

Drivers of Variation in Aboveground Net Primary Productivity and Plant Community Composition Differ Across a Broad Precipitation Gradient

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ABSTRACT

Aboveground net primary production (ANPP) is a key integrator of C uptake and energy flow in many terrestrial ecosystems. As such, ecologists have long sought to understand the factors driving variation in this important ecosystem process. Although total annual precipitation has been shown to be a strong predictor of ANPP in grasslands across broad spatial scales, it is often a poor predictor at local scales. Here we examine the amount of variation in ANPP that can be explained by total annual precipitation versus precipitation during specific periods of the year (precipitation periods) and

nutrient availability at three sites representing the major grassland types (shortgrass steppe, mixed-grass prairie, and tallgrass prairie) spanning the broad precipitation gradient of the U.S. Central Great Plains. Using observational data, we found that precipitation periods and nutrient availability were much stronger predictors of site-level ANPP than total annual precipitation. However, the specific nutrients and precipitation periods that best predicted ANPP differed among the three sites. These effects were mirrored experimentally at the shortgrass and tallgrass sites, with precipitation and nutrient availability co-limiting ANPP, but not at the mixed-grass site, where nutrient availability determined ANPP exclusive of precipitation effects. Dominant grasses drove the ANPP response to increased nutrient availability at all three sites. However, the relative responses of rare grasses and forbs were greater than those of the dominant grasses to experimental nutrient additions, thus potentially driving species turnover with chronic nutrient additions. This improved understanding of the factors driving variation in ANPP within

Received 8 April 2015; accepted 23 October 2015;

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-015-9949-7) contains supplementary material, which is available to authorized users.

Author contributions All authors conceived the study; KJL, DMB, CSB, and JAK performed the research; KJL analyzed the data; KJL wrote the paper with editorial assistance from all authors.

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ecosystems spanning the broad precipitation gradient of the Great Plains will aid predictions of alterations in ANPP under future global change scenarios.

INTRODUCTION

Aboveground net primary productivity (ANPP) is a vital ecosystem process, and ecologists have long been interested in understanding what factors drive patterns of variation in terrestrial productivity (Rosenzweig 1968; Noy-Meir 1973; Sala and Austin 2000). Across broad spatial scales, total annual precipitation has been shown to be a strong predictor of ANPP, particularly in grassland systems (Sala and others 1988; Knapp and Smith 2001; Huxman and others 2004). A well-known example of this pattern is the precipitation-production gradient of the U.S. Central Great Plains, across which production increases from roughly 100–800 g m⁻² with a 500 mm increase in precipitation (Sala and others 1988; Lane and others 1998; Paruelo and others 1999). At smaller spatial scales, limitations by other resources, such as soil nutrient availability, may have greater predictive power in describing variation in ANPP (Ditomaso and Aarssen 1989; Milchunas and others 1994; Gough and others 2000; LeBauer and Treseder 2008; La Pierre and others 2011; Craine and others 2012; Robinson and others 2012).

Variation in ANPP can also be related to total annual precipitation within sites along the Central Great Plains precipitation gradient, but these patterns are often much weaker (Lauenroth and Sala 1992; Briggs and Knapp 1995; Nippert and others 2006). This suggests that total annual precipitation may not be the best predictor of variation in site-level ANPP; rather, examining the effects of precipitation during specific periods of the year (hereafter, “precipitation periods”) may have greater predictive power. This may be particularly true if precipitation amount varies at different times of the year and if growth is seasonal. For example, La Pierre and others (2011) found that ANPP in tallgrass prairie is dependent on precipitation periods that corresponded with vegetative growth and flowering stalk elongation of the dominant C₄ grasses in the system.

Another source of variation in ANPP is the degree to which ANPP is co-limited by precipitation amount and nutrient availability. Interactions between precipitation, nutrient availability, and productivity may be highly variable across ecosystems

Key words: dominant species; Great Plains; nutrients; Nutrient Network (NutNet); rare species; precipitation periods.

(Ditomaso and Aarssen 1989; LeBauer and Treseder 2008; Cleland and Harpole 2010). If soil nutrient availability is tightly coupled with precipitation, such that water and soil nutrients co-limit production, then the relative production responses to nutrient additions should remain constant across a precipitation gradient (Schimel and others 1997; Hooper and Johnson 1999; Gough and others 2000; LeBauer and Treseder 2008). Alternatively, if water and nutrients are sequentially limiting in terrestrial systems, then the relative production responses to added nutrients should vary with precipitation amount, with a limited response in arid systems and a large response in mesic systems (Ditomaso and Aarssen 1989; Hooper and Johnson 1999; Xia and Wan 2008; Cleland and Harpole 2010; Yahdjian and others 2011).

Variation in the plant community across ecosystems may ultimately underlie variation in the response of ANPP to precipitation amount and nutrient availability (Chapin 2003). Indeed, turnover of dominant species has been shown to be a key factor in driving ecosystem responses to resource alterations (Lauenroth and others 1978; Inouye and Tilman 1995; Smith and others 2009; Avolio and others 2014). The identities and abundances of species often vary across environmental gradients due to species adaptations to environmental conditions across the gradient over evolutionary timescales (Sala and others 1988; Adler and Levine 2007), and thus the effects of precipitation and nutrient availability on ANPP may differ across ecosystems due to this variation. Examining differences in the responses of biota to alterations in precipitation and nutrient availability across sites may enhance our understanding of the interactions between these two limiting resources in determining ANPP across the precipitation gradient of the Central Great Plains.

The biota in an ecosystem may interact with precipitation and nutrient availability to affect ANPP. Individual plant-level responses to resource manipulations can rapidly produce ecosystem changes, such as changes in production (Walker and others 1999; Suding and others 2008; Lavorel and Grigulis 2012); however, the magnitude of the ecosystem response is limited by the physiology

and abundance of the species in the community (Smith and others 2009). If the dominant species in a system respond strongly to resource alteration, then a strong ANPP response could be expected. However, theory predicts that the production response of a system to an alleviation in resource limitation should depend on the growth potential of the plant community (Chapin and others 1986; Gough and others 2000; Cleland and Harpole 2010), with species in more arid environments having a lower ability to respond to changes in resource availability due to their inherently lower maximum growth rates (Grime 1977; Tilman 1990; Veron and others 2002). For example, the growth of species in water-limited systems, particularly the dominant species, which contribute most to production, may be less responsive to an alleviation of limiting resources due to their slow growth traits (Grime 1977; Chapin and others 1986; Harpole and Tilman 2006). Over time, however, species change may allow for stronger ANPP responses to resources even in more arid regions, if uncommon species have higher growth rates than dominant species, and therefore greater ability to respond to increased resource availability (Tilman 1987; Milchunas and Lauenroth 1995).

Although it is clear that precipitation and nutrient availability can each play a role in determining patterns of ANPP across a broad range of terrestrial ecosystems, we have an incomplete understanding of what controls the sensitivity of ecosystems to changes in these factors (Smith and others 2009) and how they interact. Here, we test the relative importance of natural variation in these factors in determining ANPP by examining 5 years of productivity data at three grassland sites spanning the broad precipitation gradient of the U.S. Central Great Plains. We expected that precipitation period and soil nutrient availability would be better predictors of ANPP than total annual precipitation at the site level, but that the specific precipitation periods and nutrients would differ among the three sites in their ability to predict variation in ANPP. Our second aim is to determine how nutrient availability interacts with precipitation to drive variation in productivity. We address this by experimentally increasing nutrient availability at each of the three sites to determine whether nutrient availability and precipitation are sequentially limiting or co-limiting (Cleland and Harpole 2010). In addition, we examined which plant species underlie the observed nutrient responses. While either precipitation period or nutrient availability may be the primary determinant of ANPP at each site under unmanipulated conditions,

we predicted that the relative ANPP response to experimental nutrient additions will be equal across all sites. That is, we expected that precipitation and nutrient availability will co-limit ANPP. We further predicted that the dominant plant species will drive the observed production responses to nutrient additions across all sites.

METHODS

Study System

The grasslands of central North America are an ideal system in which to study the factors controlling ANPP. These grasslands span a broad precipitation gradient (318–835 mm per year) from the semiarid shortgrass steppe in the west to the relatively mesic tallgrass prairie in the east. The productivity gradient of the U.S. Central Great Plains reflects this west–east precipitation gradient (Sala and others 1988). This spatial productivity pattern is temporally variable, shifting west in wet years and east in dry years (Sala and others 1988). In addition, plant species richness, as measured by species density, is strongly correlated with precipitation across this gradient (Adler and Levine 2007). Our study focused on three native grassland sites across the precipitation gradient of the Central Great Plains. These sites were located within shortgrass steppe (SGS; Shortgrass LTER, CO), southern mixed-grass prairie (MIX; Saline Experimental Range, western KS), and tallgrass prairie (TGP; Konza LTER, northeastern KS). All three sites are dominated by C_4 grasses and exhibit some overlap in plant species composition.

The SGS site receives an average of 318 mm of precipitation per year, with most of this occurring as rainfall during the growing season (Lauenroth and Burke 2008). The system is open, with large amounts of bare ground; therefore, light is likely not limiting, and competition is primarily for below-ground resources (Risser and others 1981; Lauenroth and Burke 2008). Shortgrass steppe plant communities are comprised of relatively few C_4 grass, forb, and shrub species, with *Bouteloua gracilis* (C_4 grass) and *Carex eleocharis* (C_3 sedge) accounting for the majority of the plant cover and productivity (Risser and others 1981; Lauenroth and Burke 2008). The MIX site is centrally positioned between the shortgrass and tallgrass prairies. The site receives an average of 603 mm of precipitation per year, again with most of this occurring as rainfall during the growing season (Adler and Levine 2007). The system is dominated by the C_4 grasses *Schizachyrium scoparium* and *Sporobolus asper*. Because it is composed of both short and tall

grasses, mixed-grass prairie community composition can vary greatly through time depending on climatic conditions (Risser and others 1981; Adler and Levine 2007). The TGP site is dominated by C_4 grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, and *S. scoparium* (Risser and others 1981; Knapp and others 1998). The flora is diverse and is thought to be controlled by grazing, fire, and the variable climate (Knapp and others 1998). The site receives an average of 835 mm of precipitation per year (Knapp and others 1998), mainly during the growing season. The tallgrass prairie site utilized in this study is under a 2-year burn management regime and was burned in odd years (2007, 2009, and 2011) during this study, with production and richness tending to increase in burned years. However, climate and nutrient effects appear to override the burn effects in both the observational and experimental data presented here.

Experimental Design

This study takes advantage of three sites from an existing network of coordinated experiments—the Nutrient Network (NutNet, <http://www.nutnet.org/>)—which was established to examine multiple resource limitation in herbaceous-dominated systems (Stokstad 2011). Experimental manipulations began at the three NutNet sites examined here in the spring of 2008 and continued through 2012.

At each site, plots were established in a randomized block design ($n = 3$) with a total of 8 nutrient addition treatment combinations per block (control, N, P, K, NP, NK, PK, NPK; $n = 24$ plots per site). Each plot is 5×5 m in area (25 m^2). The nutrient treatments were control (no nutrients added) and nitrogen (N), phosphorous (P), and potassium plus other micronutrients (K), each applied at a rate of $10 \text{ g m}^{-2} \text{ y}^{-1}$. Nitrogen was added as ammonium nitrate in 2008 and as timed-release urea from 2009 to 2012. Phosphorous was added as calcium phosphate and potassium as potassium sulfate. Micronutrients were added as Scott's Micromax fertilizer, with nutrient applications levels as follows: calcium (6 g m^{-2}), magnesium (3 g m^{-2}), sulfur (12 g m^{-2}), boron (0.1 g m^{-2}), copper (1 g m^{-2}), iron (17 g m^{-2}), manganese (2.5 g m^{-2}), molybdenum (0.05 g m^{-2}), and zinc (1 g m^{-2}). The micronutrient treatment was only applied in 2008 to prevent the build-up of these elements in the soil, some of which are toxic to plants at high levels. Nutrients were added at relatively high rates in this experiment to ensure that the treatments would result in the alleviation of nutrient limitation. Nutrient additions occurred

once yearly at the start of the growing season at each site (mid-May) and were applied for 5 years (2008–2012). All three sites examined here were in ungrazed grasslands.

Data Collection

Daily precipitation data were collected from the US Climate Reference Network (USCRN) online database (<http://www.ncdc.noaa.gov/crn/>). Total annual precipitation was calculated for each site as the sum of daily precipitation totals from the end of one growing season to the end of the following growing season (i.e., the sum of precipitation during the five precipitation periods specified below), as opposed to summing precipitation based on the calendar year. By summing precipitation based on the end of the growing season, we were able to obtain a more accurate representation of precipitation that could affect ANPP, whereas summing by calendar year incorporates precipitation that falls after the measurement of productivity has been made (Robinson and others 2012). In addition, precipitation data were aggregated into five precipitation periods (Moore and others 1991; La Pierre and others 2011) that were intended to capture specific phenology and growth phases of the dominant C_4 grasses: dormancy (P1), emergence (P2), vegetative growth (P3), flowering stalk production (P4), and anthesis (P5; see Appendix 1 in Electronic supplementary material for specific dates for each precipitation period).

ANPP was estimated by collecting all above-ground biomass once yearly at each site. Specifically, two 0.1 m^2 quadrats were clipped at ground level within each plot at the time of peak biomass accumulation for each site (August–September). The locations of the clipping quadrats were moved within each plot every year to prevent a clipping effect. Biomass was separated into current year's and previous year's biomass. Current year's biomass was separated to functional group (graminoid, woody, forb, and N-fixing forb) in 2008 and to species in 2009–2012, dried, and weighed. Previous year's growth was sifted to remove soil and rocks, dried, and weighed. ANPP was estimated as the sum of all current year's biomass and was averaged across the two quadrats within each experimental plot for analysis.

Snapshot levels of plant available N, P, and K were determined from soil cores collected from the control plots in June 2009. Three soil cores were collected from along the center of each control plot, each spaced 1 m apart. The soil cores were aggregated by plot and sieved through a 2 mm sieve.

Table 1. Model Descriptions for Four Multiple Regression Models Examining Predictors of Aboveground Net Primary Production (ANPP)

Model #	Model name	Model details
1	Total annual precipitation	ANPP = P _{tot}
2	All abiotic factors	ANPP = P ₁ + P ₂ + P ₃ + P ₄ + P ₅ + N + P + K
3	Precipitation periods	ANPP = P ₁ + P ₂ + P ₃ + P ₄ + P ₅
4	Nutrient availability	ANPP = N + P + K

Models 3 and 4 are subsets of Model 2. Year was included as a random factor in the site-level models and year, site, and site nested within year were included in the cross-site model (not shown in table for simplicity; see text for details).
P_{tot} = total annual precipitation; P₁ = dormant season precipitation; P₂ = precipitation during emergence of the dominant grasses; P₃ = precipitation during vegetative growth of the dominant grasses; P₄ = precipitation during flowering stalk elongation of the dominant grasses; P₅ = precipitation during anthesis of the dominant grasses; N = nitrogen; P = phosphorus; K = potassium and micronutrients.

Potassium chloride extractions were performed on wet sieved soil to obtain available nitrate and ammonium (nitrate and ammonium values were summed to obtain available N). Melich III extractions were performed on dried sieved soil to obtain available P. Ammonium acetate extractions were performed on dried sieved soil to obtain available K.

Statistical Analysis

We tested a total of four mixed-model multiple regressions (Table 1) both across the three sites studied here and within each site to determine which model best explained variation in ANPP. All models were analyzed using multiple regressions and only the control plots (that is, no nutrient additions) were included in these analyses. For all models, year was included as a random factor. Additionally, for each cross-site model, site and site nested within year were included as random factors. Factors that were collinear were removed from the model in a stepwise fashion using BIC to determine the best model. More specifically, within one model type (that is, Model 1, Model 2, and so; see Table 1), collinear variables were removed one at a time and the resulting models were compared using BIC. The model with the lowest BIC within each model type was considered the final model for that type.

No collinearities were observed for the cross-site models. For the TGP models, P₅ was collinear with P₃ and therefore removed from models 2 and 3, and K was collinear with N and therefore removed from models 2 and 4. For the MIX models, P₅ was collinear with P₁ and P₃ and therefore removed from models 2 and 3, and K was collinear with P and therefore removed from models 2 and 4. For the SGS models, P₃ and P₅ were collinear with P₂ and therefore removed from models 2 and 3, and K

was collinear with N and therefore removed from models 2 and 4.

Final models were compared using BIC both across all sites and within each of the three sites to determine which factor(s) best explained variation in ANPP. BIC was used to determine the best model within each site and across all sites, with all models whose BIC was within two of the lowest BIC-value considered equally supported (Raftery 1995). When more than one model was identified as being within two BIC of the lowest BIC-value, the more parsimonious model was selected as the best fit model. Adjusted R^2 was used to determine the amount of variation explained by each model.

To determine whether the response to experimental nutrient additions varied across the precipitation gradient, we compared response ratios (RR) across the three sites using a repeated measures analysis of variance (rmANOVA), with site and N, P, and K treatments as fixed factors and year as the repeated factor. RR were used to determine the magnitude of the ANPP response to nutrient additions for each block, site, and year as follows:

$$RR = (\text{trt}_x - \text{ctl}_x) / \text{ctl}_x,$$

where trt_x is ANPP in a nutrient addition treatment plot (for example, N alone, N + P, N + P+K, and so) in block x and ctl_x is ANPP in the control plot (that is, no N, P, or K added) in block x .

The biomass data that were separated by species from 2009 to 2011 were used to determine whether the responses of specific species affected the ANPP response to nutrient additions at each site. The differences between the control and treatment plots were calculated for each species within each site and year by subtracting the control plot values from the treatment plot values within each block. RRs were calculated for each species' biomass within each site and year, as described above. A repeated measures analysis of covariance (rmAN-

COVA), with year as a repeated factor, species as a fixed factor, and N, P, and K treatments as covariates, was conducted separately for each site. Additionally, a rmANCOVA was conducted separately for each site for species grouped according to dominance and functional type (vegetation classes: dominant C₄ grasses, dominant forbs, rare grasses, and rare forbs), with year as a repeated factor, vegetation class as a fixed factor, and the N, P, and K treatments as covariates. Dominant C₄ grasses and dominant forbs were defined as species that made up greater than 30% of the cover within each category (that is, grasses and forbs, respectively) on average across all plots at a site. The identity of these dominant species were fixed for each site based on the average abundances of the species at the site (that is, a species was considered one of the dominant species at a site if its average cover across all plots was greater than 30% of its category, regardless of its cover within any one plot). All other species were categorized as “rare” grasses or “rare” forbs. Because of the nature of the rank abundance curves for each site, the results presented here did not vary with the use of a more or less strict cutoff for dominant species (20–40%). The rmANCOVAs for each site were performed on both the difference and the RR of ANPP to examine both the absolute and relative responses to nutrient addition treatments. Post-hoc pairwise comparisons of the responses of each vegetation class were performed using Tukey’s HSD test.

For all rmANCOVAs, the null hypothesis was that there is no difference in ANPP difference/RR for each nutrient treatment compared to plots where that nutrient was not added (i.e., N addition plots compared to non-N addition plots, regardless of the P or K treatment). Although interactions among nutrients were tested, no significant interactions were observed and were therefore not included in the models presented here. The mixed effects multiple regressions were performed in R using the lme4 and AICcmodavg packages. All other analyses were performed using SAS version 9.3 (SAS Institute Inc, Cary, NC, USA).

RESULTS

Effect of Natural Variation in Precipitation and Nutrient Availability on ANPP

In the cross-site models, model 1 (total annual precipitation) was the best predictor of ANPP, explaining 86.1% of the variation (Figure 1; Table 2). However, total annual precipitation was not the best predictor of

variation in ANPP for each individual site (Figure 1; Table 2). Rather, precipitation periods of the year and nutrient availability were better predictors of variation in ANPP within sites (Table 2).

For the mesic TGP site, model 3 (precipitation periods) was the best predictor of variation in ANPP, explaining 85.7% of the variation. Specifically, precipitation during the period corresponding to vegetative growth of the dominant C₄ grasses (P3) was by far the best predictor of variation in ANPP within this model, explaining 74.5% of the variation (see Appendix 3 in Electronic supplementary material). For the intermediate MIX site, model 4 (nutrient availability) was the best predictor of variation in ANPP (71.3% of variation explained), with phosphorus availability explaining the majority of the variation in ANPP (51.5%; see Appendix 3 in Electronic supplementary material). For the semiarid SGS site, model 2 (all abiotic factors) was the best predictor of variation in ANPP (87.0% of variation explained). Precipitation during emergence of the dominant grasses (P2) explained 47.4% of the variation, with precipitation during dormancy (P1) and P explaining an additional 17.8 and 13.2% of variation, respectively.

Magnitude of ANPP Response to Nutrient Additions

There was an effect of N and P additions on RR across all three sites (Table 3), indicating that the experimental N and P treatments had a significant effect on ANPP across all sites. However, there were no significant interactions between N or P and site and/or year (Table 3), indicating that the relative magnitude of the ANPP response was constant across sites and years.

Species-Specific Responses to Nutrient Additions

When analyzed separately, no individual species’ biomass significantly responded to nutrient additions at any of the three sites in this experiment (data not shown), perhaps because each individual species was not ubiquitously distributed enough across the replicate plots to provide the statistical power needed to see a change. However, when species were combined into different vegetation classes (dominant grass, dominant forb, rare grass, and rare forb), the groups responded differently to nutrient additions at each site (Figure 2; see Appendices 4 and 5 in Electronic supplementary material). For the mesic TGP site, the difference in biomass between treatment and control plots dif-

Table 2. Results from Multiple Regressions for Three Grassland Sites Spanning the Precipitation Gradient of the U.S. Central Great Plains

		<i>k</i>	Adj. <i>R</i> ²	BIC
Across sites				
1	Total annual precipitation	1	0.861	560.81
2	All abiotic factors	6	0.872	572.70
3	Precipitation periods	4	0.871	565.18
4	Nutrient availability	2	0.892	568.72
TGP				
1	Total annual precipitation	1	0.851	177.48
2	All abiotic factors	6	0.863	175.14
3	Precipitation periods	4	0.857	170.29
4	Nutrient availability	2	-0.863	183.47
MIX				
1	Total annual precipitation	1	-0.027	189.48
2	All abiotic factors	6	0.759	181.30
3	Precipitation periods	4	0.201	193.85
4	Nutrient availability	2	0.713	180.72
SGS				
1	Total annual precipitation	1	0.714	162.62
2	All abiotic factors	5	0.870	147.92
3	Precipitation periods	3	0.720	154.04
4	Nutrient availability	2	0.869	158.42

See Table 1 for model descriptions. Bold text indicates the best model within each grouping, based on BIC (lowest BIC-value within 2; where more than one model is within 2 of the lowest BIC-value, the most parsimonious model is considered the best model). Note that these models may not include all variables listed in Table 1, as some variables were removed from select models due to collinearities; see text for details.

TGP = tallgrass prairie = MIX: mixed-grass prairie; SGS = shortgrass steppe.

Table 3. Results of a rmANCOVA Examining the Effects of Nutrient Additions on the Relative Production Response (RR) over Five Years (2008–2012) Across Three Grassland Sites Spanning the Precipitation Gradient of the U.S. Central Great Plains

	<i>F</i> -value	df	<i>p</i> value
Nitrogen			
N	28.12	1359	<0.001
Site*N	0.97	2359	0.382
Year*N	2.26	4359	0.063
Site*Year*N	0.79	8359	0.613
Phosphorus			
P	16.49	1359	<0.001
Site*P	1.10	2359	0.335
Year*P	0.72	4359	0.578
Site*Year*P	0.87	8359	0.540
Potassium			
K	0.58	1359	0.448
Site*K	1.97	2359	0.142
Year*K	1.26	4359	0.287
Site*Year*K	0.80	8359	0.602

Significant effects are indicated in bold.

ferred significantly between vegetation classes for N, P, and K, with the dominant grasses exhibiting the greatest response to nutrient additions, and dominant and rare forbs exhibiting no response to

nutrient additions (see Appendices 4 and 5 in Electronic supplementary material; Figure 2A–C). There was also a significant interactive effect of vegetation class on the difference in aboveground

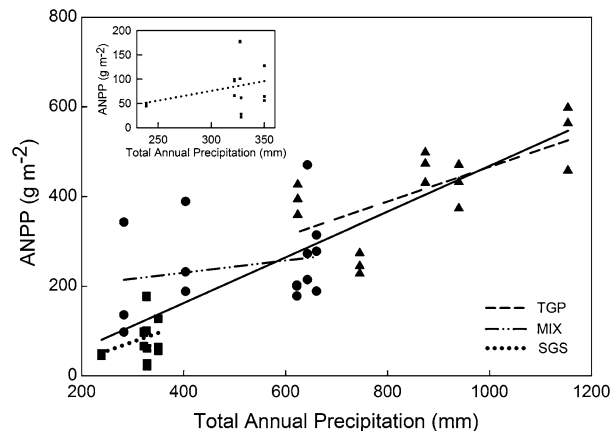


Figure 1. Regression showing the response of ANPP (g m^{-2}) to total annual precipitation (mm) across three sites spanning the precipitation gradient of the U.S. Central Great Plains (*solid black line*). Additionally, regressions were performed within each site to determine the response of ANPP to total annual precipitation in shortgrass steppe (SGS *squares, dotted line*), mixed-grass prairie (MIX; *circles, dashed-dotted line*), and tallgrass prairie (TGP; *triangles, dashed line*). Each point represents one unmanipulated plot within 1 year. *Inset* shows the SGS data in more detail.

biomass with nutrient additions in the intermediate MIX site, with the dominant grasses exhibiting the greatest response to N and K additions (see Appendices 4 and 5 in Electronic supplementary material; Figure 2D–F). Finally, significant interactive effects were observed between vegetation class and N, P, and K additions in the semiarid SGS site. A significant three-way interaction between year, N, and vegetation class was also observed (see Appendices 4 and 5 in Electronic supplementary material), with the dominant grasses increasing in biomass with N additions the most in 2009 and the rare forbs increasing in biomass with N additions in 2010 and 2011. In response to P additions at SGS, the dominant grasses increased the most and the dominant forbs and rare grasses did not respond (see Appendices 4 and 5 in Electronic supplementary material; Figure 2G–H); however, in response to K additions, the rare grasses and rare forbs increased in biomass, while the dominant grasses and forbs did not respond (see Appendices 4 and 5 in Electronic supplementary material; Figure 2I).

When examining the RR of the vegetation classes in response to nutrient additions, a significant vegetation class by N interaction was observed for TGP (see Appendices 4 and 5 in Electronic supplementary material; Figure 2A), with the rare forbs response being the greatest and the dominant grasses not responding. In MIX, the rare forbs and

rare grasses increased the most with P additions (see Appendices 4 and 5 in Electronic supplementary material; Figure 2E). In SGS, significant vegetation class by N and K interactions were observed (see Appendices 4 and 5 in Electronic supplementary material; Figure 2G, I), with the relative response of the rare forbs to N being the highest and the relative responses of the rare forbs and rare grasses to K being the highest, with no response to N or K by either the dominant grasses or forbs.

DISCUSSION

We found that the total annual precipitation predicted a significant amount of variation in ANPP across the U.S. Central Great Plains, consistent with previous studies examining the effects of precipitation on ANPP across environmental gradients (Figure 1) (Sala and others 1988; Lane and others 1998; Knapp and Smith 2001; Huxman and others 2004). However, as we hypothesized, at the site level, we found that precipitation periods and nutrient availability explained variation in ANPP better than total annual precipitation (Table 2). At both the semiarid and mesic ends of the precipitation gradient, precipitation period rather than total annual precipitation played the dominant role in driving temporal variation in ANPP.

In SGS, precipitation during the emergence of the dominant grasses (P2) explained the majority of the temporal variation in ANPP (see Appendix 3 in Electronic supplementary material). However, because precipitation during vegetative growth and anthesis (P3 and P5, respectively) were collinear with precipitation during emergence at the SGS site, the direct effects of precipitation during each of these periods cannot be determined from the data presented here. Arguments have previously been put forward for the importance of precipitation during emergence and vegetative growth in semiarid systems. Specifically, precipitation at the beginning of the growing season (P2) provides a larger base supply of water for the growing season (that is, “filling the bucket”, *sensu* Knapp and others 2006). Particularly in semiarid systems, this extra base of water could result in an earlier start to the growing season or sustained growth in the absence of rainfall during the season, thus affecting ANPP (Schwinning and Sala 2004). Additionally, precipitation during vegetative growth (P3) likely plays a role in determining the length of the growing season and can directly impact plant growth and reproduction (Schwinning and Sala 2004; Wilcox and others 2015). However, further experimental research is needed to tease apart the

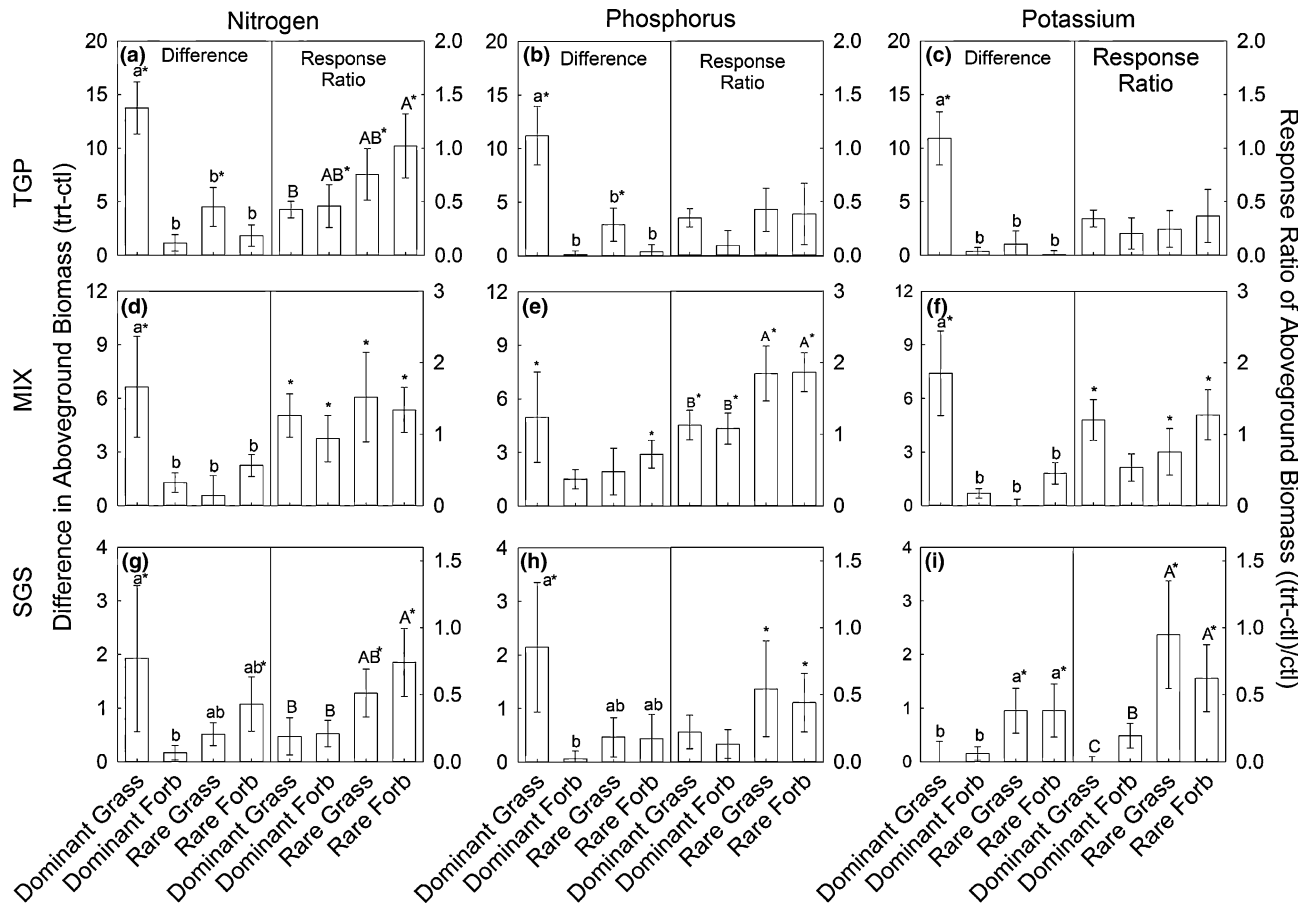


Figure 2. The difference (*left*) and response ratio (*right*) of aboveground biomass of four vegetation classes (dominant grasses, rare grasses, dominant forbs, and rare forbs) to nitrogen (panels **A**, **D**, and **G**), phosphorus (panels **B**, **E**, and **H**), and potassium plus micronutrient (panels **C**, **F**, and **I**) addition treatments across three grassland sites spanning the precipitation gradient of the U.S. Central Great Plains (*TGP* = tallgrass prairie, panels **A–C**; *MIX* = mixed-grass prairie, panels **D–F**; *SGS* = shortgrass steppe, panels **G–I**). Significant differences in response to the nutrient addition treatments among the vegetation classes is indicated by the *lowercase* (difference) and *uppercase* (response ratio) letters. Significant differences from zero are indicated with *asterisk*. Shown are means \pm standard errors.

direct and interactive effects of precipitation during emergence, vegetative growth, and anthesis on ANPP in SGS.

In TGP, precipitation during vegetative growth (P3) explained the vast majority of temporal variation in ANPP (see Appendix 3 in Electronic supplementary material). The effect of precipitation during vegetative growth on ANPP in TGP is consistent with previous findings from this system (La Pierre and others 2011). Flowering stalk production of two of the dominant C_4 grasses in tallgrass prairie has been shown to be a major component of primary production, with an increase in flowering stalk production during high precipitation years contributing to an increase in ANPP (La Pierre and others 2011). Therefore, favorable soil moisture conditions driven by precipitation during vegeta-

tive growth may trigger increased flowering in the dominant species, resulting in increased ANPP. Although precipitation during vegetative growth and anthesis (P3 and P5, respectively) were collinear in our model, previous experimental work directly manipulating precipitation amount and timing in the TGP system studied here indicates that precipitation during vegetative growth is a strong determinant of ANPP through its effect on flowering stalk production (Dietrich 2015). However, further work investigating the role of precipitation during anthesis (P5) is needed to evaluate its direct effects on ANPP. The results from SGS and TGP confirm the importance of the growing trend to examine intra-annual timescales when describing how precipitation influences production (Ditomaso and Aarssen 1989; Milchunas

and others 1994; Gough and others 2000; Jobbágy and Sala 2000; Chou and others 2008; LeBauer and Treseder 2008; Muldavin and others 2008; La Pierre and others 2011; Robinson and others 2012).

In contrast to the sites at the ends of the precipitation gradient, ANPP in MIX was less sensitive to temporal variation in annual or seasonal precipitation, and more sensitive to spatial variation in nutrient availability. MIX is an ecotone between TGP and SGS, with semiarid and mesic-adapted species coexisting in a complex spatial array (Risser and others 1981; Adler and others 2006). As a result, production in dry years can be driven by semiarid-adapted species and simultaneously limited by mesic-adapted species, whereas production in wet years can be driven by mesic-adapted species and simultaneously limited by the semiarid-adapted species. Therefore, temporal variation in ANPP is likely buffered from fluctuations in precipitation due to the mixed nature of the MIX plant community. In the absence of strong temporal variation in ANPP, we found that natural spatial variation in P and/or K availability (which were collinear in our model) was the primary determinant of ANPP in MIX (see Appendix 3 in Electronic supplementary material). This response may be due to the high abundance of *Psoralea tenuiflora*, a putative nitrogen-fixing legume, within this system. The high abundance of a nitrogen-fixer likely increases N cycling in mixed-grass prairie, thereby increasing the demand for P, K, and micronutrients. Additionally, the soils at MIX are lower in P than those in SGS (see Appendix 2 in Electronic supplementary material), further explaining the result that P availability may drive variation in ANPP at this site. Interestingly, our experimental nutrient addition treatments revealed an increase in absolute biomass of the dominant grasses with K additions, while all vegetation classes exhibited positive relative responses to P additions. These responses indicate that P and K may be important drivers of ANPP the MIX system, as has been recently shown for grasslands worldwide (Fay and others 2015).

Although ANPP at the SGS and TGP sites responded most strongly to natural temporal variation in precipitation, we did find evidence for limitation by N and P at all three sites when these nutrients were experimentally added at relatively high levels (Table 3). Additionally, our results showed that relative production responses to nutrient additions were consistent across the precipitation gradient of the Central Great Plains (Table 3). These results suggest that responses to altered nutrient availability are not restricted by precipitation levels across these three sites. Rather,

both precipitation and nutrients appear to co-limit ANPP under our experimental framework in SGS and TGP, as increases in either precipitation or N and P availability independently resulted in increases in ANPP. However, it is important to note that the levels of nutrients added in this experiment were quite high ($10 \text{ g m}^{-2} \text{ y}^{-1}$) relative to natural variation in nutrient availability at these sites. Thus, under natural conditions, or even reasonable global change scenarios, precipitation is likely the dominant driver of variation in ANPP at the SGS and TGP sites studied here. In contrast, ANPP at the MIX site appears to be primarily limited by natural variation in nutrient availability, with a more limited role of precipitation.

The dominant C_4 grasses responded the most in absolute biomass to nutrient additions at all three sites (Figure 2). This is due to the higher initial biomass of the dominant grasses at each site. Because the dominant grasses had a greater initial abundance, they were better able to respond to nutrient additions in the absolute sense (that is, a priority effect; Houseman and others 2008). The observed increase in the dominant grasses was much greater than the absolute increases in biomass of the other vegetation classes with the addition of all nutrients in TGP. However, in MIX and SGS the absolute production responses of the rare species were more similar in magnitude to those of the dominant grasses in response to N and P additions, although still lower. This production response of the rare species may be augmenting the ANPP response of these more xeric systems, thus resulting in similar proportional responses to nutrient additions across all systems, despite the lower intrinsic growth rates of the dominant grasses in the dry-adapted systems.

The rare species at these sites were, by definition, less abundant than the dominant species; therefore, in most cases, the rare species exhibited a lower absolute production response to the experimental nutrient additions than the dominant grasses. However, the rare species often had a higher relative production response (RR) to the experimental nutrient additions than the dominant C_4 grasses (Figure 2). That is, the rare species performed better than the dominant grasses with experimental nutrient additions relative to their initial abundance in the community. These differences in the RR of the dominant versus rare species may either be trait-based (that is, the rare species have traits that allow them to better respond to nutrient additions, such as annual growth forms, and rapid nutrient uptake and utilization.) or due to the limitation of the dominant species by other

resources (for example, space), thus reducing their potential to respond disproportionately to their initial abundances (Chapin and others 1986; Braakhekke and Hooftman 1999; Suding and others 2005; Harpole and Tilman 2007; Hautier and others 2009). Overall, the greater RR of the rare species provides evidence that a priority effect limits the response of the rare species to resource limitation, rather than asymmetrical competitive interactions with the dominant plant species (Ditommasso and Aarssen 1989).

The absolute response of the rare species at each site did not drive the observed ANPP response to experimental nutrient additions because of their low initial abundance in the community. However, over time with chronic nutrient additions, the rare species could come to dominate at each of the three sites as they overcome the priority effect (Lauenroth and others 1978; Inouye and Tilman 1995; Milchunas and Lauenroth 1995; Avolio and others 2014). Once this species turnover occurs, then the current rare species will be the ones that drive the ANPP response to the experimental nutrient additions. This appeared to be occurring rapidly in SGS, where the dominant grasses showed the greatest absolute biomass response to nutrient additions in 2009, but the rare grasses and forbs showed the greatest absolute biomass response to nutrient additions in 2010. In SGS, 2009 had higher than average precipitation during the growing season, which likely resulted in greater seed set of the rare species in the system, similar to the response seen in response to experimental N and water manipulation at the site (Milchunas and Lauenroth 1995). Thus, in 2010, the rare species were able to overcome the priority effect and drive the ANPP response to the nutrient addition treatments, which was then maintained for the duration of the experiment regardless of precipitation amount. The rare species that increased in abundance with the experimental nutrient additions at all three sites studied here tend to be fast-growing, weedy species. The fast-growing growth strategy of these rare species contrasts with the slow-growing, resource conservation strategies of the current dominant species at this site (Sims and others 1978; Lauenroth and Burke 2008). Thus, once they become dominant in the community, their different traits will likely have a large effect on variation in ANPP (Milchunas and Lauenroth 1995; La Pierre and Smith 2015).

Global changes, such as climate change and nutrient deposition and runoff, are affecting nutrient and water availability worldwide (Vitousek and

others 1997; Solomon and others 2007). These factors may, in turn, have a large effect on grassland production. Predicting production responses, however, will require an understanding of how the importance of these factors varies by ecosystem type, depending on the sensitivity of each system. Here we found that while the specific nutrients and the timing of precipitation that drove variation in ANPP differed among the sites across the precipitation gradient, precipitation and nutrient availability do co-limit ANPP at each site across the broad precipitation gradient of the U.S. Central Great Plains. We also found that dominant species drove the ANPP responses to nutrient additions due to a priority effect, but that the rare species exhibited a greater production response relative to their initial abundance in the community. Thus, as species turnover occurs with chronic nutrient additions (Smith and others 2009), the ANPP response observed will likely shift to be driven by particularly responsive species that are typically rare in the community. As a result, our ability to predict variation in ANPP both within and across sites could be severely impaired. Overall, a better understanding of the factors driving variation in ANPP across different spatial and temporal scales will aid predictions of alterations in ANPP under future global change scenarios. Our study suggests that a combined approach of incorporating spatial and temporal drivers of ANPP within and among sites will enhance our ability to predict changes in key ecosystem processes, such as ANPP, at local to regional scales.

ACKNOWLEDGEMENTS

Thanks are due to M. Avolio, C. Blair, C. Chang, C. Davis, L. Dev, K. Harmony, J. Kray, S. Koerner, A. Kuhl, A. Monty, P. O'Neil, M. Parsons, R. Ramundo, T. Schreck, and the SGS field crew for field assistance. M. Avolio, K. Gross, D. Post, O. Schmitz, and two anonymous reviewers provided helpful feedback on earlier drafts of the manuscript. K. La Pierre was supported by an NSF Graduate Research Fellowship. Additional funding was provided by a Yale Institute for Biospheric Studies Center for Field Ecology Pilot Grant to K. La Pierre, Konza Prairie LTER (NSF-DEB-0823341), and Shortgrass Steppe LTER (NSF-DEB-1027319). This work was generated using data from three sites within the Nutrient Network, coordinated through Research Coordination Network funding from NSF to E. Borer and E. Seabloom (NSF-DEB-1042132). Nitrogen fertilizer was graciously donated by Crop Production Services, Loveland, CO.

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