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Interactions between species richness, herbivory and precipitation affect standing biomass in Mongolian rangelands

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Abstract

Questions: Livestock management in rangelands depends on the production of plant biomass. Biomass production is driven by the temporal and spatial variability in precipitation, but our understanding of how precipitation variability mediates grazing effects on biomass production is still fragmented. Along a 600-km precipitation gradient we extracted biomass data to ask the questions: (a) what are the effects of grazing intensity on biomass production; (b) does grazing intensity interact with plant species richness to affect biomass production; and (c) how do plant functional groups respond to grazing and precipitation?

Location: Mongolia.

Methods: Biomass was sampled along 15 grazing intensity transects within the precipitation gradient over two consecutive years. We modeled spatial variability in above-ground plant biomass using mixed-effects models. Normalized difference vegetation index (NDVI) data were combined with field-sampled biomass data to correct for inter-annual precipitation variation. The effects of species richness were modeled with respect to possible interactions with grazing intensity, and the composition of plant functional groups was modeled with respect to possible interactions between grazing intensity and precipitation.

Results: Biomass was negatively correlated with grazing intensity and this effect increased as precipitation increased. Biomass was positively correlated with species richness in both years, but the strength of this effect and the interaction between species richness and grazing intensity differed between 2014 and 2015 in line with highly variable precipitation between both years. The plant functional groups grasses, sedges, legumes, wormwood and forbs had contrasting responses to grazing and precipitation.

Conclusion: Biomass production in drylands is more vulnerable to changes in precipitation variability and grazing intensities in relatively moist and productive rangelands than in dry and unproductive ones. Future rangeland management needs to address potentially increasing precipitation variability in order to promote desired forage plants, and to preserve the positive effects of biodiversity for biomass production.

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KEYWORDS

drylands, grasslands, livestock, NDVI, plant functional groups, precipitation gradient, species richness

1 | INTRODUCTION

Rangelands are the major form of land use in drylands and support the livelihoods of millions of people in Africa, America, Asia and Australia (Uriel et al., 2005; Lund, 2007). Biomass production is the critical ecosystem service provided by rangelands because it directly supports the production of livestock (Sala & Paruelo, 1997; Yahdjian et al., 2015). The production of biomass in drylands is determined mostly by precipitation and thus livestock productivity is tightly coupled to precipitation and, more importantly, its variability (Le Houerou et al., 1988).

The temporal variability of precipitation in rangelands determines the onset of biomass production and biomass availability to livestock. The spatial variability of precipitation determines spatial patterns in biomass production and the extent of exploitable rangelands. The combination of temporal and spatial variability of precipitation thus determines the carrying capacity of rangelands for livestock production (Bai et al., 2004; Uriel et al., 2005). Rangelands with greater precipitation variability usually provide less biomass for livestock, and face higher risk of extreme climatic events such as droughts or harsh winters (Vetter, 2005; Liu et al., 2020). Extreme climate events can be disastrous for livestock production and livelihoods (Middleton & Sternberg, 2013), yet also severely reduce livestock densities which may allow the vegetation to recover over time (Ellis & Swift, 1988; Müller et al., 2007). Rangelands with less precipitation variability provide more stable resources for more livestock, but stability of resource availability can increase the risk of overgrazing by livestock (von Wehrden et al., 2012).

Precipitation variability may also increase the uncertainty about where and when to expect biomass for livestock grazing. Sustainable rangeland management therefore requires either an active balancing of livestock densities and available resources (Westoby et al., 1989), or taking into account the specific climatic constraints which limit livestock numbers in space and time (Wiens, 1984; Ellis & Swift, 1988). Under both circumstances, changing climate patterns may threaten today's rangeland management systems by higher uncertainty of biomass availability production in time and space.

Climate models predict that the production of biomass in drylands will decline as precipitation becomes more spatially and temporally variable (IPCC 2019; Yao et al., 2020). In the still relatively intact Mongolian rangelands, climate and vegetation models predict declining biomass production across a vast share of these rangelands (Sato et al., 2007). The predicted reduction in available biomass for livestock grazing would have direct consequences for people's livelihoods in rangelands. Lower biomass production could increase grazing intensity on the remaining productive lands, if livestock numbers are not adjusted to the available forage (Filei et al., 2018). This might push the rangeland systems toward a degraded state, further threatening the sustainability of livelihoods.

Changes in biodiversity have the potential to alter the stability in biomass production (Gross et al., 2014). Plant species richness can enhance multifunctionality and stability of dryland ecosystems (Maestre et al., 2012; García-Palacios et al., 2018). In rangeland ecosystems, higher precipitation availability is positively correlated with species diversity (Bai et al., 2007) while higher precipitation variability has negative effects on species diversity (Zhang et al., 2018). Grazing, on the other hand, can increase plant species richness at intermediate levels (Roxburgh et al., 2004; Fox, 2013), yet this relationship differs depending on the availability of precipitation and nutrients (Cingolani et al., 2005; Ahlborn et al., 2020). However, effects of climate extremes on biodiversity–productivity relationships remain poorly understood (Boeck et al., 2018). Studying the functional properties of grassland communities can help to explain biomass patterns (Sonkoly et al., 2019). In dry rangelands, separating the vegetation into functional types can improve assessments of grazing effects (Linstädter et al., 2014) and their interactions with precipitation (Guo et al., 2016).

This paper presents data and analyses on plant biomass production along a 600 km long spatial gradient in Mongolian rangelands during 2014 and 2015, representing a mean precipitation range of 150 mm. We had three research questions: (a) what are the effects of grazing intensity on biomass production along a precipitation gradient; (b) does grazing intensity interact with plant species richness to affect biomass production; and (c) how do plant functional groups respond to grazing and precipitation? Answering these questions should increase our understanding of biomass distribution in rangelands and contribute to the development of sustainable grassland management systems. Based on existing rangeland theory, we hypothesized:

1. Increasingly negative effects of livestock grazing on biomass with increasing mean annual precipitation (Ellis & Swift, 1988; Cingolani et al., 2005)
2. Positive effects of species richness on biomass production, which are mediated by grazing intensity (Bernhardt-Römermann et al., 2011)
3. Differentiated interactions of plant functional group biomass to grazing intensity along the precipitation gradient (Linstädter et al., 2014; Gherardi & Sala, 2015; Guo et al., 2016).

2 | METHODS**2.1 | Study area and design**

The study was located in central Mongolia (Figure 1a,b) with a climate typical of Central Asia: hot summers, cold winters and frequent droughts. Rainfall occurs mainly during the summer months. Grassland

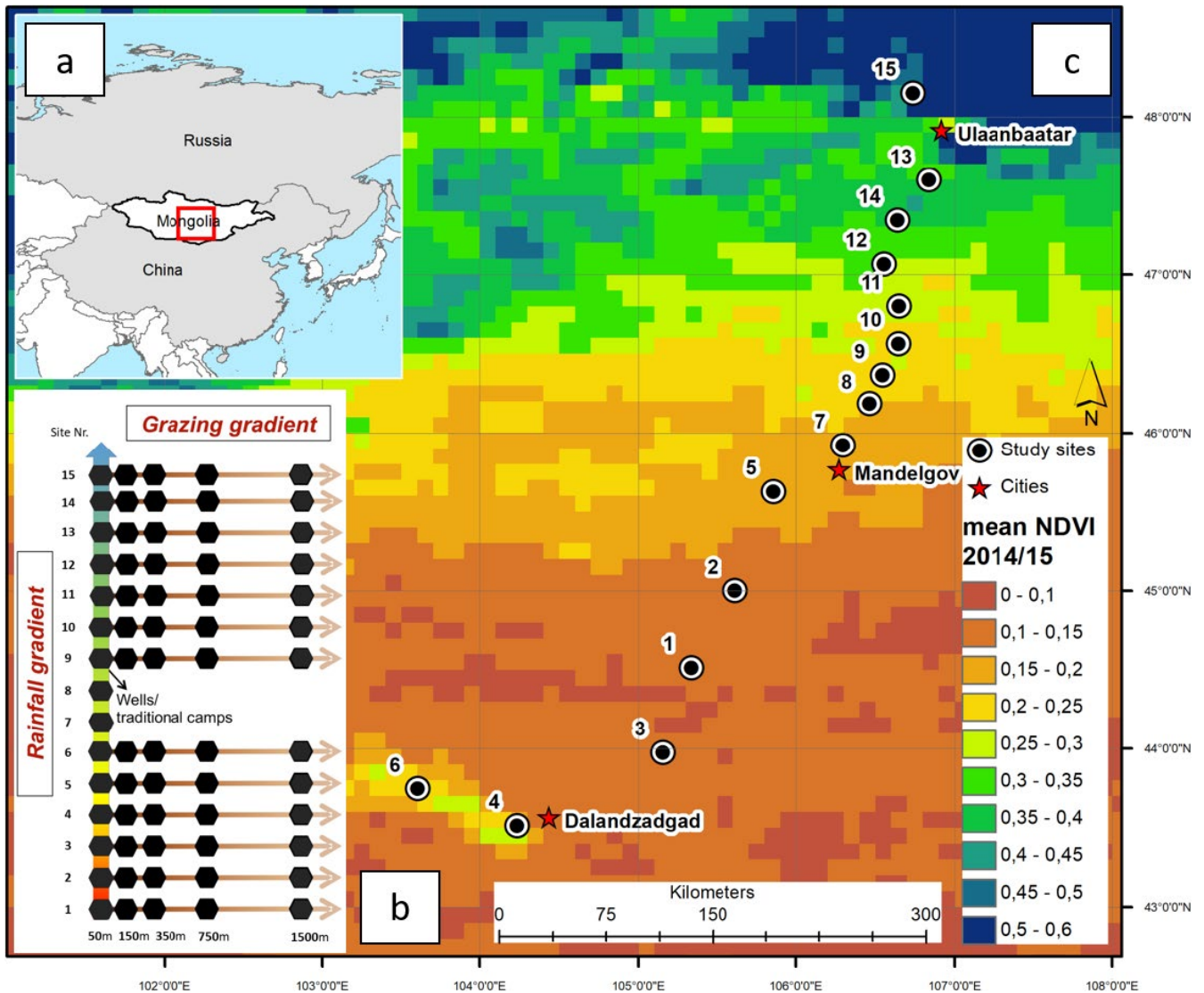


FIGURE 1 Study area and sampling design. (a) Location of the study area within Mongolia. (b) Scheme of the study design. Each black hexagon stands for five replicate 100-m² vegetation plots per distance from a grazing hotspot; the color represents the increasing mean annual precipitation. (c) Map of the study area. The colors indicate the average normalized difference vegetation index (NDVI) for the observed growth periods of 2014 and 2015, based on the MODIS product MOD13Q1 Version 6 (source: <https://lpdaac.usgs.gov/>)

is the main vegetation type in the study region (Ahlborn et al., 2020). Nomadic livestock herding is the main type of land use, with goats and sheep being the most abundant livestock species (Fernández-Giménez, 2006). Larger livestock like horses, cattle and camels are kept where there are sufficient supplies of water and biomass. Fifteen study sites within the study region were located along a precipitation gradient that ranged from 250 mm of mean annual precipitation in the north (48.15° N, 106.71° E), to 100 mm in the south (43.97° N, 105.14° E; Figure 1b; see Ahlborn et al., 2020; Lang et al., 2020).

A grazing intensity transect was placed at each site within the precipitation gradient. Each grazing transect consisted of a grazing intensity hotspot such as a camp, a well or a winter place. From there five sampling areas were arranged at distances of 50 m, 150 m, 350 m, 750 m and 1,500 m in a straight line from the grazing hotspots, and at each distance five plots were placed

perpendicular to the medium-scale grazing gradient (Figure 1c, Appendix S1). This method has shown to be adequate for capturing gradients of grazing intensity in Central Asia (Stumpp et al., 2005; Manthey & Peper, 2010). Each plot was surveyed on 10 m × 10 m, and the plots were spaced 20 m from each other. Data from a total of 375 plots were collected over two years ($n = 750$).

2.2 | Data collection

2.2.1 | Precipitation and normalized difference vegetation index

Climate stations were scarce in our study area and were far away from our study sites. We used modeled precipitation data as the

basis for the precipitation gradient (Hijmans et al., 2005, worldclim.org). The employed precipitation values represent the annual precipitation sum averaged across the period 1980–2000. In areas with high precipitation variability, the comparison of biomass samplings within and between two extended periods of field work can be problematic due to the seasonal variation in precipitation and vegetation phenology. To avoid potential intra-annual sampling errors and detect deviations of our observed biomass from the maximum biomass during the respective sampling periods, we processed satellite-based normalized difference vegetation index (NDVI) data from both sampling periods. NDVI expresses the "greening" of the landscape and can therefore be used to capture the start of the vegetation period and the peak of the standing biomass (Testa et al., 2014). NDVI data were derived from MODIS 16-day composite Imagery at 250 m resolution for the time spans mid of May to end of August in 2014 and 2015 (MOD13Q1, <https://lpdaac.usgs.gov/>). The available resolution of 250 m per pixel was too coarse to get a data point for each sampling distance within a site so we extracted the data from each pixel that intersected with a site (approximately 6–8 per site) and averaged them. We calculated the difference between the maximum NDVI value at a site within each year and the NDVI value for each site near the time of sampling. This difference was used to correct for differences in biomass samples between years and within years.

2.2.2 | Biomass sampling

Biomass samples were collected from June until August in 2014 and 2015. This period coincides with peak biomass (Pfeiffer et al., 2019). Within each of the 375 plots, the vascular vegetation was cut to ground level on one randomly chosen subplot of 50 cm × 50 cm. The samples were stored in paper bags, air-dried in the field and later oven-dried in the laboratory at 65°C for 24 h. The samples were then cooled down in desiccators and weighted to an accuracy of ±1 mg. For the analyses, we used dry weight of fresh biomass in gram per m² by extrapolating original values. We lost 68 samples (9% in total, Appendix S2) due to unsuitable air-drying conditions in the field.

2.2.3 | Species richness

Species richness was estimated by recording every vascular plant species within each 10 m × 10 m plot along the grazing transects. Nomenclature followed the standard checklist for Flora of Mongolia (Urgamal et al., 2014).

2.2.4 | Plant functional groups

During sampling, biomass was separated into pre-defined plant functional groups (PFG), whose classifications were based on growth forms (Box, 1996). We chose PFGs that should be responsive to

variability in grazing and precipitation as well as being easy to detect in the field. We classified species using standard literature for Mongolia (Hilbig, 1995; Jigjidsuren & Johnson, 2003):

1. Grasses: easy to detect and often decreasing under heavy grazing
2. Sedges: like grasses, but being less preferred as forage because of their often lower digestibility (Jigjidsuren & Johnson, 2003)
3. Legumes: easy to observe in Mongolian rangelands, have several strategies to tolerate grazing (e.g., spines such as *Caragana*, cushion-like growth forms such as *Astragalus*), having a competitive advantage in nitrogen-limited drylands (James et al., 2005)
4. Wormwood (*Artemisia* spp.): with high content of essential oils and bitter substances which provide resistance to herbivory and the harsh climate
5. Forbs: representing the most diverse group contributing to overall biomass, including the abundant and nutrient-rich *Allium* species and several less palatable Chenopodiaceae

In 2015, the last two groups, wormwood and forbs, were reordered into:

6. Shrubs: having different protection strategy against harsh climates compared to herbaceous plants
7. Herbs: representing all plants not belonging to the groups 1–4 or 6

The species spectra within the groups 4 and 5 on the one hand, and groups 6 and 7 on the other differed slightly between 2014 and 2015. In 2014, the wormwood species observed (all *Artemisia* species) and all other species with woody parts from the forbs group were considered shrubs, while all other remaining species were assigned to herbs. In each biomass sample, we calculated the proportion of each PFG by dividing the dry biomass of the respective PFG by the total dry biomass in the respective plot (Appendix S3).

2.3 | Statistical analysis

All analyses were conducted using R version 3.5.1. (R Core Team, 2018) and all predictors were scaled (centered and standardized) prior to the analysis. Graphics were coded using *lattice* (Sarkar, 2008) and *ggplot2* (Wickham, 2016).

2.3.1 | NDVI data

We analyzed NDVI data in a first step and used the results of this analysis to correct the relationship between biomass, grazing and precipitation for the described sampling bias. Differences between the sum of all processed NDVI values between May and August in the years 2014 and 2015 were tested using paired *t* tests. The development of NDVI during the summer months of 2014 and 2015

was analyzed by multiple regressions. We constructed a set of eight models that included sets of variables that are hypothesized to explain NDVI data in space and time (Appendix S4).

2.3.2 | Total biomass

The relationship between biomass, grazing and precipitation was analyzed using mixed-effects model functions from the *lme4* package (Bates et al., 2014). We constructed a set of 14 models that included sets of variables that were hypothesized to explain biomass (Appendix S5). The mixed-effects models were constructed assuming a Gaussian distribution for the residual errors, where biomass was the response variable and the distance to grazing hotspots (distance), mean annual precipitation (precipitation) and year (year) were the predictor variables. The models were structured so that each site (site) and sampling area (area) were included as random effects with sampling area nested within sites to account for the study design, and where each random effect had separate intercepts for each level of the group. The difference between the maximum NDVI value during the year of sampling and the NDVI value at the time of sampling was used in a random-effects structure to correct for the intra-annual differences in precipitation.

2.3.3 | Plant species richness

To test the effect of plant species richness and its interaction with grazing on biomass production, 13 mixed-effects models were constructed and compared using species richness, year and distance as predictor variables (Appendix S6). This resembles the approach above with two exceptions: NDVI was not included as a random intercept in the models, because NDVI cannot be used to correct for the occurrence of species. Precipitation was not included in the

model because precipitation and richness are highly correlated in drylands (Ahlborn et al., 2020).

2.3.4 | Plant functional group biomass

The biomass of PFGs was also modeled using mixed-effects models. The data are proportions and are thus bounded between zero and one. Therefore, we chose to model these data assuming a beta distribution for proportions using the *glmmTMB* package (Brooks et al., 2017). The PFG sets of 2014 and 2015 were modeled separately (Appendixes S7, S8, S9).

2.3.5 | Model selection

Each model was fitted to the data and then compared to other models using an information-theoretic ranking (Burnham & Anderson, 2002) based on the Akaike information criterion adjusted for sample size (AIC, and AICc for small sample sizes). We used the package *AICmodavg* (Mazerolle, 2016) for ranking candidate models and producing the model tables. The models with the lowest AIC and $\Delta AIC > 1.8$ to the next best models were selected as best-fitting models.

3 | RESULTS

3.1 | NDVI

The estimates of the model that described NDVI best showed that there was a positive correlation between the growth of biomass and mean annual precipitation, and that biomass growth started earlier in 2014 compared to 2015 (Table 1, Figure 2, Appendix S10). Paired t tests of the sums of NDVI values of all sites between May to August revealed a significantly higher total biomass production

TABLE 1 The sets of candidates of the generalized linear mixed models (GLMMs) explaining (a) normalized difference vegetation index (NDVI) as a function of precipitation (P), year (Y) and month (M) during 2014 and 2015; (b) total biomass as a function of precipitation (P), distance to grazing hotspot (D) and year (Y); and (c) total biomass as a function of species richness (R), distance (D) and year (Y)

Set	Model	k	LL	AICc	$\Delta AICc$	AICw	Cum.Wt
(a) NDVI as a function of precipitation (P), year (Y) and month (M)							
	$Y \times M \times P$	33	437	-808	0	1	1
(b) Biomass as a function of precipitation (P), distance (D) and year (Y)							
	$P \times D$	11	-4599.90	9,221.79	0.00	0.70	0.70
	$P + D$	10	-4602.59	9,225.18	3.39	0.13	0.83
	P	9	-4604.13	9,226.26	4.46	0.08	0.90
(c) Biomass as a function of species richness (R), distance (D) and year (Y)							
	$R \times D \times Y$	11	-4674.34	9,370.67	0	0.704	0.70
	$R \times Y$	7	-4679.59	9,373.17	2.5	0.201	0.90

Note: The models are ranked by their model weights (AICw). Model, predicted model; k, number of terms; AICc, Akaike Information Criterion (corrected for small sample sizes), $\Delta AICc$, difference to the next best model; AICw, weighted AIC; LL, log-likelihood; Cum.Wt, cumulative sum of the model weights. The table only includes the subset of candidate models that accounted for 90% of the accumulated model weights. The remaining models can be found in the Appendixes S4, S5, S6. Predictions of the models highlighted in bold were used for Figures 2a, 3b and 4c.

in 2014 than in 2015 ($p < 0.005$, Appendix S11). Comparison of the NDVI values between the time of sampling and the maximum NDVI within the respective year revealed that sampling was done during the peak of the growth period in 2014. The sampling of biomass in 2015 missed the peak growth period when sampling the sites at the end of the gradient with high mean annual precipitation (Appendix S12).

3.2 | Total biomass

The model that best explained the NDVI-corrected biomass data included an interaction between precipitation and distance (Table 1, Appendix S13). According to this model, biomass increased with mean annual precipitation. Increasing distance to grazing hotspots was correlated with slightly decreasing biomass in the dry areas, and with strongly increasing biomass in the moist areas of the precipitation gradient (Figure 3). No differences of these effects were found between 2014 and 2015.

3.3 | Species richness

When species richness was included in the candidate set of explanatory variables, the best-fitting model included interactions between species richness, distance and year (Table 1, Appendix S6). For 2014, the model predicted positive correlations of biomass with the interactions between richness and distance to grazing hotspots. Biomass increased with species richness, and distance to grazing hotspots had increasingly positive effects on biomass production with increasing species richness. For 2015, the model predicted strongly reduced effects of richness on biomass compared to 2014 (Figure 4, Appendix S14).

3.4 | Plant functional group biomass

There were no consistent effects of precipitation, distance or their interactions on the proportion of PFGs in the subplots (Table 2). The effects of precipitation and distance on the single PFGs were not the same between 2014 and 2015 (Figure 5). The proportion of grass biomass increased with distance from grazing hotspots in both years, yet in 2014 this effect was modulated by precipitation, with less pronounced grazing effects at higher precipitation. The proportion of sedge biomass increased in both years with precipitation, but was unaffected by distance to grazing hotspots. The proportion of legumes increased with precipitation only in 2014. The proportion of PFG forbs in 2014 decreased with both precipitation and distance to grazing hotspots, but the distance effect became weaker with increasing precipitation. In 2014 the proportion of the wormwood PFG increased with precipitation. The proportion of the PFG herbs changed little with distance to grazing hotspots in 2015 and there was no effect of precipitation. Effects of precipitation or distance to grazing hotspots on the PFG shrubs could not be detected at all in 2015.

4 | DISCUSSION

Biomass production differed strongly in space and time. Grazing intensity had increasingly negative impacts on biomass with increasing mean annual precipitation. Higher grazing intensity also had negative effects on the overall positive species richness–biomass relationship, and affected the functional composition of biomass along the climate gradient. Inter-annual differences in the onset of precipitation had clear effects on these relationships. We now discuss our findings with respect to our three research questions and reflect on important future challenges of livestock management in Mongolia.

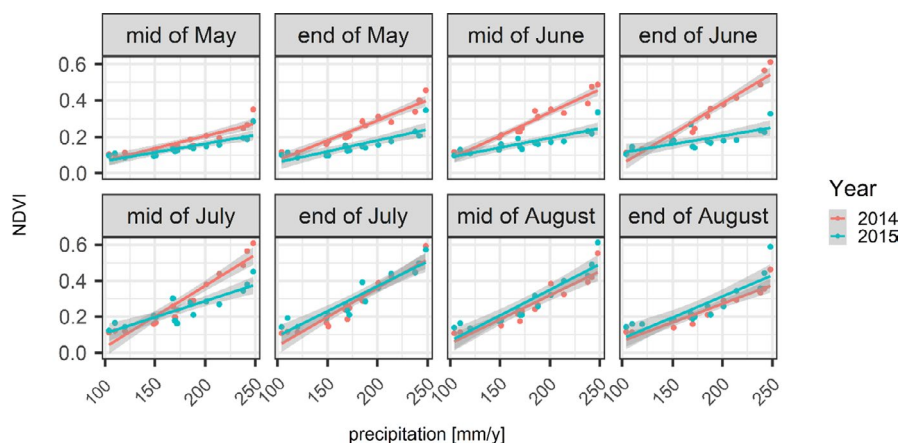


FIGURE 2 Development of above-ground biomass on our study sites during the vegetation periods of 2014 and 2015. The graphs are based on a multiple regression of normalized difference vegetation index (NDVI) data as a function of mean annual precipitation, time within the year and year (Table 1a). NDVI is the site-wise averaged NDVI data (MOD13Q1). Note the delayed start of biomass growth in 2015, which was effective especially at the moister end of the large-scale climate gradient (May–June). The points mark our study sites, the lines are the regression models with 95% confidence interval. See Appendixes S4 and S10 for further detail on the model estimates

4.1 | What are the effects of grazing intensity on biomass production along a precipitation gradient?

Biomass production is correlated with precipitation variability in dry rangelands (Le Houerou et al., 1988). This refers both to spatial gradients, such as the observed precipitation gradient in Mongolia, as well as temporal gradients, such as the two studied vegetation periods. Intra-annual precipitation variability can change the expected biomass distribution (Bai et al., 2004), which was also illustrated by our analysis of NDVI data across the vegetation periods. In 2014, biomass was correlated with mean annual precipitation (Figure 2).

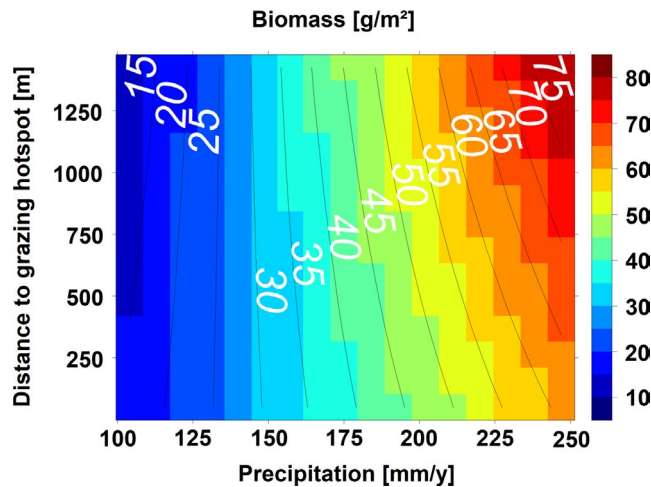


FIGURE 3 Predicted relationship between grazing intensity (expressed as distance from grazing hotspots; the larger the distance, the lower the intensity), mean annual precipitation (precipitation [mm/y]) and biomass production, based on the best fitting generalized linear mixed model (GLMM; Table 1b). Colors indicate changes of biomass with precipitation and distance; white numbers are predicted biomass weights in g per m². Biomass increases with precipitation, and is positively affected by grazing in dry areas, but negatively in more moist areas. The model includes data from 2014 and 2015 and was corrected for the delayed vegetation period and the resulting sampling bias (see Figure 2)

The late onset of precipitation in 2015 was responsible for an overall decrease of biomass along our climate gradient compared to 2014, and this decrease was especially evident in the wetter part of the precipitation gradient. Toward the end of the growth period in 2015, biomass production became more similar to the conditions in 2014.

Importantly, our analysis suggests that increasing precipitation is associated with increasingly negative effects of grazing on biomass production. Total biomass and biomass composition in the dry desert steppe of southern Mongolia were less affected by high grazing intensity than in the moist rangelands in its north. In Mongolia, livestock numbers usually correlate with precipitation and productivity of the area (Pfeiffer, 2019 #577). Lower impacts of grazing intensity on biomass production in dry areas could be a result of the harsh climate events which can drastically reduce livestock numbers (Vetter, 2005), or of the low provision of biomass in time and space (Cingolani et al., 2005). Either way, biomass production in dry rangelands seems to be more resilient to grazing than in moister rangelands. The fact that inter- and intra-annual variability in precipitation has a stronger impact on biomass production in the more productive rangelands in Mongolia's north might relate to a higher risk for overgrazing. Stocking densities are higher there (Pfeiffer et al., 2019; Ahlborn et al., 2020), and the generally higher precipitation results in much shorter phases of recovery for the vegetation compared to the dry areas in the south (Müller et al., 2007). Therefore, potentially increasing precipitation variability in the future in combination with decreasing water availability calls for adaptation of future management schemes to the respective climate regime to avoid rangeland degradation.

4.2 | Does grazing intensity interact with plant species richness to affect biomass production along the grazing gradient?

The stability of biomass production in rangelands is positively correlated with species richness (Tilman & Downing, 1996; Hector et al., 2010). The acceleration of climate change has recently

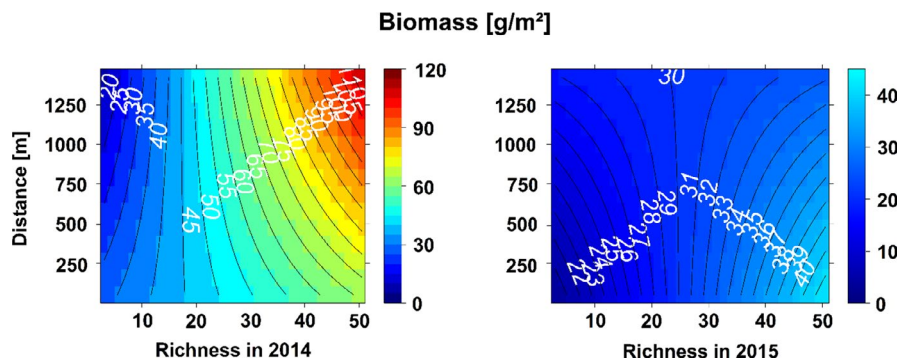


FIGURE 4 Predicted relationship between richness, grazing intensity (expressed as distance from grazing hotspots; the larger the distance, the lower the intensity) and biomass in 2014 and 2015 based on the best-fitting generalized linear mixed model (GLMM; Table 1c). Colors indicate changes of biomass with precipitation and distance; white numbers are predicted biomass weights in g per m². Distance to grazing hotspots had an increasing, positive effect on biomass with increasing richness in 2014. This effect was absent in 2015. Note the difference in the color code

TABLE 2 The sets of candidates of the generalized linear mixed models (GLMMs) explaining the proportion of biomass in each functional group as a function of distance to grazing hotspot (*D*) and precipitation (*P*) within the respective years 2014 and 2015

Functional group	Year	Model	K	LL	AIC	Δ AIC	AICw	Cum.Wt
Full	2014	PFG \times (<i>P</i> + <i>D</i>)	18	2,807.66	-5579.33	0	1	1
Grasses		<i>P</i> \times <i>D</i>	7	272.49	-530.98	0	0.593	0.59
		<i>D</i>	5	269.56	-529.13	1.85	0.234	0.82
		<i>P</i> + <i>D</i>	6	270.26	-528.52	2.46	0.172	1
Sedges		<i>P</i>	5	799.42	-1588.85	0	0.63	0.63
		<i>P</i> + <i>D</i>	6	799.50	-1587.01	1.84	0.25	0.88
		<i>P</i> \times <i>D</i>	7	799.72	-1585.45	3.40	0.12	0.99
Legumes		<i>P</i>	5	1,207.16	-2404.33	0	0.53	0.53
		<i>P</i> + <i>D</i>	6	1,207.23	-2402.47	1.85	0.21	0.74
		NULL	4	1,204.70	-2401.40	2.93	0.12	0.86
		<i>P</i> \times <i>D</i>	7	1,207.30	-2400.6	3.73	0.08	0.95
Forbs		<i>P</i> \times <i>D</i>	7	199.02	-384.05	0	0.80	0.80
		<i>P</i> + <i>D</i>	6	196.59	-381.19	2.86	0.20	0.99
Wormwood		<i>P</i>	5	576.98	-1143.97	0	0.51	0.51
		<i>P</i> + <i>D</i>	6	577.00	-1142.00	1.96	0.19	0.70
		<i>P</i> \times <i>D</i>	7	577.76	-1141.53	2.43	0.15	0.85
		NULL	4	574.43	-1140.86	3.10	0.10	0.95
Full	2015	PFG \times (<i>P</i> + <i>D</i>)	18	3,264.96	-6508.39	0	0.9	0.9
Grasses		<i>P</i> \times <i>D</i>	7	330.4652	-646.9304	0	0.4794	0.4794
		<i>D</i>	5	328.2221	-646.4442	0.4861	0.376	0.8554
		<i>P</i> + <i>D</i>	6	328.2281	-644.4562	2.4742	0.1391	0.9945
Sedges		<i>P</i>	5	788.2119	-1566.424	0	0.5622	0.5622
		<i>P</i> + <i>D</i>	6	788.2772	-1564.554	1.8695	0.2208	0.783
		NULL	4	785.4658	-1562.931	3.4923	0.0981	0.8811
		<i>P</i> \times <i>D</i>	7	788.2782	-1562.556	3.8674	0.0813	0.9624
Legumes		<i>P</i>	5	1,293.962	-2577.924	0	0.3064	0.3064
		NULL	4	1,292.93	-2577.86	0.0636	0.2968	0.6031
		<i>P</i> + <i>D</i>	6	1,294.358	-2576.716	1.208	0.1675	0.7706
		<i>D</i>	5	1,293.321	-2576.643	1.2807	0.1615	0.9321
Herbs		<i>D</i>	5	219.6757	-429.3514	0	0.3736	0.3736
		<i>P</i> \times <i>D</i>	7	220.9537	-427.9074	1.444	0.1815	0.5552
		NULL	4	217.946	-427.8919	1.4595	0.1801	0.7353
Shrubs		<i>P</i> + <i>D</i>	6	219.9374	-427.8749	1.4766	0.1786	0.9138
		NULL	4	841.6539	-1675.308	0	0.4407	0.4407
		<i>D</i>	5	841.7619	-1673.524	1.7839	0.1806	0.6213
		<i>P</i>	5	841.6617	-1673.323	1.9843	0.1634	0.7847
		<i>P</i> \times <i>D</i>	7	843.5654	-1673.131	2.177	0.1484	0.933

Note: The models are ranked by their model weights (AICw). Functional group = 'Full' is the full model explaining differences between groups (PFG), *P* and *D*. Grasses, Sedges, Legumes, Forbs, Wormwood, Herbs and Shrubs are the proportions of the single groups to the total biomass. Model, predicted model; k, number of terms; AIC, Akaike Information Criterion; Δ AIC, difference to the next best model; AICw, weighted AIC; LL, log-likelihood; Cum.Wt, cumulative sum of the model weights. The table only includes the subset of candidate models that accounted for 90% of the accumulated model weights. The remaining models can be found in the Appendix S8. Predictions of the models highlighted in bold were used for Figure 5.

raised concerns about the impact of climatic extremes on this relationship (Boeck et al., 2018). In fact, there is good evidence for the positive and stabilizing effects of biodiversity on the

productivity and stability of grassland ecosystems after extreme climatic events (Isbell et al., 2015). Most of the evidence supporting a positive biodiversity–stability relationship comes from rather

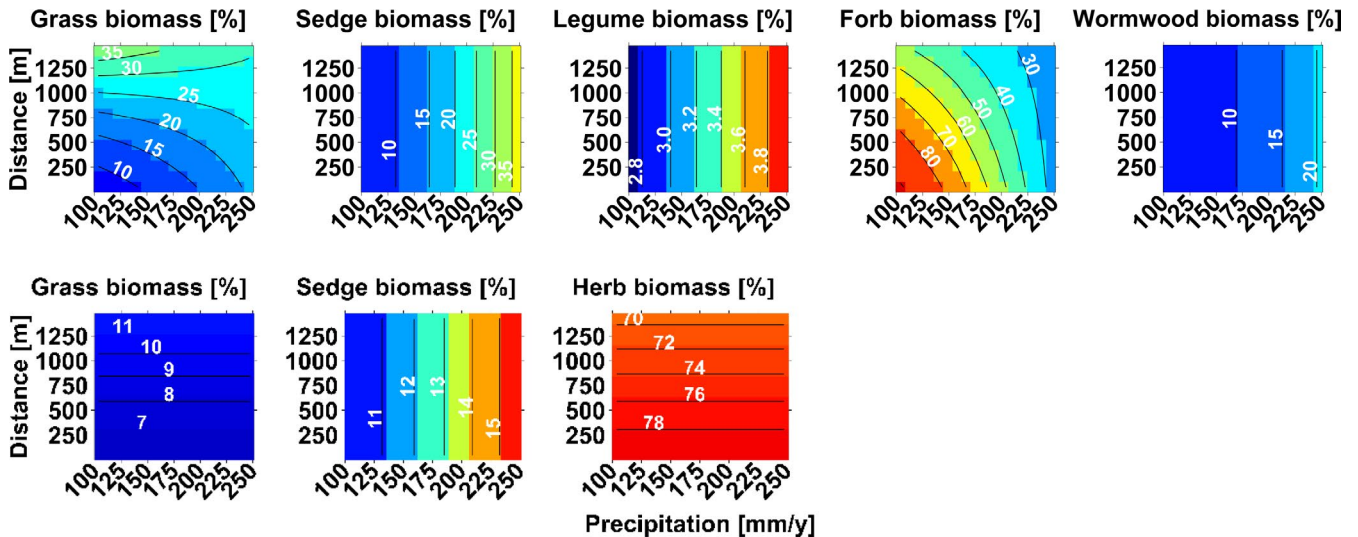


FIGURE 5 Predicted relationships of the single PFGs with annual mean precipitation and grazing intensity (expressed as distance from grazing hotspots) in 2014 (top row) and 2015 (bottom row) based on the selected generalized linear mixed models (GLMMs) of Table 2. Colors indicate changes of biomass with precipitation and distance; white numbers are predicted proportions of the PFGs on the total biomass in %. Note the differences in the scaling of the color codes of 2014’s legume and 2015’s sedge biomass. Models for the PFGs shrubs and legumes did not differ from the null model in 2015

productive grasslands, and disregards the importance of precipitation patterns for the diversity–productivity relationships in dry rangeland systems (Adler & Levine, 2007). Our data suggest that the positive relationship between biomass production and biodiversity also holds for dry rangeland systems, but the data highlight the importance of both grazing *and* precipitation variability in this relationship (Figure 3). This is basically in line with the general negative grazing effect on species richness and productivity (Adler et al., 2011), which is also true for semi-arid ecosystems (Dingaana et al., 2016). Grazing negatively affected the positive effect of diversity on biomass production in 2014 in our data as well, but not in 2015 (Figure 3, Table 1). This might be due to the fact that the most diverse communities occur on sites which received sufficient precipitation only relatively late in the growth period in 2015. Previous studies showed that higher precipitation provides more resources for more species in dry rangeland systems (Adler & Levine, 2007; Hejcman et al., 2010), leading to a higher biomass production (Hector et al., 2010) and to higher grazing impacts through higher livestock numbers (Fernández-Giménez, 2006). Our data highlight the effects of overall climate, and suggest that precipitation variability has stronger effects on the diversity–productivity relationship in more productive, wetter areas than in drier areas. This is either because the magnitude of variability of the biomass production is higher, or because higher resource availability can have negative effects on the stability of biomass production (Hautier et al., 2014). Taken together, we can confirm that the positive diversity–productivity relationship also applies to dry rangeland systems, yet that precipitation variability can introduce detrimental effects for the more productive among the dry grassland systems.

4.3 | How do plant functional groups respond to grazing and precipitation?

Recent evidence supports the theory that grazing affects the productivity and stability of above-ground biomass production in dry rangeland systems via compensatory effects between PFGs (Ren et al., 2018), not through plant species loss per se. We found large differences of biomass productivity among PFGs in response to grazing, and more importantly, found that grazing–climate interactions did not uniformly affect biomass distribution across all PFGs. The main biomass producers, i.e., grasses, are more negatively affected by grazing in wetter regions. They might thus profit from increasing water scarcity in the future, but only under lower grazing pressure. The other two main biomass producers, forbs and herbs, on the other hand built up the main share of the biomass under higher grazing pressure and lower water availability.

Plant species at grazing hotspots are often the less preferred forage (Urgamal et al., 2014; Ahlborn et al., 2020), which could explain the dominance of forbs and herbs in standing biomass toward grazing hotspots and also the higher total biomass at grazing hotspots in dry areas in our data (Figure 3). However, a surprisingly high share of Mongolian plant species are commonly considered forage (Jigjidsuren & Johnson, 2003). They have broadly varying contents of protein, fiber and mineral content (Olson et al., 2010), and these are subject to change over the course of a given year (Campos-Arceiz et al., 2004). Digestibility of forage differs between life stages and the type of livestock (Jigjidsuren & Johnson, 2003; van Soest, 2018).

Although many of the species which constitute most of the herbaceous biomass belong to less (but still) palatable plants, a high diversity of these PFGs could be beneficial. High forb or herb biomass in

combination with a high diversity might act as an insurance for forage quality in harsh times (Shanafelt et al., 2015). Legumes and sedges could suffer from decreasing water availability, since their contribution to the total biomass significantly decreases toward drier regions. However, these seem to be largely unaffected by grazing and could play at least a minor role as “emergency” forage during harsh times. Finally, we want to point out that although our results imply PFG-specific adaptations to a decrease of moisture availability, further studies have shown that plant communities of steppe have low functional diversity, and that losses of biodiversity might therefore have serious consequences for the provisioning of forage (Jäschke et al., 2019).

5 | CONCLUSION

This study provides evidence that biomass production and thus livestock forage availability is more vulnerable to changes in precipitation variability and grazing intensities in wetter and more productive rangelands as compared to drier and less productive ones. The impacts of grazing intensity increase with productivity, reflecting generally higher stocking densities and therewith increased risks of degradation during times of low resource availability. Plant species richness has distinct effects on the production of forage through its positive association with biomass production and likely through the diversity of forage plants in time and space, but changing climate might decrease the positive effect through species loss and an increased frequency of droughts. Especially under higher mean annual precipitation, dominant grasses suffer from higher grazing intensities and temporally lacking moisture, while herbaceous species benefit from temporally dry conditions.

Climate change is therefore particularly problematic for more productive rangelands, since dry rangelands are more adapted to higher precipitation variability and prolonged periods of drought. Changing precipitation variability in the future could be tackled by livestock management strategies that increase the mobility and flexibility of livestock herds to deal with lower and more sparsely distributed forage production. Further research needs to address quality of biomass for forage production and its resistance to grazing and climatic extremes in time and space.

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AUTHOR'S CONTRIBUTIONS

JA collected data, conducted the analysis, and wrote most of the manuscript. JA, KW, CR and HVW drafted the paper idea. BL and MO contributed in data collection. OB organized field work. NC assisted with the analysis and coding and made major contributions to the writing style and language. CR, KW and HW designed the study, raised funding and significantly improved the quality of the

manuscript. All authors gave approval to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data publication is still in process.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Basic information on the 15 study sites

Appendix S2. Summary table on response and predictor variables

Appendix S3. Model selection table for NDVI analysis

Appendix S4. Model estimates for the model used to produce Figure 2

Appendix S5. Model selection table for biomass – grazing – climate models

Appendix S6. Model estimates for the model used to produce Figure 3

Appendix S7. Model selection table for biomass – grazing – richness models

Appendix S8. Model estimates for the model used to produce Figure 4

Appendix S9. Model selection tables for the global effects of grazing and precipitation on PFGs

Appendix S10. Model selection tables for the effects of grazing and precipitation on single PFGs

Appendix S11. Summary of the models of the single PFGs

Appendix S12. Comparison of the sums of NDVI values in 2014 and 2015

Appendix S13. Comparison of the NDVI values at the time of sampling against the maximum NDVI within the respective year

Appendix S14. Tables of the sampled biomass of the PFGs

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