Grazing intensity differentially regulates ANPP response to precipitation in North American semiarid grasslands

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Abstract. Grazing intensity elicits changes in the composition of plant functional groups in both shortgrass steppe (SGS) and northern mixed-grass prairie (NMP) in North America. How these grazing intensity-induced changes control aboveground net primary production (ANPP) responses to precipitation remains a central open question, especially in light of predicted climate changes. Here, we evaluated effects of four levels (none, light, moderate, and heavy) of long-term (>30 yr) grazing intensity in SGS and NMP on: (1) ANPP; (2) precipitation-use efficiency (PUE, ANPP:precipitation); and (3) precipitation marginal response (PMR; slope of a linear regression model between ANPP and precipitation). We advance prior work by examining: (1) the consequences of a range of grazing intensities (more grazed vs. ungrazed); and (2) how grazing-induced changes in ANPP and PUE are related both to shifts in functional group composition and physiological responses within each functional group. Spring (April–June) precipitation, the primary determinant of ANPP, was only 12% higher in NMP than in SGS, yet ANPP and PUE were 25% higher. Doubling grazing intensity in SGS and nearly doubling it in NMP reduced ANPP and PUE by only 24% and 33%, respectively. Increased grazing intensity reduced C_3 graminoid biomass and increased C_4 grass biomass in both grasslands. Functional group shifts affected PUE through biomass reductions, as PUE was positively associated with the relative abundance of C_3 species and negatively with C_4 species across both grasslands. At the community level, PMR was similar between grasslands and unaffected by grazing intensity. However, PMR of C_3 graminoids in SGS was eightfold higher in the ungrazed treatment than under any grazed level. In NMP, PMR of C_3 graminoids was only reduced under heavy grazing intensity. Knowing the ecological consequences of grazing intensity provides valuable information for mitigation and adaptation strategies in response to predicted climate change. For example, moderate grazing (the recommended rate) in SGS would sequester the same amount of aboveground carbon as light grazing because ANPP was nearly the same. In contrast, reductions in grazing intensity in NMP from moderate to light intensity would increase the amount of aboveground carbon sequestered by 25% because of increased ANPP.

Key words: northern mixed-grass prairie; precipitation marginal response; precipitation-use efficiency; rain-use efficiency; rangeland ecosystems; shortgrass steppe.

INTRODUCTION

Grazing by domestic herbivores is the primary land use of semiarid rangelands worldwide (Vitousek et al. 1986, Herrero and Thornton 2013). In semiarid ecosystems, aboveground net primary production (ANPP) is the main determinant of forage consumption by large herbivores, resultant meat production (McNaughton et al. 1989, Oesterheld et al. 1992, Derner et al. 2008a, Craine et al. 2013, Reeves et al. 2013), and hence

economic returns (Ritten et al. 2010, Torell et al. 2010). In these water-limited systems, the response of ANPP to precipitation is central to sustainable management (Fang et al. 2014, Kachergis et al. 2014). Mean ANPP is positively correlated with mean annual precipitation across widely different terrestrial ecosystems including semiarid grasslands (Le Houerou 1984, McNaughton 1985, Sala et al. 1988, McNaughton et al. 1993, Knapp and Smith 2001, Bai et al. 2008). Within a given site, there is also a positive association between ANPP and precipitation (Lauenroth and Sala 1992, Jobbágy and Sala 2000, Derner and Hart 2007). The interaction between such spatial and temporal dynamics has provided major

insights to the function of semiarid rangelands: (1) dispersion of the data around the temporal model is larger than the spatial model; (2) temporal slope of the relationship between ANPP and current year precipitation changes across a regional gradient; and (3) the importance of current year precipitation on ANPP increases as mean annual precipitation decreases (Lauenroth and Sala 1992, Paruelo et al. 1999, Sala et al. 2012). However, the degree to which grazing modulates relationships between ANPP and precipitation has not been quantitatively evaluated, despite the primacy of grazing as a land use in semiarid rangelands.

Grazing intensity can elicit vegetation changes through shifts in plant functional group dominance (Manley et al. 1997, Biondini et al. 1998, Derner and Hart 2007, Milchunas et al. 2008), which may alter ANPP response to precipitation (Verón et al. 2006, Verón and Paruelo 2010). In the shortgrass steppe (SGS) and northern mixed-grass prairie (NMP), increasing grazing intensity results in increased dominance of perennial, C_4 grasses at the expense of perennial, C_3 graminoids (Manley et al. 1997, Biondini et al. 1998, Derner and Hart 2007, Milchunas et al. 2008). C_3 and C_4 functional groups exhibit differential responses to precipitation across these two grassland ecosystems (Epstein et al. 1997, Derner et al. 2008b). By comparing a wet year to a dry year, Derner et al. (2008b) showed that C_3 species production had a higher relative increase in response to increased precipitation than C_4 species. However, such shifts in functional group biomass and shifts in the capacity of each functional group to respond to precipitation have only been evaluated within a single grazing intensity for a limited time period (Derner et al. 2008b).

Here, we examine how multiple long-term grazing intensity treatments affect ANPP responses to annual and seasonal precipitation in both SGS and NMP using: (1) precipitation-use efficiency (PUE), defined as the ANPP: precipitation ratio (Le Houerou 1984, but see also Verón et al. 2006); and (2) precipitation marginal response (Verón et al. 2005, 2006), defined as the slope of a linear regression of annual ANPP on annual or key seasonal precipitation. This precipitation marginal response is also known as the "temporal model" for the relationship between precipitation and ANPP (Noy-Meir 1973, Sala et al. 1988, Lauenroth and Sala 1992). Increased grazing intensity is predicted to reduce precipitation-use efficiency by reducing ANPP. However, for comparisons between grasslands, differences in both ANPP and total precipitation may influence precipitation-use efficiency responses to grazing intensity (Le Houerou 1984, Verón et al. 2006).

For precipitation marginal response, grazing may have lesser or no effect when compared to precipitation-use efficiency, as functional group shifts might result in species with a similar capacity to respond to precipitation (Verón et al. 2006). Within a grassland, the intuitive prediction is that precipitation marginal response should decrease with increasing grazing intensity, as a result of reduced productivity with increasing grazing intensity (Milchunas et al. 1994, Derner and Hart 2007), which is tied to meristematic tissue density, an important mechanism for plant responses to precipitation (Paruelo et al. 2008, Reichmann et al. 2013, Reichmann and Sala 2014). However, for SGS and NMP, grazing intensity also induces shifts in functional group composition, with higher grazing intensities favoring C_4 grasses over C_3 graminoids (Milchunas et al. 1994, Derner and Hart 2007) and has possible implications for other functional groups, such as forbs and/or sub-shrubs. Since water-use efficiency is greater for C_4 than C_3 grasses (Taylor et al. 2014), precipitation marginal response should be influenced by grazing intensity through: (1) the shift in plant functional group contribution to ANPP, from K-type species toward r-type species or vice versa (Verón and Paruelo 2010); (2) concurrent shifts in meristem density and the proportion of these that are active; and (3) reductions in total ANPP with increased grazing intensity. For comparisons between grasslands, the seasonal distribution of precipitation and temperature may favor a specific functional group by influencing soil water during the growing season. For both SGS and NMP, spring precipitation explains a higher proportion of ANPP interannual variation than annual precipitation (Lauenroth and Sala 1992, Derner and Hart 2007), which could potentially favor C_3 species over C_4 species.

Here, we examined ANPP responses to precipitation under four levels of long-term (>30 yr) grazing intensity (none, light, moderate, and heavy). We hypothesized that ANPP response differences across grazing intensities in both SGS and NMP would be driven by influences of the contribution of functional groups, especially C_4 grass and C_3 graminoid biomass. ANPP was measured as peak growing season biomass and we used both annual and spring precipitation to compare: (1) ANPP; (2) precipitation-use efficiency; and (3) precipitation marginal response across the four levels of grazing intensity for the two grasslands. Our primary goals were to better understand if grazing intensity affects community ANPP, precipitation-use efficiency, and precipitation marginal response in a similar way between the two major grasslands of North America, and to better understand how functional groups shifts affect precipitation-use efficiency and precipitation marginal response. Our specific hypotheses were that: (1) as grazing intensity increases, C_4 grass biomass will increase and C_3 graminoid biomass will decrease; (2) compared to C_3 graminoids, C_4 grasses will produce less biomass per unit precipitation; (3) within each functional group, increased grazing intensity will reduce plant capacity to respond to increased precipitation; and (4) as a consequence of these multiple mechanisms, ANPP, precipitation-use efficiency, and precipitation marginal response should all decrease with increased grazing intensity.
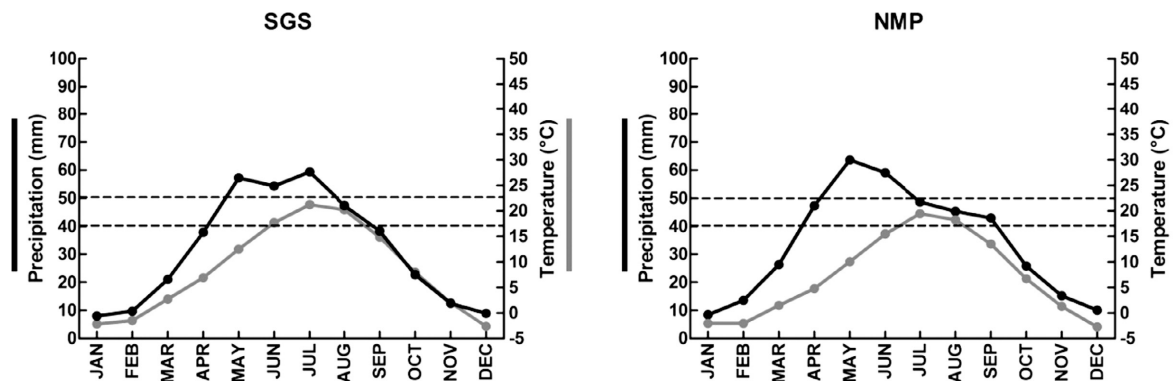
Fig. 1.　Climate of shortgrass steppe (SGS) and northern mixed-grass prairie (NMP). Data represent mean values for 1981–2014. Dotted lines are reference lines for 40 and 50 mm.

Materials and Methods

Site description

Research was conducted on the USDA-Agricultural Research Service sites (1) Central Plains Experimental Range (SGS), a Long Term Agro-ecosystem Research (LTAR) Network site, located ~12 km northeast of Nunn, in north-central Colorado, USA (40°49′ N, 107°46′ W); and (2) High Plains Grasslands Research Station (NMP), located 7 km northwest of Cheyenne, Wyoming, USA (41°11′ N, 104°53′ W). The primary ecological sites are Loamy Plains for SGS, and Loamy for NMP (Site ID: R067BY002CO, and R067AY122WY, respectively). Mean annual precipitation at SGS and NMP (1981–2014) is 376.8 ± 82.0 mm (mean ± standard deviation [SD]), and 405.9 ± 112.1 mm, respectively. Spring precipitation (April + May + June) was 149.2 ± 64.1 mm at SGS and 169.8 ± 70.1 mm at NMP during this period. Spring precipitation represents ~40% of annual precipitation at both grasslands. Precipitation in early spring (April + May) is greater for NMP compared to SGS, whereas the opposite relationship is observed for summer precipitation as the amount in SGS exceeds NMP (Fig. 1). Previous reports demonstrate that spring precipitation has impacts on ANPP (Lauenroth and Sala 1992, Derner and Hart 2007) and net secondary production (Derner et al. 2008a, Reeves et al. 2015). Spring temperature was 12.3°C ± 1.5°C at SGS and 10.0°C ± 1.4°C at NMP. For both ecosystems, spring precipitation and temperature were negatively correlated (SGS, $r = -0.72$, $P < 0.0001$; NMP, $r: = -0.50$, $P = 0.001$).

For both the SGS and NMP, species composition is similar and predominately perennial grasses. *Bouteloua gracilis* (blue grama) is the dominant perennial warm season (C_4) shortgrass species, and increases with increasing grazing (Milchunas and Lauenroth 1993, Derner and Hart 2007). Important perennial cool season (C_3) mid-height grasses are *Pascopyrum smithii* (western wheatgrass) and *Hesperostipa comata* (needle-and-thread). *Carex duriuscula* (needle leaf sedge) is a frequent,

short-statured, C_3 perennial graminoid. *Sphaeralcea coccinea* (scarlet globemallow) is the primary forb, while *Artemisia frigida* (fringed sagewort) and *Eriogonum effusum* (buckwheat) are the main sub-shrubs. Annual grasses consist almost entirely of *Vulpia octoflora* (six weeks fescue).

Grazing intensity treatments

Grazing intensity experiments were initiated in 1939 at SGS (Hart and Ashby 1998) and in 1982 at NMP (Hart et al. 1988). For both grasslands, there were four levels of grazing intensity: (1) none; (2) light (targeted for 20% utilization of peak growing season biomass); (3) moderate (40% utilization); and (4) heavy (60% utilization). Grazing seasons typically began mid-May (SGS) or early June (NMP) and ended in mid-October. Field sizes for grazing treatments were the same for SGS (125 ha), but differed for NMP among grazing treatments; light (80 ha), moderate (12 ha), and heavy (9 ha). Grazing animals for both grasslands were British-breed yearlings. Mean yearling densities applied to achieve the desired grazing intensities were 9.3 animal unit days (AUD)/ha (light), 12.5 AUD/ha (moderate), and 18.6 AUD/ha (heavy) at SGS (J. D. Derner et al., *unpublished manuscript*) and 15.7 AUD/ha (light), 32.6 AUD/ha (moderate), and 43.4 AUD/ha (heavy) for NMP (Reeves et al. 2013).

For both grasslands, we estimated ANPP as the peak growing season biomass harvested from 12–15, 1.5-m^2 temporary exclosures (moved each year a random distance and cardinal direction from established transects prior to the grazing season) for each grazing intensity. Within each temporary exclosure, biomass was hand-clipped to ground level from one 0.10-m^2 (SGS) or 0.18-m^2 (NMP) quadrat in late July or early August each year from 2003 to 2013. Milchunas and Lauenroth (1992) showed that estimates of ANPP based on this method provided a close approximation of ANPP measured via ^{14}C turnover. Although our method of estimating ANPP does not account for potential compensatory regrowth of grasses within a growing season,

it does account for the cumulative effects of grazing on plant productivity over time scales longer than 1 yr. We note that analyses of seasonal growth patterns of grazed vegetation in SGS indicate limited potential for within-season compensatory growth (Milchunas et al. 2008). Total current year biomass (standing dead biomass from prior year was excluded) was separated into five plant functional groups: perennial C_3 cool-season graminoids, perennial C_4 warm-season grasses, annual grasses, forbs, and sub-shrubs. Biomass was dried at 60°C to constant mass.

Statistical analyses

We used linear mixed models to evaluate the effects of grassland ecosystem, grazing intensity, and both spring and annual precipitation on ANPP at the community level and by two key functional groups (C_4 grasses and C_3 graminoids). Fixed effects included grassland (SGS or NMP), grazing intensity (stocking rate was included as a continuous variable either in a linear or quadratic form, allowing us to test a linear or nonlinear effect of grazing intensity on any of the response variables), precipitation, and all two- and three-way interactions. For precipitation, we compared models that included either annual precipitation or spring precipitation (April–June). In all cases, spring precipitation performed better (higher R^2) than annual precipitation, therefore we only discuss these models. We included pasture ($n = 8$; one pasture for each grazing intensity at each grassland) as a random factor and used a compound symmetry covariance structure to address the non-independence of repeated measurements within the same pasture. Since ANPP and functional groups biomass did not have a normal distribution, we square-root-transformed values before analysis.

Precipitation-use efficiency was estimated as the ratio between annual ANPP and spring precipitation for each grazing intensity level and grassland for each year. We analyzed the influence of grassland and grazing intensity on precipitation-use efficiency using linear mixed models (random effects and covariance structures as described previously). The models included grassland, grazing intensity, and their interactions as fixed effects.

Precipitation marginal response was estimated by determining the slope of a linear regression between untransformed total ANPP or functional group (C_3 graminoids or C_4 grasses) and ANPP and spring precipitation for each grazing intensity level and grassland ($n = 8$). As a result, we had a parameter estimator that we used to test the effect of grazing intensity on total, C_3 graminoid, or C_4 grass precipitation marginal response for each grassland. To accomplish this, we used ANOVAs where the dependent variable was precipitation marginal response (either at the community level or by functional group) and the fixed factors were grassland, grazing intensity, and their interaction.

Finally, we analyzed the effect of functional group abundance on ANPP response to precipitation by means of linear regression. The dependent variables were both precipitation-use efficiency and precipitation marginal response of each grassland and grazing treatment, and the independent variables were the relative abundance of either C_3 gramioids or C_4 grass biomass. All analyses were conducted in JMP (version 10.0.0, SAS Institute, Cary, North Carolina, USA). Results are reported as means ± 95% confidence interval (CI).

TABLE 1. Linear mixed model results.

Fixed factors, by response variable	Fixed factor F ratio (num df:den df)	P
Aboveground net primary productivity (ANPP)		
G	**28.1 (1:4)**	**0.0060**
GI	**142.3 (1:4)**	**0.0211**
Spring precipitation	**18.4 (1:75)**	**<0.0001**
G × GI	1.1 (1:4)	0.3420
G × Spring precipitation	0.08 (1:75)	0.7726
GI × Spring precipitation	0.34 (1:75)	0.5606
G × GI × Spring precipitation	1.27 (1:75)	0.2634
C_4-biomass		
G	**79.7 (1:4)**	**0.0009**
GI	**10.1 (1:4)**	**0.0314**
Spring precipitation	**31.5 (1:75)**	**<0.0001**
G × GI	0.22 (1:4)	0.6653
G × Spring precipitation	**4.7 (1:75)**	**0.0336**
GI × Spring precipitation	1.78 (1:75)	0.1852
G × GI × Spring precipitation	0.20 (1:75)	0.6510
C_3-biomass		
G	**88.3 (1:4)**	**0.0007**
GI	**35.4 (1:4)**	**0.0037**
Spring precipitation	**37.9 (1:75)**	**<0.0001**
G × GI	5.9 (1:4)	0.0713
G × Spring precipitation	**11.3 (1:75)**	**0.0012**
GI × Spring precipitation	**11.7 (1:75)**	**0.0010**
G × GI × Spring precipitation	**8.8 (1:75)**	**0.0129**
Spring precipitation-use efficiency(PUE)		
G	**28.2 (1:4)**	**0.0060**
GI	**14.1 (1:4)**	**0.0152**
G × GI	1.94 (1:4)	0.2364
Spring C_4 PUE		
G	**109.2 (1:4)**	**0.0005**
GI	**10.8 (1:4)**	**0.0263**
G × GI	0.49 (1:4)	0.5184
Spring C_3 PUE		
G	**98.7 (1:4)**	**0.0006**
GI	**39.4 (1:4)**	**0.0030**
G × GI	6.03 (1:4)	0.0684

Notes: Fixed factors include grassland (G), grazing intensity (GI), and precipitation-use efficiency (PUE). Statistically significant factors ($P < 0.05$) are bolded.

RESULTS

Grazing intensity influence on ANPP and spring precipitation-use efficiency

Both ANPP and spring precipitation-use efficiency were 25% greater in NMP (ANPP: 1471 ± 211 kg/ha; precipitation-use efficiency: 10.7 ± 1.2 kg·mm^{-1}·ha^{-1}) compared to SGS (ANPP: 1179 ± 205 kg/ha; precipitation-use efficiency: 8.6 ± 0.9 kg·mm^{-1}·ha^{-1}; Table 1, Fig. 2A, B) even though observed spring precipitation in NMP was only 12% higher than SGS. Within each grassland, both ANPP and spring precipitation-use efficiency declined linearly with increasing grazing intensity

(Table 1; Fig. 2A, B). For SGS, doubling of grazing intensity from light (9.3 AUD/ha) to heavy (18.6 AUD/ha) reduced ANPP and precipitation-use efficiency by 24%. Thus, for each unit of grazing intensity increase in SGS, ANPP is reduced by 32 kg and precipitation-use efficiency is lowered by 0.18 kg/mm. For NMP, a 175% increase in grazing intensity from light (15.7 AUD/ha) to heavy (43.4 AUD/ha) reduced ANPP and spring precipitation-use efficiency by 33%. This represented a 20-kg reduction of ANPP or a 0.15 kg/mm reduction of precipitation-use efficiency for every unit increase of grazing intensity. Across grasslands, total ANPP increased significantly with increasing spring precipitation (Table 1, Fig. 3A, D). Relationships among
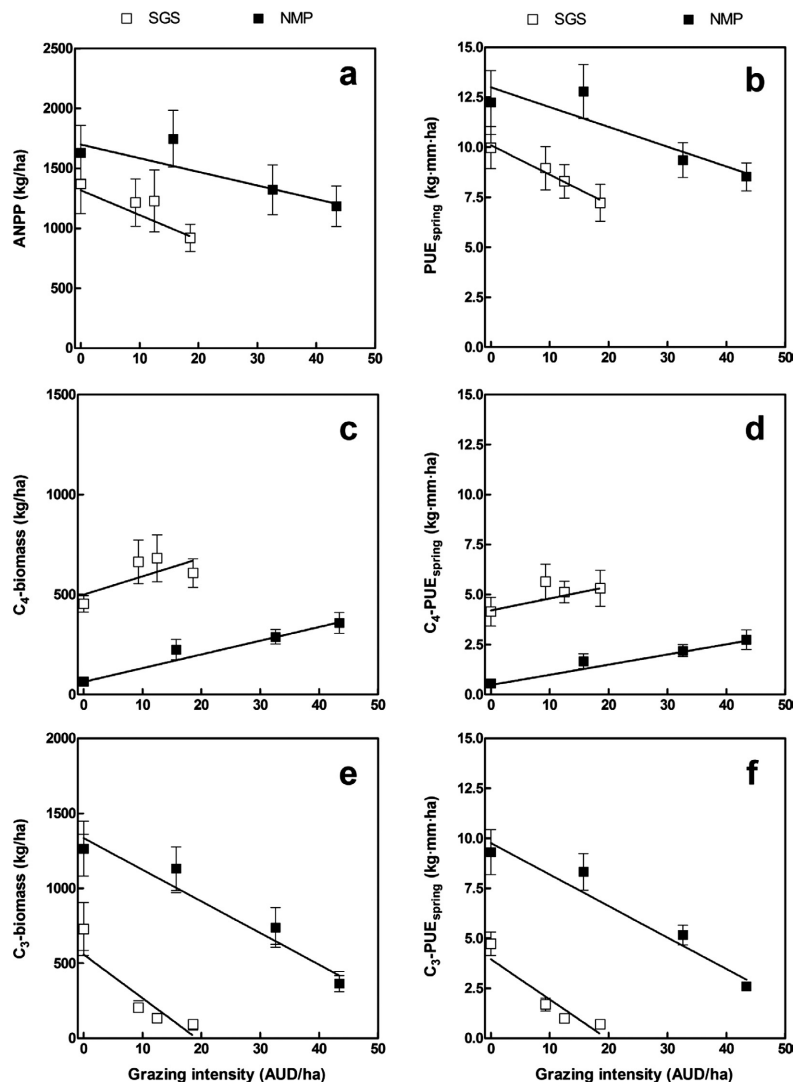

FIG. 2. Relationships between (a) aboveground net primary production (ANPP), (b) precipitation-use efficiency (PUE$_{spr}$, ratio between ANPP and spring precipitation), (c) C$_4$ grass biomass, (d), C$_4$-PUE$_{spr}$ (ratio between C$_4$ grass biomass and spring precipitation), (e) C$_3$ graminoid biomass, and (f) C$_3$-PUE (ratio between C$_3$ graminoid biomass and spring precipitation) relative to grazing intensity (animal unit days, AUD/ha) for SGS and NMP. Points are mean values and error bars represent the 95% confidence intervals (CI). Lines represent the fitted values from linear mixed models.
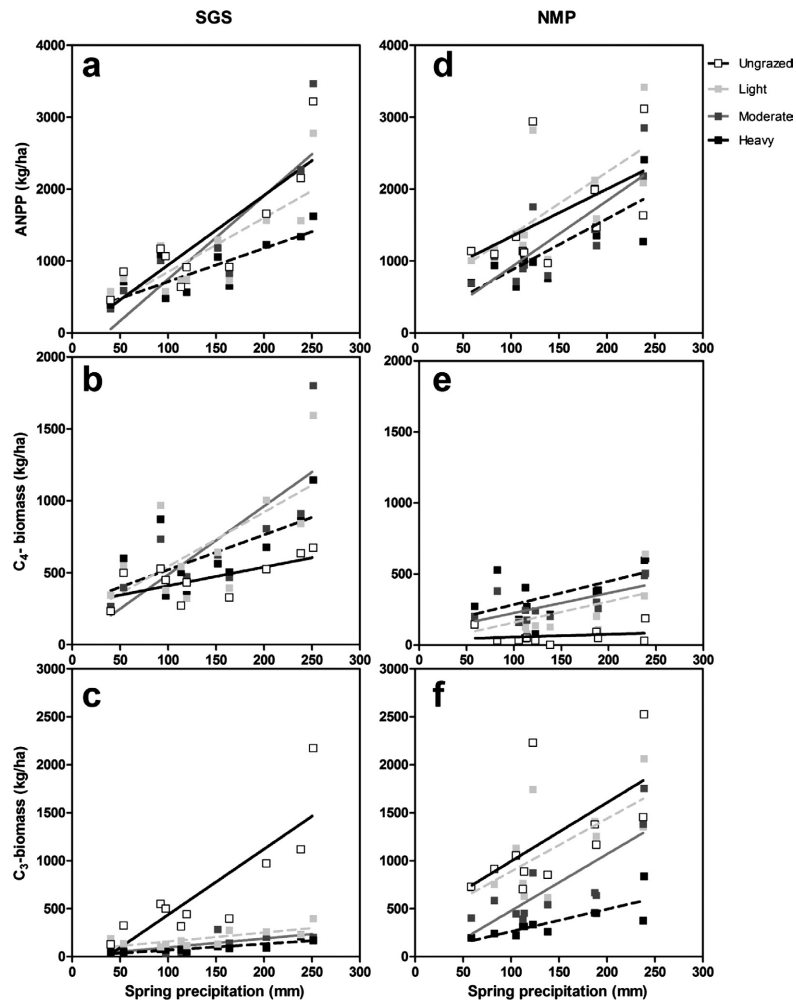
FIG. 3. Temporal relationships between ANPP, C_4 grass biomass, and C_3 graminoid biomass, and spring precipitation (mm, sum of April–June). Points are raw data and lines show the linear regression between ANPP and spring precipitation for each grazing intensity level and grassland (same as in Fig. 1).

ANPP, grazing intensity, and spring precipitation did not vary significantly by grassland, and grazing intensity did not significantly affect the relationship between ANPP and spring precipitation (all interactions nonsignificant, Table 1).

At the functional group level, C_4 grass biomass and its precipitation-use efficiency were 2.6- and 2.8-fold greater in SGS (C_{4mass}, 605 ± 91 kg/ha; precipitation-use efficiency, 5.1 ± 0.7 $kg \cdot mm^{-1} \cdot ha^{-1}$) than NMP ($C_{4mass}$, 234 ± 50 kg/ha; precipitation-use efficiency, 1.8 ± 0.4 $kg \cdot mm^{-1} \cdot ha^{-1}$) respectively (Table 1, Fig. 2C,D). Moreover, both C_4 biomass and C_4-precipitation-use efficiency increased with increasing grazing intensity at both grasslands (Table 1; Fig. 2C,D). For SGS, the raw data show a potential plateau that was not captured by the statistical models; there was a large difference in C_4 biomass between no versus light grazing, but doubling of grazing intensity from light to heavy resulted in minimal change in C_4

biomass (Fig. 2C). Similarly, the doubling of grazing intensity from light to heavy only increased C_4-precipitation-use efficiency by 6% (Fig. 2D). In contrast, for NMP, a 175% increase in grazing intensity from light to heavy increased C_4 biomass by 37% and precipitation-use efficiency by 39% (Fig. 2C, D). This represented a 5-kg or a 0.04 kg/mm increase of C_4 biomass and precipitation-use efficiency for every unit increase of grazing intensity in NMP. C_4 biomass responded positively to spring precipitation, and this response was significantly stronger at SGS than NMP (Table 1; Fig. 3B, E).

For C_3 graminoids, biomass and C_3-precipitation-use efficiency were 3.1- and 3.2-fold greater in NMP (C_{3mass}, 874 ± 167 kg/ha; precipitation-use efficiency, 6.3 ± 1.1 $kg \cdot mm^{-1} \cdot ha^{-1}$; mean of 11 yr) than SGS (C_{3mass}, 279 ± 108 kg/ha; precipitation use-efficiency, 2.0 ± 0.6 $kg \cdot mm^{-1} \cdot ha^{-1}$; mean of 11 yr), respectively. Across grasslands, C_3 biomass and C_3-precipitation-use

efficiency both decreased substantially with increasing grazing intensity (Table 1; Fig. 2E, F). For SGS, the largest decline in C_3 biomass was from no to light grazing (Fig. 2E). Doubling of grazing intensity from light to heavy in SGS reduced C_3 biomass by 53% and reduced precipitation-use efficiency by 58%. This represented a 12-kg and 0.10 kg/mm reduction of C_3 biomass and precipitation-use efficiency, respectively, for every unit increase of grazing intensity in SGS. For NMP, the changes in C_3 biomass and precipitation-use efficiency exhibited a linear decline from no to heavy grazing intensity. A 175% increase in grazing intensity from light to heavy reduced C_3 biomass by 67% and precipitation-use efficiency by 69%. This represented a 27-kg and a 0.2 kg/mm reduction of C_3 biomass and precipitation-use efficiency for every unit increase of grazing intensity. Relationships between C_3 biomass and spring precipitation were sensitive to both grassland and grazing intensity (significant three-way interaction, Table 1). C_3 biomass increased with increasing precipitation at both grasslands, but increases were much weaker in grazed treatments at SGS (Table 1, Fig. 3C, F). Thus, with an increase in grazing intensity from light to heavy, the decline in C_3 biomass and C_3-precipitation-use efficiency was greater in NMP compared to SGS.

Grazing intensity influence on spring precipitation marginal response

The spring precipitation marginal response was similar between the two grasslands (NMP, 8.0 ± 1.2 kg·mm^{-1}·ha^{-1}; SGS, 8.4 ± 2.9 kg·mm^{-1}·ha^{-1}). We did not observe a significant effect of grazing intensity on precipitation marginal response of the total plant community (ANOVA: R^2: 0.25; P was nonsignificant). For C_4 grasses, precipitation marginal response was 2.6-fold greater in SGS (3.0 ± 1.5 kg·mm^{-1}·ha^{-1}) compared to NMP (1.2 ± 0.6 kg·mm^{-1}·ha^{-1}), indicating the SGS has the capacity to produce more C_4 biomass (and correspondingly less of other functional groups) per unit precipitation received (ANOVA: grassland effect $F = 0.36$; df = 1 $P = 0.07$). Grazing intensity did not significantly affect precipitation marginal response for C_4 grasses at either grassland (ANOVA: $F = 6.1$; df = 1; $P =$ nonsignificant).

For C_3 graminoids, precipitation marginal response was 2.1-fold greater in NMP (5.0 ± 1.7 kg·mm^{-1}·ha^{-1}) compared to SGS (2.3 ± 2.9 kg·mm^{-1}·ha^{-1}; ANOVA: $F = 14.5$; df = 1; $P = 0.02$). In addition, increased grazing intensity reduced C_3 graminoid precipitation marginal response (Fig. 4; ANOVA $F = 10.5$; df = 1; $P = 0.03$). Moreover, and similar to C_3-precipitation-use efficiency (Table 1), there was a marginal effect of the interaction between grassland and grazing intensity (ANOVA: $F = 4.6$; df = 1; $P = 0.09$). This suggests that the rate of change in precipitation marginal response with increasing grazing intensity differed among
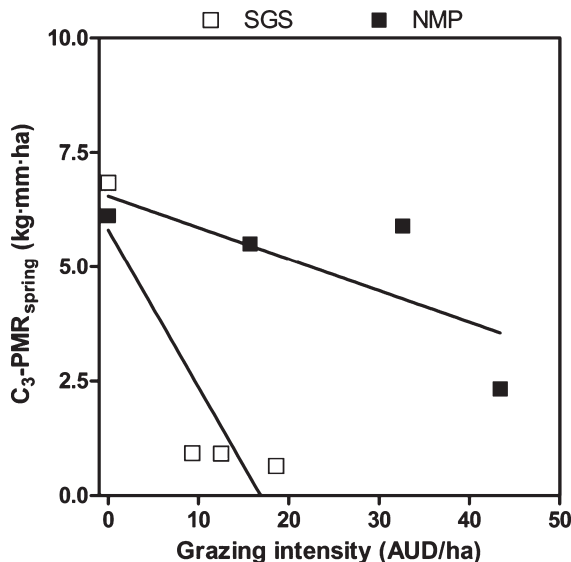

FIG. 4. Relationship between C_3-PMR$_{spr}$ (slope of a linear regression between C_3 graminoid biomass and spring precipitation) relative to grazing intensity (AUD/ha) for SGS and NMP. Lines represent the fitted values through ANOVA.

grasslands. For SGS, precipitation marginal response dropped by more than 6.01 kg/mm between the ungrazed and lightly grazed treatments, but then declined by only 0.03 kg/mm per unit of grazing intensity from light to heavy. For NMP, precipitation marginal response was similar across ungrazed, lightly grazed, and moderately grazed treatments, but then declined by 3.51 kg/mm when grazing intensity increased from moderate to heavy.

Changes in spring precipitation-use efficiency with shifts in functional group relative abundance

Increases in the relative abundance of C_3 graminoids versus C_4 grasses had a clear impact on precipitation-use efficiency (Fig. 5), but there was not a statistical association with precipitation marginal response. We observed a positive association between precipitation-use efficiency and the relative abundance of C_3 graminoids (Fig. 5A; PUE$_{spr}$ = 6.9 + 6.8 C_{3abun}; R^2 = 0.80; P = 0.0025), and a negative association with C_4 grasses (Fig. 5B; PUE$_{spr}$ = 12.3–7.0 C_{4abun}; R^2 = 0.73; P = 0.0065). Thus, as C_4 species replace C_3 species, community-level precipitation-use efficiency declines.

Aboveground carbon allocation scenarios for SGS and NMP under different grazing intensity levels

Extrapolation of our results to the entire two grasslands has major implications for regional aboveground carbon allocation (Table 2). For example in SGS, increasing from recommended moderate stocking rates (12.5 AUD/ha in this study) to heavy stocking for
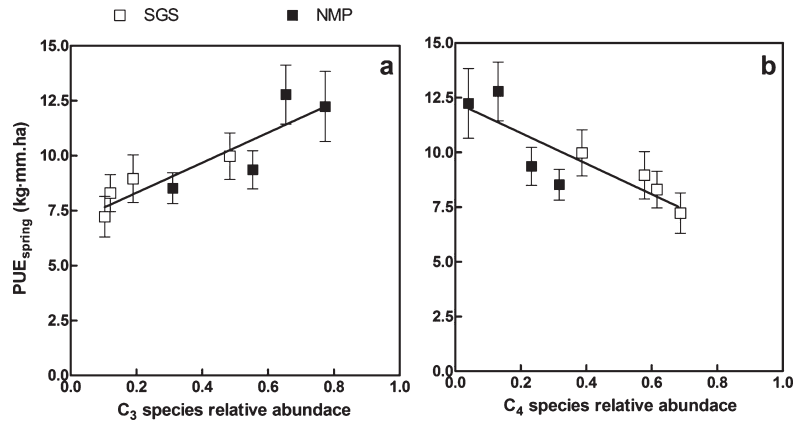
□ SGS ■ NMP

FIG. 5. Relationships between PUE_{spr} and functional groups relative abundance for SGS and NMP. Error bars represent the 95% CI. The lines represent the fitted model by means of linear regression.

greater secondary production and economic returns per ha over the entire 20 million ha of this grassland translates to a 6.2 Mg decrease in ANPP, and a consequent 2.9 Mt reduction in aboveground carbon storage (Table 2). Conversion from moderate stocking to light stocking in SGS, however, would not impact aboveground carbon stocks (Table 2). Increasing stocking rate in NMP from the recommended rate of 32.6 AUD/ha (moderate in this study) to heavy would decrease ANPP by 4.1 Mt annually, assuming a change in management across the entire 30 million ha of NMP (Table 2). This would represent a reduction of 1.9 Mt in aboveground carbon storage. Changing grazing management in NMP from moderate to light grazing across the entire grassland would yield 12.7 Mt additional ANPP, or 6.0 Mt of aboveground carbon stock. Collectively, across these two grasslands, there exists potential to greatly alter regional ANPP and aboveground carbon storage.

DISCUSSION

We quantified relationships between grazing intensity, variable precipitation, shifts in plant functional groups, and ANPP for the two largest native remaining grasslands in the North American Great Plains, both of which are highly grazing-resistant grasslands relative to other grasslands worldwide (Milchunas et al. 1988, 2008). Increasing grazing intensity by twofold in SGS and 1.75-fold in NMP reduced ANPP by 24% and 32% respectively. This key finding emphasizes two points: (1) relationships between precipitation and ANPP are sensitive to grazing intensity; and (2) the magnitude of grazing intensity effects on these relationships is site dependent. Both of these implications have critical consequences for understanding and predicting primary and secondary production across the world's semiarid rangelands, especially in the context of climate change and associated increases in weather variability.

TABLE 2. Aboveground carbon allocation scenarios under different grazing intensity levels for the short-grass steppe (SGS) and the northern mixed-grass prairie (NMP).

Grazing intensity, by grassland type (AUD/ha)	ANPP (kg/ha)	Aboveground total biomass (Mg)	Aboveground total carbon (Mg)
SGS			
Ungrazed (0)	1370	27.40	12.88
Light (9.3)	1216	24.32	11.43
Moderate (12.5)	1228	24.56	11.54
Heavy (18.6)	920	18.40	8.64
NMP			
Ungrazed (0)	1631	48.93	22.99
Light (15.7)	1746	52.40	24.63
Moderate (32.6)	1322	39.66	18.64
Heavy (43.4)	1185	35.56	16.71

Notes: Grazing intensity is shown in animal unit days (AUD) per ha. Semiarid grassland areas were 20 million ha for SGS, and 30 million ha for NMP (Holechek et al. 1998). We assumed that each total region is grazed under one of the four described long-term grazing intensities. ANPP values represented the mean values of our research sites and grazing intensity treatments. A 47% carbon content was assumed for ANPP conversion (Schlesinger 1991).

In both systems, grazing-induced reductions in C_3 graminoid productivity were accompanied by replacement of C_3 graminoids by less-productive C_4 grasses and an associated reduction in precipitation-use efficiency. The negative effect of grazing intensity on precipitation-use efficiency concurs with prior findings that increased disturbance leads to greater ecosystem water loss, and consequently a reduction in precipitation-use efficiency (Le Houerou 1984, Prince et al. 1998). However, the magnitude of the decline in precipitation-use efficiency with increased grazing intensity can vary substantially among rangeland ecosystems, and may be related to the kinds of plant functional groups that persist under heavy grazing. Modeling studies from semiarid rangelands in Patagonia (South America) with similar MAP as the North American grasslands in the current study showed a sixfold reduction in precipitation-use efficiency from non-grazed to heavily grazed areas (Paruelo et al. 2008), which is notably greater than the 1.6- or 1.4-fold reduction in precipitation-use efficiency we documented here for either NMP or SGS. The larger reduction in precipitation-use efficiency associated with increasing grazing intensity in Patagonia is attributable to substantial increases in bare soil and shrubs (Paruelo et al. 2008), whereas in North American grasslands, increased grazing intensity elicits only modest increases in bare soil (Augustine et al. 2012) and partially compensatory increases in production and cover of grazing-resistant C_4 shortgrasses (Fig. 2).

Our analyses identified key differences between SGS and NMP in how grazing intensity affects the capacity for C_3 and C_4 graminoids to respond to temporal fluctuations in precipitation. In SGS, we found a dramatic decline in precipitation marginal response of C_3 graminoids with the change from no grazing to light grazing (Fig. 3C). This indicates that in the presence of even low levels of grazing intensity in the SGS, the capacity for C_3 grasses to respond to variable precipitation is impaired, which could be explained by a combination of reduced belowground storage by C_3 graminoids and grazing facilitating increased competitive ability of C_4 grasses. However, as grazing increased from light to moderate to heavy grazing, the capacity of C_3 graminoids to respond to variable rainfall did not change (Fig. 3C). Thus, reducing grazing intensity from heavy to light, which has major economic costs for producers (Hart and Ashby 1998), does not increase capacity for the C_3 component of the vegetation to respond to variable precipitation. In contrast, for the NMP we found the capacity for C_3 graminoids to respond to variable precipitation was similar under no, light, and moderate grazing intensities, but then declined substantially under heavy grazing (Fig. 3F). Thus, changing management from heavy to moderate grazing could have substantially greater benefits in terms of C_3 graminoid response to variable precipitation in NMP compared to SGS.

Although precipitation-use efficiency and precipitation marginal response are both expressed in the same units ($kg \cdot mm^{-1} \cdot ha^{-1}$), and have been used synonymously in some studies (Paruelo et al. 1999, Lauenroth et al. 2000, Huxman et al. 2004), precipitation-use efficiency expresses the amount of ANPP produced by a unit of precipitation, while precipitation marginal response represents the change in ANPP per unit change in precipitation (Verón et al. 2005). Across broad environmental gradients (e.g., Sala et al. 1988, Knapp and Smith 2001, Bai et al. 2008), precipitation-use efficiency increases as mean annual precipitation increases (Bai et al. 2008), but precipitation marginal response shows an optimal response, with a maximum at 600 mm of MAP (Paruelo et al. 1999) or no pattern at all (Lauenroth et al. 2000). We found that precipitation marginal response was similar between SGS and NMP, and consistent across grazing intensities. However, at the functional group level, C_4 grass precipitation marginal response was higher in SGS than NMP; C_3 graminoid precipitation marginal response had the opposite pattern and was affected by grazing intensity. These patterns are in contrast to those reported from Patagonian rangelands, where grazing intensity reduced precipitation marginal response due to increased shrub abundance (which lack the capacity to respond rapidly to precipitation variability) and reductions in C_3 grasses (Verón and Paruelo 2010, Gaitán et al. 2014). These differences among ecosystems with similar mean annual precipitation may be attributed to both the direct, within-year effects of seasonal distribution of precipitation (Hsu et al. 2012), as well as long-term shifts in the relative abundance of C_3 versus C_4 graminoids (Epstein et al. 2002).

Grazing-induced changes to plant communities have implications for how semiarid grasslands may respond to rising atmospheric [CO_2] and temperatures (Morgan et al. 2007, 2011, Reyes-Fox et al. 2014), as well as altered precipitation event sizes and seasonal distribution that are anticipated with climate change (Heisler-White et al. 2008, Wilcox et al. 2014). In particular, experimental manipulations of atmospheric [CO_2] and temperature demonstrate differential responses between C_3 and C_4 species (Morgan et al. 2011). In ungrazed SGS, increasing precipitation event sizes, without changes in the annual value, positively affected ANPP (Heisler-White et al. 2008). However, manipulation of precipitation did not affect ANPP in the NMP (Wilcox et al. 2014). Our results highlight that studies conducted in the absence of grazing cannot be extrapolated to grazed communities without careful consideration of how grazing influences the relative abundance of C_3 and C_4 functional groups, as well as responses of these functional groups to atmospheric [CO_2] and precipitation variability. In this sense, the use of the long-term grazing treatments, where there are substantial shifts in community compositional structure, could provide the experimental framework for precipitation manipulation.

Overall, these results provides insights for conversion in land management from moderate stocking to light stocking for possible provisioning of a greater suite of

ecosystem services (including carbon sequestration) and enhanced vegetation heterogeneity (e.g., Derner et al. 2009, Fuhlendorf et al. 2012). With respect to carbon sequestration, our results suggest that in the SGS moderate grazing (the recommended rate) would sequester the same amount of aboveground carbon as light grazing, without the loss of the economic revenue of beef production. In contrast, reductions from moderate grazing intensity (the recommended rate) to light intensity in the NMP would dramatically increase the amount of aboveground carbon sequestered. Future studies should address the economic tradeoff between increasing carbon sequestration over the loss of the provision of secondary production (livestock gain). Setting a market value based on lost profit could help policy makers establish a price for aboveground carbon sequestration under different grazing intensity scenarios.

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