

Asymmetric responses of primary productivity to climate extremes: A synthesis of grassland precipitation manipulation experiments

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Abstract:

Climatic changes are altering Earth's hydrological cycle, resulting in altered precipitation amounts, increased interannual variability of precipitation, and more frequent extreme precipitation events. These trends will likely continue into the future, having substantial impacts on net primary productivity (NPP) and associated ecosystem services such as food production and carbon sequestration. Frequently, experimental manipulations of precipitation have linked altered precipitation regimes to changes in NPP. Yet, findings have been diverse and substantial uncertainty still surrounds generalities describing patterns of ecosystem sensitivity to altered precipitation. Additionally, we do not know whether previously observed correlations between NPP and precipitation remain accurate when precipitation changes become extreme. We synthesized results from 83 case studies of experimental precipitation manipulations in grasslands worldwide. We used meta-analytical techniques to search for generalities and asymmetries of aboveground NPP (ANPP) and belowground NPP (BNPP) responses to both the direction and magnitude of precipitation change. Sensitivity (i.e., productivity response standardized by the amount of precipitation change) of BNPP was similar under precipitation additions and reductions, but ANPP was more sensitive to precipitation additions than reductions; this was especially evident in drier ecosystems. Additionally, overall relationships between the magnitude of productivity responses and the magnitude of precipitation change were saturating in form. The saturating form of this relationship was likely driven by ANPP responses

to very extreme precipitation increases, although there were limited studies imposing extreme precipitation change, and there was considerable variation among experiments. This highlights the importance of incorporating gradients of manipulations, ranging from extreme drought to extreme precipitation increases into future climate change experiments. Additionally, policy and land management decisions related to global change scenarios should consider how ANPP and BNPP responses may differ, and that ecosystem responses to extreme events might not be predicted from relationships found under moderate environmental changes.

Keywords: aboveground net primary productivity | belowground net primary productivity | biomass allocation | climate change | grasslands | meta-analysis | root biomass

Article:

1 Introduction

Global warming has intensified many hydrological processes (Huntington, 2006), and general circulation models predict diverse responses of the water cycle to climate change. These include increases or decreases in precipitation amount depending on geographic region (Hartmann & Andresky, 2013; Zhang et al., 2007), increased interannual variability of precipitation, and increased frequency of extreme wet and dry years (Easterling et al., 2000; Jentsch & Beierkuhnlein, 2008; Singh, Tsiang, Rajaratnam, & Diffenbaugh, 2013; Smith, 2011), all of which will likely have large effects on primary productivity (Breshears et al., 2005; Del Grosso et al., 2008; Gherardi & Sala, 2015; Weltzin et al., 2003). It is especially important to understand the magnitude of these impacts in grasslands, most of which are strongly water limited (Knapp, Briggs, & Koelliker, 2001; Sala, Parton, Joyce, & Lauenroth, 1988), cover a large proportion of the terrestrial land surface (Chapin, Chapin, Matson, & Vitousek, 2011), and provide valuable ecosystem services (e.g., forage production, soil C storage: Sala, Yahdjian, Havstad, & Aguiar, 2017). Observational precipitation studies have shown robust relationships between climatic context (e.g., mean annual precipitation—MAP) and the sensitivity of ecosystems to altered precipitation (i.e., the magnitude of change in production standardized by the magnitude of precipitation change; Huxman et al., 2004; Sala, Gherardi, Reichmann, Jobbágy, & Peters, 2012; Guo et al., 2012). Yet, findings from individual experiments often conflict with these broad patterns (Byrne, Lauenroth, & Adler, 2013; Cherwin & Knapp, 2012; Koerner & Collins, 2014; White, Cahill, & Bork, 2014; Wilcox, Blair, Smith, & Knapp, 2016; Wilcox, Fischer, Muscha, Petersen, & Knapp, 2015), highlighting the need for synthesis across experiments (Carpenter et al., 2009; Knapp et al., 2004).

Most existing knowledge concerning patterns of ecosystem sensitivity to precipitation is based on aboveground net primary productivity (ANPP) data, even though belowground net primary productivity (BNPP) represents a large proportion of NPP in many grasslands (Sims & Sing, 1978). Furthermore, recent evidence suggests that BNPP responses to altered precipitation are often different in magnitude from those of ANPP (Byrne et al., 2013; Wilcox et al., 2015). Existing theory states that plants shift biomass allocation (above- vs. belowground) depending on soil resource availability (Bloom, Chapin, & Mooney, 1985; Gao, Chen, Lin, Giese, & Brueck, 2011; Giardina, Ryan, Binkley, & Fownes, 2003). If soil moisture decreases due to drought, plants may increase allocation of carbohydrates to roots to maximize resource uptake, thus

minimizing BNPP loss while exacerbating ANPP loss. Alternately, if soil moisture increases due to high precipitation levels, plants may allocate growth aboveground to maximize light capture, resulting in larger responses above- vs. belowground. Under this framework, we would predict allocation patterns to offset BNPP increases and decreases under increased and decreased precipitation, respectively. If generalizable, these allocation patterns should lead to higher ANPP sensitivity than BNPP. Empirical evidence for optimal allocation theory concerning soil nutrients is abundant (McConaughay & Coleman, 1999; Poorter & Nagel, 2000; Poorter et al., 2012), whereas a smaller number of studies have shown such allocation responses under altered soil moisture (Milchunas & Lauenroth, 2001; Wilcox, Blair, & Knapp, 2016). However, some experimental evidence has shown BNPP to be *more* sensitive than ANPP to changes in precipitation (Frank, 2007; Wilcox et al., 2015).

Another critical knowledge gap is whether the sensitivity of net primary productivity (ANPP+BNPP) differs under precipitation increases vs. decreases. Knapp and Smith (2001) showed that ANPP responded more strongly in wet vs. dry years, and they posited that this was due to drought tolerance mechanisms of resident plants. Yet, we lack similar information for BNPP responses; currently, our synthetic knowledge of BNPP responses to altered precipitation in grasslands consists of a few experiments conducted across 2–3 sites (e.g., Byrne et al., 2013; Fiala, Tuma, & Holub, 2009; Wilcox et al., 2015), and portions of two meta-analyses with limited numbers of studies documenting BNPP responses (Wu, Dijkstra, Koch, Penuelas, & Hungate, 2011; Zhou et al., 2016). Recently, a number of additional grassland precipitation studies have reported BNPP responses in individual ecosystems, and this presents an opportunity to examine and identify trends of BNPP responses to increased and decreased precipitation amounts across studies.

As precipitation extremes such as widespread drought (e.g., Midwestern United States in 2012) and high precipitation years become more frequent (IPCC, 2013), understanding patterns of ecosystem responses in extreme wet and dry years will be vital for assessing future provisioning of ecosystem services. Currently much of our knowledge comes from ecosystem responses to naturally occurring climatic variation (Huxman et al., 2004; Knapp, Ciais, & Smith, 2016; Knapp & Smith, 2001; La Pierre, Blumenthal, Brown, Klein, & Smith, 2016), or from experiments implementing mild-to-moderate alterations relative to the inherent interannual variation at the site (e.g., Miranda, Armas, Padilla, & Pugnaire, 2011; Cherwin & Knapp, 2012; Byrne et al., 2013; Koerner & Collins, 2014; Wilcox et al., 2015; all *sensu* Knapp et al., 2015). Extreme precipitation manipulations are more rare (Evans & Burke, 2013; Hoover, Knapp, & Smith, 2014; Yahdjian & Sala, 2006), and syntheses of extreme precipitation experiments are even more uncommon. Understanding whether ecosystem responses to mild/moderate precipitation change are predictive of ecosystem responses to larger magnitude precipitation changes is necessary to assess and update projections of future ecosystem functioning under climate change scenarios.

We synthesized results from 83 experimental case studies that measured ANPP and/or BNPP responses to manipulated precipitation amounts to address these knowledge gaps. Precipitation alterations in these case studies ranged in magnitude from –86% to +431% relative to control plots. We used meta-analytical techniques with this compiled data set to test the following hypotheses: (1) BNPP is less sensitive than ANPP to altered precipitation amount; (2) both ANPP and BNPP have greater sensitivity to increased vs. decreased precipitation; (3) ANPP and

BNPP sensitivities vary across temperature and precipitation gradients; and (4a) ANPP and BNPP responses to precipitation change are linear across the magnitude of precipitation change; or (4b) ANPP and BNPP responses to precipitation change are saturating across precipitation magnitudes. Compared with a linear relationship, a saturating relationship would indicate larger responses to extreme drought and lesser responses to extreme precipitation increases (Knapp et al., 2016). Assessment of these hypotheses is integral for assessing climate change impacts on ecosystem services across larger spatial scales, as well as identifying where/when impacts of climatic extremes are likely to be severe.

2 Materials and Methods

2.1 Data compilation

We collected publications that reported on primary productivity responses to experimental precipitation manipulations in grassland ecosystems by searching Web of Science. This included both increased (+PPT) and decreased (−PPT) precipitation treatments. We used the following search terms to obtain papers from January 1st, 1900, to November 14th, 2016: (“plant growth” OR “primary product*” OR “plant product*” OR “ANPP” OR “BNPP”) AND (“altered precipitation” OR “drought” OR “decreased precipitation” OR “increased precipitation” OR “increased summer precipitation” OR “decreased summer precipitation” OR “water addition” OR “water reduction” OR “water treatment*”) AND (“herbaceous” OR “grass*”) AND (“experiment*” OR “treatment*”). The search resulted in 322 peer-reviewed papers. We then went through these papers and removed all that did not meet the following criteria:

1. Study described a unique experiment. In the case of multiple publications of the same responses, we used the latest published paper. However, if the newest paper did not present annual responses, we used the most recent paper presenting annual data.
2. Plant communities were not artificially constructed, with the exception of species assemblages planted to approximate community abundances of a natural study site.
3. Experiment was conducted in the field, or using monolith plots in a greenhouse.
4. Treatment was consistent in all years.
5. Raw productivity values were reported (not just proportional change, or biomass with woody species).
6. Productivity was measured <2 months after treatment stopped.
7. Total community productivity was reported (not just species productivity).
8. Reported primary productivity in mass per area units.
9. A control precipitation treatment was present, and replication was greater than one.
10. Reported the amount or proportion of precipitation change.
11. Reported the standard deviation or standard error and sample size.

We also added multiple studies fitting these criteria obtained via personal communications and from literature cited sections of published papers. Production responses were excluded when ANPP incorporated previous year woody growth or if belowground standing crop root biomass was measured instead of BNPP in all perennial ecosystems. We limited our analyses to results from plots that solely manipulated precipitation—results from plots receiving precipitation combined with other resource manipulations were excluded. We compiled annual means,

standard deviations, and sample sizes of ANPP and BNPP from the literature or directly from the authors. We also compiled mean annual temperature (MAT), mean annual precipitation (MAP), and the amount and/or proportion of precipitation added or subtracted in each year of the study, obtained from the papers or authors. When studies reported results from experiments conducted in different locations or having multiple distinct treatments, these components were treated as individual case studies. In total, our meta-analysis included 47 published papers providing 83 precipitation manipulation case studies. Most (62 of the 83) of the case studies occurred in North America and Europe (Table S1). See Table 1 for summary information regarding the compiled data set and Text S1 for a bibliography of the papers used.

Table 1. Summary information for experimental precipitation addition (+PPT) and reduction (-PPT) treatments included in the meta-analysis

	Avg. ΔPPT (%)	Range ΔPPT (%)	Avg. duration (year)	Range duration (year)	Avg. MAP (mm)	Range MAP (mm)	Avg. MAT (°C)	Range MAT (°C)
+PPT	43.1	1.9–431	3.2	1–23	551	161–1526	7.5	-4.8–16.3
-PPT	48.7	18.1–86.0	2.0	1–4	572	168–1632	10.4	1.6–22.0
All	49.7	-86–431	2.7	1–23	554	161–1632	8.7	-4.8–22.0

ΔPPT, percent change of precipitation manipulation relative to control plots; MAP, mean annual precipitation; MAT, mean annual temperature.

2.2 Calculating sensitivity for meta-analysis

We employed a meta-analytic approach to assess the overall sensitivity of ANPP and BNPP to altered precipitation (Hedges, Gurevitch, & Curtis, 1999; Luo, Hui, & Zhang, 2006). Sensitivity (Sens) was calculated to represent the magnitude of response relative to the amount of precipitation change, as previously used by others (e.g., Huxman et al., 2004; Knapp et al., 2016; Sala et al., 2012; Smith, Wilcox, Power, Tissue, & Knapp, 2017; Wilcox, Blair, Smith, et al., 2016; Wu et al., 2011). The benefit of this calculation is that ecosystem responses are made comparable by standardizing by the magnitude of precipitation change:

$$\text{Sens} = \frac{\bar{X}_c - \bar{X}_t}{\text{PPT}_c - \text{PPT}_t} \quad (1)$$

where \bar{X}_t and \bar{X}_c are the productivity means across replicates of treatment and control groups, respectively, and PPT_t and PPT_c are the precipitation amounts in treatment and control groups, respectively. A variance (v_{sens}) associated with sensitivity was approximated using Equation 2.

$$v_{\text{sens}} = \left(\frac{1}{\text{PPT}_c - \text{PPT}_t} \right)^2 \times (s_c^2 + s_t^2) \quad (2)$$

where s_t and s_c are standard deviations of treatment and control groups, respectively. We validated our calculated variance using Monte Carlo simulations (Text S2).

We aggregated sensitivity across studies by calculating a weighted sensitivity estimate, similar to how previous meta-analyses have aggregated response ratios (Hedges et al., 1999; Luo et al., 2006). We calculated the weighted sensitivity (Sens_{++}) as:

$$\text{Sens}_{++} = \frac{\sum_{i=1}^k w_i \text{Sens}_i}{\sum_{i=1}^k w_i} \quad (3)$$

where w is the weighting factor ($w = \frac{1}{v_{\text{sens}}}$) and k is the number of studies. Standard error (SE) associated with Sens_{++} was computed using Equation 4.

$$SE(\text{Sens}_{++}) = \sqrt{\frac{1}{\sum_{i=1}^k w_i}} \quad (4)$$

Significance of Sens_{++} was assessed using a mixed-effects meta-analytic model where individual studies are weighted by the following equation:

$$w = \frac{1}{\tau^2 + v_{\text{sens}}} \quad (5)$$

where w is the weighting factor for an individual study, τ is the amount of variability not accounted for using the existing parameters in the model, and v_{sens} is the study variance as calculated from Equation 2. Many of the experiments were conducted over multiple years, and responses often varied interannually due, in large part, to year-to-year variation in ambient rainfall. To account for this, case study was designated as a random effect within the mixed-effects model to account for pseudoreplication originating from studies spanning multiple years.

2.3 Sensitivity vs. climatic factors

To assess patterns of sensitivity across climatic gradients, we averaged sensitivity values across years for ANPP or BNPP under increased or decreased precipitation treatments within each case study. This resulted in up to four sensitivity calculations per case study, which occurred if a study measured ANPP and BNPP and imposed both precipitation additions and reductions (one sensitivity value each for PPT+ ANPP, PPT- ANPP, PPT+ BNPP, and PPT- BNPP). Linear and various nonlinear models were compared using AIC values to determine the most appropriate model structure for correlating sensitivity with MAP and MAT (see Table S2 for identity and form of relationships tested).

2.4 Magnitude of precipitation change vs. magnitude of ANPP or BNPP response

Because the percentage change of precipitation varies in most studies from year to year, depending on ambient precipitation, we assessed relationships between the percentage precipitation change and the percentage productivity response for each year of each case study. First, we did this to determine whether relationships between the magnitude of production response and the magnitude of precipitation change differed for ANPP vs. BNPP. We also determined whether this relationship differed for precipitation additions vs. subtractions. To this end, we calculated the percentage precipitation change— $\% \Delta \text{PPT} = (\text{PPT}_t - \text{PPT}_c)/\text{PPT}_c$, percentage productivity response for ANPP— $\% \Delta \text{ANPP} = (\text{ANPP}_t - \text{ANPP}_c)/\text{ANPP}_c$, and

$\text{BNPP} - \% \Delta \text{BNPP} = (\text{BNPP}_t - \text{BNPP}_c) / \text{BNPP}_c$. We used percentage change for this analysis—instead of the raw amount of precipitation change—because percentage change is comparable across ecosystems spanning climatic gradients, whereas the absolute amount of precipitation change may have very different implications in dry vs. wet sites. We constructed a mixed-effects weighted-estimation metaregression model (van Houwelingen, Arends, & Stijnen, 2002) (Equation 5), with case study as a random factor, to look for significant interaction terms between productivity type (ANPP vs BNPP) and $\% \Delta \text{PPT}$ as well as between treatment (increased vs decreased precipitation) and $\% \Delta \text{PPT}$.

Second, we looked at whether these relationships were linear or saturating. We did this through AIC comparisons of linear and natural log transformed (Table S4) models relating $\% \Delta \text{PPT}$ with $\% \Delta \text{ANPP}$ or $\% \Delta \text{BNPP}$. We again weighted the regressions using mixed-effects weighted-estimation metaregression models. If the more appropriate model is linear, this suggests that ecosystem responses to precipitation extremes are proportional to their responses to mild or moderate alterations in precipitation (i.e., levels of precipitation change similar to those commonly found in historical precipitation records; Knapp et al., 2015). If the more appropriate model is saturating, primary production responses under precipitation extremes may not conform to patterns assessed under milder precipitation change. Intercepts for $\% \Delta \text{PPT}$ - $\% \Delta \text{ANPP}$ (or $\% \Delta \text{BNPP}$) regressions were set at zero because, in an experimental framework, $\% \Delta \text{ANPP}$ (or $\% \Delta \text{BNPP}$) should be zero when $\% \Delta \text{PPT}$ is zero. Five outliers were removed from the increased precipitation vs. $\% \Delta \text{ANPP}$ using a threshold of $\alpha = 0.05$ (r -student: 6.29, 5.62, 4.36, 3.95, 3.80; all Bonferroni $p < .05$). Results were qualitatively similar when these points were included (Table S5). We did not detect publication bias when examining plots showing the observed effect size and study variance (funnel plots; Sterne & Egger, 2001).

All analyses were conducted in r (R Core Team, 2016), and mixed-effects models were conducted using the nlme package (Viechtbauer, 2010).

3 Results

Across all studies, we found that the sensitivity of ANPP and BNPP to both precipitation increases and decreases was greater than zero (Figure 1; ANPP+: $F_{1,71} = 32.2, p < .01$; ANPP-: $F_{1,39} = 36.7, p < .01$; BNPP+: $F_{1,25} = 5.71, p = .02$; BNPP-: $F_{1,10} = 6.97, p = .02$). ANPP sensitivity to increased precipitation was 147% greater than ANPP sensitivity to decreased precipitation ($z = 3.0$, Tukey-adj. $p = .01$). In contrast, BNPP sensitivity to precipitation increases and decreases was not significantly different ($z = -1.8$, Tukey-adj. $p = .28$). Sensitivity to increased precipitation was 118% greater for ANPP than BNPP ($z = -3.4$, Tukey-adj. $p < .01$), but sensitivity to decreased precipitation was not significantly different between ANPP and BNPP ($z = 1.5$, Tukey-adj. $p = .44$).

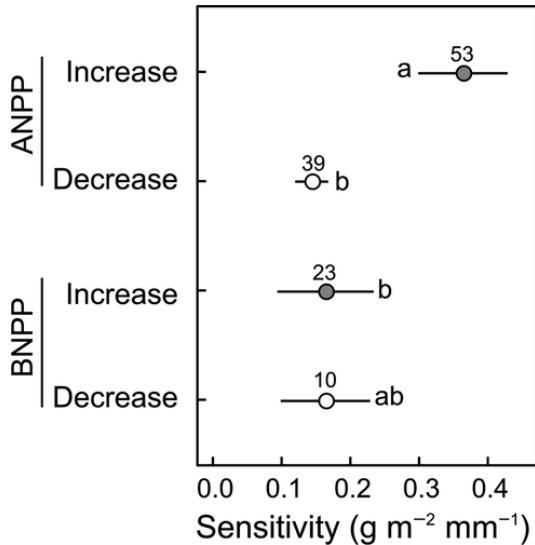


Figure 1. Sensitivity of aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP) aggregated across experiments simulating increased (filled circles) and decreased (open circles) precipitation. Sensitivity is calculated as the amount of productivity response divided by the amount of precipitation change. Numbers above symbols represent the number of studies incorporated in each estimate. Different letters represent different sensitivity at $\alpha = 0.05$, and error bars represent one standard error from the mean

3.1 Precipitation sensitivity and background climate

The broad range of MAP and MAT of sites used in this meta-analysis (Table 1) allowed us to examine patterns of precipitation sensitivity across large climatic gradients. We first tested whether sensitivity-MAP and sensitivity-MAT relationships varied between precipitation increases and decreases. We found that the sensitivity-MAP relationship was marginally different under precipitation increases vs. decreases ($F_{1,85} = 3.82, p = .05$; different trend lines in Figure 2a). The sensitivity of ANPP to precipitation additions was higher in arid sites than in mesic sites. We found no relationship between MAP and sensitivity of ANPP to precipitation reduction treatments (Figure 2a, Table S2). BNPP sensitivity-MAP relationships were not different for precipitation increases vs. decreases ($F_{1,29} = 0.18, p = .67$), and sensitivity of BNPP to precipitation manipulations generally decreased with MAP (Figure 2c). We did not find a significant interaction between MAT-sensitivity and precipitation increases vs. decreases for ANPP ($F_{1,85} = 0.04, p = .84$) or BNPP ($F_{1,29} = 0.85, p = .36$). We did not find a significant relationship between MAT and ANPP sensitivity (Table S2), while BNPP sensitivity was greater in colder sites (Figure 2b, d). See Table S2 for information about the form, coefficients, and selection of each regression.

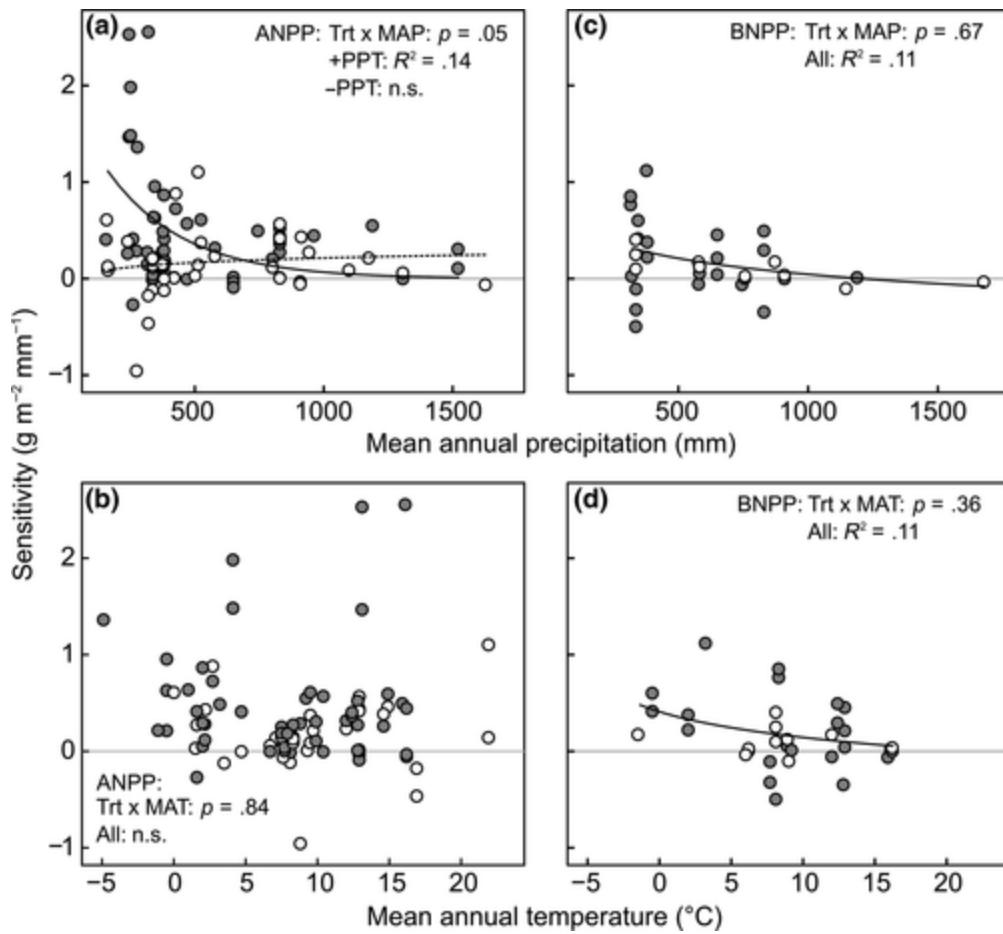


Figure 2. Relationships between site-level climate and sensitivity of ANPP (a, b) and BNPP (c, d) to increased (filled circles) and decreased (open circles) precipitation treatments (Trt). Climatic variables tested were mean annual precipitation (a, c) and mean annual temperature (b, d). Trendlines in (a) are split into precipitation increases and decreases because slopes were significantly different. Trendlines in (b–d) represent overall regressions because sensitivity-MAP or MAT relationships were not different between increased and decreased precipitation treatments (nonsignificant Trt \times MAP or Trt \times MAT interactions). Relationships without trendlines and the dotted trendline in (a) are not significant at $\alpha = 0.1$.

3.2 Comparing $\% \Delta \text{PPT}$ and $\% \Delta \text{NPP}$ linear vs. saturating relationships

In our full models comparing the percentage change of productivity ($\% \Delta \text{NPP}$) vs. percentage change of precipitation ($\% \Delta \text{PPT}$), we found the natural log transformed model was a better fit than the linear model (linear model AIC: 177.7, natural log model AIC: 175.2; Table S3). Within the full natural log model, we found significant interactions between $\% \Delta \text{PPT}$ and precipitation direction (precipitation increases vs. decreases) and between $\% \Delta \text{PPT}$ and productivity type (ANPP vs BNPP; Table S3). This was due to steeper $\% \Delta \text{PPT}$ - $\% \Delta \text{NPP}$ slopes for ANPP (0.24 ± 0.11 ; slope \pm standard error) vs BNPP (0.15 ± 0.07) and for precipitation increases (0.59 ± 0.17) vs. decreases (0.22 ± 0.07). Additionally, we found significant interactions between $\% \Delta \text{PPT}$ and precipitation direction for both ANPP and BNPP analyzed separately (Table S3). These interactions indicated that relationships between the magnitude of productivity response

and $\% \Delta \text{PPT}$ may vary between ANPP and BNPP as well as under precipitation increases vs. decreases.

We then analyzed $\% \Delta \text{PPT}$ - $\% \Delta \text{NPP}$ relationships separately for ANPP and BNPP under precipitation increases and decreases to assess whether linear or saturating (natural logarithmic) models better fit the data for each category. We found that the saturating model was a better fit for ANPP under precipitation increases (linear model AIC 47.1 vs ln model AIC 44.6; Figure 3; Table S4). The better fit of the saturating model was maintained even after removal of the point having very large $\% \Delta \text{PPT}$, but the AIC differentiation was weaker (Table S5). For ANPP under precipitation decreases and BNPP under precipitation increases and decreases, we found weak or no evidence for saturating models as a better fit to the data (Figure 3; Table S4).

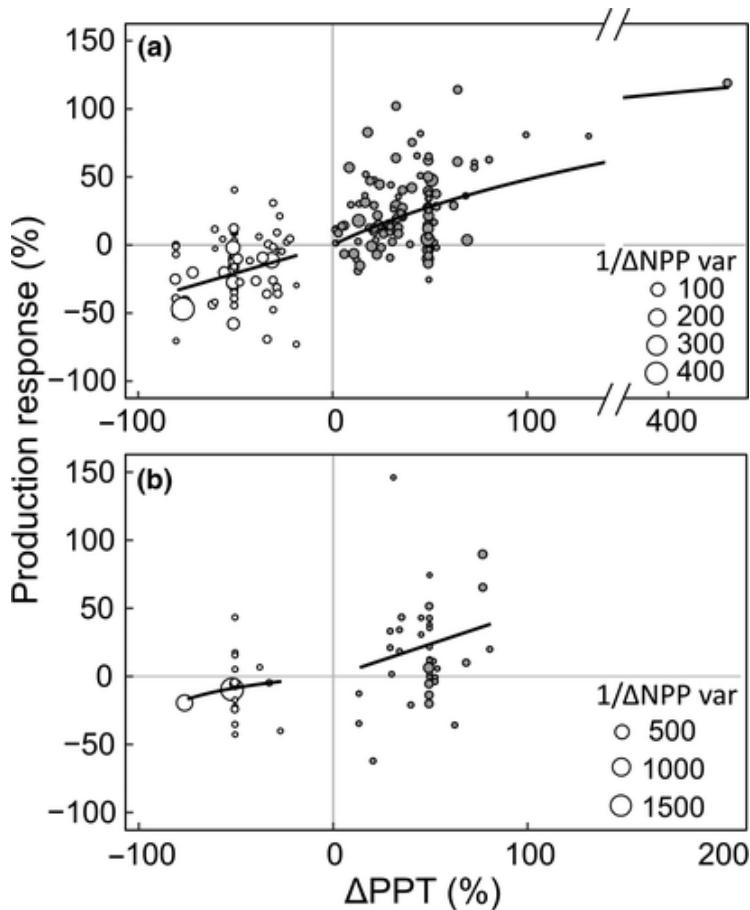


Figure 3. Relationships between percentage responses of (a) ANPP or (b) BNPP and the magnitude of experimental precipitation manipulation (ΔPPT ; increased (filled circles) and decreased (open circles)). Circle sizes are inversely correlated with the estimated sampling variance of the percentage response of productivity, which was used to weight points within the metaregression (i.e., larger circles influence the regression more, see Methods). In panel (a), the far right point is included in the regression, but results are qualitatively similar when this point is removed (Table S5)

4 Discussion

Plant growth accounts for a large fraction of the terrestrial carbon cycle and acts as an important buffer against fossil fuel emissions (Le Quéré et al., 2015). Making accurate assessments of future carbon budgets depends upon understanding influences of altered precipitation on primary productivity. Fortunately, many recent precipitation studies have documented responses of various components of NPP, allowing for synthesis to identify key general patterns of herbaceous responses to precipitation change. We found that sensitivity to precipitation change often differed between ANPP and BNPP, and depended on whether precipitation was increased or decreased. We also found that drier and cooler sites had higher sensitivity to precipitation change, especially to precipitation additions. Lastly, we found evidence that productivity responses to increased precipitation may saturate under very wet conditions. In the paragraphs below, we discuss implications and potential mechanisms underlying these findings.

4.1 Overall ANPP vs. BNPP sensitivity to precipitation change

BNPP was less sensitive than ANPP to increased precipitation treatments (Figure 1), coinciding with previous work (Wu et al., 2011). One interpretation is that root:shoot plasticity may be strong under wet conditions (Knapp, 1984) and may result in decreased root allocation to facilitate greater light capture during periods of high soil resources (Joslin & Wolfe, 1998). Additionally, saturated soil moisture conditions may limit root development (Kozlowski, 1997). These changes in allocation may limit increased BNPP under increased precipitation, as well as heighten ANPP responses, compared with overall NPP responses. Secondly, longevity of live roots is typically greater under moderately wet soil conditions (Facette, McCully, & Canny, 1999), which may reduce the need/space for increased BNPP to replace root systems under wetter conditions (Hayes & Seastedt, 1987). However, under extremely wet conditions, root lifespan can decrease (Kozlowski, 1997), which may result in a threshold response at a certain magnitude of precipitation increase. The methodology used to measure roots in most of these studies (root ingrowth cores) would likely not detect this second mechanism as competition for space is not typically a factor for roots growing in root ingrowth cores during much of the growing season. For this reason, we suggest that plasticity in root:shoot allocation may be the important factor driving different above vs. belowground productivity responses to increased precipitation observed in this study. Conversely, we found that ANPP and BNPP sensitivities to drought were similar in magnitude. This may be due to a limitation of carbohydrates available for growth (and thus allocation shifts) during periods of low soil moisture in drought treatments. In the early portion of the growing season, soil moisture is often high in both drought and control conditions due to winter inputs and low evaporation rates occurring with cooler spring temperatures. However, as soil moisture is depleted later in the growing season and drought effects become more evident (Denton, Dietrich, Smith, & Knapp, 2016), carbohydrates may be similarly deficient for both root and aboveground growth, which may limit the potential for changes in allocation above- or belowground.

4.2 PPT sensitivity across climatic gradients

Previous observational studies have assessed patterns of climatic context (e.g., MAP) vs. the sensitivity of primary production to altered precipitation amount by examining the slope between primary production and annual precipitation (Huxman et al., 2004; Sala et al., 2012). We used a similar sensitivity metric to assess whether similar patterns exist for ANPP and BNPP based on

experimental data. We found the sensitivity of ANPP and BNPP to altered precipitation was negatively related to MAP (Figure 2a, c), coinciding with these observational studies (Huxman et al., 2004; Sala et al., 2012). To our knowledge, this pattern has not been previously identified through synthesis of experimental findings. Wu et al. (2011) found no relationship between sensitivity and MAP, potentially because they limited their analysis to linear regression, a relationship we found to be substantially less predictive than the negative exponential relationship shown in Figure 2 (Table S2). The nonlinearity of the ANPP sensitivity-MAP relationship (Figure 2a, c) highlights the importance of understanding precipitation impacts in more xeric ecosystems, due to their potential for much higher sensitivity to precipitation increases than more mesic systems. We found no significant relationship between MAP and ANPP sensitivity to drought. The different sensitivities to precipitation increases vs. decreases in arid ecosystems may be due to buffering capacity of drought tolerant plant traits (Knapp & Smith, 2001) possessed by dominant plant species in these ecosystems.

We found BNPP was generally less sensitive to precipitation changes in warmer ecosystems. This may be due to longer residence times of added soil moisture in cooler sites, resulting in a higher proportion of soil water being utilized by plants vs. being evaporated directly from the soil and cooler sites having higher water use efficiency (Vermeire, Heitschmidt, & Rinella, 2009). In addition, this could be driven by deeper rooting profiles in cooler, high latitude sites. Root growth tends to occur more homogenously throughout the soil profile due to more homogenous soil moisture levels across soil depths (e.g., Schenk & Jackson, 2002; Wilcox et al., 2015), so it may be that the additional soil depths available for root production in cooler systems leads to greater BNPP sensitivity to water additions.

4.3 ANPP and BNPP responses across magnitudes of precipitation manipulation

If relationships between $\% \Delta \text{PPT}$ and $\% \Delta \text{NPP}$ are nonlinear and saturating, then using linear models from historical precipitation-productivity regressions will not accurately predict the impacts of extreme drought or extreme precipitation increases (Knapp et al., 2016). In our full models, we found that the saturating model relating $\% \Delta \text{PPT}$ and $\% \Delta \text{ANPP}/\text{BNPP}$ was a better fit to the data than the linear model (Table S3). Past observational studies have looked for, but have not been able to identify, nonlinear patterns of primary productivity and precipitation change through site-level historical records of ANPP and annual precipitation (Hsu & Adler, 2014). This may stem from the fact that, by definition, years having extreme precipitation amounts occur very infrequently in the historical record. For example, Hoover et al. (2014) examined a 27-year ANPP-precipitation data set from the Konza Prairie Biological Station, and in the context of a 111-year precipitation record from this same area, found only one year of ANPP data that was linked with extreme precipitation. This highlights the value of climate change experiments for quantifying future ecosystem responses under novel climatic conditions, as experimental manipulations are able to push systems beyond historical climatic limits within sites (e.g., Evans, Byrne, Lauenroth, & Burke, 2011; Zhu, Chiariello, Tobeck, Fukami, & Field, 2016).

The nature of the overall saturating relationship could be driven by (1) lower magnitude of productivity responses under extreme precipitation increases, (2) greater magnitude of productivity responses under extreme drought, or (3) both. When we analyzed $\% \Delta \text{ANPP}$ vs $\% \Delta \text{PPT}$ separately for +PPT and -PPT, we only found convincing evidence for a saturating

relationship for +PPT (Table S3; Figure 3). We did not find that the saturating curve was a substantially better fit for % Δ BNPP under +PPT or -PPT. We think this may be due to a few factors. First, the range of % Δ PPT was much greater for studies increasing precipitation and measuring ANPP, so perhaps saturating relationships are only evident under very extreme changes in precipitation (Knapp et al., 2016). Second, perhaps extreme drought impacts require multiple successive years of precipitation reductions to fully develop (Hoover et al., 2014) due to depletion of soil water or carbohydrate reserves. The majority (51 of 83; Table S6) of our case studies were only 1–2 years in length, which may be why we failed to detect logarithmic relationships under drought alone—even though we included a number of experiments with large drought magnitudes (Table 1). Third, extreme heat waves often co-occur with extreme drought during real-world climatic extremes. This is likely to cause larger productivity responses than typically found in single factor drought experiments through further depletion of soil moisture (Hoover et al., 2014).

We found substantial variation surrounding the trends shown in Figures 2 and 3. Much of the variation seen in these relationships may stem from cross-site variation of nonclimate characteristics, such as soil texture, soil fertility, plant species composition, fire regime, or presence/absence of grazing. For example, nitrogen limitation may constrain a site's sensitivity to increased precipitation (Ladwig et al., 2012), or drought tolerant plant species may reduce sensitivity of an ecosystem to changes in water availability (Wilcox, Blair, Smith, et al., 2016). Unfortunately, many studies did not report sufficient site-level characteristics for robust assessment of these factors as drivers of ecosystem sensitivity to precipitation change. We encourage future precipitation studies to report ecosystem characteristics such as soil available nutrients, soil texture, and plant species/functional composition. We also see considerable value in conducting experiments within single sites manipulating a gradient of precipitation levels—ranging from extreme precipitation increases to extreme precipitation decreases—while controlling for other variables that may affect sensitivity (e.g., Gherardi & Sala, 2015; Luo, Jiang, Niu, & Zhou, 2017).

To provide accurate projections of how ecosystems will respond to future precipitation scenarios, generalities informing patterns of precipitation impacts on ecosystem function are needed. Using meta-analytic methods, we explored overall ANPP and BNPP sensitivity to precipitation change, the climatic context of sensitivity, and how patterns of primary productivity change as precipitation changes become extreme. First, we suggest that shifts in allocation of biomass above- vs. belowground may lower NPP during high rainfall years, compared with expectations based on ANPP responses alone. Second, we identified drier ecosystems as being especially sensitive to precipitation increases, while cooler ecosystems were somewhat more sensitive to any changes in precipitation. Lastly, we found that previously identified asymmetries—showing greater productivity responses in wet vs. dry years (Knapp & Smith, 2001)—may be reversed when precipitation alterations become very extreme. In the future, we advocate for (1) increased attention to BNPP responses to extreme precipitation changes, and (2) more long-term experiments that implement multiple levels of increased and decreased precipitation amount.

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Supplemental Materials

Additional Supporting Information may be found online: <https://doi.org/10.1111/gcb.13706>

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