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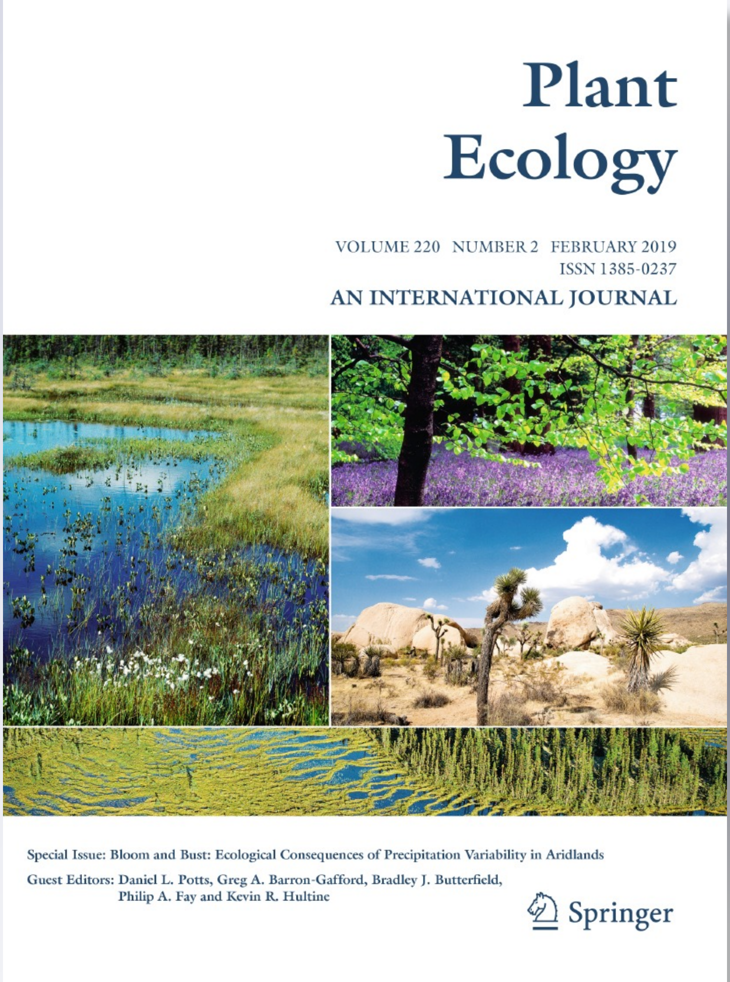

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Drought and small-bodied herbivores modify nutrient cycling in the semi-arid shortgrass steppe

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Abstract Climate change will increase the frequency of droughts over the next century, with severe consequences for ecosystem function in semi-arid grasslands. The shortgrass steppe (SGS) experiences some of the largest interannual variation in precipitation among terrestrial biomes and exhibits extremely high sensitivity to drought. Yet despite decades of research describing the consequences of drought for ecosystem function in the SGS, we currently have little information regarding the impact of drought on bioavailability of important nutrients other than nitrogen, the contribution of herbivores to bioavailable concentrations of these nutrients, and whether drought alters herbivore-derived nutrient cycling. To quantify the impacts of long-term drought and small-bodied herbivores on nutrient cycling and aboveground net primary production (ANPP), we factorially manipulated rainfall and herbivore presence in the SGS of northern Colorado. Specifically, we measured the impacts of drought and herbivores on bioavailability of ten important nutrients: aluminum, calcium, iron, potassium, magnesium, manganese, nitrate, phosphorus, sulfur, and zinc. We then correlated these nutrients with grass production to determine whether reduced plant growth under drought conditions causes a belowground buildup of nutrients. Drought reduced ANPP as expected, and also altered concentrations of many nutrients apart from N, which clustered in their drought response. In contrast, small-bodied herbivores did not affect ANPP or soil N. However, they did contribute to the bioavailable soil concentrations of two important nutrients: PO_4-P and S. Importantly, drought generally did not modify the contribution of herbivores to nutrient cycling, suggesting that herbivores might be a critical component of biogeochemical cycling regardless of precipitation in semi-arid grasslands.

Keywords Biogeochemistry · Ecosystem function · Grasshoppers · Grasslands · Climate change

Introduction

Climate change will increase the frequency, duration, and intensity of droughts over the next century (IPCC 2014), with severe consequences for ecosystem function in arid and semi-arid grasslands. Dry ecosystems, such as the shortgrass steppe (SGS), undergo the largest interannual variation in precipitation among terrestrial biomes and exhibit the highest sensitivity to drought (Huxman et al. 2004a; Knapp et al. 2015b).

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For example, severe drought reduces aboveground net primary production (ANPP) by 50–75% in xeric grasslands (Knapp et al. 2015a), and this collapse of ANPP impacts a number of other important ecosystem functions. Plant nitrogen (N) uptake rates decline during drought as a consequence of lower growth demand, which in turn causes a buildup of bioavailable soil N accessible by plant roots (Evans and Burke 2013). Soil CO_2 flux also generally declines during drought due to reduced soil microbial activity, thereby increasing the pool of belowground soil carbon in the SGS (Huxman et al. 2004b; Munson et al. 2010; Evans and Burke 2013). Low ANPP also prefaces long-term shifts in plant community composition, which persist for several years following severe drought (Rondeau et al. 2018). Yet despite decades of research describing the consequences of drought for ecosystem function in the SGS, several important knowledge gaps remain. We currently have little information regarding (1) the impact of drought on bioavailability of important nutrients other than N, (2) the contribution of herbivores to bioavailable concentrations of these nutrients, and (3) whether drought alters herbivore nutrient cycling in semi-arid grasslands.

Although N has received the most attention as a limiting nutrient in grassland ecosystems, ANPP and ecosystem function depend on several other important, but often overlooked, nutrients (Fay et al. 2015). Phosphorus (P) and potassium (K) can limit ANPP as strongly as N (Fay et al. 2015; Koerner et al. 2016), and both nutrients potentially affect grassland resilience to drought. For example, accumulation of soil P disrupts mycorrhizal-plant mutualisms, thereby weakening plant tolerance of water stress and destabilizing long-term ANPP (Augé 2001; Yang et al. 2014; Shantz et al. 2016). Potassium, on the other hand, can mitigate plant water stress during drought by acting as an antioxidant and facilitating stomatal regulation of water loss (Egilla et al. 2005). The minerals magnesium (Mg), iron (Fe), and zinc (Zn) are all integral components of photosynthesis, enabling capture of light energy and facilitating transport of light energy through the photosystem (Balakrishnan et al. 2000). Soil P and K concentrations decline during drought in forests (Sardans and Peñuelas 2007), and it is likely that nutrient availability in grasslands also depends on soil moisture and ANPP. Thus, drought-induced changes in any number of macro- or micronutrients can potentially impact ecosystem function, but the extents to which drought alters soil concentrations of P, K, or other micronutrients are unknown.

In addition to precipitation, nutrient cycling and ANPP in the SGS might be affected by the presence of herbivores. Herbivores reduce ANPP through direct consumptive effects (Bakker et al. 2006; La Pierre et al. 2015) or stimulate ANPP by converting refractory detritus into labile organic matter and bioavailable soil nutrients (Belovsky and Slade 2000; Nitschke et al. 2015). Unfortunately, herbivore-driven nutrient cycling in grasslands, specifically the contributions of invertebrate and small mammal herbivores, has received relatively little attention. Limited evidence hints that these herbivore groups might contribute substantially to soil nutrient availability. Soil N availability in tallgrass prairies doubles in the presence of large mammal grazers like cattle or bison (Bakker et al. 2009). Since bison biomass density (g m^{-2}) in tallgrass prairies is comparable to that of grasshoppers (Branson et al. 2006), invertebrate herbivores represent a potentially large nutrient cycling pathway via frass deposition. Indeed, insect frass deposition accelerates N cycling by 42–600% in temperate forests (Reynolds et al. 2000; Frost and Hunter 2004) and accounts for over a quarter of N and P soil inputs in tropical forests (Metcalf et al. 2014). In a cold, mixed grass prairie, grasshoppers increased soil N concentrations by ~ 5% (Belovsky and Slade 2000). Many other nutrients [e.g., K, Mg, calcium (Ca)] also positively correlate with grasshopper density, and grasshopper frass contains high concentrations of N, P, and sulfur (S) (Joern et al. 2012; Nitschke et al. 2015). Yet the contribution of insects and small mammals to bioavailable soil nutrients is unknown in grasslands.

Furthermore, herbivore-dependent biogeochemical cycling might vary with abiotic conditions, such as drought (Irisarri et al. 2016). Rain limitation can alter the nutritional content of plants by decreasing plant water content, thereby increasing leaf toughness and reducing plant palatability (Avolio and Smith 2013; Koerner et al. 2014). Lower consumption rates result in lower frass and fecal production rates by insects and small mammals (Lemoine and Shantz 2016), such that herbivore contributions to biogeochemical cycling could be reduced under drought. Drought can also reduce decomposition and leaching rates of insect frass into soils. Indeed, Frost and Hunter (2004) reported that insect frass deposition in an oak forest must be temporally matched with precipitation events for herbivore nutrients to significantly contribute to soil nutrient pools. Given that soil biogeochemcial processes in the SGS largely depend on rainfall (Evans and Burke 2013), it is likely that drought mediates herbivore contributions to nutrient cycling in semi-arid grasslands. However, no study to date has manipulated both herbivory and rainfall to test how drought influences herbivore nutrient cycling.

Here, we factorially crossed growing season drought with herbivore removals to quantitate the impacts of long-term drought and small-bodied herbivores on nutrient cycling and ANPP in the SGS. We tested three hypotheses: (1) Drought should increase the pool of bioavailable nutrients related to plant growth (N, P, and K) and photosynthesis (Fe, Mn, and Zn) because of lower ANPP and nutrient uptake rates under water limitation; (2) herbivore presence will increase soil bioavailability of macronutrients, like N and P, but would have little effect on minerals that exhibit little herbivore turnover, like Mn and Fe; and (3) drought will reduce the importance of herbivore nutrient cycling because herbivore contributions to soil nutrient pools will be relatively small and therefore decrease in importance as baseline nutrient levels increase.

Methods

Study site

Our study took place in the Central Plains Experimental Range (CPER; 40.8°N, − 104.7°W), an experimental station situated in the SGS of northern Colorado. The SGS is a semi-arid grassland with low annual rainfall (mean annual precipitation: 375 mm; mean growing season precipitation: 293 mm) and primary production (mean annual ANPP: 88.9 g m^{-2}) (Knapp et al. 2015a). Up to 90% of ANPP in the Colorado SGS derives from the perennial C_4 grass *Bouteloua gracilis* (Oesterheld et al. 2001), although the graminoids *B. dactyloides* (C_4), *Carex* spp. (C_3), *Elymus elymoides* (C_3), *Pascopyrum smithii* (C_3), and *Vulpia octoflora* (C_3), the forb *Sphaeralcea coccinea,* and the shrubs *Artemisia frigida* and *Gutierrezia sarothrae* also contribute substantially to ANPP.

Our study site at the CPER has not been grazed by cattle for over 15 years, and the primary herbivores in this pasture are invertebrates and small mammals. Grasshoppers (Orthoptera: Acrididae) are the dominant invertebrate herbivore by biomass in the SGS and consist of a diverse assemblage of species. *Arphia pseudonietana*, *Eritettix simplex*, *Melanoplus sanguinipes*, and *Opeia obscura* are the most abundant early- and late-season orthopterans in northern Colorado along the Front Range, occurring in densities as high as 10–20 individuals per 100 m^2 during non-outbreak years (Welch et al. 1991; Craig et al. 1999). Small mammal herbivores are a combination of lagomorphs (*Lepus californicus*, *Sylvilagus audubonii*) and rodents (*Dipodomys ordii*, *Onchyomys leucogaster*) (Grant et al. 1982), although lagomorph feces were the most common indication of small mammal herbivory in the experimental plots. Pronghorn antelope (*Antilocapra americana*) are common in the SGS but were excluded from both control and treatment plots by cages.

Drought treatment

To simulate drought, we took advantage of a long-term rainfall exclusion experiment ongoing in the CPER since 2014. In 2014, twenty 6 × 6 m experimental plots were arrayed into ten blocks. Within each block, the two plots were randomly assigned to either 'Ambient' or 'Drought' treatments ($n = 10$ per precipitation treatment). The 'Ambient' plot was unmanipulated and received 100% of growing season precipitation each year. Growing season precipitation was reduced by 66% in the 'Drought' plots with a passive rainout shelter design (Yahdjian and Sala 2002). Each passive rainout shelter consisted of a 6 × 6 m cold frame greenhouse structure enclosing a 5 × 5 m measurement plot and covered by a roof made of 60 3.7 m × 15 cm clear polycarbonate strips. The plastic strips were evenly spaced across the roof to cover 66% of shelter area and angled to deliver intercepted rainfall into a gutters at the base of each side of the shelter roof. Gutters transported all intercepted rainfall several meters away from each plot via corrugated plastic tubes. All plots, including 'Ambient' plots, were trenched to a depth of 0.5 m and lined with plastic to prevent subsurface groundwater movement into the plot. Every year (2014–2017), we installed shelter roofs in May prior to green up and removed the roofs in September at the end of the growing season. This design was successful in reducing annual precipitation by ∼ 50% and volumetric soil moisture by ~ 10% within the 'Drought' plots compared to 'Ambient' plots (Lemoine et al. in prep). Removing 50% of rainfall constitutes an extreme drought in the SGS (< 1% percentile).

In both 'Ambient' and 'Drought' plots, a 0.5 m buffer around the edge of the plot minimized rainfall blow-in into the central 5 × 5 m measurement plot. The measurement plot was further subdivided into four 2 × 2 m subplots bisected by 1 × 1 m buffer strips. Three randomly chosen subplots were designated sampling units in a different project, so herbivore manipulations in this study occurred within the remaining 2 × 2 m subplot.

Herbivore exclosures

We tested our hypotheses regarding the effects of herbivores on ecosystem function by comparing plots exposed to herbivores to plots protected from herbivores (Lemoine et al. 2017b). We excluded herbivores using cages constructed of a 0.5 × 0.5 × 0.5 m PVC frame. The frame was anchored in place with rebar spikes inside each hollow PVC leg and covered with 14 mm mesh aluminum screen. The window screen had a 20-cm skirt fastened tightly to the ground using common garden staples to prevent invertebrate herbivore immigration into cages. In May 2017, we haphazardly placed two cages in each 2 × 2 m subplot ($n = 10$ per drought × herbivore treatment) while attempting to minimize differences in plant species compositions between cages and avoiding cacti where possible. For each pair of cages, one cage was randomly designated the 'No Herbivores' treatment, and remained fully enclosed. The 'Herbivores' cage had large holes cut in the window screen to allow herbivore movement into the cage, while allowing the screen to mimic the reduction in light imposed by the 'No Herbivores' treatment (La Pierre and Smith 2016). Since both herbivore treatments were present in every subplot, this design was a split-plot design with precipitation (ambient vs. drought) as the whole-plot factor and herbivore presence (No herbivores vs. herbivores) as the subplot factor.

Every week throughout the growing season, we checked cages for damage and repaired window screen when needed. We also removed any invertebrates found within the 'No Herbivores' cages. However, only one grasshopper was ever found within an exclusion cage throughout the course of this experiment. Furthermore, small-bodied herbivores regularly occurred within the 'Herbivores' cages, as evidenced by small mammal dung (usually lagomorphs) regularly observed within the open cages.

Bioavailable nutrients

We quantified soil nutrient bioavailability in each drought × herbivore treatment using Plant Root Simulator (PRS) probes (Western Ag, Saskatoon, Saskatchewan, CA) (Evans and Burke 2013). PRS probes consist of a pair of plastic stakes (15 × 2 × 0.5 cm), each with a 17.5 cm^2 charged ion membrane. The ionic membrane of one stake in the pair is made of a general purpose R-NH_4^+ cation base that absorbs anions. The other stake in the pair has a general purpose R-SO_3^- anion base to absorb cations. We buried two pairs of PRS probes within each cage in early August prior to the period of maximum insect activity (T. Joern—pers. comm.). Pairs of probes were buried at opposite corners of the cage by making a small slit in the soil surface with a garden knife. Probes were then inserted into each slit at a 30°–35° angle and gently driven into the ground using a rubber mallet. Loose soil was back-filled into the slit to maximize contact between the ion membrane and the soil. After 30 days, we removed probes from the cages and pooled the two probe pairs within a single cage for nutrient analysis. Nutrient analyses, conducted by Western Ag, provided uptake rates ($\mu\text{g}\ 10\ \text{cm}^{-2}\ \text{day}^{-1}$) for aluminum (Al), calcium (Ca), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), nitrate-derived nitrogen (NO_3-N), phosphate-bound phosphorus (PO_4-P), sulfur (S), and zinc (Zn).

ANPP sampling

We estimated annual ANPP in each plot via destructive biomass harvest at the end of the growing season. In late August, cages were removed, and a 20 × 50 cm (0.1 m^2) metal frame was placed within the footprint of each cage. We harvested all biomass within the metal frame, sorted it by grass, forb, and woody functional types, and dried it at 60 °C for 48 h. Because the site is not annually burned, some harvested biomass from each cage was dead production from previous years. To avoid measuring past production, we removed any stems, shoots, or leaves with > 50% dead tissue. We weighed the remaining biomass to the nearest 0.1 g and calculated ANPP as g m^{-2} for each functional type.

Statistical analyses

We tested our hypothesis that drought should modify herbivore contributions to nutrient cycling using a split-plot MANOVA (Lemoine et al. 2017b). The MANOVA included all ten nutrients as a multivariate response matrix. The predictor variables were herbivore treatment and the drought × herbivore interaction at the subplot level, with the main effect of drought estimated at the whole-plot level. We used a similar split-plot ANOVA model to analyze the effects of drought and herbivore presence on forb and grass ANPP. Forb and grass ANPP were analyzed separately because six plots were missing forb data ($n = 34$), and a multivariate analysis would have required removing grass ANPP observations from those plots. Since grass and forb ANPP were only weakly correlated ($r = -0.16$), we chose to use a univariate model to incorporate all available data. Forb data were log-transform prior to analysis to mitigate heteroscedasticity.

Many nutrient uptake rates were correlated, and it appeared that nutrients clustered by their response to drought. To better visualize the correlations among nutrients, we used principal component analysis to the reduced variation in soil nutrient bioavailability to two orthogonal axes. We then constructed a distance biplot of the first two principal component axes, overlaid with vectors of nutrient uptake rates. Distance biplots preserve the relationship among plots (and thus accurately representing separation among treatments), while slightly distorting the correlation among nutrient uptake rates. However, nutrient uptake rates clustered strongly in this case, such that any distortion in correlations among nutrient bioavailability had little impact on the results.

We hypothesized that soil nutrient bioavailability would be negatively correlated with ANPP. To test this hypothesis, we calculated the partial correlation coefficient between grass ANPP and nutrient uptake rates for all ten nutrients. We used MCMC sampling to generate a posterior distribution from 40,000 samples for the correlation matrix $\boldsymbol{R}$ containing the correlations among all variables. For each posterior sample, we calculated the partial correlation coefficients as:

$$\boldsymbol{P} = \boldsymbol{R}^{-1},$$

$$r_{i,j} = p_{i,j} \Big/ \sqrt{p_{i,i} p_{j,j}},$$

where $r_{i,j}$ is the partial correlation coefficient between the ith and jth variables accounting for all other correlations. For example, $r_{\text{Grass,Al}}$ is the partial correlation between grass ANPP and Al uptake rates, accounting for any correlations between grass ANPP and all other nutrients and Al uptake rates and all other nutrients.

We conducted all ANOVAs and MANOVAs in a Bayesian framework so that we could place weakly informative priors of $N(0,1)$ on all parameters (Lemoine et al. 2016a, b). Weakly informative priors constrain effect sizes to reasonable estimates in the presence of small samples sizes and weak effects, thereby making our tests more conservative but less prone to magnitude errors (Button et al. 2013; Gelman and Carlin 2014; Lemoine et al. 2016). Since all variables were standardized prior to analyses, the $N(0,1)$ prior states that effect sizes should be smaller than one standard deviation of the response unless strongly supported by the data. Such a prior is more conservative, but reduces the probability of Type I errors for underpowered studies. To assess the impact of prior choice on our results, we repeated all analyses with noninformative priors, which yield quantitatively identical results to traditional statistics. Qualitative patterns of results did not depend on prior choice ("Appendix 1").

The correlation among responses and the variances of each response were given uninformative $LKJ(1)$ and $Cauchy(0,\ 25)$ priors, respectively. Models were allowed 10,000 warm-up iterations in four independent MCMC chains. We saved the next 10,000 estimates from each chain for posterior distributions of each parameter (40,000 total samples per parameter). Kernel density plots indicated good convergence among chains. Due to small sample sizes ($n = 10$ per precipitation × herbivore treatment) and our use of weakly informative priors, we consider any effect with $\Pr \geq 0.90$ as marginally significant and $\Pr \geq 0.95$ as statistically significant. A $\Pr = 0.5$ is the lowest value because it indicates that the effect is just as likely to be positive or negative (i.e., centered at 0) (Lemoine and Shantz 2016; Lemoine et al. 2017a, b).

All statistical analyses were conducted in Python v3.6 using *numpy*, *scipy*, and *pandas* modules (Jones

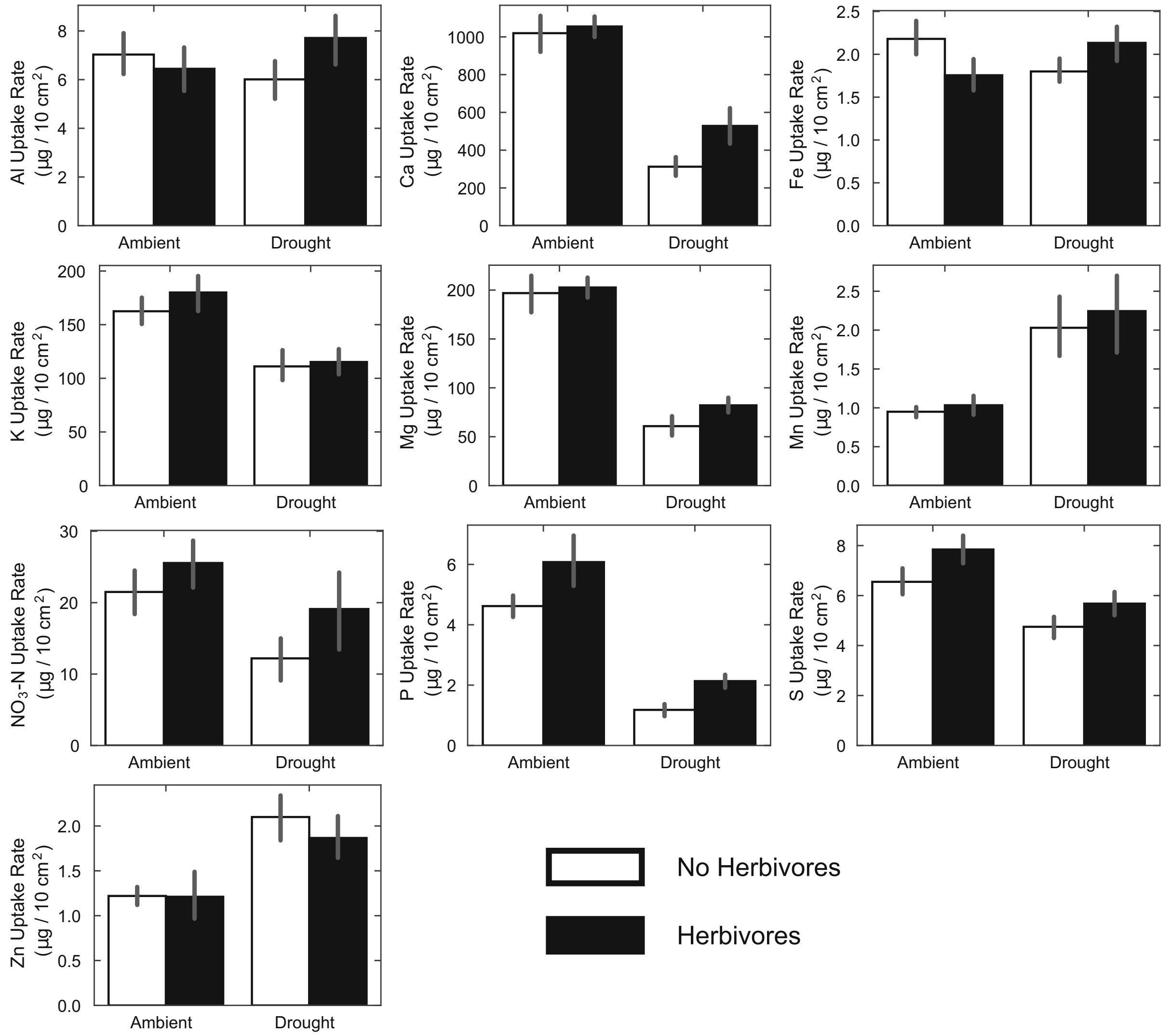

Fig. 1 Nutrient uptake rates (µg 10 cm^{-2} day^{-1}) of all ten nutrients in each of the drought × herbivore treatments. Note the different scale of each *y*-axis. Bars denote means ± 1 SE

et al. 2001; McKinney 2010; van der Walt et al. 2011). Bayesian models were run with STAN v2.17 accessed by PySTAN (Stan Development Team 2016). Unless otherwise stated, all results are reported as mean ± 1 SE.

Results

Bioavailable nutrients

Bioavailable nutrient concentrations varied by several orders of magnitude among nutrients, indicative of considerable variability in nutrient standing stocks in the SGS. Calcium uptake rates, for example, ranged between 200 and 1000 µg 10 cm^{-2} day^{-1}, while uptake rates of Zn and Mn rarely exceeded 2 µg 10 cm^{-2} day^{-1} (Fig. 1). Nutrient bioavailability was highest for alkali/alkaline earth metals Ca, K, and Mg, and lowest for transition metals Fe, Mn, and Zn (Fig. 1).

Long-term drought imposed significant changes in soil nutrient bioavailability, although the direction of change depended on nutrient identity. Ca, K, Mg, NO_3-N, PO_4-P, and S all decreased uptake rates under drought (Fig. 1, Table 1), and reductions were most

Table 1 Pr(Effect) values from the split-plot MANOVA for all nutrients

	Al	Ca	Fe	K	Mg	Mn	NO_3-N	PO_4-P	S	Zn
Drought	0.589	**1.000****	0.793	**0.986****	**1.000****	**0.974****	**0.907***	**1.000****	**0.986****	**0.981****
Herbivores	0.504	0.835	0.858	0.831	0.789	0.513	0.786	**0.989****	**0.975****	0.627
Drought × herbivores	0.789	0.640	**0.941***	0.731	0.509	0.669	0.643	0.786	0.726	0.579

The Pr values indicate the probability that a parameter is < or > 0, such that Pr = 0.5 indicates the parameter is equally likely to be positive or negative and therefore centered around 0. Bold indicates parameters that were either marginally (*) or statistically (**) significant

severe for Ca (− 54.5 ± 6.8%), Mg (− 61.0 ± 5.6%), and PO_4-P (− 65.6 ± 7.8%). In contrast, drought increased uptake rates of both Mn and Zn by + 113.7 ± 231.7% and + 51.53 ± 28.5%, respectively (Fig. 1, Table 1). Neither Al nor Fe was affected by drought (Fig. 1, Table 1). Fe did respond to drought with noninformative priors (Appendix 1“), but given the small sample sizes used here, we prefer the more conservative estimates based on weakly informative priors.

Herbivore presence generally had weak effects on soil nutrient bioavailability, with three notable exceptions. Uptake rates of PO_4-P increased with herbivore presence (+ 40.5 ± 21.0%, Fig. 1, Table 1). Likewise, S uptake rates also increased with herbivore presence, but to a lesser degree than did PO_4-P (+ 17.5 ± 9.5%, Fig. 1, Table 1). Only Fe exhibited a moderate interaction between drought and herbivore presence (Table 1), suggesting that the effect of herbivore presence on Fe availability depends on rainfall. Under ambient rainfall conditions, herbivore presence decreased Fe uptake rates by ~ 20%, whereas herbivore presence increased Fe uptake rates by ~ 20% under drought conditions (Fig. 1, Table 1).

Principal components analysis revealed strong correlations among nutrient availability, such that the first two principal axes explained over 60% of the variance among nutrients (Fig. 2). Nutrients clustered into three groups along the first principal component, distinguished by their relative availability under drought conditions: nutrients with positive PC 1 loadings demonstrated decreased uptake rates during drought (Ca, K, Mg, NO_3-N, PO_4-P, S), nutrients with negative PC 1 loadings exhibited increased uptake rates during drought (Mn, Zn), and nutrients that were unrelated to PC 1 for which drought had little effect (Al, Fe). Indeed, PC 1 strongly demarcated plots by rainfall treatment, whereas plots did not cluster by herbivore presence along either PC 1 or PC 2. These results confirm that soil nutrient bioavailability is primarily regulated by rainfall in the SGS, although herbivores do regulate the availability of a small subset of nutrients (e.g., PO_4-P, S).

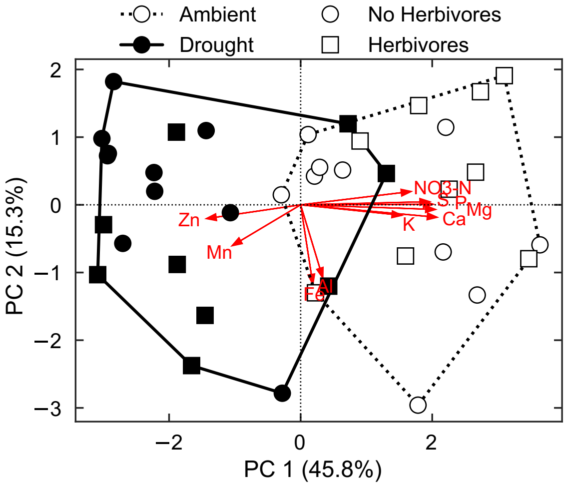

Fig. 2 Distance biplots of the first two principal component axes. Plots have been coded by drought × herbivore treatment. The lines are the convex hull enclosing all sites from their respective drought treatments

ANPP

Drought suppressed grass ANPP in the SGS by 32.1 ± 11.0% (Pr(Drought) = 0.99), but had no detectable effect on forb ANPP (Pr(Drought) = 0.61, Fig. 3). Herbivore presence, on the other hand, did not strongly affect either grass (Pr(Herbivores) = 0.71) or forb ANPP (Pr(Herbivores) = 0.53, Fig. 3). Grass ANPP was slightly lower in the presence of herbivores, but this effect was relatively small and highly variable (− 10.4 ± 16.3%), suggesting that insect and

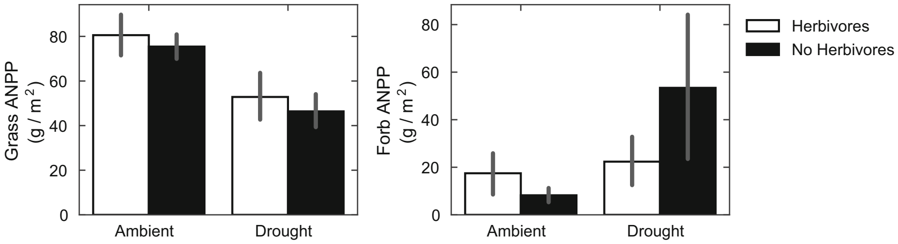

Fig. 3 Aboveground net primary production (ANPP) for both forbs and grass (g m^{-2}) in each of the drought × herbivore treatments. Note the different scales of each *y*-axis. Bars denote means ± 1 SE

Table 2 Partial correlation coefficients between grass ANPP (mean ± 1 SE in parentheses) and each of the nutrient uptake rates

Al	Ca	Fe	K	Mg	Mn	NO$_3$-N	PO$_4$-P	S	Zn
0.08 (0.14)	− 0.02 (0.16)	− 0.08 (0.15)	**− 0.21*** **(0.14)**	0.11 (0.16)	− 0.17 (0.14)	**0.24*** **(0.15)**	− 0.17 (0.16)	**0.21*** **(0.15)**	**0.18*** **(0.14)**

Bold indicates parameters that were either marginally (*) or statistically (**) significant

small mammal herbivores do not strongly suppress ANPP in this semi-arid system.

Correlations between nutrient flux and ANPP

We hypothesized that bioavailable soil nutrient concentrations would be negatively correlated with ANPP due to reduced nutrient uptake by plants. However, many nutrients were positively correlated with ANPP (Table 2). Specifically, NO$_3$-N, S, and Zn uptake rates all increased with ANPP (Pr(> 0) = 0.94, 0.91, 0 and 0.90, respectively). Only K demonstrated a marginally significant, negative correlation with grass ANPP (Pr(< 0) = 0.92), conforming to our initial hypotheses.

Discussion

Drought and herbivores are expected to independently impact ANPP and nutrient cycling in terrestrial SGS grasslands (Huxman et al. 2004b; Munson et al. 2010; Evans and Burke 2013). In our experiment, ANPP and nutrient cycling of many micro- and macronutrients were affected by growing season drought. Interestingly, drought did not have a consistent directional impact on nutrient cycling. Of the ten measured nutrient uptake rates, six decreased, two increased, and two did not change under drought. In contrast, small-bodied herbivores, including both insects and small mammals, did not affect ANPP or soil N in our study. However, they did contribute to the bioavailable soil concentrations of two important nutrients: PO$_4$-P and S. Importantly, drought did not modify the contribution of herbivores to nutrient cycling, suggesting that herbivores might be a critical component of biogeochemical cycling regardless of precipitation in semi-arid grasslands.

Semi-arid grasslands experience high interannual variability in precipitation, making these ecosystems vulnerable to extreme drought (Knapp et al. 2015b). The drought of 2012, for example, caused a 40% decline in annual precipitation throughout US grasslands, resulting in a 50% reduction in ANPP in the SGS. We found a similarly strong effect; ANPP declined by 32.1 ± 11.0% under a 66% reduction in growing season precipitation. However, our study contradicts previous work examining the effects of drought on bioavailable soil nutrients. Evans and Burke (2013) found that drought increased resin-captured NO$_3$-N by 200–400%, whereas we documented a 22.0 ± 17.5% decline in bioavailable NO$_3$-N. This discrepancy might be due to intra- or interannual variation in soil N pools, which can vary by an order of magnitude among years and between early- and late-season periods within a year (Evans and Burke 2013). Other nutrients showed drought sensitivities similar to those reported in other ecosystems. In Mediterranean forests and shrublands, total P concentrations increase during drought, but this increase is caused by an accumulation of plant-unavailable organic P and a decrease in plant-available inorganic P (Sardans and Peñuelas 2004, 2007; Sardans et al. 2008). Inorganic P (PO_4-P) declined during drought in our study as well, but did so more severely than in forests. Soil K availability also declined more severely under drought in this study compared to other ecosystems (Sardans and Peñuelas 2007; Sardans et al. 2008). Given the large reductions, or in some cases increases, in soil nutrient bioavailability reported here compared to other ecosystems, semi-arid grasslands like the SGS might be more sensitive to drought in multiple aspects of ecosystem function beyond ANPP.

Changes in soil nutrient availability during drought potentially initiate feedback loops that make semi-arid grasslands more or less susceptible to drought in the future. High P concentrations, for example, disrupt the mycorrhizal-plant mutualism, making plants less tolerants of water stress (Augé 2001; Shantz et al. 2016). Drought-induced declines in soil P might therefore strengthen the mycorrhizal association and assist plants in avoiding drought stress in the future. However, it is unlikely that ambient soil P concentrations in the SGS exceed the threshold required to shut down mycorrhizal mutualisms. Instead, P deficiency under drought conditions could further reduce leaf water potential and water-use efficiency of many plant species, exacerbating the negative effects of water stress (Wu et al. 2018). Likewise, K hinders the formation of reactive oxygen species and protects chloroplasts from damage, such that reduced K concentrations are associated with low photosynthetic rates (Cakmak 2005). Photosynthesis also suffers under sulfur deficiency because sulfur-based proteins comprise nearly 10% of the thykaloid membrane of chloroplasts (Maréchal et al. 1997). Numerous other mineral nutrients help plants maintain physiological function under water stress, including Fe and Mg which are both integral to the photosystem, and Ca, which provides antioxidant protection during abiotic stress (Jiang and Huang 2001). Any drought-imposed reduction in soil concentrations of these important mineral nutrients could potentially make plants more susceptible to drought in the future. Legacy effects are common in the SGS (Sala et al. 1982) and in grasslands worldwide (Sala et al. 2012), and it is possible that drought-induced changes in soil nutrient availability represent an underappreciated legacy effect that might influence the ability of a system to tolerate or recover from drought in the future.

Herbivores might also enhance ecosystem drought tolerance via herbivore nutrient cycling, but the magnitude of herbivore contributions to SGS soil nutrient bioavailability, up to now, remains largely unexplored. Bakker et al. (2009) reported no effect of large mammals on bioavailable N in the SGS, and insect herbivores increased soil N concentrations by only 5% in a dry, cool-season grassland (Belovsky and Slade 2000). These results, coupled with the absence of herbivore effects reported here, suggests that N cycling is largely decoupled from herbivore presence in the SGS. In forests, however, insect frass alone increases soil bioavailable N by 15–500%, likely due to the greater density of insect herbivores and higher frass throughfall (Reynolds et al. 2000; Frost and Hunter 2004; Metcalf et al. 2014). Phosphorus and S in throughfall are also elevated by 200–800% in the presence of insect herbivores (Nitschke et al. 2015). Therefore, herbivore nutrient cycling could be important for other minerals in semi-arid grasslands. In the SGS, herbivores increased soil bioavailable P by nearly 50% and S by almost 20%, more than double the contribution of insects to P deposition in forests (Fonte and Schowalter 2005; Metcalf et al. 2014). Given the importance of P as a determinant of grassland community composition (Koerner et al. 2016), and the roles of P and S in plant photosynthesis and drought tolerance (Maréchal et al. 1997; Wu et al. 2018), herbivores might be an integral component of ecosystem stability and drought tolerance in the face of high interannual rainfall variability.

The magnitude of herbivore nutrient cycling depends, however, on the density of herbivores present at a given site in a given year (Schade et al. 2003; Burkepile et al. 2013). Small-bodied herbivore populations in semi-arid grasslands exhibit extreme interannual fluctuations in population densities. Grasshopper densities, for example, vary three- to tenfold over a relatively short time period (Capinera and Thompson 1987; Belovsky and Slade 1995), and rodent population sizes can oscillate over two orders of magnitude from year to year (Garsd and Howard 1981; Brady and Slade 2004). Since herbivore population sizes in semi-arid systems typically track annual precipitation and the concomitant increase and decrease of vegetative cover (Capinera and Horton

1989), the magnitude of herbivore nutrient cycling probably also depends, to some extent, on annual precipitation. Unfortunately, this study was limited to a single growing season, and we are therefore unable to determine the environmental constraints on herbivore nutrient cycling. However, our study occurred during a year of below-average annual and growing season precipitations (293 mm and 221 mm, respectively). We may have therefore underestimated the average, long-term contribution of small herbivores to nutrient cycling in the SGS, and multiyear studies that encompass drier and wetter years provide an opportunity for future research.

Increased frequency and intensity of droughts will no doubt adversely affect ecosystem function of the SGS ecosystem. Numerous previous studies have reported the consequences of rainfall shortages on ANPP, soil N, and soil CO_2 fluxes, and here we show for the first time that extreme drought depletes the belowground availability of other important nutrients. Many of these minerals enhance the drought tolerance of plants, and the reduced availability of these nutrients might impose significant drought legacies, initiating a negative feedback loop during recovery or recurrent drought events. Herbivores might be able to offset some of the negative impacts of drought be enhancing bioavailable concentrations of several important nutrients. Thus, our research demonstrates that incorporating consumer effects on nutrient cycles of minerals important to plant growth and drought response could help elucidate the consequences of single or recurrent droughts in semi-arid ecosystems.

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Appendix 1: Comparison of priors for Bayesian models

Weakly informative priors constrain large effect sizes in the presence of lower statistical power (i.e., small sample sizes, noisy data). These priors are therefore more conservative than noninformative priors, which are analogous to conducting frequentist statistics (the *p*-values and confidence intervals are identical between noninformative priors and frequentist methods). To assess the impact of prior choice on model output, we conducted all analyses with both weakly informative [$N(0,1)$] and noninformative [$N(0,10000)$] on regression coefficients.

MANOVA of nutrient availability

See Tables 3 and 4.

Results from weakly informative priors were qualitatively similar to, but slightly weaker than, noninformative priors. This is to be expected, due to the ability of $N(0,1)$ priors to constrain effect sizes. The biggest difference occurred for Fe, where weakly informative priors negated marginally significant main effects of herbivory and drought and reduced the significant interaction to marginal significance.

Table 3 Pr(effect) values from the split-plot MANOVA for all nutrients using weakly informative priors (this is identical to Table 1 of the main text)

	Al	Ca	Fe	K	Mg	Mn	NO_3-N	PO_4-P	S	Zn
Drought	0.589	**1.000****	0.793	**0.986****	**1.000****	**0.974****	**0.907***	**1.000****	**0.986****	**0.990****
Herbivores	0.504	0.835	0.858	0.831	0.789	0.513	0.786	**0.989****	**0.975****	0.503
Drought × herbivores	0.789	0.640	**0.941***	0.731	0.509	0.669	0.643	0.786	0.726	0.700

The Pr values indicate the probability that a parameter is < or > 0, such that Pr = 0.5 indicates the parameter is equally likely to be positive or negative and therefore centered around 0. Bold indicates parameters that were either moderately (*) or strongly (**) significant

Table 4 Pr(Effect) values from the split-plot MANOVA for all nutrients using noninformative priors

	Al	Ca	Fe	K	Mg	Mn	NO_3-N	PO_4-P	S	Zn
Drought	0.757	**1.000****	**0.900***	**0.986****	**1.000****	**0.976****	**0.945***	**1.000****	**0.991****	**0.981****
Herbivores	0.664	0.626	**0.937***	0.806	0.619	0.567	0.765	**0.978****	**0.959****	0.627
Drought × herbivores	0.875	0.856	**0.976****	0.687	0.735	0.584	0.645	0.694	0.643	0.579

The Pr values indicate the probability that a parameter is < or > 0, such that Pr = 0.5 indicates the parameter is equally likely to be positive or negative and therefore centered around 0. Bold indicates parameters that were either moderately (*) or strongly (**) significant

Thus, the weakly informative priors were more conservative then traditional statistics.

ANOVA of ANPP

See Tables 5, 6.

Table 5 Pr(Effect) values from the split-plot ANOVAs for forb and grass ANPP using weakly informative priors

	Grass	Forbs
Drought	**0.990****	0.603
Herbivores	0.610	0.556
Drought × Herbivores	0.789	0.614

The Pr values indicate the probability that a parameter is < or > 0, such that Pr = 0.5 indicates the parameter is equally likely to be positive or negative and therefore centered around 0. Bold indicates parameters that were either moderately (*) or strongly (**) significant

Table 6 Pr(Effect) values from the split-plot ANOVAs for forb and grass ANPP using noninformative priors

	Grass	Forbs
Drought	**0.981****	0.634
Herbivores	0.636	0.579
Drought × herbivores	0.532	0.621

The Pr values indicate the probability that a parameter is < or > 0, such that Pr = 0.5 indicates the parameter is equally likely to be positive or negative and therefore centered around 0. Bold indicates parameters that were either moderately (*) or strongly (**) significant

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