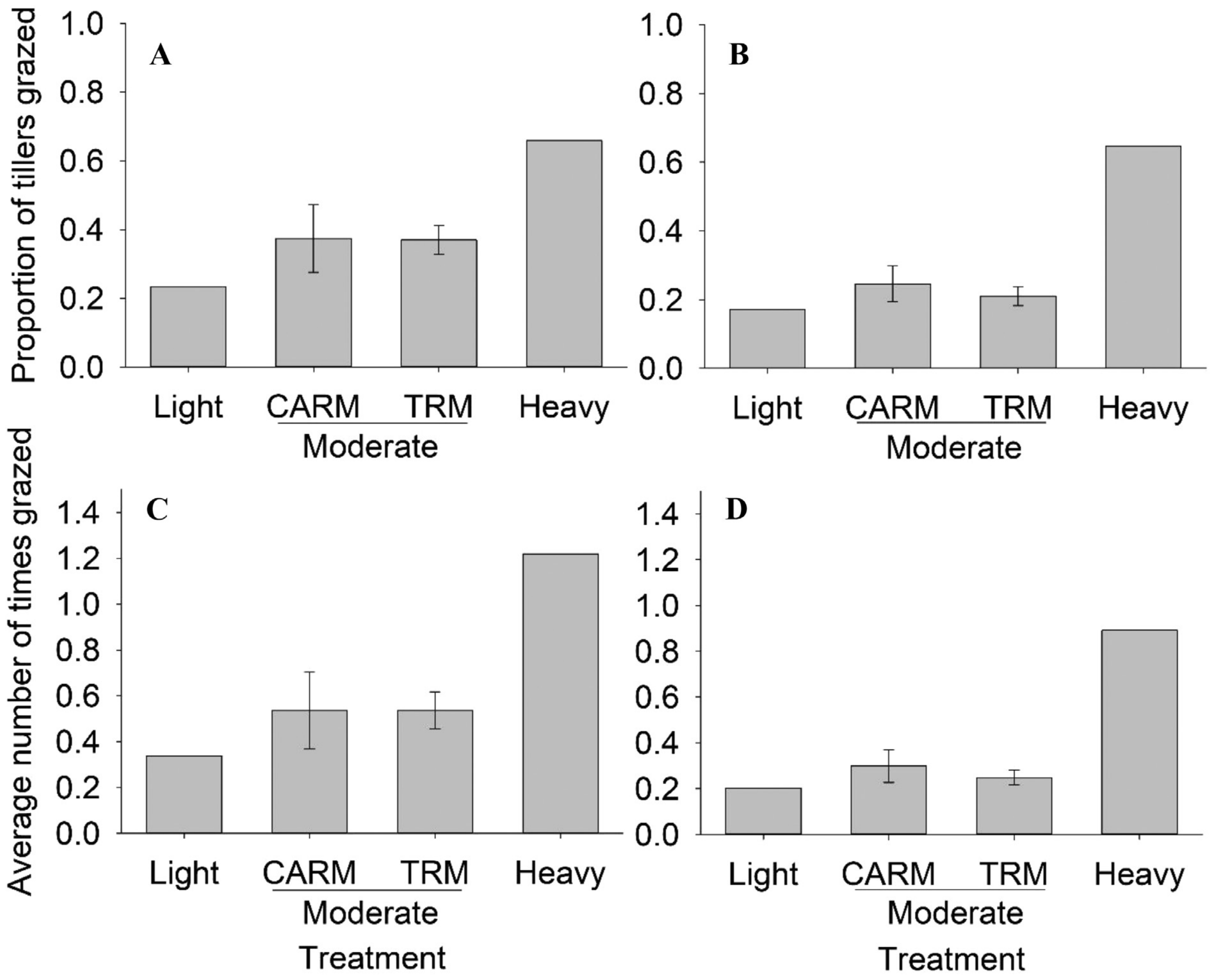


**Figure 2.** Proportion of western wheatgrass tillers grazed in each of four grazing management treatments implemented at the Central Plains Experimental Range in northeastern Colorado in **A,** 2017 and **B,** 2018 and the average number of times a tiller was grazed by treatment in **C,** 2017 and **D,** 2018. CARM indicates collaborative adaptive rangeland management using multipaddock rotational grazing ($N=10$ pastures); TRM, traditional rangeland management using continuous season-long grazing at the same stocking rate as CARM ($N=10$ pastures); heavy, continuous, season-long grazing at a stocking rate 50% greater than TRM ($N=1$ pasture); and light, continuous, season-long grazing at a stocking rate 50% lower than TRM ($N=1$ pasture).

not differ between treatments ($F_{1,10}=0.08$, $P=0.8$). In the lightly and heavily grazed pastures in 2018, 18% and 65% of marked tillers were grazed, respectively (see Fig. 2b).

In 2017, tillers experienced equal amounts of regrazing in the CARM and TRM treatments (see Fig. 2c; $F_{1,9}=0.06$, $P=0.8$). Averaged across CARM and TRM treatments, 25% of tillers were grazed once, 11% were grazed twice, and 4% were grazed more than twice (Fig. 3a). In the heavily grazed pasture, 30% of marked tillers were grazed once, 21% were grazed twice, and 15% were grazed more than twice, whereas in the lightly grazed pasture, 15% of tillers were grazed once, 7% were grazed twice, and 2% were grazed more than twice (see Fig. 3a).

In 2018, tillers again experienced equal amounts of regrazing in the CARM and TRM treatments (see Fig. 2d; $F_{1,10}=0.08$, $P=0.8$). Across CARM and TRM treatments, 20% of tillers were grazed once, 4% were grazed twice, and 1% were grazed more than twice (see Fig. 3b). In the heavily grazed pasture, 46% of marked tillers were grazed once, 13% were grazed twice, and 6% were grazed more than twice, whereas in the lightly grazed pasture, 15% of tillers were grazed once, 3% were grazed twice, and none were grazed more than twice (see Fig. 3b).

Starting and ending tiller lengths were not different between CARM and TRM treatments in 2017 or 2018 (Fig. 4a and 4b; $P$ values > 0.07). However, in 2017, tillers in CARM experienced a season-long reduction in length of about 2 cm, on average, while tiller length in TRM remained constant (see Fig. 4c; $F_{1,7}=10.1$, $P=0.02$). In 2018, tillers in CARM and TRM experienced a similar season-long change in length (see Fig. 4d; $F_{1,10}=0.90$, $P=0.4$).

*Treatment effects on heterogeneity in defoliation rates*

Although levels of defoliation were similar between CARM and TRM at the scale of the whole experiment, individual pastures experienced very different patterns of defoliation in the two treatments. In 2017, western wheatgrass tillers in the two CARM pastures grazed earliest in the season experienced defoliation rates greater than the long-term heavily grazed pasture (Table 1; Fig. 5a). Tillers experienced moderate-to-heavy defoliation in three other CARM pastures and very light defoliation in five pastures, including the one rested pasture (see Fig. 5a). In contrast to the CARM treatment, western wheatgrass tillers in the TRM treatment did not experience defoliation rates greater than the long-term heavily grazed pasture in any TRM pasture, with moderate defoliation rates in seven pastures and light defoliation rates in three pastures (see Fig. 5b).

Overall tiller defoliation rates were lower in 2018 compared with 2017, with defoliation rates again varying more among CARM pastures than among TRM pastures. In CARM, western wheatgrass tillers experienced higher defoliation rates in the two pastures used earliest in the season, light to moderate defoliation in five

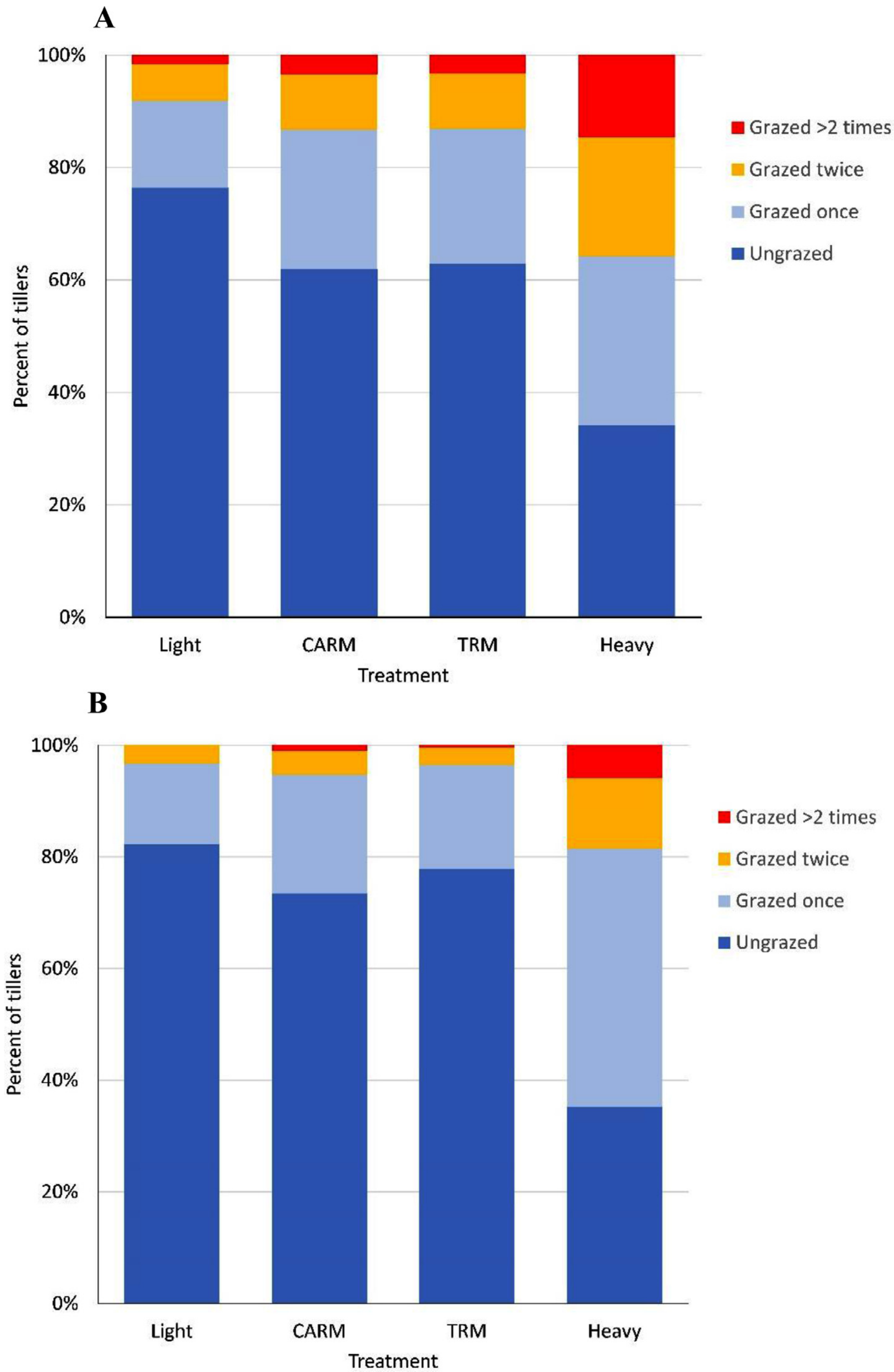


**Figure 3.** Proportion of western wheatgrass tillers grazed or regrazed in each of four grazing management treatments implemented at the Central Plains Experimental Range in northeastern Colorado in **A,** 2017 and **B,** 2018. Treatment labels follow Figure 2.

pastures, and very light defoliation in three pastures, including the rested pasture (Fig. 6a). In contrast, for the TRM pastures, western wheatgrass tillers experienced light-to-moderate defoliation in six pastures and light defoliation in four pastures (see Fig. 6b). Thus, for both years, defoliation rates were more variable across pastures in CARM than TRM.

*Drivers of defoliation rates within CARM*

Both pasture-scale stocking rate and timing of grazing had strong effects on defoliation rates within grazed CARM pastures in 2017. Tillers were more likely to be grazed when pasture-scale stocking rates were higher (Fig. 7a; $F_{1,6} = 23.3$, $P = 0.002$), and there was weaker evidence that tillers were more likely to be grazed in pastures grazed earlier in the season (see Fig. 7b; $F_{1,6} = 5.39$, $P = 0.06$). Tillers were regrazed more often when pasture-scale stocking rates were higher or grazing occurred earlier in the season (see Fig. 7c and 7d; stocking rate $F_{1,7} = 7.34$, $P = 0.03$; start date $F_{1,6} = 8.93$, $P = 0.02$).

In 2018, the duration of grazing time was more similar across the 10 CARM pastures than in 2017, which resulted in pasture-level stocking rates differing less among CARM pastures (see Table 1).

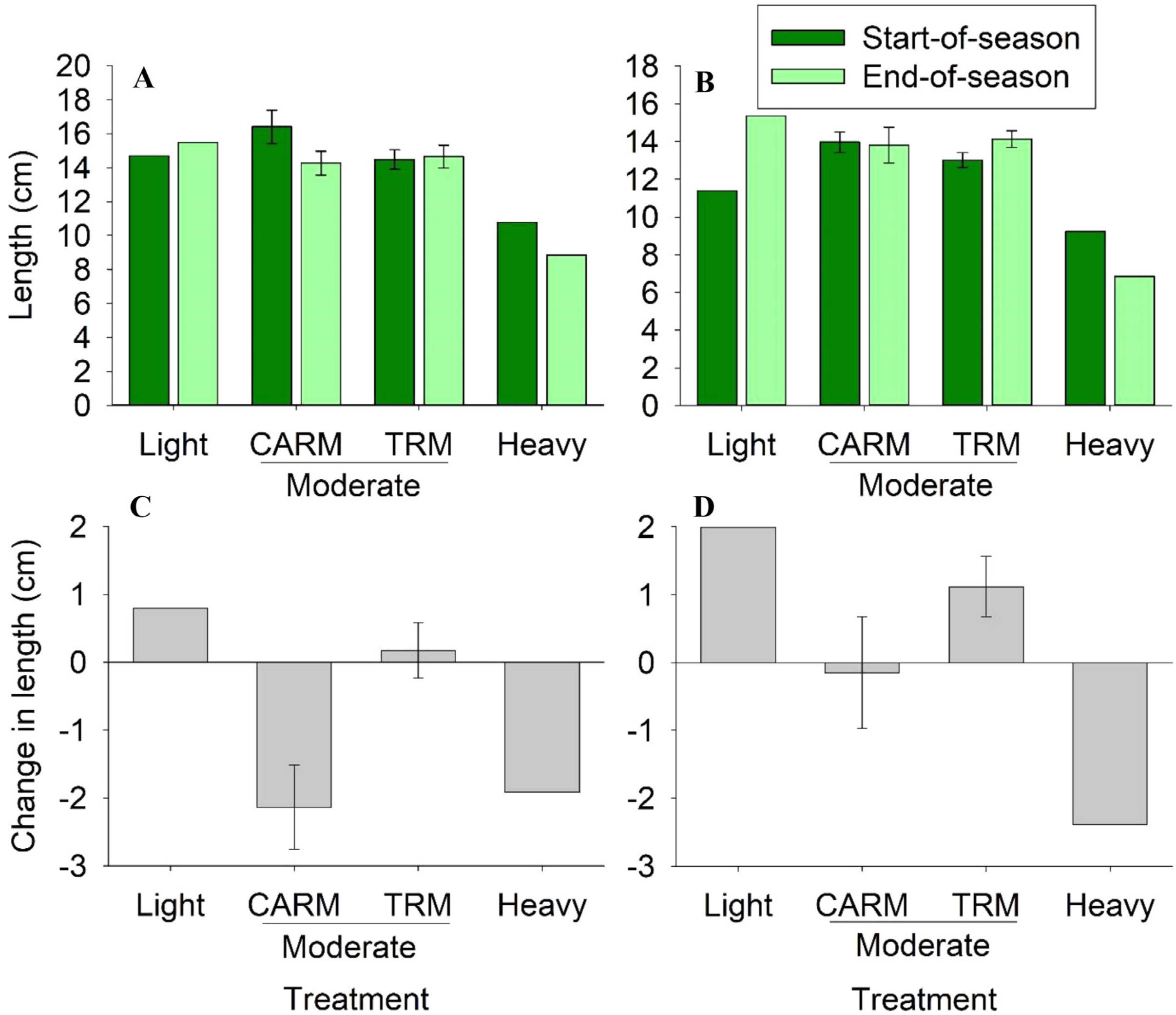


**Figure 4.** Average length of western wheatgrass tillers at the start of the grazing season (mid-May) and end of the grazing season (early October) in each of four grazing management treatments in **A,** 2017 and **B,** 2018 and season-long net change in length by treatment in **C,** 2017 and **D,** 2018. Treatment labels follow Figure 2.

Under this pattern of rotation, pasture-scale AUDs were not significantly associated with defoliation rates (see Fig. 7a and 7c; $P$ values > 0.5). In 2018, we again found that earlier grazing timing was associated with a higher proportion of tillers grazed (see Fig. 7b; $F_{1,5} = 6.09$, $P = 0.05$) and a higher rate of regrazing per tiller (see Fig. 7d; $F_{1,5} = 7.43$, $P = 0.04$).

### *Tiller-scale patterns*

In both years, the number of times a tiller was grazed had a large impact on its season-long change in length (Fig. 8; 2017 $F_{1,2234} = 100$, $P < 0.0001$; 2018 $F_{1,2825} = 280$, $P < 0.0001$). Ungrazed tillers either did not change or increased in length between mid-May and early October, whereas tillers grazed once declined in length by 1–4 cm. Tillers grazed two or more times declined in length by 2–6 cm.

In 2017, tillers grazed once ($N = 695$) exhibited little capacity for regrowth (average tiller-scale length change from date of grazing to the end of the grazing season was 1.1 ± 0.3 cm in CARM, −0.4 ± 0.4 cm in TRM, −0.06 ± 0.7 cm in light and −0.06 ± 1 cm in heavy), and post-grazing length change did not differ between CARM and TRM treatments ($F_{1,10} = 0.85$, $P = 0.4$). Tillers grazed before June 15 ($N = 307$) had more capacity for regrowth, particularly in CARM (average tiller-scale length change from date of grazing to the end of the grazing season was 3.4 ± 0.5 cm in CARM, 0.4 ± 0.6 cm in TRM, −0.6 ± 1.6 cm in light and 0.5 ± 1 cm in heavy), but regrowth amount still did not differ between CARM and TRM treatments ($F_{1,3} = 1.45$, $P = 0.3$).

In 2018, tillers grazed once ($N = 582$) again exhibited little capacity for regrowth (1.2 ± 0.3 cm in CARM, 0.8 ± 0.3 cm in TRM, 0.9 ± 1.5 cm in light and −0.6 ± 0.5 cm in heavy). Postgrazing length change did not differ between CARM and TRM treatments in 2018 ($F_{1,11} = 0.70$, $P = 0.4$). Tillers grazed before June 15 ($N = 221$) had more capacity for regrowth (1.8 ± 0.5 cm in CARM, 1.5 ± 0.7 cm in TRM, 5.9 ± 3.2 cm in light and −0.5 ± 1 cm in heavy), but regrowth amount did not differ between CARM and TRM treatments ($F_{1,5} = 0.25$, $P = 0.6$).

## Discussion

To our knowledge, this was the first ranch-scale experimental investigation into tiller defoliation dynamics in the context of adaptive multipaddock rotational grazing. Consistent with many previous studies conducted in smaller paddocks and without CAM (Morris 1969; Briske and Stuth 1982; Hart and Balla 1982; Gillen et al. 1990; Jensen et al. 1990; Hart et al. 1993; Derner et al.

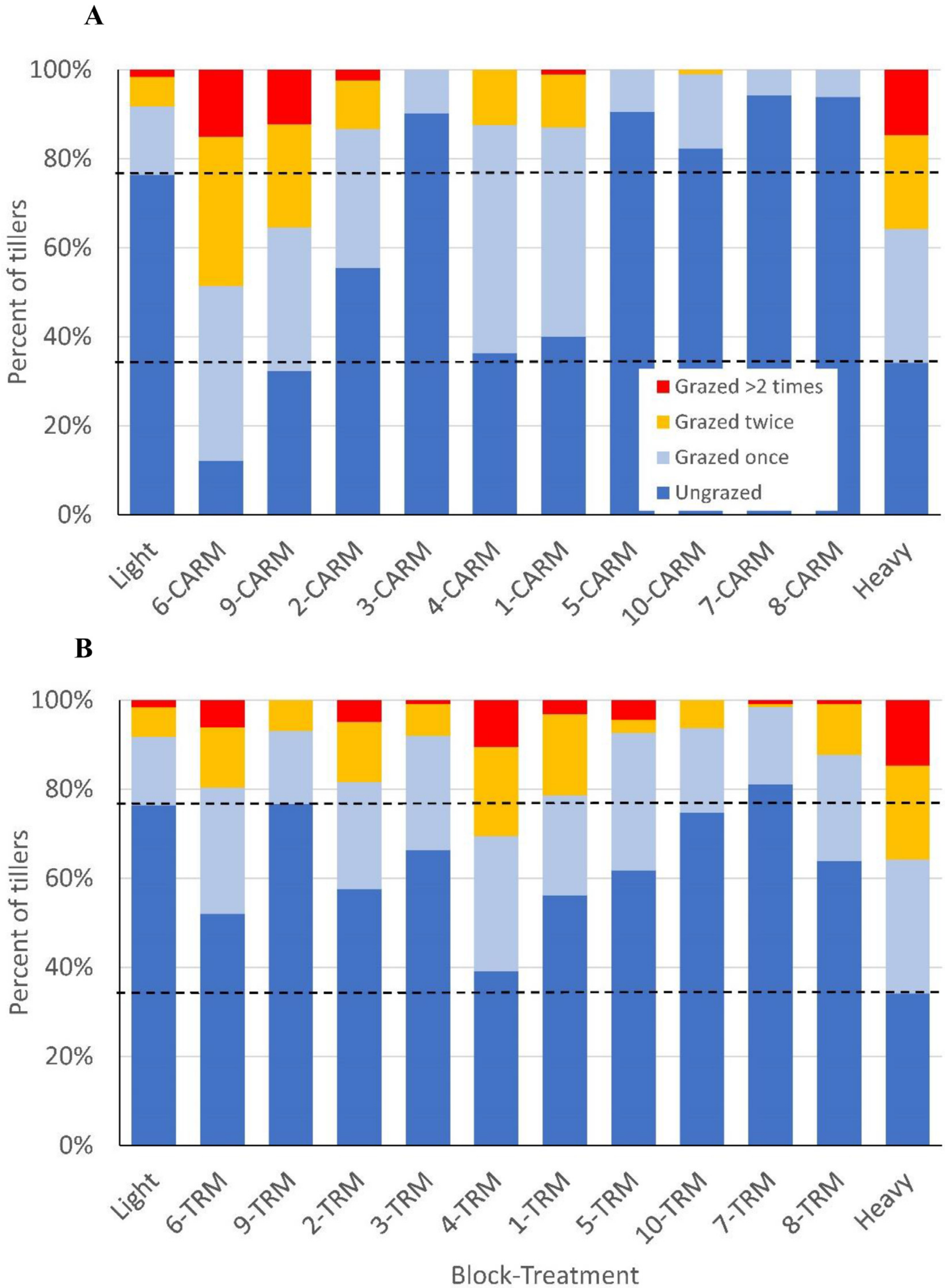


**Figure 5.** Proportion of western wheatgrass tillers grazed or regrazed in each of the 10 replicate pastures in each treatment in 2017 for **A,** collaborative adaptive multipaddock rotational grazing treatment (CARM) and **B,** traditional rangeland management. Treatment labels follow Figure 2. Pastures are paired into 10 blocks, which are sorted on the basis of the order in which CARM pastures were grazed (left-most CARM pasture was grazed first). For reference, *dashed black lines* show the percent of tillers that remained ungrazed in the light and heavy treatments.

1994; Volesky 1994; O'Reagain and Grau 1995; Cullan et al. 1999), we observed that frequencies of grazing and regrazing on a palatable, cool-season grass (western wheatgrass) were much more sensitive to stocking rate than grazing system. Under the moderate stocking rates used in both CARM and TRM treatments, roughly two-thirds of western wheatgrass tillers remained ungrazed annually, regardless of grazing system. At the ranch scale, rates of regrazing in CARM and TRM were low (5–15% of tillers, see Fig. 3). This is consistent with several previous studies (e.g., Gammon and Roberts 1980; Hart et al. 1993; Derner et al. 1994), though other studies in both rotational and continuous systems have reported substantially higher rates of regrazing (e.g., Morris 1969; Briske and Stuth 1982; Hart and Balla 1982; Heitschmidt et al. 1990). Compared with moderately grazed CARM and TRM pastures, rates of grazing and regrazing were noticeably higher in the long-term heavily grazed pasture and lower in the long-term lightly grazed pasture included in our study. Within the CARM treatment, pasture-level stocking rate was also a strong driver of temporal

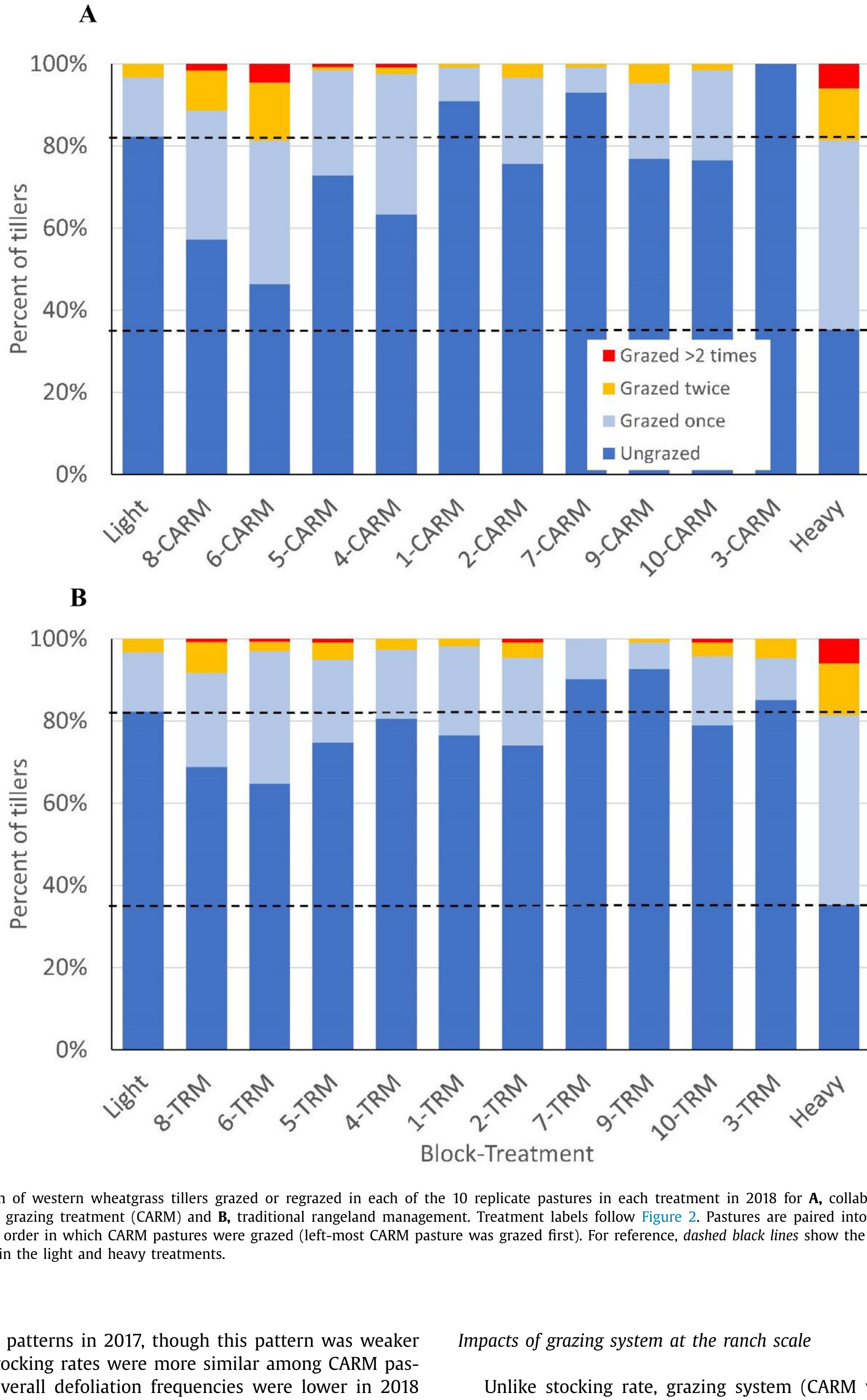


**Figure 6.** Proportion of western wheatgrass tillers grazed or regrazed in each of the 10 replicate pastures in each treatment in 2018 for **A,** collaborative adaptive multipaddock rotational grazing treatment (CARM) and **B,** traditional rangeland management. Treatment labels follow Figure 2. Pastures are paired into 10 blocks, which are sorted based on the order in which CARM pastures were grazed (left-most CARM pasture was grazed first). For reference, *dashed black lines* show the percent of tillers that remained ungrazed in the light and heavy treatments.

tiller defoliation patterns in 2017, though this pattern was weaker in 2018 when stocking rates were more similar among CARM pastures (Fig. 7). Overall defoliation frequencies were lower in 2018 than 2017, possibly because a rapid dry-down in early summer 2018 led to relatively rapid senescence of western wheatgrass, which reduced the temporal window during which it was highly palatable and selected over other species.

*Impacts of grazing system at the ranch scale*

Unlike stocking rate, grazing system (CARM vs. TRM) had little influence on the frequency and intensity of grazing experienced by western wheatgrass tillers at the ranch-scale. Grazing treatment did not affect the proportion of tillers grazed or the average number of times a tiller was grazed in either year. Similar defoliation patterns between the two grazing treatments are consistent with

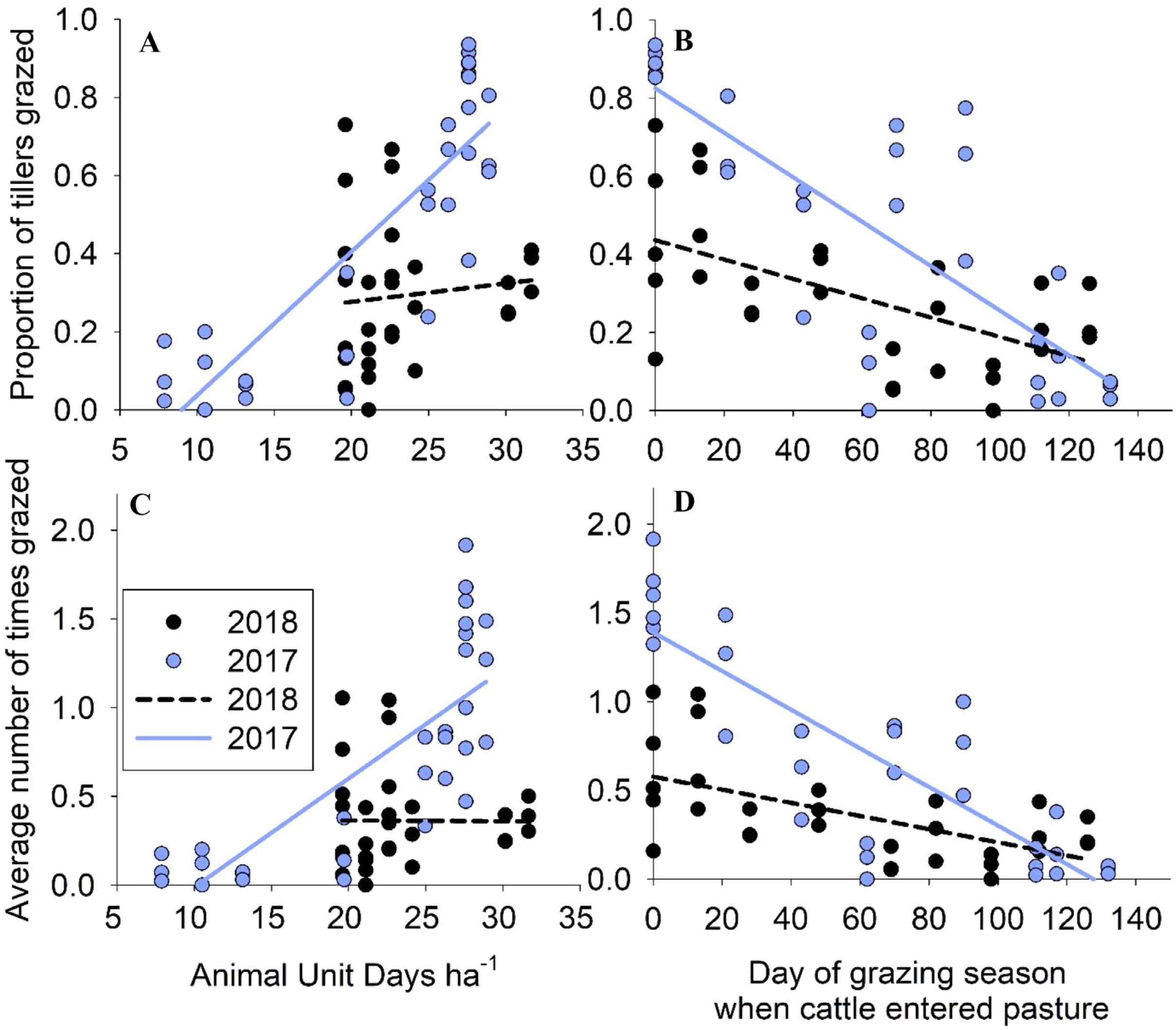


**Figure 7.** The proportion of western wheatgrass tillers grazed **(A, B)** and the average number of times a tiller was grazed **(C, D)** as a function of pasture-scale stocking rate **(A, C)** and grazing timing **(B, D)** for grazed pastures within the collaborative adaptive multipaddock rotational grazing treatment employing multipaddock rotational grazing.

previous studies (Hart et al. 1993; Volesky 1994) and tiller density results from this study (Augustine et al. 2020).

Why did regrazing frequencies remain low and similar at the ranch scale between CARM and TRM treatments in our study? Gammon and Roberts (1980) suggested that both plant height and forage quality can control regrazing frequencies. Given the short stature of grasses in the semiarid shortgrass steppe, we suggest that livestock attempting to maximize bite size are likely to preferentially select ungrazed tillers due to greater height and biomass. Moreover, western wheatgrass possesses elevated growth points that increase the culm-to-leaf ratio relatively early in the growing season (Branson 1953). Higher culm-to-leaf ratios are known to reduce forage quality and influence foraging dynamics (Ganskopp et al. 1992), and this may have led to selection against previously grazed tillers (which have even higher culm-to-leaf ratios than ungrazed tillers). Finally, forage quality is highly variable and driven mostly by precipitation timing in our system, where highly variable precipitation patterns limit the windows of time in which resources for vegetation regrowth are available. Thus, high-quality regrowth of western wheatgrass is uncommon, unpredictable, and unlikely to drive foraging patterns in the shortgrass steppe.

In some systems, forage quality may be a more important driver of selection than bite size, and plant regrowth capacity may be more robust. In such systems, defoliation can be effective in helping to maintain high forage quality by preventing plants from producing low-quality stems and reproductive culms. Thus, there should be more potential for within-season regrazing (and more potential for tiller-scale benefits of rotation) in systems where two conditions are met: 1) forage quality is a stronger driver of foraging behavior than other factors like bite size, and 2) palatable plants are able to quickly regrow after defoliation. These conditions would be more common in mesic or fertile systems where overall biomass is higher and grazed plants have more resources available for regrowth after defoliation (Maschinski and Whitham 1989; Heitschmidt et al. 1990; Hawkins 2017; Venter et al. 2020). However, several studies in mesic systems have failed to document strong effects of grazing system on levels of selectivity or regrazing rates at the plant scale (Volesky 1994; Venter et al. 2019). Further research is needed to identify the specific conditions under which rotation may influence regrazing frequencies.

Effects of grazing system on plant defoliation patterns may also depend on the scale of observation. Venter et al. (2019) found that when compared with holistic planned (high-density, short-

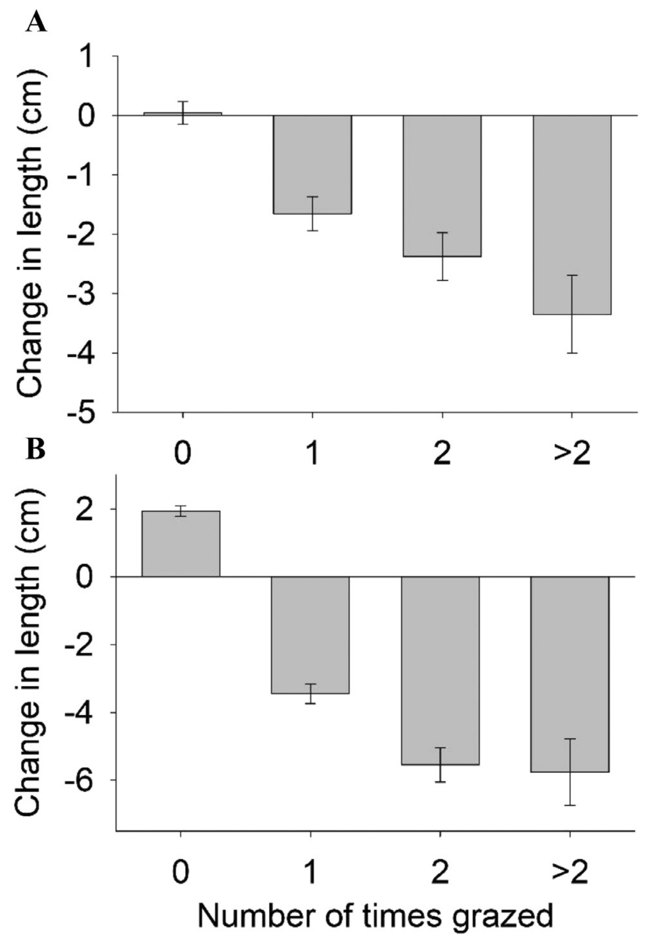


**Figure 8.** Effect of the number of times a tiller was grazed on its season-long net change in length in **A,** 2017 and **B,** 2018.

duration) grazing, season-long continuous grazing led to more heterogeneous grazing patterns and more regrazing of patches with high greenness within a pasture. However, these patterns did not carry through to the plant scale; cattle in high-density rotational systems were able to select for palatable species at similar rates as cattle in low-density continuous systems (Venter et al. 2019). Thus, rotational grazing may affect within-pasture heterogeneity in vegetation structure and greenness without impacting plant species composition. Supporting this, a multidecadal study in South Africa found little effect of different rotational grazing systems on plant species composition (Morris and Tainton 1996).

Several studies also suggest that the ratios between different defoliation frequencies are relatively consistent; regrazing often commences once ≈50–60% of tillers of a given species have been grazed once (Jensen et al. 1990; O'Reagain and Grau 1995). These consistent ratios make it difficult to design a grazing management strategy in which livestock graze all tillers once but do not regraze any tillers. This further demonstrates why grazing management strategies may be limited in their ability to control defoliation frequency and intensity at the ranch scale (Briske et al. 2008).

*Impacts of grazing system at the pasture scale*

Despite the lack of difference in overall tiller defoliation patterns between CARM and TRM, we found that the two grazing treatments differed dramatically when it came to variation in defoliation rates among the 10 pastures within each treatment (Figs. 5 and 6). Across both years of the study, pastures grazed by the CARM herd early in the growing season experienced the most grazing and regrazing on western wheatgrass (Fig. 7); this corresponds to the time of year when western wheatgrass is most palatable (high leaf–to–stem ratio) and $C_4$ grass species like blue grama have limited new growth available to livestock (Monson et al. 1983). In contrast, tillers in pastures grazed by the CARM herd later in the grazing season experienced much lower rates of grazing and regrazing. These early-season results are counter to the assumption that adaptive multipaddock rotational grazing should lead to reduced grazing of the most palatable species. Pastures grazed for shorter time periods within CARM experienced less defoliation (e.g., Block 3 in 2017, see Fig. 5a), but this was fully offset by other CARM pastures, which were grazed for longer and experienced more defoliation. Thus, we have no reason to suspect that faster rotation speeds would lead to less defoliation at the ranch scale. Defoliation patterns were much more similar across pastures assigned to the TRM treatment, likely due to more uniform pasture-scale stocking rates across TRM pastures.

The high and predictable heterogeneity in western wheatgrass defoliation patterns among CARM pastures could prove useful for managers seeking to achieve pasture-scale objectives. For example, if pasture-scale objectives include reducing western wheatgrass abundance to enhance habitat for thick-billed longspurs (Wilmer et al. 2019), which require short structure for nesting, our data suggest that repeated early-season grazing may help accomplish this goal. Alternatively, early-season rest would be most beneficial for pastures in which managers are trying to enhance the abundance of western wheatgrass. More generally, varying the timing of grazing between years should result in more variable grazing pressure at the pasture scale. In any given year, western wheatgrass plants within pastures grazed early in the season will experience defoliation rates equivalent to season-long heavy stocking, whereas plants in pastures grazed later will experience defoliation rates equivalent to light stocking. The long-term effects of this more variable defoliation regime on western wheatgrass population dynamics are unclear, though tiller densities have not yet been affected over 5 yr in our study (Augustine et al. 2020).

*Tiller-scale patterns*

It is important to emphasize that our results do not suggest grazing and regrazing are benign for western wheatgrass. On the contrary, our data indicate that grazing and regrazing lead to significant reductions in tiller length (Fig. 8). Moreover, regrowth capacity of this plant was limited in this highly variable environment where rest from grazing may occur during periods of low precipitation or during periods when the species is not physiologically active (Briske et al. 2008). Regrowth is likely also limited by this species' elevated growth points, which increase the probability that new tiller (ramet) initiation from rhizomes is needed for regrowth after defoliation. These findings suggest that western wheatgrass has little capacity for compensatory regrowth in response to defoliation in this ecosystem and are consistent with previous studies showing that defoliation, particularly repeated defoliation, can reduce aboveground production in western wheatgrass (Everson 1966; Buwai and Trlica 1977; Lauenroth et al. 1985; Eneboe et al. 2002; Bork et al. 2017; Broadbent et al. 2018). Although we did not measure root responses, previous research indicates that grazing also leads to reductions in root biomass and increased carbon allocation to shoots, relative to roots, in this species (Branson 1956; Painter and Detling 1981; Polley and Detling 1989; Augustine et al. 2011).

Relatively long deferment periods are needed for western wheatgrass plants to fully recover from growing season defoliation (Trlica et al. 1977; Menke and Trlica 1981; Reece et al. 1996). One hypothesized benefit of CARM and other adaptive multipaddock rotational grazing strategies is the potential to incorporate pasture-scale rest (especially early in the growing season) for some pastures each year, which would allow plants in those pastures to recover from grazing the previous season. However, our data convincingly show that regardless of grazing treatment, approximately two-thirds of western wheatgrass tillers experienced season-long rest (i.e., no grazing) under moderate stocking rates. Thus, rest is effectively "built in" to continuous grazing systems, if not heavily stocked, and cattle do not have to be removed from a pasture to create opportunities for season-long rest at the scale of individual grass plants. At the same time, season-long rest at the pasture scale may be beneficial for achieving other objectives (e.g., grassland bird habitat or drought resilience, Davis et al. 2019).

*Collaborative adaptive management*

Our study of tiller defoliation was inspired and guided by the hypotheses and mental models of the CARM stakeholder group. Designing the study within an existing collaborative process allowed us to examine applied ecological questions at a manager-relevant spatial scale in a rigorous way and then feed our findings back into the group's decision-making process, following the CAM model (Fernández-Giménez et al. 2019). In the case of this study, CARM stakeholders participated in the research question selection (2015), discussed initial findings while the study was being conducted (2017–2018), applied these results to CARM herd management (2019–2020), and copresented results in various venues. These activities are evidence of enhanced stakeholder ownership and understanding of the research process and findings in the CARM approach. Such an approach may be useful in other contexts where different stakeholders (e.g., researchers, agency managers, ranchers) have competing or conflicting mental models regarding the nature of specific management-ecosystem relationships. The CAM model enabled our team to directly address key stakeholder hypotheses and enhanced stakeholder trust of research results.

While many grazing studies evaluate the effects of relatively rigid management "treatments" designed at the study's onset, our study provides a novel comparison of management "scenarios," informed by continual structured social learning supported by regular monitoring and stakeholder deliberation. The CARM process involves quarterly meetings, regular digital communications on changing pasture and livestock conditions during the grazing season, and other activities during which stakeholders and researchers establish and update management objectives, implement treatments, evaluate results, and adjust management actions within grazing seasons and over multiple years. An ongoing challenge of the project is to balance this attentive adjustment and collaborative decision-making process with the research objective of developing transferable, evidence-based management triggers and recommendations that inform ranch-scale adaptive management for diverse objectives at regional or national scales.

*Limitations*

We note several important limitations of our study. First, although the continuous grazing TRM treatment was truly replicated across 10 pastures, all CARM pastures were grazed by the same herd within a given year, so these pastures are not truly independent. Nevertheless, we have no reason to suspect some kind of herd-scale bias that would have systematically altered western wheatgrass tiller defoliation patterns across the 10 CARM pastures. Moreover, our results from CARM were consistent across years, despite a completely different set of yearling steers being used in the CARM herd each year. Second, as with most previous studies on tiller defoliation (e.g., Gammon and Roberts 1978; Derner et al. 1994), our data on regrazing may have slightly underestimated regrazing occurrences within CARM pastures, which were monitored somewhat less intensively than TRM pastures per AUD of grazing. However, our results for the proportion of tillers grazed and season-long changes in length should not have been affected by this issue. Third, defoliation results for the light and heavy pastures may have been affected by the large differences in the abundance of western wheatgrass between these pastures (Porensky et al. 2017). We tried to minimize this issue by placing all monitoring transects in portions of the pastures that had similar western wheatgrass abundance, regardless of pasture-scale plant community composition. The fact that pasture-level stocking rate was also an important driver of defoliation patterns within the CARM treatment, which included pastures spanning a wide range of variation in background plant community composition, suggests that background community composition was not a strong driver of results. Our study did not explore defoliation patterns in rotational systems where cattle return to previously grazed pastures within the same growing season, though other studies have done this and arrived at similar conclusions (e.g., Hart et al. 1993; Volesky 1994). Finally, we only studied one species here; previous studies have shown that defoliation dynamics and regrowth capacity vary across species (e.g., Heitschmidt et al. 1990; Broadbent et al. 2018).

## Management Implications

We found that CARM grazing did not lower rates of grazing and regrazing on western wheatgrass tillers at the ranch scale in the shortgrass steppe, when compared with season-long continuous grazing at the same stocking rate. Thus, the use of adaptive multipaddock rotational grazing strategies should not be expected to enhance the production or abundance of this palatable, cool-season species. In fact, when viewing the world from the humble perspective of a western wheatgrass tiller, it is apparent that season-long rest is built into season-long continuous grazing and rotational systems. More than 50 yr ago, Morris (1969) wisely summarized that "under the system of 'correctly [moderately] stocked' continuous grazing, described here, plants were grazed neither frequently nor severely … Individual small areas in these 'continuously grazed' swards were thus grazed rotationally." While Morris studied continuously grazed, nonadaptively managed pastures in a mesic grassland, our work extends the same finding to an adaptively managed, multipaddock rotational grazing system implemented in a semiarid grassland. In the end, like many previous studies, we conclude that stocking rate is a far more important driver of ranch-scale defoliation intensity and frequency than the spatiotemporal movement of cattle among paddocks.

Although defoliation patterns were similar between CARM and TRM at the whole-ranch scale, the spatial and temporal heterogeneity created by CARM (i.e., higher and predictable variability in defoliation frequency among pastures) could be used to strategically minimize or maximize the impacts of grazing on western wheatgrass or other palatable grasses at the individual pasture scale. Ocular or quantitative estimates of western wheatgrass defoliation could serve as a key indicator for determining when to move cattle to the next pasture in the current grazing sequence within a season, especially considering plant physiology and recovery periods (Grissom and Steffens 2013). Defoliation patterns could also inform decisions about the timing of use across grazing seasons for longer-term (e.g., decadal scale) potential improvement to populations of palatable species in selected pastures (Grissom and Steffens 2013).

## Declaration of Competing Interest

None.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2021.06.008.

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