Multiple resource limitations explain biomass-precipitation relationships in grasslands

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Abstract

Interannual variability in grassland primary production is strongly driven by precipitation, nutrient availability and herbivory, but there is no general consensus on the mechanisms linking these variables. If grassland biomass is limited by the single most limiting resource at a given time, then we expect that nutrient addition will not affect biomass production at arid sites. We conducted a distributed experiment manipulating nutrients and herbivores at 44 grassland sites in 8 regions around the world, spanning a broad range in aridity. We estimated the effects of 5-11 years of nutrient addition and herbivore exclusion treatments on precipitation sensitivity of biomass (proportional change in biomass relative to proportional change in rainfall among years), and the biomass in the driest year (to measure treatment effects when water was most limiting) at each site. Grazer exclusion did not interact with nutrients to influence driest year biomass or sensitivity. Nutrient addition increased driest year biomass by 74% and sensitivity by 0.12 (proportional units), and that effect did not change across the range of aridity spanned by our sites. Grazer exclusion did not interact with nutrients to influence sensitivity or driest year biomass. At almost half of our sites, the previous year's rainfall explained as much variation in biomass as current year precipitation. Overall, our distributed fertilization experiment detected co-limitation between nutrients and water governing grasslands, with biomass sensitivity to precipitation being limited by nutrient availability irrespective of site aridity and herbivory. Our findings refute the classical ideas that grassland plant performance is limited by the single most limiting resource at a site. This suggests that nutrient eutrophication will destabilize grassland ecosystems through increased sensitivity to precipitation variation.

1   Introduction

The productivity of grassland ecosystems around the world is strongly driven by precipitation. Anthropogenic global change is expected to increase interannual variation in precipitation (Fischer et al., 2013). Aboveground plant biomass in grasslands (henceforth "biomass") is additionally governed by soil resource availability (Fay et al., 2015) and consumption by grazers (Borer, Seabloom, et al., 2014), and both of these should influence how variation in precipitation over time affects biomass production at a site (Huxman et al., 2004; Irisarri et al., 2016). Understanding the nature of this temporal relationship across different sites and regions of the world is crucial for predicting how rainfall variability will interact with other global changes such as nutrient eutrophication (Stevens et al., 2015).

The temporal relationship between annual aboveground biomass and annual precipitation in grasslands has been extensively measured in long-term ecological studies (Hsu et al., 2012; Sala, Gherardi, et al., 2012; Sala, Parton, et al., 1988). Two aspects of this relationship at a site are important to this study. Firstly, the 'sensitivity' of biomass to interannual precipitation variation at a site measures how much biomass changes for a given change in rainfall among years. Secondly, the biomass produced during the driest year for a specific site, and the effects of resource addition treatments on that, gives an understanding of the importance of other resources when water is most limiting (see Figure 1a). Both of these measures (sensitivity and
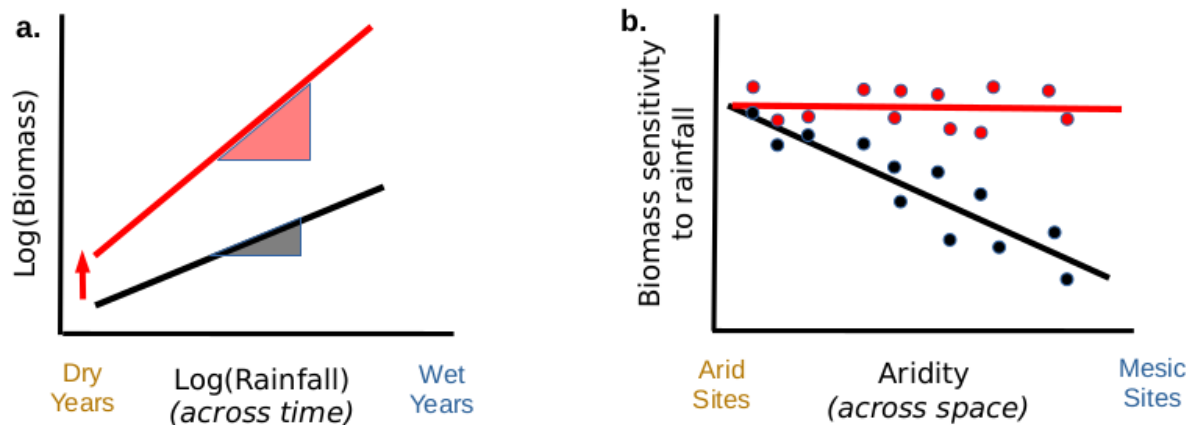
Figure 1: **Expectations of single resource limitation driving grassland sensitivity to rainfall, from Huxman et al. (2004)**. **a.** Nutrient addition is expected to increase both biomass measured in the driest year (b_d), and the precipitation sensitivity S (proportional response of biomass to a change in rainfall), estimated from the graph of biomass vs. precipitation across time at a site. Black denotes the relationship in control plots, red in nutrient added plots. **b.** Across space, precipitation sensitivity is expected to decline from arid to mesic sites. Since sensitivity is already maximum at arid sites, nutrient addition is expected to have no effect on sensitivity at arid sites, but a strong effect at mesic sites.

74   driest year biomass) are expected to vary among sites, especially with relation to site aridity
75   (Bai et al., 2008; Hsu et al., 2012; Huxman et al., 2004). Since limitation by water should be
76   stronger in arid sites, the sensitivity of biomass to precipitation should decrease as we move
77   from arid to mesic sites (Huxman et al., 2004; Sala, Gherardi, et al., 2012, Figure 1b). Mean
78   grassland biomass and driest year biomass should increase as we move from arid to mesic sites
79   (Sala, Gherardi, et al., 2012; Sala, Parton, et al., 1988), though there can be variations in these
80   patterns among grassland regions (Bharath et al., 2020; O'Halloran et al., 2013).

81   However, precipitation-production patterns may depend on nutrient limitation. Most grass-
82   lands are not only limited by water, but also by the supply of available soil nutrients; e.g.,
83   nitrogen or phosphorus (Fay et al., 2015). The degree of nutrient limitation is expected to
84   vary based on the aridity of the site (Yahdjian et al., 2011). Experimental nutrient addition
85   should alleviate limitations, thus increase the sensitivity of biomass to precipitation in mesic,
86   but not arid sites (Figure 1, Bharath et al., 2020; Huxman et al., 2004; Wang et al., 2017).
87   Water availability should primarily limit biomass in dry years, and therefore nutrient addition
88   should have little effect on driest year biomass at arid sites, but increase biomass at mesic sites
89   (Yahdjian et al., 2011). Alternatively, if biomass production of a plant community is equally
90   constrained by multiple resources (Rastetter and Shaver, 1992), nutrient addition can increase
91   biomass production even in dry years at arid sites (Hooper and Johnson, 1999). Examining how
92   alleviation of nutrient limitation interacts with moisture limitation across time and space en-

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ables us to evaluate the utility of the multiple resource limitation framework for understanding grassland productivity.

The effects of herbivory on plant biomass should interact with nutrient availability and precipitation in grasslands (Anderson et al., 2018; Frank et al., 2018; McNaughton et al., 1989). The net effect of grazers on biomass across years at a site can alter biomass-precipitation relationships in different ways. Depending on how consumption by grazers changes between wet and dry years, their exclusion might either increase or decrease sensitivity of biomass to precipitation. If grazers at a site are consuming the additional biomass generated by fertilization, their exclusion will increase the effects of nutrients on sensitivity (Gruner et al., 2008). If grazing enhances production by releasing the plant community from light limitation (Borer, Seabloom, et al., 2014), nutrients will have smaller effects on sensitivity when grazers are excluded. In spite of all these possible mechanisms, the generality and degree to which grazing by mammalian herbivores modulates the relationship between grassland biomass and interannual variation in precipitation has not been quantitatively evaluated (Campbell and Stafford Smith, 2000; Frank et al., 2018).

We quantified how precipitation sensitivity and driest year biomass were affected by 5-11 years of continuous nutrient addition in 44 grassland sites around the world. We also tested whether effects of nutrients were altered by the gradient of aridity among sites and the simultaneous experimental exclusion of vertebrate herbivores (at 36 sites). We specifically examined the following predictions derived from the hypothesis that water is among multiple resources that co-limit grassland productivity –

1. Precipitation sensitivity of biomass will decline from arid to mesic sites (Huxman et al., 2004; Sala, Gherardi, et al., 2012).

2. Nutrient addition will increase precipitation sensitivity at mesic sites but not at arid sites (Huxman et al., 2004).

3. Driest year biomass will increase from arid to mesic sites, as the amount of water received in the driest year is higher at mesic sites as compared to arid sites.

4. Nutrient addition will have no effect on driest year biomass at arid sites, yet will have larger effects at mesic sites (Yahdjian et al., 2011).

5. Herbivore exclusion could increase or decrease the effects of nutrients on precipitation sensitivity.

2 Methods

2.1 Experimental setup

We used data generated within the Nutrient Network (NutNet) experiment, a distributed research cooperative focused on the study of the diversity, productivity, and composition of grasslands worldwide (Borer, Harpole, et al., 2014). Within the network, we selected all sites that had

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129 at least 5 years of biomass data from nutrient treatments, and reliable weather data (described
130 below), which came to a total of 44 sites. Nutrient treatment (N, P, K, and micronutrients
131 added) and fencing were crossed in a factorial design to test for the effects of multiple nutrient
132 limitation and grazing on plant composition and ecosystem function. Experimental plots were
133 5m x 5m in size, with one set of all treatments arranged in a spatial block, and there were 3-6
134 blocks per site. Nutrient addition rates and sources were: 10 g N m^{-2}year^{-1} as timed-release
135 urea [(NH$_2$)$_2$CO], 10 g P m^{-2}year^{-1} as triple-super phosphate [Ca(H$_2$PO$_4$)$_2$], 10 g K m^{-2}year^{-1}
136 as potassium sulfate [K$_2$SO$_4$] and 100 g m^{-2} of a micronutrient mix of Fe (15%), S (14%), Mg
137 (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%), and Mo (0.05%). N, P, and K were applied
138 annually; micronutrients were applied once at the start of the experiment to avoid toxicity (see
139 Borer, Harpole, et al., 2014, for details). The goal of nutrient addition was to overcome resource
140 limitation for plant growth. Each plot was sampled annually for aboveground biomass, clipped
141 from two 0.1 m^2 quadrats per plot, dried to constant mass at 60°C and weighed to the nearest
142 0.01g.

143   At 36 of the 44 sites, we established fences designed to exclude aboveground mammalian
144 herbivores larger than 50 g around two plots in each block, one receiving experimental nutrient
145 addition and one used as an ambient nutrient control plot. Fences were 230 cm tall with the
146 lower 90 cm surrounded by 1-cm woven wire mesh. An additional 30-cm outward-facing flange
147 was stapled to the ground to exclude digging animals (such as rabbits or echidnas), although
148 not fully subterranean animals (such as gophers or mole rats). Four strands of barbless wire
149 were strung at equal vertical distances above the wire mesh. Although most sites built fences
150 exactly to these specifications, 5 sites made minor modifications (described in Appendix S2).

151   2.2   Site selection and weather data

152 We obtained weather data (total precipitation, average monthly maximum and minimum tem-
153 peratures) from the nearest reliable source, validated by PIs to be representative of weather at
154 their site (detailed in Appendix S2). Weather data started at least 3 years prior to the first
155 biomass observations. For 43 sites, this was obtained as daily resolution data from weather
156 stations, for 1 site this was as monthly resolution globally gridded data (see list of sources and
157 methodology in Appendix S2). We used a modified form of the Hargreaves equation (Droogers
158 and Allen, 2002) to estimate total potential evapotranspiration (PET) at the monthly scale for
159 each site. Water availability metrics over the growing season are better predictors of annual
160 biomass than annual precipitation (Robinson et al., 2013). We summed precipitation over the
161 growing season months at each site (henceforth abbreviated to GSP); the months that consti-
162 tute the growing season were determined by site PIs (See Appendix S2: Table S2). We defined
163 aridity of a site as the log$_2$ ratio of mean GSP divided by mean growing season PET at a site.

2.3 Measuring biomass-precipitation relationships

Temporal biomass-precipitation relationships were found to be nonlinear or saturating in many long term studies (Hsu et al., 2012; Rudgers et al., 2018). We examined the relationships between annual aboveground biomass and GSP at each site by log_2 transforming both variables and then fitting linear models to the data. This allowed us to fit nonlinear relationships, meet assumptions of normality for linear models, and prevent model predictions of negative biomass in dry years.

We fit linear mixed effects models of the following form at each site:

$$log_2(Biomass_t) \sim log_2(GSP_t) \times Nutrients \times Fencing + SPEI_{t-1}$$

Peak biomass at year t (log_2 transformed) was the response variable. Predictors were GSP, fencing, nutrient addition, as well as all interactions between the these three, allowing both slope and intercept to vary for each treatment at a site. Legacies of the previous year's precipitation can influence biomass by changing the soil seed bank, bud bank, tiller density, soil nutrient pools or soil moisture availability in the current year (Reichmann et al., 2013; Sala, Gherardi, et al., 2012). Therefore, we included the Standardized Precipitation Evapotranspiration Index (SPEI) calculated over the growing season for the previous year as a predictor variable. The SPEI is a normalized metric of water availability in a given year relative to the precipitation and temperature history of the site. This metric is positive if the previous year was wetter than the mean, and negative if it was drier than the mean. We also included a random effect for blocks within sites, to correctly account for the design of our experiment. All analyses were performed in R version 4.0.0 (R Core Team, 2020).

We measured precipitation sensitivity (S) as the slope of the relationship between log_2(Biomass) and log_2(GSP). A slope value of 1 means that biomass value doubles when precipitation doubles. $S < 1$ indicates that a change in precipitation results in a less than proportional change in biomass, and $S > 1$ indicates a greater than proportional change. Fitted models and parameters are shown in Appendix S1.

Driest year biomass (b_d) was directly estimated as the measured biomass in the driest year during our experiment. We calculated the effects of treatments on this biomass as the log_2 ratio of biomass in treatment plots over control plots in each block, during that driest year.

We also fit linear relationships to the data of biomass and precipitation (Huxman et al., 2004; Irisarri et al., 2016; Verón et al., 2005), to match earlier studies in the literature. These are reported in Appendix S3.

2.4 Examining variation in responses among sites

We then examined the effects of nutrient addition treatments (inside and outside fences) on sensitivity (S) and driest year biomass (b_d) along the gradient of aridity (GSP/PET) among

our sites. We tested 3 possible models of the relationship between response parameters (y) and GSP/PET (x) -

1. A simple linear regression.

2. A linear regression with different intercepts for each region.

3. A linear regression with different slopes and intercepts for each region.

Since there are differences in uncertainty of the response parameters among sites, we carried out weighted linear regressions where the contribution of a data point to the sums of squares during regression was weighted by the inverse of the standard error of that data point.

Four regions in our study had more than 5 sites each, and were amenable to examination of regional relationships. Thus we first fitted all 3 models to the data of 36 sites, located in the regions of Europe (9 sites), Australia (8 sites), North America Pacific Coast (7 sites) and North America Central Plains (12 sites). This excluded sites in North America Montane West (4 sites), South America (2 sites), sub-Saharan Africa (1 site) and Asia (1 site). For each response variable, we used AIC_c based model selection to identify which of these models best describes the data, and report those results. If model selection showed that region was unimportant (models 2 and 3 did not perform well), we then re-fit and reported the results of model 1 on the whole dataset of 44 sites.

We chose this two-stage analyses instead of fitting a linear mixed effect model (MEM) to the global data with random effects for sites. We are interested in examining the variation in biomass-precipitation relationships at many sites. Shrinkage of random parameter estimates towards global means in MEM results in very poor (and in many cases wrong) estimations of biomass-precipitation relationships at individual sites. Global MEM additionally faced convergence issues.

3 Results

Average results across all sites

Across our 44 sites, we found much variation in the shape of biomass-precipitation relationships (Figure 2a). The log-log models used in our study better predicted biomass-precipitation relationships, resulting in 32% less residual variance than the linear models (variance calculated on arithmetic scale for both). The sensitivity of biomass to interannual precipitation at each site (S) varied in value from -1.9 to 4.5, with a median value of 0.35. Positive sensitivity values indicate a constant proportional increase in biomass with increasing precipitation. Fifteen out of 44 sites had negative values of sensitivity, indicating that water was not limiting biomass at those sites, or excess water negatively affected biomass. The driest year biomass (b_d) estimated at each site varied from 18 g m^{-2} to 1003 g m^{-2} (Figure 2b).

Nutrient addition significantly increased driest year biomass (median = + 60%, Wilcoxon signed rank exact test, V = 788, p < 0.001, Figure 3b). It resulted in a marginal, but non-
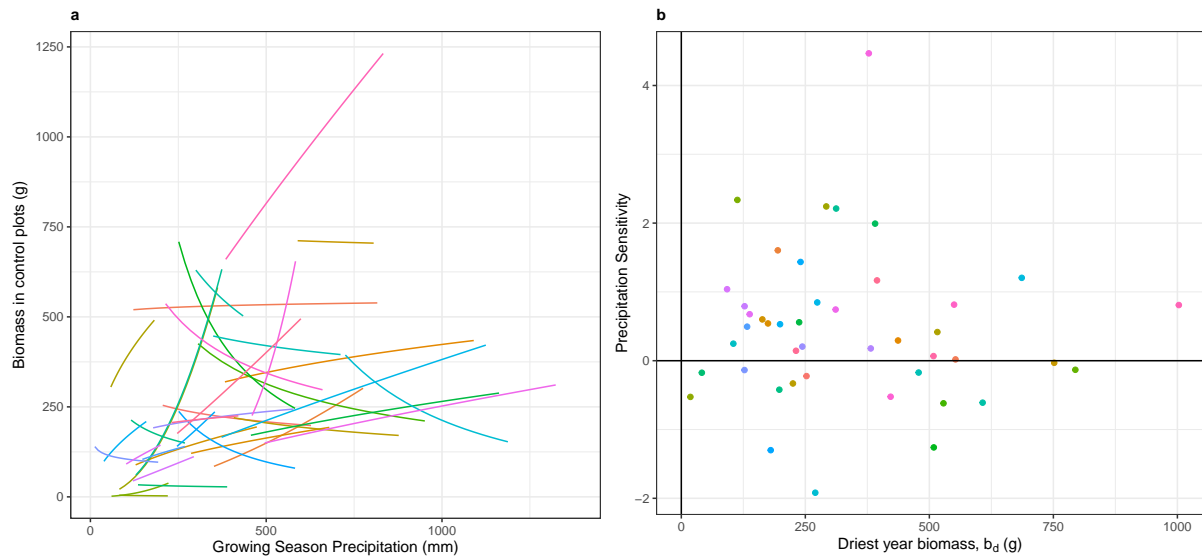
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Figure 2: **Biomass-precipitation relationships in unmanipulated plots at 44 grassland sites.** Relationships were estimated by fitting linear models to log_2 transformed data of both biomass and growing season precipitation (GSP). **a.** Fitted relationships in control plots in our study. **b.** Values of precipitation sensitivity S (proportional response of biomass to a change in rainfall) and biomass measured in the driest year b_d.

significant increase of precipitation sensitivity (median +0.08, V = 640, p = 0.09, Figure 3a). Since our study is on natural temporal variation in precipitation at each site, we also checked whether the observed effect of nutrient addition on driest year biomass depended on how extreme the driest year was at each site. We found that the nutrient effect on b_d was not significantly associated with the $SPEI_gs$ value of that driest year (Appendix S1: Figure S4).

On average, excluding herbivores did not change the effect of fertilization on biomass-precipitation relationships. There was no interaction effect between the nutrient addition and fencing treatments on either sensitivity (median 0.06, V = 360, p = 0.68, Figure 3a) or driest year biomass (median -12%, V = 273, p = 0.35, Figure 3b).

Precipitation in the previous growing season was an important factor for explaining current year biomass at many sites. While the mean effect was not different from zero, there were sites with both strongly positive and strongly negative legacy effects (Figure 3c, Appendix S1: Figure S5). The proportion of total biomass variance explained by legacy effects ranged from 0% to 74% (median 14%, IQR = 5% to 33%). In 21 out of 44 sites (48%), previous year's water availability explained more variance in biomass than current year growing season precipitation.

Changes with site aridity and fencing

Next, we examined how the parameter values of sensitivity and driest year biomass, and the effects of fertilization on both, varied across the aridity gradient.
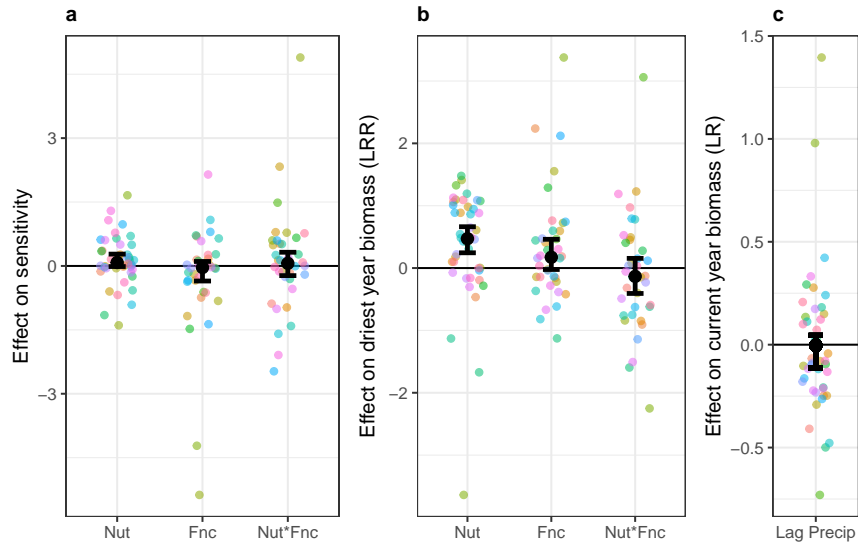
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Figure 3: The effects of nutrient addition (Nut, n = 44), grazer exclusion (Fnc, n = 36), and their interaction (n=36) on biomass - precipitation relationships. Nut and Fnc effects are change relative to control plots. 'Nut*Fnc' denotes the interaction between the two treatments. Error bars denote 95% confidence intervals from Wilcoxon signed rank tests. **a.** The $\log_2$ response ratio of treatment effects on driest year biomass at each site (b_d), **b.** The additive effects of treatments on precipitation sensitivity (S). **c.** The $\log_2$ effect of precipitation in the previous year (measured as SPEI) on current year biomass.

Sensitivity did not significantly change from arid to mesic sites (p =0.4, Figure 4b). Driest year biomass strongly increased from arid to mesic sites (p = 0.02), with arid sites having low biomass and mesic sites having large variation in biomass (Figure 4b).

Nutrient addition increased both driest year biomass and precipitation sensitivity regardless of site aridity (Figure 5b,d). The increase in driest year biomass caused by nutrient addition was constant across the aridity gradient, and was unaffected by the exclusion of grazers (Figure 5c,d). Nutrient addition also increased driest year biomass irrespective of how relatively dry that year was in comparison to the site's climate history i.e. there was no correlation between the nutrient effect on driest year biomass and the SPEI value of that year (Appendix S1: Figure S4). Due to our effects being measured on a $\log_2$ scale, and biomass increasing from arid to mesic sites (Figure 4b), the constant relative nutrient effect corresponds to an absolute increase in the biomass added by nutrients in mesic versus arid sites.

Nutrient effects on biomass sensitivity to precipitation had a larger variance in ungrazed plots as compared to grazed plots ($F_{43,35} = 0.35$, p = 0.001). Nutrient addition marginally increased sensitivity in grazed plots (mean = +0.12, Wilcoxon signed rank test V = 641, p = 0.09), and did not significantly increase sensitivity in ungrazed plots (V = 422, p = 0.16, Figure 5a). The effects of grazers on nutrient addition did not significantly change across the aridity
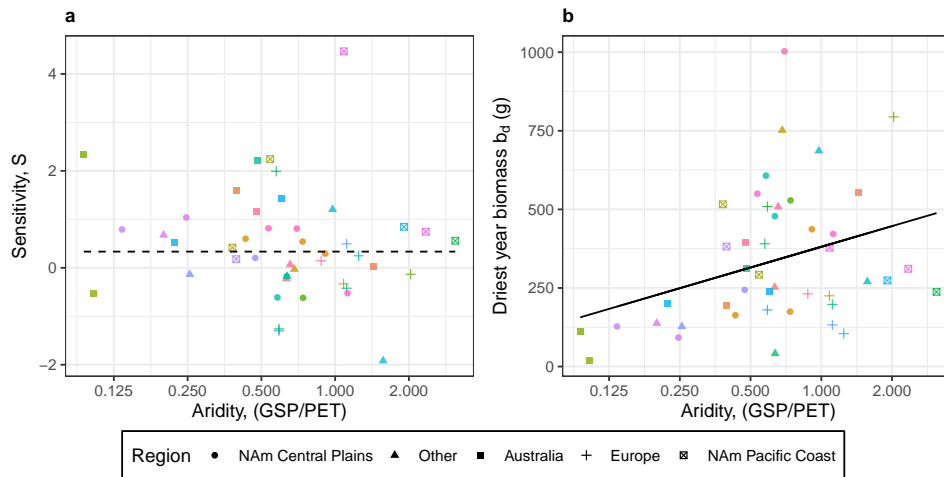
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Figure 4: Change of **a.** precipitation sensitivity (S) and **b.** driest year biomass (b_d) across the gradient of aridity among sites in this study. Aridity is measured by the ratio of mean precipitation to potential evapotranspiration over the growing season at each site. (GSP/PET) < 1 indicates dry sites where evapotranspiration exceeds precipitation, and (GSP/PET) > 1 indicates mesic sites with greater water availability Points denote individual sites, with shape varying by region.
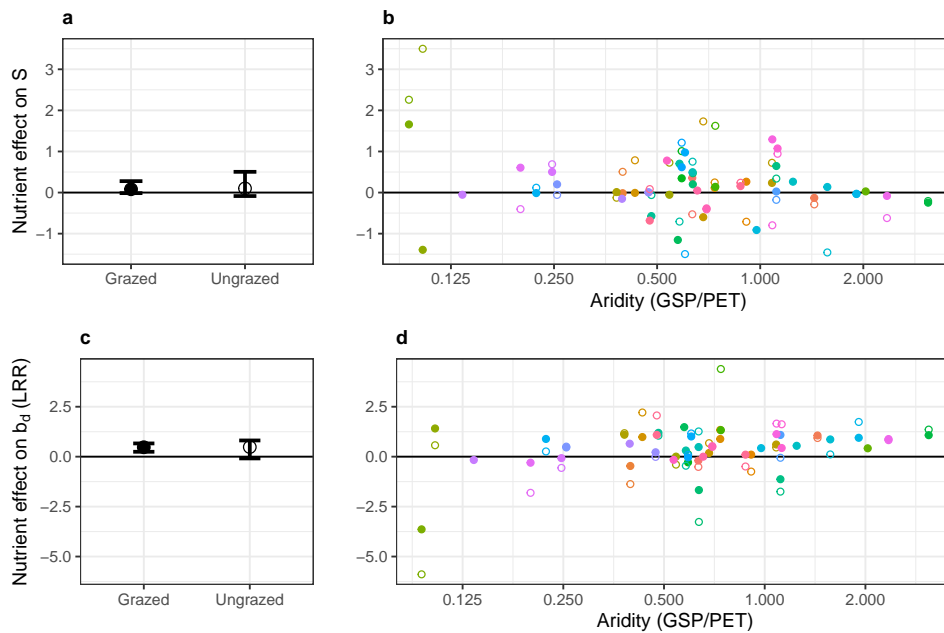

Figure 5: Effect of nutrient addition on sensitivity (a,b) and driest year biomass (c,d) across the aridity gradient among sites and experimental grazer exclusion in this study. Filled points denote mean effects for grazed plots at a site, whereas open points denote fenced plots. Error bars (panels a, c) show 95% confidence intervals estimated from Wilcoxon signed-rank tests. There is no significant relationship between site aridity and any of the response variables.

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268 gradient (Figure 5b). When we estimated sensitivity as the slope of linear biomass-precipitation
269 relationships (units: $gm^{-2}mm^{-1}$), then we found that nutrient addition significantly increased
270 sensitivity in grazed plots (V = 733, p = 0.005, Appendix S3:Figure S2). The linear slope
271 corresponds to the increase in biomass per unit rainfall, whereas our relative sensitivity metric
272 measures the proportional change in biomass for a change in rainfall.

4 Discussion

274 We examined the interaction between spatial and temporal variation in water availability on
275 grassland biomass at 44 sites around the world, and how that was influenced by nutrient addition
276 and herbivore removal. In spite of the significant heterogeneity in all responses, nutrient addition
277 increased both driest year biomass and precipitation sensitivity across the whole range of aridity.
278 This was contrary to our expectation that nutrients would not affect driest year biomass or
279 sensitivity at arid sites. These findings are consistent with models of plant biomass being co-
280 limited by nutrients and water. In almost half of our sites, the previous year's rainfall explained
281 as much variation in biomass as current year precipitation, highlighting the importance of
282 accounting for legacies in estimations of biomass-precipitation relationships (Sala, Gherardi,
283 et al., 2012; Silvertown et al., 1994).

284 Resource co-limitation occurs when primary production is simultaneously limited by multi-
285 ple resources, and shows non-additive responses to factorial resource additions (Harpole et al.,
286 2011; Sperfeld et al., 2016). Species interactions (Danger et al., 2008), optimal foraging by
287 plants (Rastetter and Shaver, 1992), variation in the availability of multiple resources over time
288 (Yahdjian et al., 2011), and the dependence of plant mineral uptake on soil water availabil-
289 ity (Everard et al., 2010; Plett et al., 2020) frequently result in biomass being co-limited by
290 multiple resources. The degree of limitation can vary between different resources, thus leading
291 to biomass in some ecosystems being functionally limited by just a single resource (Fay et al.,
292 2015; Harpole et al., 2011). This underlies the expectation that arid ecosystems are fundamen-
293 tally limited by water, and should be unresponsive to added nutrients in the absence of added
294 water (Eskelinen and Harrison, 2015; Yahdjian et al., 2011). We found that nutrient addition
295 increased driest year biomass at most sites in our study, suggesting that these grasslands are
296 independently responsive to both water and nutrients (as per Harpole et al., 2011) Thus, our
297 study demonstrates the ubiquity of co-limitation between water and nutrients in grasslands
298 across a globally-representative range of aridity.

299 Multiple resource limitation has been proposed as a framework to explain variation in
300 biomass sensitivity to precipitation across aridity gradients (Huxman et al., 2004). Compari-
301 son of site responses across the aridity gradient in our study directly tested and supported this
302 framework, building on earlier meta-analyses (Hooper and Johnson, 1999; Yahdjian et al., 2011).
303 We found that sensitivity did not significantly change between arid and mesic sites, matching

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304 other cross site observational studies (Bai et al., 2008; Hsu et al., 2012). Experimental nutrient
305 addition increased sensitivity all across the gradient of aridity spanned by our sites, refuting our
306 expectations from Huxman et al. (2004) that nutrient addition would have stronger effects at
307 mesic, rather than arid sites. Many studies have sought to undertand the the effects of global
308 change on the stability of grassland ecosystems, by examining the variation of biomass over time
309 in different treatments (Gilbert et al., 2020; Hautier et al., 2014). In this study we focused on
310 one aspect of that variation - how biomass is driven by inter-annual variation in rainfall. Our
311 findings of co-limitation extend our understanding of the controls on grassland ecosystem pro-
312 cesses across space and time, thus providing mechanistic bases for future predictions of grassland
313 responses to global change.

314 Herbivores and climate can influence ecosystems by changing the availability of nutrients
315 and water for plants (Frank et al., 2018). Our fencing treatments enabled us to evaluate the
316 role of grazers in shaping multiple resource limitation of biomass. On average, the effect of
317 nutrients on biomass-precipitation relationships was similar in the presence and absence of
318 grazers. However, excluding grazers both increased and decreased the effect of nutrients on
319 sensitivity (overall increasing the variance of nutrient effects). Excluding grazers can increase
320 nutrient effects on sensitivity if grazers are consuming the additional biomass generated by
321 fertilization (Gruner et al., 2008). Leaf litter can suppress plant growth, and grazers can reduce
322 and remove standing litter, enhancing plant growth (Borer, Seabloom, et al., 2014). In such
323 situations, excluding grazers can dampen the effects of nutrients on biomass sensitivity, which
324 is visible in our study. Fencing also directly affected biomass-precipitation relationships. At
325 some sites, excluding grazers increased the precipitation sensitivity of biomass, implying that
326 grazing dampens the variation in biomass caused due to interannual variation in precipitation.
327 At other sites, excluding grazers decreased precipitation sensitivity, implying that grazing can
328 potentially exacerbate the effects of rainfall change (Staver et al., 2019). Thus, grazer exclusion
329 had context-dependent effects on the interaction between nutrients and biomass precipitation
330 relationships.

331 Our study is the first large scale evaluation of the effects of nutrient addition on the rela-
332 tionship between plant biomass and annual precipitation in grasslands, with sites spanning the
333 range of precipitation variation experienced by global grasslands (Gilbert et al., 2020). Though
334 there was significant variation in the shape of biomass-precipitation relationships across sites,
335 the effects of nutrient addition supports a model of grassland biomass being co-limited by both
336 nutrients and water, irrespective of whether a site is arid or mesic. Thus nutrient eutrophica-
337 tion has the potential to increase temporal biomass variation, reducing the stability of even arid
338 grasslands (Hautier et al., 2014; Sloat et al., 2018). The presence or absence of grazers did not
339 consistently change the resource co-limitation, although grazer effects did vary strongly among
340 sites. Ongoing efforts of coordinating distributed experiments across regions of the world (Borer,
341 Grace, et al., 2017; Knapp et al., 2017) will deepen our understanding of processes, patterns

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342 and contingencies driving ecosystem functions.

5   Acknowledgments

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