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Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions?

KEVIN R. WILCOX,^{1,3} JOHN M. BLAIR,² MELINDA D. SMITH,¹ AND ALAN K. KNAPP¹

¹Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado 80523, USA

²Division of Biology, Kansas State University, 116 Ackert Hall, Manhattan, Kansas 66506-4901, USA

Abstract. Central to understanding global C cycle dynamics is the functional relationship between precipitation and net primary production (NPP). At large spatial (regional) scales, the responsiveness of aboveground NPP (ANPP) to interannual variation in annual precipitation (AP; ANPP_{sens}) is inversely related to site-level ANPP, coinciding with turnover of plant communities along precipitation gradients. Within ecosystems experiencing chronic alterations in water availability, plant community change will also occur with unknown consequences for ANPP_{sens}. To examine the role plant community shifts may play in determining alterations in site-level ANPP_{sens}, we experimentally increased precipitation by ~35% for two decades in a native Central U.S. grassland. Consistent with regional models, ANPP_{sens} decreased initially as water availability and ANPP increased. However, ANPP_{sens} shifted back to ambient levels when mesic species increased in abundance in the plant community. Similarly, in grassland sites with distinct mesic and xeric plant communities and corresponding 50% differences in ANPP, ANPP_{sens} did not differ over almost three decades. We conclude that responses in ANPP_{sens} to chronic alterations in water availability within an ecosystem may not conform to regional AP–ANPP patterns, despite expected changes in ANPP and plant communities. The result is unanticipated functional resistance to climate change at the site scale.

Key words: climate change; ecosystem function; grasslands; Konza Prairie Biological Station; plant community; precipitation; primary productivity; sensitivity.

INTRODUCTION

Global climate models forecast both increases and decreases in mean annual precipitation, the predictions varying with geographic location (Zhang et al. 2007, Hartmann et al. 2013). When combined with alterations of other modifiers of ecosystem water balance (increased atmospheric CO₂, warmer air temperatures, altered humidity), a substantial proportion of terrestrial ecosystems are expected to become either drier or wetter, with recent analyses confirming this forecast (Greve et al. 2014). Climate models also predict an increase in interannual precipitation variability for the majority of terrestrial ecosystems (Hartmann et al. 2013). These predictions are important because precipitation is a major determinant of local temporal dynamics in terrestrial aboveground net primary productivity (ANPP; i.e., responses to interannual rainfall variation within

an ecosystem), as well as at regional (>1000 km) to continental scales (i.e., across ecosystems with different mean annual precipitation [MAP]; Sala et al. 1988, 2012, Huxman et al. 2004). Indeed, the functional relationship between precipitation and ANPP both temporally and spatially is central to understanding the dynamics of Earth's C cycle.

A key difference between temporal (within-system) and spatial (across-system) relationships is that plant community composition often remains relatively constant in temporal models, but varies dramatically over regional gradients. As a result, in addition to precipitation amount, the attributes of more xeric vs. more mesic plant communities help determine regional-scale responses to interannual variation in precipitation (Lauenroth and Sala 1992, Lavorel and Garnier 2002, La Pierre and Smith 2015). Spatial and temporal models describing ANPP–precipitation relationships have been linked by observations that the temporal sensitivity of ANPP to precipitation variability (response in ANPP per mm difference in annual precipitation, ANPP_{sens})

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³E-mail: Wilcoxkr@gmail.com

varies inversely with MAP and ANPP at regional to continental scales (Huxman et al. 2004, Del Grosso et al. 2008, Sala et al. 2012). Thus, as MAP increases across large spatial gradients, plant communities shift from those dominated by xeric (less productive, shorter statured) species to more mesic (more productive, taller) species and ANPP increases (Sala et al. 1988). Yet, the temporal responsiveness of ANPP to wet and dry years decreases (Huxman et al. 2004). As a consequence, ecosystems that become chronically wetter with climate change would be predicted to become more productive and shift towards plant communities with more mesic species, but they would have reduced ANPP_{sens}, with the opposite predictions made for ecosystems that become drier.

Here, we assess how well regional models relating patterns of MAP, ANPP, plant community composition, and ANPP_{sens} predict responses within an ecosystem subjected to long-term differences in water availability with attendant alterations in plant community composition and ANPP (Collins et al. 2012, Knapp et al. 2012). We used two long-term (>20 yr) data sets, one experimental and one observational, that directly linked altered water availability and differences in plant community composition to expected changes in the temporal sensitivity of ANPP to precipitation variability. With the experimental data set, we were able to assess productivity responses and shifts in ANPP_{sens} to a chronic increase in water availability both before and after community change occurred. Whereas the observational data set allowed us to assess ANPP_{sens} in relatively stable plant communities that reflected long-term differences in water availability due to differences in soil depth and topographic position in the landscape. We tested a key prediction from regional models (Huxman et al. 2004, Sala et al. 2012), that with chronic increases or decreases in water availability and concurrent plant community changes, ANPP_{sens} would be altered. Specifically, that increased water availability and more mesic plant communities would have lower ANPP_{sens} whereas decreased water availability and more xeric communities would have greater ANPP_{sens}.

METHODS

Study sites

We utilized long-term data from the Konza Prairie Biological Station (KPBS), an NSF Long-Term Ecological Research (LTER) site located in the Flint Hills region of northeastern Kansas, USA. The Flint Hills region is characterized by relatively steep topography (~120 m difference in elevation from lowland to upland sites at KPBS; Knapp et al. 1998). KPBS is a native tallgrass prairie ecosystem that receives an average of 834 mm of precipitation annually, most of which falls during the growing season (April–September; Knapp et al. 1998), has a mean annual temperature of 12.5°C (USCRN

data), and a mean ANPP in productive lowland sites of 528 g/m² (Knapp et al. 1998). Vegetation is dominated by a few rhizomatous, C₄ perennial grass species, namely *Andropogon gerardii* and *Sorghastrum nutans*, but species found more commonly in wetter ecosystems to the east (e.g., *Panicum virgatum*, *Spartina pectinata*) and drier grasslands to the west and south (e.g., *Schizachyrium scoparium*, *Bouteloua curtipendula*) also occur throughout the site.

Data sets

We examined two data sets from annually burned (>20 yrs), ungrazed (>40 yrs) sites at KPBS consisting of ANPP, plant species composition, and precipitation measurements. Frequent fire is important for the origin and maintenance of tallgrass prairie (Axelrod 1985) and is a common management tool today (Briggs and Gibson 1992). The first data set is from the Irrigation Transect Experiment (IrrT) where transects spanning uplands to lowlands were irrigated from 1991 to 2011 (average of 256 mm added during May–September in addition to ambient rainfall; see Collins et al. 2012 and Appendix S1 for more information on the experimental design). We used the lowland portion of this experiment ($n = 9$) because this was where species composition shifted consistently and strongly due to irrigation (Collins et al. 2012). The second data set (upland-lowland comparison [ULC]) encompassed 50-m transects ($n = 4$) located in upland areas with relatively shallow soils (average ~20 cm) and close-by lowland areas with deeper soils (average ~50 cm [Schimel et al. 1991], $n = 4$ transects; 1984–2011 PAB01 data set, Konza Prairie LTER). Water availability in this grassland is primarily determined by soil depth, as runoff (and runoff) due to topographic position is of minor importance (Schimel et al. 1991, Knapp et al. 1993, 1998, Dodds 1997).

Plant species composition

Plant community composition was measured by visually estimating aerial cover of each species separately two times per season (May–June and August–September) for the ULC study and once annually in late July for the IrrT study using a modified Daubenmire cover scale. For the IrrT experiment, aerial cover was sampled within permanent 10-m² circular plots for irrigated and control plots ($n = 9$ for each treatment), and in upland and lowland plots for the ULC study ($n = 20$ for each topographic position). For analysis, cover classes were converted to the midpoint of the cover range and maximum cover values between early and late season sampling were used for each species.

ANPP measurements

Estimates of ANPP were obtained in IrrT from 1991 to 2011 by clipping all aboveground live plant biomass

to ground level in six 0.1-m² subplots per plot, and in five 0.1-m² subplots per transect in ULC (1984–2011) yearly in late August–early October. Biomass was dried for 48 h at 60°C, sorted to major functional type (e.g., graminoid, forb, woody), and weighed. In these annually burned sites, woody plant biomass was minimal (Briggs and Knapp 1995) and was excluded from analyses. Measurements from subplots were averaged across each plot for the IrrT dataset and averaged across each transect for the ULC data set.

Statistical analyses

We assessed differences in plant community composition between treatments for the IrrT experiment and between topographic position for the ULC study in each year by testing for differences between centroid locations using 999 permutational MANOVA with a Bray-Curtis dissimilarity matrix. For the IrrT experiment, Bray-Curtis dissimilarities between treatment centroids in each year were used in a general linear regression analysis comparing community differences with the annual standardized ANPP response to irrigation ($[\text{ANPP}_{\text{Irr}} - \text{ANPP}_{\text{Ctrl}}]/\text{mm}$ of irrigation). We determined which species were most important in determining differences between treatments (IrrT) or topographic position (ULC) by pooling community data for all years where communities were significantly different and conducting similarity percentages analyses (SIMPER). Plant compositional analyses were conducted using PRIMER v6 (Primer, Plymouth, UK).

We used repeated-measures mixed-model ANOVAs (Proc MIXED; SAS v9.3; SAS Institute, Cary, North Carolina, USA) with autoregressive covariance structure, based on corrected Akaike information criterion (AIC_c), to examine differences in relative cover of functional groups and of the five species that contributed most to differences of community centroids between treatments or topographic position. Cover values were logit transformed as necessary to satisfy normality assumptions.

We compared productivity responses in each data set between treatments/topographic position using repeated measures ANOVA, with year as the repeated variable, a compound symmetry covariance matrix based on AIC_c , and Satterthwaite approximations of standard error. In IrrT, the nine plots were located along two transects, which constitutes simple spatial pseudoreplication in the experiment; we accounted for this by using transect as a random effect within mixed effects models (Millar and Anderson 2004).

We first assessed and then compared $\text{ANPP}_{\text{sens}}$, defined as the slope of the relationship between annual growing season precipitation and ANPP using general linearized regressions (ULC) or mixed model regressions (IrrT with transect as a random factor), for each treatment (in IrrT) or topographic location (in ULC) within each data set. ANPP was log-transformed as necessary to satisfy assumptions of normality. Differences between

sensitivities were determined in one of two ways: (1) if one regression was significant and another was not, sensitivities were determined to be different, and (2) if both slopes were significant, sensitivity was determined to be different in the case of a significant interaction between treatment (or topographic position) and growing season precipitation. Statistical significance was set using $\alpha = 0.05$ for all analyses.

RESULTS

IrrT experiment

Over the entirety of the experiment (1991–2011), ANPP was significantly higher in irrigated plots (772.3 ± 18.1 g/m²; mean \pm model SE) than in control plots (503.8 ± 16.8 g/m²; Table S1). Plant community composition was not significantly different between control and irrigated treatments during the first 9 years of the experiment (1991–1999) based on a permutational MANOVA (all $P > 0.1$; Table S2). However, starting in 2000, plant community centroids differed significantly in every year (Table S2; Fig. 1A, note that $P = 0.052$ in 2004). We subsequently assessed community composition for those years after the community shift had occurred to identify which species were driving differences between irrigated and control communities. The five species contributing most to divergence of plant communities cumulatively explained 60.3% of the difference between community centroids (Table S3). The most important of these was *P. virgatum*, for which relative cover was almost two-fold higher in irrigated ($34\% \pm 2.2\%$) than in control plots ($19\% \pm 2.2\%$; Table S4). The other species driving community change were *S. scoparium*, *Andropogon gerardii*, *Helianthus rigidus*, and *Dalea candida*, yet their covers were not found to be significantly different between treatments using univariate statistical methods (Fig. 1B; Table S4). Species richness (S) and Shannon's diversity (H') were not significantly different between irrigated and control plots from 1991 to 1999 ($F_{1,18.7} = 1.70$ and $F_{1,19} = 0.12$, respectively; $P = 0.21$ and 0.74 , respectively), yet during 2000–2011 richness was marginally lower ($F_{1,21.7} = 3.56$; $P = 0.07$) while H' was significantly less ($F_{1,20.7} = 5.17$, $P = 0.03$) in irrigated (S , 12.2 ± 1.32 ; H' , 1.45 ± 0.05) vs. control plots (S , 14.2 ± 1.32 ; H' , 1.55 ± 0.05 ; Fig. S1). Despite changes in species relative abundances and diversity, no differences in functional group abundance were found after the community shift (Table S5) indicating a switch in the identity of the dominant C_4 grass species rather than an overall shift in functional group abundance. Bray-Curtis dissimilarity between irrigated and control plant communities varied among years, and dissimilarity was positively correlated with the standardized ANPP response ($P < 0.01$, $R^2 = 0.54$; Fig. 1C).

Two major plant-community–ecosystem-function groupings were discerned, with 1999 being a transition year (Fig. 1C). For this reason, we excluded 1999

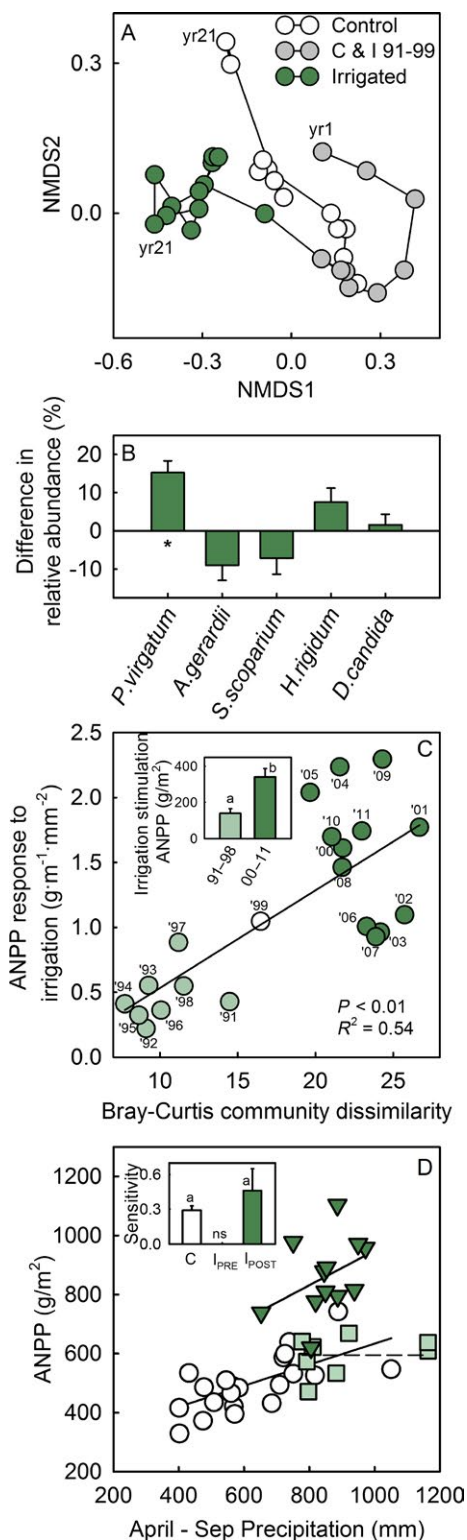


FIG. 1. Plant community and productivity responses over 21 years of irrigation: (A) nonmetric multidimensional scaling centroids over time representing plant communities in control and irrigated plots together before community change (gray circles), and in both control (open circles) and irrigated (dark green circles) plots after community change. (B) Differences in relative cover (mean and SE) between control and irrigated plots of the five species most responsible for community dissimilarity. Cover differences incorporate averaged data from all years after the communities diverged (2000–2011). Species are *Panicum virgatum*, *Andropogon gerardii*, *Schizachyrium scoparium*, *Helianthus rigidus*, and *Dalea candida*. Asterisks represent significant differences between control and irrigated relative species abundances at $\alpha = 0.05$. (C) Bray-Curtis dissimilarity between treatment community centroids in each year compared with that year's aboveground net primary productivity (ANPP) response to irrigation standardized by the amount of water added. Numbers represent the year of the response. Inset: average increase in ANPP due to irrigation before the plant community shift (1991–1998; light green bar) and after the community shift (2000–2011; dark green bar). (D) Relationship between growing season precipitation and ANPP in plots receiving control (i.e., ambient) precipitation from 1991 to 2011 (open circles), control + irrigation during 1991–1998 (before community change, squares) and 2000–2011 (after community change, triangles). Inset: control (C) and irrigated slope estimates before (I_{pre} : 1991–1998) and after (I_{post} : 2000–2011) community change. Different letters indicate significant differences between treatments at $\alpha = 0.05$, and error bars represent standard error.

from analyses including 1999). Mean ANPP response to irrigation was lower in 1991–1998 ($139.4 \pm 27.0 \text{ g/m}^2$) than in 2000–2011 ($340.4 \pm 47.7 \text{ g/m}^2$; Fig. 1C inset; Table S6). We then compared ANPP_{sens} of irrigated plots before and after the community shift with the baseline sensitivity of the system, which we identified as the ANPP–precipitation slope of the control plots over the entirety of the experiment. The slope coefficient in control plots from 1991 to 2011 was significantly positive (0.29 ± 0.04 ; $R^2 = 0.14$) whereas interannual variability in ANPP in the irrigated plots prior to community change was not related to growing season precipitation (Table S6; Fig. 1D). As a result, we found a significant difference between the slopes of control and pre-composition change irrigated plots (treatment \times precipitation interaction, Table S6). Conversely, during 2000–2011, a significant slope was detected in irrigated plots (0.46 ± 0.19 ; $R^2 = 0.04$; Table S6), and we found no significant difference between slopes of control and post-composition change irrigated plots (Table S6; Fig. 1D).

Upland–lowland comparison (ULC)

Over this 28-year data set (1984–2011), ANPP in the lowlands ($585.3 \pm 17.1 \text{ g/m}^2$; mean \pm model SE) was significantly higher than in the uplands ($384.7 \pm 17.1 \text{ g/m}^2$; Table S1) as observed previously (Briggs and Knapp 1995). Also, plant community composition was significantly different between upland and lowland areas in every year based on permutational MANOVA (Table S2; Fig. 2A). The top five species contributing to divergence of upland and lowland communities cumulatively

irrigated ANPP data from further analyses to examine ANPP responses before and after distinct plant community change (but see Table S7 showing similar results

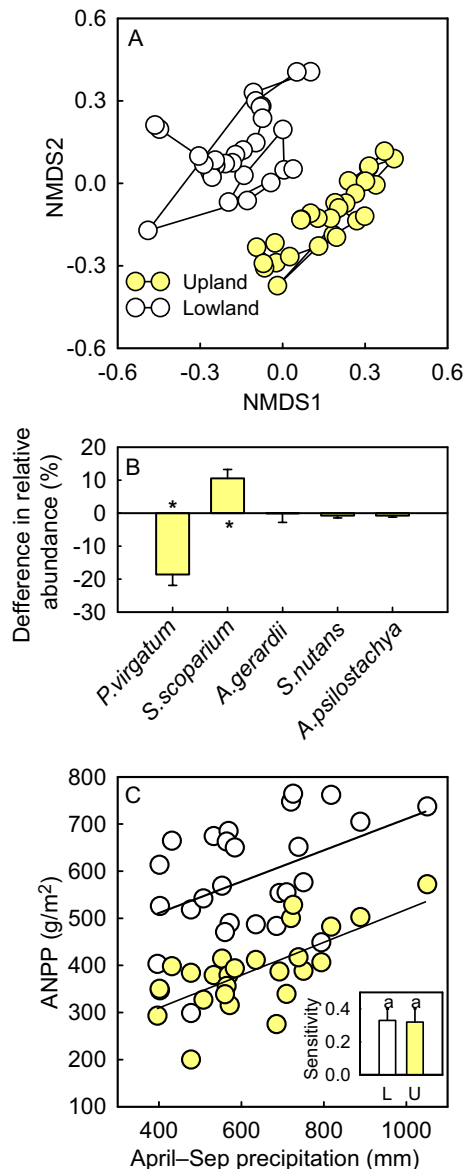


FIG. 2. (A) Nonmetric multidimensional scaling centroids over time representing upland (solid circles) and lowland (open circles) plant community composition in each year from 1984 to 2011. Community centroids for upland vs. lowland sites were significantly different for all years based on a permutational MANOVA. (B) Differences in relative cover (mean and SE) between upland and lowland plots of the five species most responsible for community dissimilarity between the treatments based on SIMPER analysis. Cover differences shown are averages of data spanning 1984–2011. Species are *Panicum virgatum*, *Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans*, and *Ambrosia psilostachya*. Asterisks represent significant differences between average upland and lowland relative species abundances at $\alpha = 0.05$. (C) Relationship between growing-season precipitation and ANPP in upland (solid circles) and lowland (open circles) plots. Yearly ANPP means are shown for clarity. Inset: upland (U) and lowland (L) sensitivities (slope estimates; mean and SE) for upland vs. lowland sites. Different letters indicate significant differences between upland vs. lowland sites at $\alpha = 0.05$.

explained 63.8% of the difference between communities (Table S3). When we examined these five species individually, *P. virgatum* relative cover was significantly less in upland ($3.3\% \pm 1.9\%$) than in lowland plots ($19\% \pm 1.9\%$; Table S4), and *S. scoparium* cover was significantly greater in upland ($24\% \pm 1.3\%$) than in lowland plots ($18.5\% \pm 1.3\%$; Table S4), while *A. gerardii*, *Sorghastrum nutans*, and *Ambrosia psilostachya* relative cover values were not significantly different (Fig. 2B; Table S4). Richness and H' were both greater ($F_{1,103} = 43.86$ and $F_{1,106} = 28.5$, respectively; both $P < 0.01$) in upland (S , 21.1 ± 0.26 ; H' , 1.88 ± 0.02) than in lowland (S , 18.6 ± 0.26 ; H' , 1.75 ± 0.02) plots (Fig. S1). Again, despite changes in relative abundances of species and H' , only slight differences in functional group abundance were found between topographic positions (Table S5). Although (1) overall ANPP was greater in lowland than in upland areas, (2) plant communities differed substantially, and (3) the ANPP–precipitation relationships were both significantly positive (lowland slope coefficient: 0.33 ± 0.08 , upland: 0.32 ± 0.07 ; $R^2 = 0.13$ and 0.18 , respectively; Table S6), we found no significant difference between ANPP_{sens} in upland vs. lowland areas (Fig. 2C; Table S6).

Predictions of relative changes in sensitivity

For comparison of ANPP_{sens} to existing regional sensitivity models, we calculated predictions based on MAP–sensitivity relationships from Huxman et al. (2004) described by the equation: $0.455 \times e^{-0.0015\text{MAP}}$. Since our sensitivity calculations were based on growing season precipitation while the relationships from Huxman et al. (2004) were based on annual precipitation (the different scales resulting in inherently different slope estimates), we calculated the expected relative changes in sensitivity for comparison. In the ULC, MAP was the same in upland and lowland plots, so by applying the reduction in ANPP in the uplands relative to the lowlands within a robust, spatial MAP–ANPP relationship for Central U.S. grasslands (Sala et al. 1988), we were able to estimate the MAP (and sensitivity prediction) for the uplands. Based on these calculations, we would expect a ~64% increase in sensitivity in upland vs. lowland areas, and a ~31% reduction in sensitivity in irrigated plots relative to the control transect (see Fig. S2 for more details concerning sensitivity predictions).

DISCUSSION

Spatial and temporal models relating ANPP to precipitation differ fundamentally in the way that plant community composition influences responses to variation in precipitation. In temporal models, plant communities are relatively constant over time (or are assumed to be so), with variability in ANPP mostly

explained by responses of the extant plant community to interannual variability in precipitation (Lauenroth and Sala 1992). In contrast, the relationship between ANPP and precipitation in spatial (or regional) models appears to be primarily determined by covariation in MAP and plant community composition across space (La Pierre and Smith 2015). These two models are linked by the expectation that long-term chronic changes in precipitation (or water availability in general) at a site will lead to eventual community change (Smith et al. 2009). Thus, while the temporal model may be a better predictor of ANPP responses prior to community change, the spatial model (incorporating community change) should be a better predictor of future ANPP_{sens} under an altered climate. Indeed, theory predicts that with chronic changes in water availability for any particular ecosystem, responses in function (e.g., ANPP) will initially be modest and determined by physiological responses of the extant plant community, consistent with the local temporal model (Smith et al. 2009). However, as communities adjust to new resource levels, greater responses in ecosystem function congruent with spatial models may occur as species better able to take advantage of increased resource availability (or cope with reduced resources) become more abundant (i.e., via species reordering; Smith et al. 2009), and this has been shown empirically (Knapp et al. 2012, Peters et al. 2012, Smith et al. 2014).

With the IrrT experiment, we show how species reordering with increased resource availability over time may result in greater ecosystem responses through a robust relationship between the development of a more mesic plant community and an increase in the magnitude of ANPP response to irrigation (Fig. 1C). We used long-term data from this experiment as well as data from adjacent sites that differed in ANPP and community composition to evaluate a previously untested prediction derived from spatial models; namely, that with change in community composition and ANPP driven by chronic alterations in water availability, ecosystem sensitivity to interannual variability in precipitation (ANPP_{sens}) will also change inversely with precipitation and ANPP (Huxman et al. 2004, Sala et al. 2012). Surprisingly, despite variation in ANPP of >450 g/m² (>50% of the range in ANPP used to develop the spatial ANPP_{sens} relationship in Huxman et al. 2004), we did not observe the predicted changes in ANPP_{sens}. In the IrrT experiment, we observed shifts in community composition towards greater abundances of more mesic grass species, and ANPP was increased much more than predicted by the temporal model (Fig. 1), but ANPP_{sens} did not decrease as predicted by the spatial model. Indeed, the trend we observed was for increasing sensitivity (Fig. 1D). Similarly, when comparing functionally drier uplands vs. more mesic lowlands, no difference in ANPP_{sens} was detected; this was despite significant differences in community composition (Fig. 2A) that included higher abundances of

species in uplands more characteristic of drier grasslands (*S. scoparius*) compared to lowlands (Fig. 2B). Moreover, ANPP in the uplands was similar to grasslands with much lower MAP (e.g., mixed-grass prairie; Sala et al. 1988). This lack of differences in sensitivity despite shifts to both more productive mesic and less productive xeric communities contrasts with predictions from spatial MAP–ANPP_{sens} models, which estimates a twofold range in ANPP_{sens} from the least to the most productive site.

Why doesn't ecosystem sensitivity to precipitation change as predicted by regional models?

We propose two mechanisms, not mutually exclusive, to explain this lack of response in ANPP_{sens} for this mesic grassland. First, the Huxman et al. (2004) spatial ANPP_{sens} model is driven by dramatic differences in dominant plant growth forms in ecosystems ranging from deserts to forests. Deserts and semiarid grasslands are typically characterized by short-statured vegetation interspersed with frequent patches of bare ground where evaporation rates are high and light limitation is low (Noy-Meir 1973); more mesic grasslands have continuous vegetative canopy cover, which reduces evaporation and increases the importance of light; and forests, having vertical structure, typically exhibit even lower soil evaporation rates and greater levels of light limitation. Although significant shifts in plant community composition occurred with differences in water availability in this grassland ecosystem, there was no evidence of any major shift in functional composition (i.e., C₄ grasses remained dominant). Perhaps alterations of more fine-scale plant community attributes (e.g., plant community growth traits) act to stabilize sensitivity until turnover of the dominant plant functional type occurs. Theory and empirical evidence suggest biodiversity can affect productivity through complementarity or redundancy of species and/or plant traits (Isbell et al. 2011), and an increase of diversity under chronically wetter conditions might lead to an increase in ANPP and the restoration of ANPP_{sens} (i.e., by allowing for fuller utilization of soil water even in very wet years). However, if this were the case, we would expect higher levels of biodiversity to exist in the more mesic areas of our study, yet we found both richness and diversity were lower in irrigated and lowland plots (Fig. S1). Of course, over longer time periods, immigration of species may alter biodiversity differently, and potentially impact ecosystem function and/or sensitivity.

A second mechanism that might explain the lack of shift in ANPP_{sens} is that soil nutrients and texture may not change temporally at the site-level in the same way they do across broad spatial scales. For example, regional models encompass biomes with substantially different edaphic and biogeochemical properties (Burke et al. 1989, Austin and Vitousek 1998), yet individual ecosystems may not respond over time in the same

manner under chronic changes in rainfall amount. We would like to note, however, that the vegetation and biogeochemical properties in the irrigated plots are likely still in a transitional state, and the strengths of drivers such as light and total N pools may shift over much longer time scales, potentially resulting in ANPP_{sens} more closely aligned with spatial model projections.

CONCLUSIONS

Our results provide insight into potential responses of ecosystem function under chronic alterations of soil water availability. Overall, long-term productivity responses to rainfall additions were consistent with current theory, suggesting that production may exceed values predicted from site-based temporal models after plant communities adjust to new environmental conditions. To our knowledge, temporal patterns of sensitivity and simultaneous changes in community composition have not been evaluated previously due to the lack of long-term experiments capable of linking plant community change with ecosystem sensitivity (Smith et al. 2014). Based on our analyses, we conclude that (1) spatial models of sensitivity may not provide accurate predictions for climate change scenarios at the site-level, at least on decadal time scales, and (2) within an ecosystem or biome, plant community changes may actually stabilize relationships between annual precipitation and ANPP in the near term. As a result, functional resistance to climate change at the site scale may be greater than expected based on regional models.

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