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Secondary production of the central rangeland region of the United States

Edward J. Raynor¹  | Justin D. Derner² | Melannie D. Hartman³  |
 Christopher D. Dorich³ | William J. Parton³  | John R. Hendrickson⁴ |
 Keith R. Harmony⁵ | Jameson R. Brennan⁶ | Clenton E. Owensby⁷ |
 Nicole E. Kaplan⁸  | Susan M. Lutz² | David L. Hoover⁸  | David J. Augustine⁸

¹AgNext, Department of Animal Sciences, Colorado State University, Fort Collins, Colorado, USA

²Rangeland Resources and Systems Research Unit, US Department of Agriculture–Agricultural Research Service, Cheyenne, Wyoming, USA

³Natural Resource Ecology Lab, Colorado State University, Fort Collins, Colorado, USA

⁴Northern Great Plains Research Laboratory, US Department of Agriculture–Agricultural Research Service, Mandan, North Dakota, USA

⁵Agricultural Research Center, Kansas State University, Hays, Kansas, USA

⁶West River Agricultural Center, South Dakota State University, Rapid City, South Dakota, USA

⁷Department of Agronomy, Kansas State University, Manhattan, Kansas, USA

⁸Rangeland Resources and Systems Research Unit, US Department of Agriculture–Agricultural Research Service, Fort Collins, Colorado, USA

Correspondence

Edward J. Raynor

Email: edwardraynor@gmail.com

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Abstract

Rangelands are the dominant land use across a broad swath of central North America where they span a wide gradient, from <350 to >900 mm, in mean annual precipitation. Substantial efforts have examined temporal and spatial variation in aboveground net primary production (ANPP) to precipitation (PPT) across this gradient. In contrast, net secondary productivity (NSP, e.g., primary consumer production) has not been evaluated analogously. However, livestock production, which is a form of NSP or primary consumer production supported by primary production, is the dominant non-cultivated land use and an integral economic driver in these regions. Here, we used long-term (mean length = 19 years) ANPP and NSP data from six research sites across the Central Great Plains with a history of a conservative stocking to determine resource (i.e., PPT)–productivity relationships, NSP sensitivities to dry-year precipitation, and regional trophic efficiencies (e.g., NSP:ANPP ratio). PPT–ANPP relationships were linear for both temporal (site-based) and spatial (among site) gradients. The spatial PPT–NSP model revealed that PPT mediated a saturating relationship for NSP as sites became more mesic, a finding that contrasts with many plant-based PPT–ANPP relationships. A saturating response to high growing-season precipitation suggests biogeochemical rather than vegetation growth constraints may govern NSP (i.e., large herbivore production).

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Differential sensitivity in NSP to dry years demonstrated that the primary consumer production response heightened as sites became more xeric. Although sensitivity generally decreased with increasing precipitation as predicted from known PPT–ANPP relationships, evidence suggests that the dominant species' identity and traits influenced secondary production efficiency. Non-native northern mixed-grass prairie was outperformed by native Central Great Plains rangeland in sensitivity to dry years and efficiency in converting ANPP to NSP. A more comprehensive understanding of the mechanisms leading to differences in producer and consumer responses will require multisite experiments to assess biotic and abiotic determinants of multi-trophic level efficiency and sensitivity.

KEYWORDS

aboveground net primary production, *Bouteloua gracilis*, differential sensitivity, large grazer production, net secondary production, *Poa pratensis*, regional trophic efficiency

INTRODUCTION

For decades, grassland ecologists have examined the ways in which precipitation (PPT) drives variability in aboveground net primary productivity (ANPP) across space and time (Hoover et al., 2023; Huxman et al., 2004; Knapp et al., 2017; Knapp & Smith, 2001; Sala et al., 1988). Grasslands of central North America are characterized by a broad spatial west-to-east gradient of increasing mean annual precipitation, and a north-to-south gradient in mean annual temperature, which in turn creates a linearly increasing west-to-east gradient in ANPP, and a north-to-south gradient in dominance of C_3 versus C_4 grass species (Epstein et al., 1997; Lauenroth et al., 1999). Despite some covariance in the precipitation and temperature gradient, as well as covariance in the precipitation and soil nitrogen availability gradient, the strong positive, linear relationship with mean annual precipitation (MAP) is overwhelmingly the most important driver of spatial variation in ANPP across the region (Epstein et al., 1997; Lauenroth et al., 1999; Sala et al., 1988). Hereafter we refer to this as the spatial PPT–ANPP model (Sala et al., 1988). The central North American grasslands are also characterized by substantial temporal variability in the timing, size, and frequency of precipitation events, which in turn drives local temporal variability in ANPP. Lauenroth and Sala (1992) showed that the slope of the local temporal model for PPT–ANPP is substantially lower than the slope of the regional spatial model, as productivity responses at a given locality are constrained temporally by the pool of plant species present and their collective capacity to respond to droughts and deluges. Across gradients encompassing arid to mesic grasslands and shrublands worldwide, the temporal PPT–ANPP model has been shown to have a

consistently lower slope than the spatial model (Sala et al., 2012). This difference in slopes between spatial versus temporal models arises from legacies that constrain the temporal response of ecosystems to PPT, whereby wet years led to greater than expected ANPP in the subsequent year, and dry years led to lower than expected ANPP in the subsequent year (Sala et al., 2012). Such temporal legacies are thought to arise from shifts in structural attributes of the plant community, such as changes in plant and meristem density, and belowground biomass storage (Oesterheld et al., 2001; Sala et al., 2012).

Despite the fact that livestock production is the primary land use in the remaining non-cultivated grasslands of this region, with animals converting available plant material into high-quality protein (Augustine et al., 2021; Vitousek et al., 1986), most of the literature on PPT–ANPP relationships have focused on ungrazed grasslands (Huxman et al., 2004; Knapp & Smith, 2001); little consideration has been given to how livestock grazing and its management may affect either temporal or spatial models (Sala et al., 2012). Temporal relationships between PPT, ANPP, and net secondary production (NSP; primary consumer production) have been examined at only a handful of individual long-term research sites (Craine et al., 2009; Derner et al., 2020; Smart et al., 2010). To date, regional analyses are lacking which have examined whether temporal versus spatial models for NSP are consistent with ANPP responses for the central North American grasslands.

This paucity of understanding secondary production response to PPT variability is surprising given its importance from climatological, ecological, and socioeconomic perspectives. In this era of unprecedented climate change (Cook et al., 2015; Pörtner et al., 2022), including

increasing temporal variability and unpredictability in precipitation, improved understanding of controls over NSP in addition to ANPP is needed as both trophic levels act as integrators of terrestrial ecosystem structure and function (Briske et al., 2015; Fahey & Knapp, 2007). Relationships between PPT and NSP may not follow patterns for ANPP because factors beyond the amount of precipitation can control NSP. For instance, diversity in species composition, timing, and quality of herbivore forage resources influences their productivity (Fynn, 2012).

We examined long-term measurements of ANPP and NSP from six long-term research sites: the USDA Agricultural Research Service (ARS) Central Plains Experimental Range near Nunn, Colorado; the USDA ARS High Plains Grasslands Research Station near Cheyenne, Wyoming; the South Dakota State University Cottonwood Field Station near Cottonwood, South Dakota; the USDA ARS Northern Great Plains Research Laboratory near Mandan, North Dakota; the Kansas State University Agricultural Research Center near Hays, Kansas; and the Rannells Flint Hills Prairie Preserve near Manhattan, Kansas (Figure 1). All sites have long-term observations of daily PPT, ANPP and yearling cattle (*Bos taurus*, a primary consumer) weight gains managed under moderate grazing intensity (Dorich et al., 2021). Our analysis focused on the relationships among PPT, ANPP, and NSP. Understanding these relationships should help improve production forecasting and aid managers in reducing uncertainty in decision-making for management practices to meet future human population protein needs as climate variability increases (Briske et al., 2015; Espeland et al., 2020; Shrum et al., 2018).

Here, we examine the PPT–ANPP and PPT–NSP relationships in rangelands that maintain a moderate grazing intensity level, allowing inspection of relationships given a standard and consistent livestock management practice in the Great Plains (Briske et al., 2011). We note that this differs from NSP in unmanaged ecosystems, in that livestock densities do not vary dramatically from year to year in response to variation in reproduction or mortality rates. As a result, temporal legacies in NSP cannot arise from lagged population dynamics in these managed rangelands. Rather, variation arises from how a consistent density of herbivores responds to resource variation in terms of their individual growth rate. First, we explored the relationships of interannual precipitation to ANPP and NSP (beef cattle weight gain), that is, the temporal model, to determine whether similar site-level (within-site) relationships existed across the sites. Next, we examine how ANPP and NSP respond to regional variation in PPT, that is, the spatial model, and compare our findings to previously published

temporal versus spatial PPT–ANPP relationships for these grasslands.

Our second objective determined NSP sensitivity to PPT in dry years, which are hydrological conditions that limit or co-limit resource production in some biomes more than others, as shown for ANPP (Knapp & Smith, 2001; Seddon et al., 2016). For example, plants in arid ecosystems tend to be smaller, with inherently slower absolute growth rates and reduced plant and meristem densities relative to those in more mesic ecosystems (Huxman et al., 2004; Knapp & Smith, 2001). This “vegetation constraint” results from ANPP response to excess PPT in arid ecosystems (Lauenroth & Sala, 1992) where vegetation constraints will be high if the rate of change of leaf-area index of the dominant plants per unit of resource and dominant plant relative growth rate is low. On the other hand, a biogeochemical constraint related to the magnitude of nutrient limitation should be higher toward the wet end of a precipitation gradient than at the dry end as lignin-rich forage with a high absolute growth rate reduces the conversion efficiency of plant biomass to consumer weight gain (Austin & Vitousek, 1998; Paruelo et al., 1999). Thus, we expected NSP sensitivity to be greatest in semiarid grasslands, where increasing ANPP does not lead to as rapid declines in forage digestibility, compared to mesic grasslands, where increasing ANPP leads to more rapid increases in lignin and reduced digestibility. Conversely, declines in ANPP during drought are expected to have a stronger effect on NSP in semiarid systems, where NSP is more limited by food quantity, compared with mesic systems, where quality limitations are stronger. This hypothesis is consistent with predictions by Huxman et al. (2004) for terrestrial ecosystems and, more recently by Bondaruk et al. (2022) for South American rangelands that resource sensitivity to precipitation change will be inversely related to PPT. Testing this prediction is essential for several reasons. First, the Huxman et al. (2004) sensitivity model was based on ANPP responses to interannual PPT variability, which included wet and dry years. However, ANPP may not respond symmetrically to years with above-average and below-average precipitation (Bondaruk et al., 2022; Huxman et al., 2004; Knapp & Smith, 2001; Wilcox et al., 2017). Thus, consumer responses to drought may not be predictable based on general ecosystem sensitivity patterns to PPT as investigated through PPT–ANPP relationships. Second, although the analysis of Huxman et al. (2004) was based on data sets encompassing a range of wet and dry years at each site, sensitivity estimates were based on slopes of precipitation–ANPP relationships rather than on responses to the same magnitude of PPT deviation at all locations. Thus, our sensitivity analysis focuses on years below the 25th percentile of 30-year

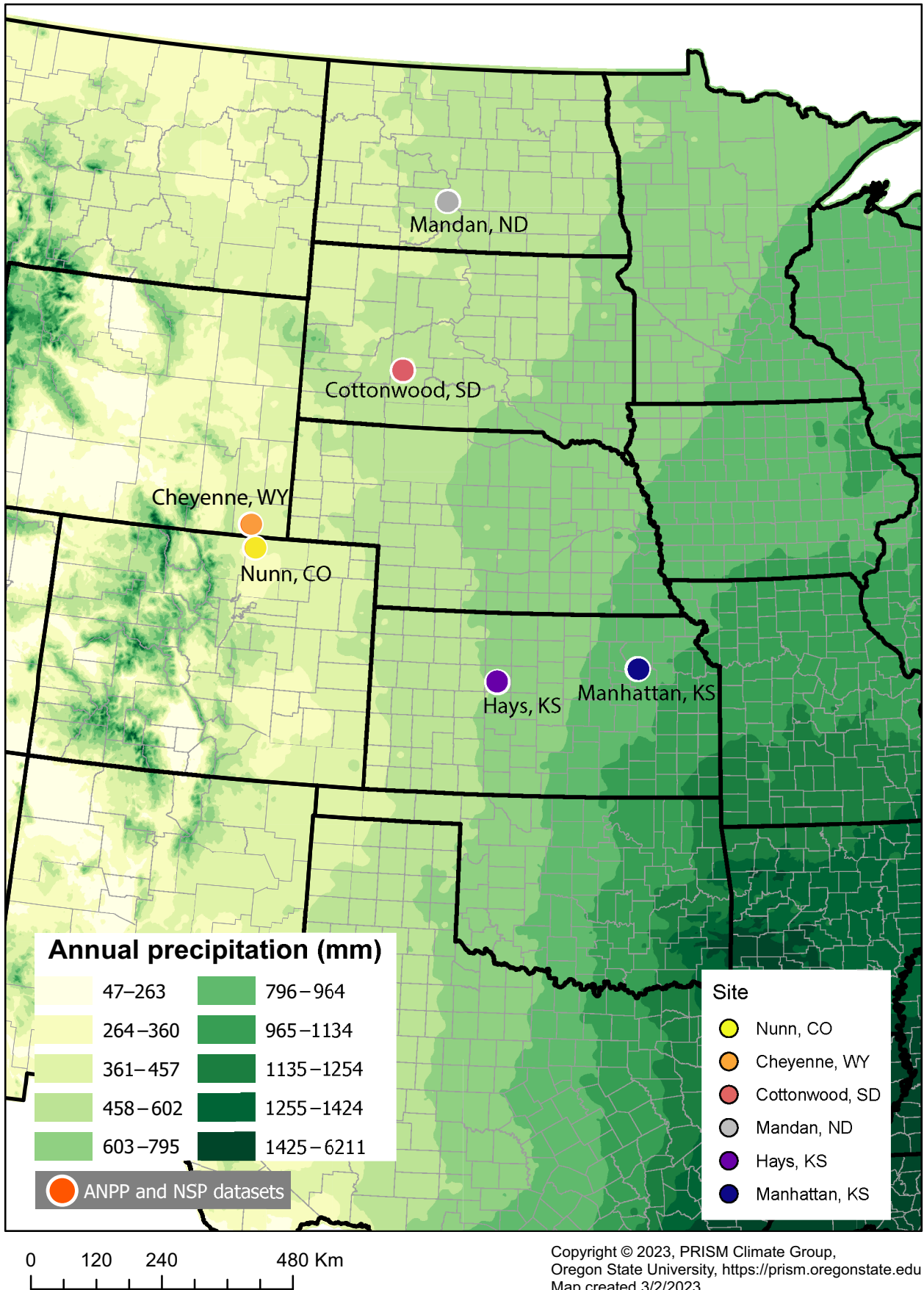


FIGURE 1 Mean annual precipitation for the 1991–2019 study period across the Central Great Plains as calculated by PRISM.

mean site-level precipitation representing dry years in each grassland. The slopes of these resource-product relationships will likely vary depending on the degree of climatic extremes experienced (Knapp et al., 2015). For instance, we expect dry-year NSP sensitivity to be reduced in mesic systems where forage quantity limitations are less severe during drought conditions than in semiarid systems.

For the third objective, we employed annual ANPP and NSP measurements to calculate trophic efficiency (NSP per unit of ANPP) across the resource gradient (Irisarri et al., 2014; McNaughton et al., 1989, 1991). Trophic efficiency is the efficiency at which mass (or energy) is transferred from one trophic level to the next. Three major consolidated factors that can govern NSP are the amount, availability, and suitability of food. Therefore, understanding differences in NSP among ecosystems depends on evaluating ANPP and trophic transfers (or efficiencies; Irisarri et al., 2014; McNaughton et al., 1991). We expect regional trophic efficiency to decline with increasing PPT because biogeochemical limitations in mesic plant communities increase investment in indigestible lignin content of forage for ruminant consumers (Craine et al., 2010; Paruelo et al., 1999). We contrast our results for the trophic efficiency of North American grasslands with those presented by Irisarri et al. (2014) for South American grasslands in light of how plant community composition varies with ANPP across regional spatial gradients in PPT.

METHODS

Study system

We assessed the response of ANPP and NSP to interannual variation of PPT at six North American rangelands (Figure 1, Table 1). This region is dominated by grasslands across a wide range of climatic conditions; annual precipitation varies two-fold from the eastern (~840 mm year⁻¹) to the western Great Plains (~330 mm year⁻¹) (Augustine et al., 2021; Burke et al., 1991; Küchler, 1965), while annual temperature decreases from >15°C in the southern Great Plains to <0°C in the Northern Great Plains (Hartman et al., 2020). These locations encompassed the major grassland types in the Central US Great Plains with blue grama (*Bouteloua gracilis*)-dominated shortgrass steppe (USDA ARS, Central Plains Experimental Range) in northeastern Colorado; northern mixed-grass prairie co-dominated by western wheatgrass (*Pascopyrum smithii*), *B. gracilis* (USDA ARS, High Plains Grasslands Research Station) in southeastern Wyoming; northern mixed-grass prairie co-dominated by *P. smithii*, green needlegrass (*Nassella viridula*), buffalograss (*B. dactyloides*), and *B. gracilis* (South Dakota State University Cottonwood Field Station) near Cottonwood, South Dakota; northern mixed-grass prairie recently dominated by perennial cool-season grasses including Kentucky bluegrass (*Poa pratensis*) in 1995 (Hendrickson et al., 2021; Kleinhesselink et al., 2023); (USDA ARS, Northern Great Plains Research

TABLE 1 Site characteristics for six North American Great Plains rangelands grazed season-long with moderate stocking of yearling cattle.

Site and no. years of measurement	Years	Grassland type	Meters (ASL)	MAP (mm)	PPT (mm; April–August)	ANPP (kg ha ⁻¹)	NSP (kg ha ⁻¹)	Stocking rate (AUM ha ⁻¹)	Average daily gain (kg day ⁻¹)
Nunn, CO (n = 28)	1991–2019	Shortgrass C ₄	1600	316 (151–518)	222 (85–407)	944 (245–2527)	18.4 (7.9–28.0)	0.52	0.87 (0.60–1.1)
Cheyenne, WY (n = 27)	1991–2019	Mixed C ₃ C ₄	2100	437 (246–578)	276 (139–427)	1386 (689–2850)	35.6 (19.1–52.8)	0.91	0.97 (0.76–1.26)
Cottonwood, SD (n = 14)	1997–2019	Mixed C ₃ C ₄	7454	441 (303–665)	302 (160–530)	1891 (696–3335)	38.5 (13.8–55.7)	1.07	0.91 (0.70–1.12)
Mandan, ND (n = 19)	1995–2016	Non-native C ₃	593	488 (270–796)	348 (154–626)	6589 (4111–10,353)	45.7 (23.1–59.2)	1.10	0.92 (0.70–1.35)
Hays, KS (n = 9)	2011–2019	Mixed C ₃ C ₄	600	633 (380–935)	419 (238–572)	3013 (2195–4052)	65.5 (49.4–88.3)	2.50	0.65 (0.54–0.81)
Manhattan, KS (n = 17)	2000–2016	Tallgrass C ₄	324	880 (568–1115)	572 (335–767)	5071 (3274–7035) ^a	88.1 (53.9–114.9)	1.62	0.94 (0.58–1.23)

Note: Mean (range) for site conditions are provided for MAP-NSP.

Abbreviations: ANPP, aboveground net primary production; AUM, animal unit months; MAP, mean annual precipitation; NSP, net secondary productivity; PPT, precipitation.

^aMissing years of ANPP data for Rannells Flint Hills Prairie Preserve were filled with neighboring estimates from Konza Prairie LTER CORE data set PAB01 (Blair & Nippert, 2023).

Laboratory) near Mandan, North Dakota; an ecotone representing shortgrass and mixed-grass prairie co-dominated by sideoats grama (*B. curtipendula*), *P. smithii*, *B. gracilis*, *B. dactyloides* and Japanese brome (*Bromus japonicus*) (Harmony & Jaeger, 2011), (Kansas State University, Hays Agricultural Research Center) near Hays, Kansas; as well as tallgrass prairie co-dominated by big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparium*; Rannels Flint Hills Prairie Preserve) near Manhattan, Kansas (Owensby & Auen, 2018). These study locations have been managed for moderate grazing intensity since the 1940s. Only the Manhattan, KS site is annually burned, a typical management practice for this historically significant process for maintaining tallgrass prairie structure and function (Anderson et al., 1970). Unlike the other study locations, Mandan, ND, is dominated by a single non-native perennial grass species, *P. pratensis*, which may (1) promote consumer production at this site, for example, livestock weight gains (Hendrickson et al., 2021; Reeves et al., 2014), but also (2) hamper plant diversity and concomitantly reduce stability of ANPP under other stresses such as drought (Wagg et al., 2017). Additional site descriptions are available in Appendix S1.

Experimental design

These locations were selected as each had a rare combination of data sets, including PPT, ANPP (in kilograms per hectare), and beef production (NSP, in kilograms per hectare), all with similar livestock management (moderately-stocked pastures grazed with British breed yearlings) (Dorich et al., 2021). ANPP estimates were obtained from clipping plant biomass at peak biomass inside of $\sim 1 \text{ m}^{-2}$ cages that excluded livestock grazing during the current growing season and were moved annually to new locations prior to the start of the growing season. Harvests occurred on representative soils exposed to grazing (in prior years) under a season-long moderate stocking rate. Individual animal weights were measured at the beginning and end of the season. In total, 114 site-years of combined ANPP and NSP measurements were available for individual sites ranging from nine to 28 years beginning in 1991. Precipitation observations collected at each site were pooled to represent the growing-season (April–August) PPT.

Statistical analysis

For our first objective, we explored the relationships of growing-season PPT and ANPP to beef cattle weight gain

(NSP) to determine whether similar relationships existed across sites. We employed two techniques to fit data: simple linear regression and polynomial linear regression of the second degree, to characterize resource-product relationships as linear or curvilinear with increasing resources using the R function, `lm()` (R Development Core Team, 2023). To ensure that studies had sufficient power to detect linear and nonlinear trends, we excluded data sets with fewer than 9 years of simultaneous PPT, ANPP, and NSP data. We conducted each regression technique for temporal (within-site) and spatial (cross-site) models.

Further, we focused analyses on growing-season PPT (April–August; Table 1), which accounts for $\sim 70\%$ of annual PPT across this gradient (Knapp et al., 2015). Growing-season PPT underlies most forage production for cattle production in this grassland biome (Derner et al., 2020; Reeves et al., 2014; Smart et al., 2021; Smith & Owensby, 1978). Spatial (cross-site) models were fitted with site-level means of a product against the site-level means of a resource. To gauge the influence of non-native plant-dominated grazing land on the relationship between resource and production across the Central Great Plains, spatial models were fit with and without the Mandan, ND site.

To quantify the NSP sensitivity of different rangeland ecosystems to variation in PPT, we calculated sensitivity via site-level slopes (product against PPT) and plotted the slopes as a function of PPT (*sensu*; Huxman et al., 2004). We quantified critical ecosystem processes (ANPP, NSP) with comparable methods across six Central Great Plains grasslands (Table 1). Grassland sites ranged from semiarid short- and mixed-grass prairie to mesic tallgrass prairie, and all were exposed to growing-season drought. Analysis of variance was performed to assess differences among year types for NSP sensitivity. We estimated marginal means (least square means) of sensitivity for dry (below 25th percentile), normal (25th to 75th percentile), and wet (above 75th percentile) years using the R function, `emmeans()` (Lenth et al., 2023).

In our estimation of trophic efficiency (E_{troph}) for our third objective, we transformed mass into energy units. We transformed in per kilogram of fresh weight (mean season end weight–mean start weight; NSP) into kilojoule using a conversion factor of 9900 kJ kg^{-1} of fresh weight (Coughenour et al., 1985), while ANPP was transformed into energy units as $16,760 \text{ kJ kg}^{-1}$ dry matter (Golley, 1968). As a result, trophic efficiency was calculated as energy-based NSP/energy-based ANPP (i.e., $E_{\text{troph}} = \text{NSP:ANPP}$; Irisarri et al., 2014). Analysis of variance was performed to assess dry-year NSP sensitivity differences among sites. We estimated the marginal

means of site-level sensitivity and conducted pairwise comparisons.

RESULTS

Temporal and spatial models

Within each individual site, we found the relationships between temporal variation in PPT and ANPP to be linear (Table 2, Figure 2a; that is, the temporal model). We report models based on growing-season (April–August) PPT because these explained more variation in ANPP than models based on annual PPT, which may explain the lower fit of temporal models based on annual PPT reported by Sala et al. (2012). Within-site temporal model slopes varied from a low of 2.37 at Cottonwood, SD to a high of 4.52 kg ha⁻¹ mm⁻¹ at Mandan, ND (Table 2), with a mean temporal slope of 3.42 kg ha⁻¹ mm⁻¹. Two sites, Cottonwood, SD and Mandan, ND, exhibited a curvilinear response to increasing PPT suggesting plant production plateaus at above-average growing-season PPT. Across sites, we also found that spatial variation in mean ANPP was strongly, positively, and linearly related to mean PPT, that is, the spatial model (Figure 2c; $R^2 = 0.399$, slope = 11.33 kg ha⁻¹ mm⁻¹), such that the slope of the spatial model was 3.3 times greater than the mean of the temporal model slopes (Table 2). The Mandan, ND site was a clear outlier in this relationship; removing it from the cross-site analysis resulted in an extremely strong linear model ($R^2 = 0.994$) with a slope of 11.8 kg ha⁻¹ mm⁻¹, which is 3.5 times greater than the mean slope of the temporal models.

For the PPT–NSP relationship, the slope of linear temporal models varied substantially across the PPT gradient. For the four driest sites, the slope was positive, varying from 0.027 at Nunn, CO to 0.042 kg ha⁻¹ mm⁻¹ at Mandan, ND (Table 2). In contrast, the relationship became negative at the two wettest sites, with slopes of –0.10 (Hays, KS) and –0.053 kg ha⁻¹ mm⁻¹ (Manhattan, KS; Figure 2b). Furthermore, for the four driest sites, the PPT–NSP relationship was better fit by quadratic than linear models, reflecting a pattern of saturating NSP at higher levels of precipitation. At the Nunn, CO and Cheyenne, WY sites, NSP increased as PPT varied from 85 to 300 mm, and then began to decline slightly with precipitation >300 mm. At Cottonwood, SD and Mandan, ND, NSP increased over the range from 140 to 400 mm, and then reached an asymptote. In contrast with these saturating or negative temporal relationships, evaluation of the PPT–NSP relationship across the region (i.e., the spatial model) revealed a very strong positive linear relationship ($R^2 = 0.981$), with a

slope of 0.201 kg ha⁻¹ mm⁻¹, which is five times greater than the mean slope of the four linear, positive temporal models (Figure 2d). These data also showed a strong fit to a quadratic model ($R^2 = 0.994$), which suggested the rate of increase in NSP may saturate as PPT exceeds 500 mm.

Sensitivity

We estimated dry-year NSP sensitivity by calculating the site-specific NSP divided by the change in PPT of different sites to variation in PPT during dry years (range: 3–6 dry years per site, mean: 4 years). Mean dry-year NSP sensitivity across all sites was two-fold greater than NSP sensitivity to PPT change in normal and wet years (ANOVA, $p < 0.01$; Figure 3a). NSP sensitivity to dry-year PPT at the two driest sites, Nunn, CO and Cheyenne, WY, was 0.14 and 0.12 kg ha⁻¹ mm⁻¹, whereas the two wettest sites showed low sensitivity in that they both showed net increases in NSP during dry years (Hays, KS = –0.21 kg ha⁻¹ mm⁻¹; Manhattan, KS = –0.21 kg ha⁻¹ mm⁻¹; Figure 3b). Pivotal outliers were Mandan, ND, with the highest sensitivity to dry-year PPT (0.30 kg ha⁻¹ mm⁻¹) and Cottonwood, SD with the lowest sensitivity to dry-year PPT (–0.25 kg ha⁻¹ mm⁻¹). We found no statistically significant relationship between PPT and NSP sensitivity in dry years (dry-year NSP sensitivity = 0.33–0.001 × PPT, $R^2 = 0.27$, $p = 0.29$). Without Mandan, ND, PPT explained more variation in dry-year NSP sensitivity, although the relationship was not significant (NSP sensitivity = 0.26–0.001 × PPT, $R^2 = 0.45$, $p = 0.22$; Figure 3b).

Trophic efficiency

Evaluation of the PPT– E_{troph} relationship did not reveal a regional influence of increasing PPT on trophic efficiency ($E_{\text{troph}} = 0.015–0.000009 \times \text{PPT}$, $R^2 = 0.08$, $p = 0.59$). Removal of Mandan, ND from this evaluation demonstrated PPT explained more variation in regional E_{troph} ($E_{\text{troph}} = 0.017–0.00001 \times \text{PPT}$, $R^2 = 0.43$, $p = 0.23$) (Figure 4a). Estimated marginal (least squares) means comparisons for annual E_{troph} across sites indicated Cheyenne, WY and Mandan, ND showed the highest and lowest trophic efficiency, respectively (Table 3). Across the Central Great Plains precipitation gradient, E_{troph} exhibited a quadratic response to increasing ANPP in kilojoule per square meter (linear $R^2 = 0.71$, $p = 0.02$; quadratic: $R^2 = 0.84$, $p = 0.03$). Central Great Plains regional E_{troph} peaked at ~2500 ANPP in kilojoule per square meter (Figure 4b).

TABLE 2 Temporal and spatial model fit, y -intercept (in kilograms per hectare), and slope coefficients (in kilograms per hectare per millimeter) for simple and quadratic linear regression models of the PPT–ANPP and PPT–NSP relationships at six rangeland sites in the Central Great Plains of North America.

Model parameters	R^2	Intercept	Slope	Slope ²
Linear PPT–ANPP				
Temporal (local) models				
Nunn, CO	0.084	542.193	2.624	
Cheyenne, WY	0.269	379.654	3.640	
Cottonwood, SD	0.118	1174.448	2.369	
Mandan, ND	0.098	5012.287	4.526	
Hays, KS	0.789	90.988	4.185	
Manhattan, KS	0.225	359.0003	3.169	
Spatial (regional) model				
Spatial model	0.399	−891.7	11.333	
Spatial model excluding Mandan, ND	0.994	−1764.4	11.796	
Quadratic PPT–ANPP				
Temporal (local) models				
Nunn, CO	0.136	−484.676	11.865	−0.018
Cheyenne, WY	0.297	−820.598	12.401	−0.015
Cottonwood, SD	0.307	−1715.308	20.327	−0.025
Mandan, ND	0.112	3445.084	13.394	−0.011
Hays, KS	0.802	−1009.421	9.902	−0.007
Manhattan, KS	0.429	7461.688	−23.509	0.023
Spatial (regional) model				
Spatial model	0.255	−9193.857	62.118	−0.075
Spatial model excluding Mandan, ND	0.830	−545.946	9.836	−0.009
Linear PPT–NSP				
Temporal (local) models				
Nunn, CO	0.196	12.404	0.027	
Cheyenne, WY	0.142	25.322	0.037	
Cottonwood, SD	0.106	27.880	0.035	
Mandan, ND	0.324	31.087	0.042	
Hays, KS	0.728	108.548	−0.103	
Manhattan, KS	0.049	120.411	−0.053	
Spatial (regional) model				
Spatial model	0.986	−22.816	0.201	
Spatial model excluding Mandan, ND	0.987	−22.428	0.201	
Quadratic PPT–NSP				
Temporal (local) models				
Nunn, CO	0.416	−1.776	0.154	−0.0003
Cheyenne, WY	0.245	−7.166	0.274	−0.0004
Cottonwood, SD	0.122	14.581	0.117	−0.0001
Mandan, ND	0.453	7.650	0.174	−0.0002
Hays, KS	0.747	142.137	−0.277	0.0002
Manhattan, KS	0.319	413.795	−1.155	0.0009

TABLE 2 (Continued)

Model parameters	R^2	Intercept	Slope	Slope ²
Spatial (regional) model				
Spatial model	0.990	-44.575	0.320	-0.0001
Spatial model excluding Mandan, ND	0.997	-53.747	0.376	-0.0002

Abbreviations: ANPP, aboveground net primary production; NSP, net secondary productivity; PPT, precipitation.

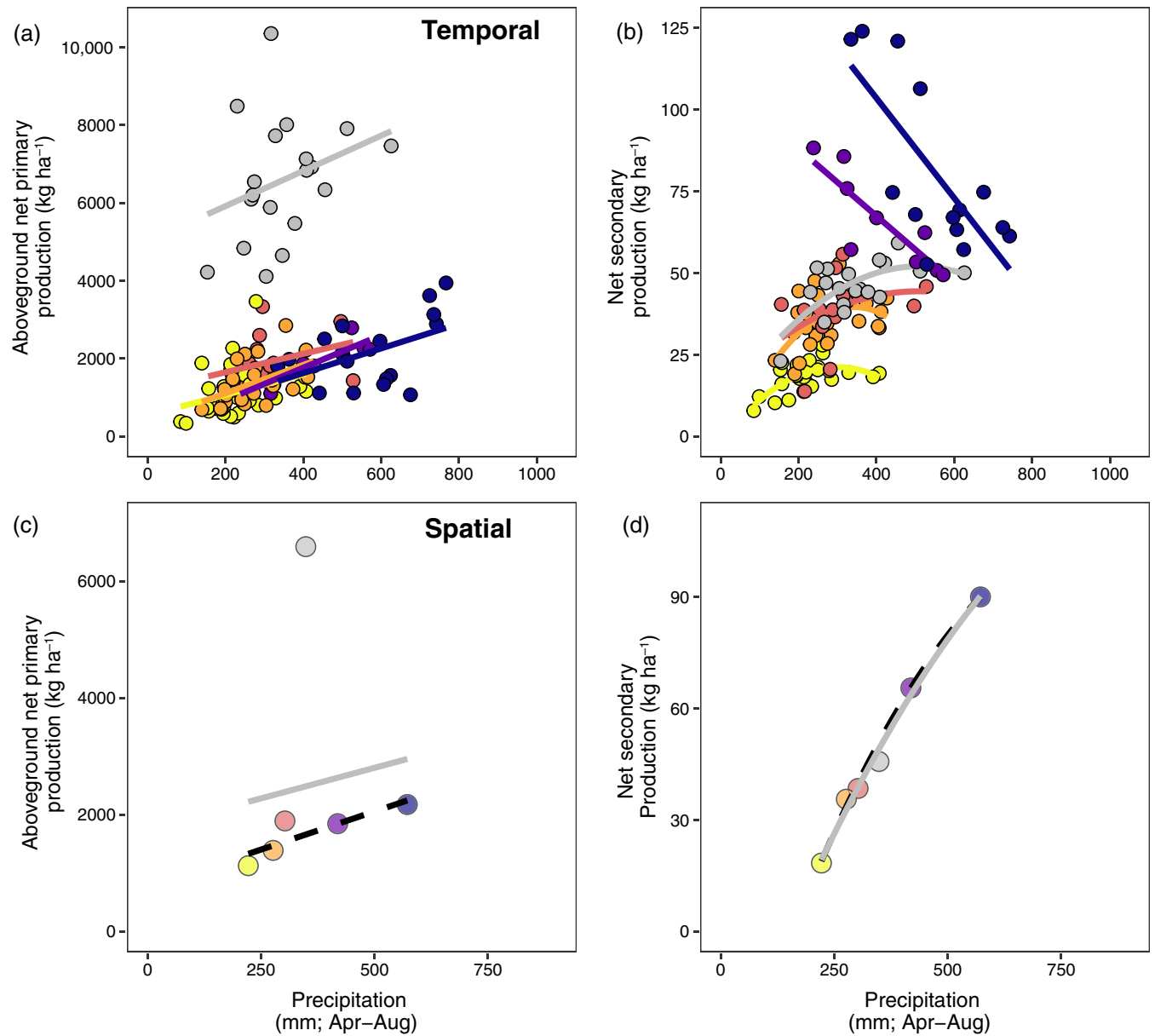


FIGURE 2 Temporal models are site-based and relate interannual variability in precipitation (PPT) to interannual variability in aboveground net primary production (ANPP) and net secondary production (NSP). Relationships between (a) ANPP and PPT and (b) NSP and PPT derived from annual observations. Spatial models relate mean PPT to mean ANPP and NSP. Relationships between (c) ANPP and PPT and (d) NSP and PPT are derived from multiyear observations. Line of best fit is shown for data set with Mandan, ND (gray) and excluding Mandan, ND (dashed black).

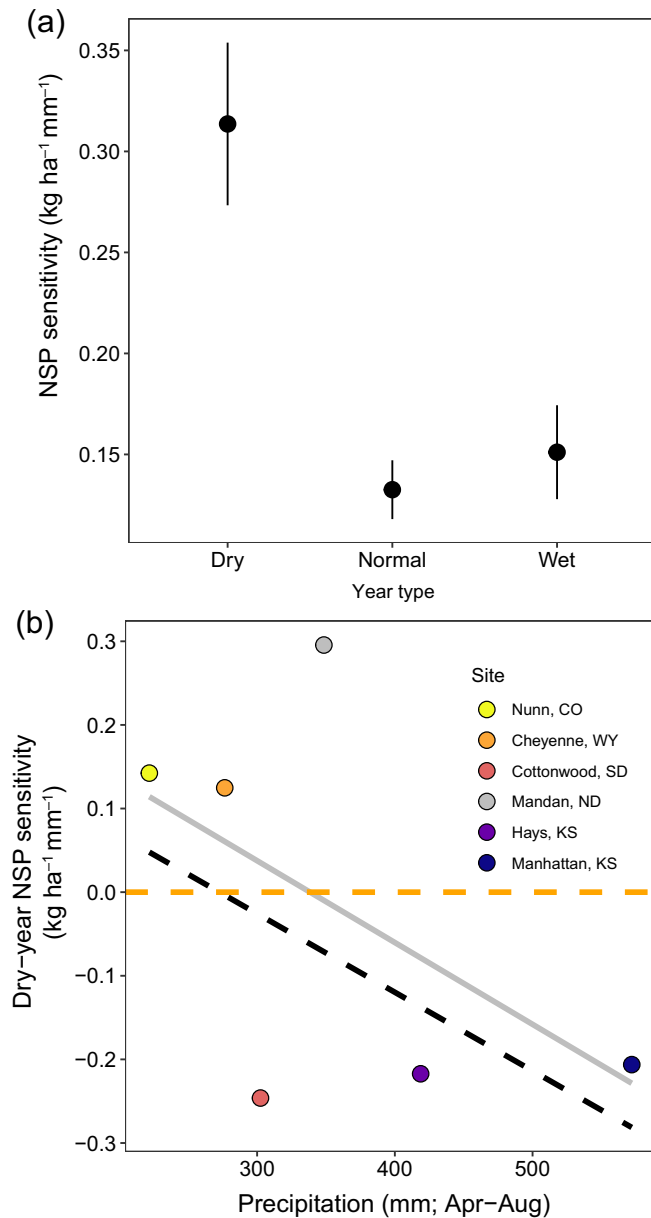


FIGURE 3 (a) Gradient-wide comparison of mean net secondary production (NSP) sensitivity for dry, normal, and wet precipitation (PPT) years based on <25th, >25 < 75th, and >75th percentiles. (b) Sensitivity of NSP to PPT in dry years along mean annual precipitation gradient. Line of best fit is shown for the data set with Mandan, ND (gray) and excluding Mandan, ND (dashed black).

DISCUSSION

Sala et al. (2012) showed that, across spatial PPT gradients in grasslands of North America, Africa, and Asia, ANPP increases more rapidly with increasing PPT compared with the response of ANPP to temporal variation in PPT within any given locality. Specifically, they found the slope of the regional, spatial model was 3.7 times

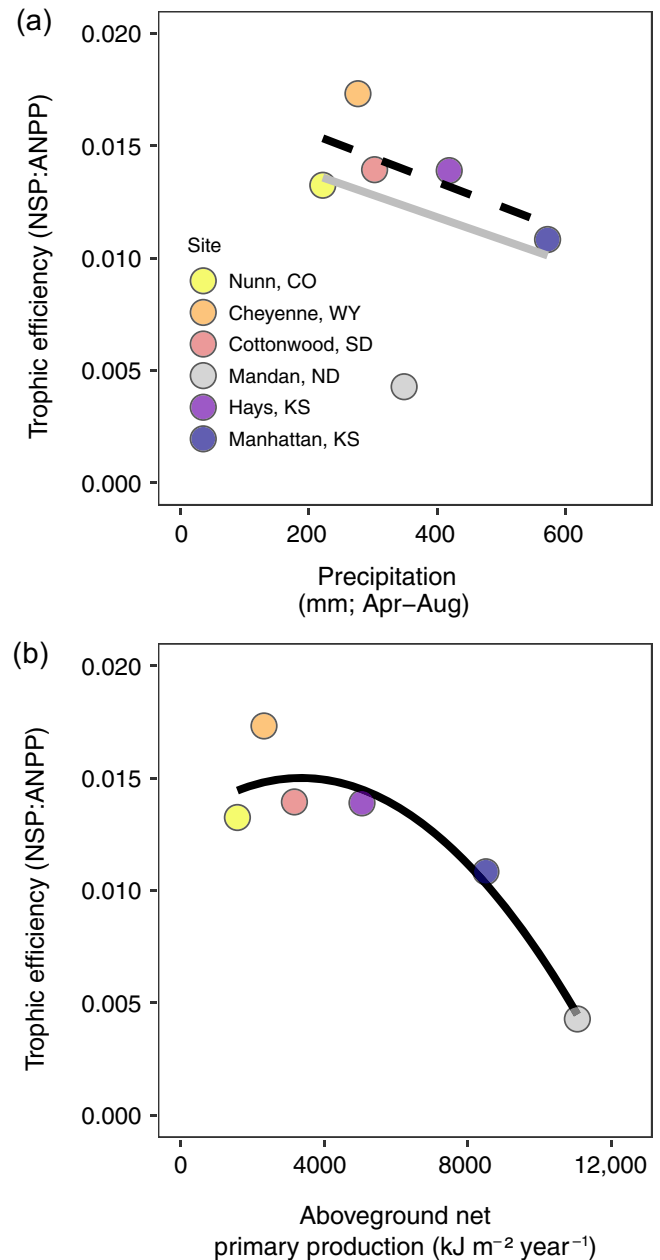


FIGURE 4 (a) Relationship of site trophic efficiency (NSP:ANPP) against growing-season precipitation (PPT) with Mandan, ND (gray line) and without (dashed black line). (b) Relationship for site trophic efficiency (NSP:ANPP) against ANPP of central North American grasslands.

greater than the mean slope of all the local, temporal models (Sala et al., 2012). In their analysis, most of the study sites consisted of ungrazed grassland, and they did not examine how NSP varied with PPT or ANPP. The Sala et al. (2012) analysis included datasets from Nunn, CO and Manhattan, KS, but they were from different specific locations and different sets of years than the datasets we analyzed here. Using independent datasets spanning the PPT gradient found in central North American

TABLE 3 Estimated marginal means of site E_{troph} , confidence limits and multiple comparisons across sites.

Site	β (E_{troph})	SE	df	Lower CL	Upper CL	Grouping ^a
Nunn, CO	0.013	0.001	98.8	0.010	0.016	B
Cheyenne, WY	0.017	0.001	99.9	0.015	0.020	C
Cottonwood, SD	0.014	0.001	107.8	0.010	0.018	BC
Mandan, ND	0.004	0.001	105.8	0.001	0.008	A
Hays, KS	0.014	0.002	107.3	0.010	0.020	BC
Manhattan, KS	0.010	0.001	106.9	0.007	0.013	B

Note: Multiple comparisons were calculated using Tukey's honest significant difference method.

^aDifferent letters represent different E_{troph} at $\alpha = 0.05$.

grasslands, we found very similar patterns, where the slope of the regional, spatial model was 3.3 times greater than the mean slope of the local, temporal models. One cause of the muted sensitivity of ANPP to variable PPT in the local, temporal models is the fact that the local plant community is constrained by long-term mean local climate, such that species adapted to increased or reduced PPT are not as abundant as they would be at a site with greater or lower long-term mean annual PPT. Furthermore, the lower slope of the temporal models arises at least in part from “legacy” effects of prior years on current-year ANPP at any given locality, whereby ANPP is greater than expected based on the spatial model following wet years, and lower than expected based on the spatial model following dry years (Sala et al., 2012). The only notable difference between our findings and those of Sala et al. (2012) arose from the site in Mandan, ND which has been invaded and dominated by non-native C_3 perennial grass, and now supports substantially greater ANPP than expected based on site-level PPT (Toledo et al., 2014). This is also the most northern (and hence coldest) site included in either analysis. Both lower water loss associated with reduced evaporative demand and less surface runoff (Kim et al., 2023), as well as more efficient conversion of cool-season moisture to biomass by the non-native C_3 invasive plant, may explain the unusually high ANPP at this site.

Furthermore, we showed that the discrepancy in spatial versus temporal model slopes is even greater for NSP than ANPP. Across the regional, spatial PPT gradient, NSP increased by 0.20 kg ha⁻¹ for each 1 mm increase in growing-season PPT. Within any given site, however, NSP increased by only 0.35 kg ha⁻¹ for a 1 mm increase in PPT across the lower half of the PPT gradient, and even declined with increasing PPT at the two wettest sites. The lack of an increase in NSP in the wettest sites can be attributed to increased plant investment in lignified stems, constraining protein acquisition and concomitant ruminant growth rates. In mesic, tallgrass prairies, forage protein content and digestibility decline rapidly as vegetation matures with increasing

stem: leaf (Raynor et al., 2015), which then strongly constrains ruminant growth rates (e.g., Craine et al., 2009). In contrast, forage quality is less sensitive to variability in PPT and growth rates in short-statured, semiarid grasslands (e.g., Augustine et al., 2018). The moderate stocking rate at each site is set based on a combination of long-term mean forage production rates (Bement, 1969; Gillen et al., 1998), the risk of extremely low forage production levels in drought years (Bement, 1969; Espeland et al., 2020), and the inability to predict PPT levels prior to the growing season (Holechek, 1988; Shrum et al., 2018). Because herbivore numbers did not increase or decrease substantially in response to annual PPT variability, it is the year-to-year variation in growth rates of individual cattle that determined temporal NSP variability within sites. In contrast, the spatial PPT–NSP relationship is driven by a combination of variation in stocking rates across the spatial gradient combined with variation in individual growth rates. At the two most mesic sites, reductions in digestibility and protein content of forages (i.e., increased forage maturation rates with increasing PPT) appear to be constraining NSP, leading to low trophic efficiency.

Even at the more arid sites that exhibited a positive PPT–NSP relationship, maximal NSP occurred with average or slightly above-average PPT levels and often declined slightly in the wettest years. This latter response again likely reflects forage quantity limitations in below-average years versus forage quality limitations in above-average years and highlights the potential value of providing protein supplements to ruminant consumers in wet years. The strong positive slope of the spatial NSP model suggests that cattle production rates could be increased substantially if stocking rates could be adjusted at the site level in response to ANPP variation, but this is constrained by uncertainty in both seasonal weather forecasts and cattle markets.

Finally, we found the highest trophic efficiencies (0.013–0.017) in central North American grasslands with ANPP below 5000 kJ m⁻² year⁻¹, whereas trophic efficiency was considerably lower (0.004–0.010) in more productive grasslands. In contrast, Irisarri et al. (2014)

examined variation in trophic efficiency across a broad PPT and ANPP gradient in South America, and found the opposite pattern, with low (<0.010) trophic efficiency when ANPP was below $5000 \text{ kJ m}^{-2} \text{ year}^{-1}$, and peak trophic efficiencies of $0.015\text{--}0.028$ in grasslands with ANPP in the range of $5000\text{--}12,000 \text{ kJ m}^{-2} \text{ year}^{-1}$. In South America, low trophic efficiency at the low end of the ANPP gradient is associated with the dominance of indigestible C_3 grasses and xerophytic shrubs. In North America, high trophic efficiency at the low end of the ANPP gradient is associated with the dominance of short-statured, digestible C_4 grasses that have minimal investment in aboveground stems (e.g., *B. gracilis*). This difference in variation in plant traits across PPT gradients on the two continents could potentially be related to differences in the evolutionary history of large grazing mammals, as North American grasslands have supported abundant ruminant grazers for the past 10,000 years whereas South American grasslands have not (Milchunas et al., 1988; Milchunas & Lauenroth, 1993).

Aboveground resource variation in the North American Central Great Plains exhibits differential responses to PPT in terms of ANPP and NSP. Both showed three to five times stronger responses to regional spatial variation than to local temporal variation in PPT. Regional dry-year sensitivity of NSP to PPT heightened as PPT decreased across the gradient. Huxman et al. (2004) and Knapp et al. (2015) reported an inverse relationship between the sensitivity of ANPP to change in interannual PPT as a function of MAP, and we found the same general pattern for NSP sensitivity to growing-season PPT.

Unlike the PPT–ANPP relationship, which exhibited linear temporal and spatial responses (Sala et al., 1988, 2012), we found saturating or negative temporal responses of NSP to PPT, and a slightly saturating regional spatial relationship between PPT and NSP. Although more datasets may reveal a more collectively linear result (Hsu et al., 2012; Knapp et al., 2017), we extend our understanding of consumer response to water availability in this water-limited system. Our findings suggest that a biogeochemical constraint is likely affecting trophic efficiency through forage maturation processes, which more strongly affect mesic than semiarid grassland systems. A comprehensive understanding of the mechanisms leading to differences in consumer and producer responses to climatic variation will require multisite experiments to assess biotic and abiotic determinants of sensitivity to precipitation variability and efficiencies across trophic levels.

AUTHOR CONTRIBUTIONS

Edward J. Raynor, Justin D. Derner, William J. Parton, David L. Hoover, and David J. Augustine conceived the ideas and designed the methodology. All authors

contributed to data collection or curation. Edward J. Raynor and David J. Augustine analyzed the data. Edward J. Raynor, David J. Augustine, Justin D. Derner, and David L. Hoover led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Dorich et al., 2021) are available on the Ag Data Commons repository at <https://doi.org/10.15482/USDA.ADC/1521120>.

ORCID

Edward J. Raynor  <https://orcid.org/0000-0003-2483-4694>

Melannie D. Hartman  <https://orcid.org/0000-0002-0675-2292>

William J. Parton  <https://orcid.org/0000-0003-4151-7869>

Nicole E. Kaplan  <https://orcid.org/0000-0003-1090-9173>

David L. Hoover  <https://orcid.org/0000-0002-9326-9791>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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