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RESEARCH ARTICLE

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A meta-analysis of primary productivity and rain use efficiency in terrestrial grassland ecosystems

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Abstract

A comprehensive understanding of annual net primary productivity (ANPP) and rain-use efficiency (RUE) along precipitation gradients is critial for grassland conservation under climate change. However, how ANPP and RUE respond to changes in precipitation at different spatial and temporal scales remains uncertain. The aim of this research was to clarify these things. Using data from 21 field experiments, with an average sampling period of 14.3 years in 32 sites, 18 of which are in China, we evaluated the relationship of mean annual precipitation (MAP) with ANPP and RUE across spatial and temporal scales in grassland ecosystems. Our study showed different degrees of sensitivity of ANPP and RUE to changing precipitation spatially and temporally. First, analysis supports the well-known positive linear relationship between ANPP and MAP. Second, we found that ANPP increases with increasing precipitation regardless of the actual precipitation amount of the study sites, whereas ANPP increased 0.2 g m^{-2} more than it declined per 1 mm change in precipitation. Third, RUE increased with increasing MAP across sites, whereas RUE generally decreased with annual precipitation within most sites. Finally, the temporal variation in RUE within sites is lower than the overall spatial pattern of variation across sites. The lack of consistency in ANPP and RUE among years and across sites in response to interannual variation in precipitation indicates the complexity of ecological indicators characterizing precipitation changes. These findings highlight the prevalence of site-specific variation in precipitation-ANPP relationships.

KEYWORDS

asymmetric responses, precipitation gradient, rain use efficiency, sensitivity of net primary productivity, spatial- and temporal-scale, vegetation and biogeochemical limitations

1 | INTRODUCTION

Substantial changes in precipitation patterns have occurred worldwide (Dukes, Classen, Wan, & Langley, 2014; IPCC, 2013). These fluctuations have motivated studies on effects of precipitation on annual net primary productivity (ANPP), productivity sensitivity to precipitation changes (the slope of annual precipitation versus ANPP), and rain-use efficiency (RUE, ratio of ANPP to annual precipitation) in grassland ecosystems (Collins et al., 2016; Fahey & Knapp, 2007; Gao et al., 2016; Hoover, Knapp, & Smith, 2014; Knapp, Ciais, & Smith, 2017; Song, Niu, & Wan, 2016; Walther, 2002). However, there is little consensus on how these measurements co-vary, despite the fact that they are inherently interrelated (Verón, Oesterheld, & Paruelo, 2005).

ANPP sensitivity and RUE are implicitly contained within the precipitation-ANPP relationship (Chapin, Matson, & Mooney, 2002; Huxman et al., 2004; Lambers, Chapin, & Pons, 1998; Lauenroth, Burke, & Paruelo, 2000; Noy-Meir, 1973; Paruelo, Lauenroth, Burke, & Sala, 1999; Tilman, Cassman, Matson, Naylor, & Polasky, 2002). For example, with respect to spatial variation, if the mean annual precipitation (MAP)- mean ANPP relationship is linear across a range of MAP (Huxman et al., 2004; Petrie et al., 2018), ANPP sensitivity and/or RUE should be relatively constant (Figure 1a). If the MAP- mean ANPP relationship shows a non-linear increase, as found in some studies at the low end of the MAP gradient (Gherardi & Sala, 2019; Hu et al., 2010), then ANPP sensitivity and/or RUE will increase with MAP (Bai et al., 2008) (Figure 1b). However, if the MAP- mean ANPP relationship is asymptotic as found in more mesic systems (Gherardi & Sala, 2019), ANPP sensitivity and/or RUE may decrease with MAP (Del Grosso et al., 2008; Luo, Jiang, Niu, & Zhou, 2017) (Figure 1b). If the conversion of rainfall into productivity is low both at the dry and the wet end of a precipitation gradient, and thus peaks at intermediate levels, ANPP sensitivity and/or RUE will be unimodal (Hein & de Ridder, 2006) (Figure 1c). Knapp et al. (2017) suggest a temporal non-linear relationship between annual precipitation and ANPP in grasslands when including extreme wet and dry years. This model predicts positive asymmetry-a greater positive response of ANPP during wet periods compared to the negative response during dry periods (Ahlstrom et al., 2015; Knapp & Smith, 2001; Unger & Jongen, 2015; Wu, Dijkstra, Koch, Penuelas, & Hungate, 2011), and also suggests negative asymmetry-a smaller positive response of ANPP in wet periods compared to negative responses in dry periods (Luo et al., 2008; Peng et al., 2013; Wu et al., 2018; Zscheischler et al., 2014) (Figure 1d). However, this 'double asymmetry' hypothesis is rarely confirmed, perhaps because many studies are short-term over relatively small ranges of interannual variability in preciptation.

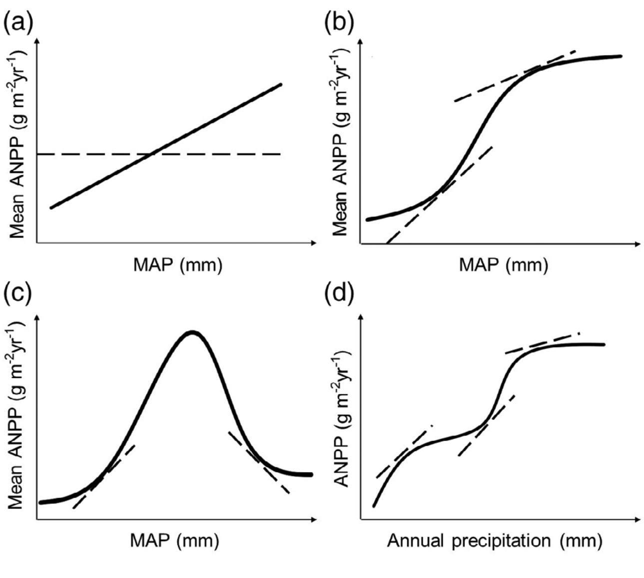

FIGURE 1 Hypothesized relationships between mean annual net primary productivity (ANPP) and mean annual precipitation (MAP) (relationships between mean ANPP and MAP, solid line; productivity sensitivity to changing precipitation, dotted line)

To better understand the patterns of ANPP sensitivity and RUE in relation to precipitation, we conducted a global synthesis to evaluate mid- to long-term effects (with an average sampling period of 14.3 years) of MAP on mean ANPP for 32 terrestrial sites in 12 grassland ecosystems. We first examined goodness of fit of linear, logarithmic, exponential, and unimodal models by assessing the relationship between mean ANPP/MAP across all of the sites using Akaike information criterion (AIC) values. Then, ANPP sensitivity was compared by regressing the slopes of annual precipitation and ANPP for each site against MAP (Huxman et al., 2004; Maurer, Hallmark, Brown, Sala, & Collins, 2020). We further tested a temporal annual precipitation-ANPP model by correlating the relative ANPP pulse [(maximum – mean)/mean] for the wettest year with the relative ANPP decline [(mean – minimum)/mean) for the driest year across the 32 sites. We also assessed whether temporal patterns of RUE and ANPP sensitivity to interannual variation in precipitation within sites were similar to patterns of variation across sites in these grasslands. Finally, to determine how well patterns of productivity, productivity sensitivity to changing precipitation, and RUE in China represented global grasslands, we compared the main findings from China to grasslands on other continents.

2 | MATERIALS AND METHODS

2.1 | Data compilation

We compiled publications that reported on primary productivity responses to changing precipitation in natural grassland ecosystems by searching Web of Science. We used the following search terms to obtain papers before December 31th, 2017: ('ANPP' OR 'biomass' OR 'production' OR 'primary productivity' OR 'plant production') AND ('precipitation' OR 'drought' OR 'rainfall') AND ('grassland' OR 'steppe' OR 'meadow' OR 'pasture' OR 'prairie'). We also added multiple studies fitting these criteria obtained via personal communication. A total of 182 peer-reviewed papers on ANPP and precipitation was collected. We then evaluated these papers and removed all that did not meet the following criteria:

1. Studies were conducted in ungrazed grassland, steppe, meadow, pasture, or prairie ecosystems, and plant communities that were not artificially constructed;
2. Studies were done under natural precipitation regimes rather than under experimental precipitation manipulations or other resource manipulations;
3. Studies that reported the absolute value of ANPP, whereas studies reporting only relative change of ANPP or cover data were excluded;

4. ANPP was measured over at least 6 years;
5. Annual precipitation was reported.

In total, our meta-analysis included 21 published papers for 32 sites in 12 grassland ecosystems (see Figure S1, Table S1 for details). These sites represent a broad annual precipitation gradient from 3 mm in desert in northern China to 1,339 mm in Mediterranean grassland in western United States.

2.2 | Data analysis

In order to analyze the effect of precipitation on net primary production, we compared mean ANPP and MAP relationships across sites, as well ANPP-annual precipitation relationships within each of the 32 sites over time. Linear and nonlinear models (exponential, logarithmic, and unimodal model) were compared using Akaike information criterion (AIC) values to determine the most appropriate model for correlating mean ANPP with MAP. ANPP sensitivity was assessed by correlating annual precipitation with ANPP over time for each site, and the resulting slopes were then regressed against MAP to determine how sensitivity of ANPP changed with MAP (Huxman et al., 2004; Maurer et al., 2020). To assess how ecosystems responded to wet versus dry years, we tested the relationships between relative precipitation maxima [$Precipitation_{max}$ = (maximum – mean)/mean] and relative ANPP pulses [$ANPP_{pulse}$ = (maximum – mean)/mean] for the wettest year and between relative precipitation minima [$Precipitation_{min}$ = (mean – minimum)/mean] and relative ANPP decline [$ANPP_{decline}$ = (mean – minimum)/mean] for the driest year, following Knapp and Smith (2001). To examine whether the response of ANPP to precipitation changes was symmetric or asymmetric, we correlated relative ANPP pulses with relative ANPP declines across the 32 sites. Linear regressions were used to evaluate effects of MAP or annual precipitation on RUE_{max}, RUE_{mean}, and RUE_{min} across 32 sites, and RUE within each site over time for all 32 sites. RUE_{max}, RUE_{mean}, and RUE_{min} were the maximum, mean, and minimum RUE in each site, respectively. RUE was calculated directly as the ratio of ANPP to annual precipitation (Bai et al., 2008). Linear and unimodal models were compared using AIC values to determine the most appropriate models that influence RUE_{max}, RUE_{mean}, and RUE_{min}. To predict whether RUE converged to a common maximum RUE (RUE_{max}) when water was the primary limiting resource, and converged to a common minimum RUE (RUE_{min}) when water was abundant, we separately related ANPP with annual precipitation in the driest years and ANPP with annual precipitation in the wettest years. We also quantified interannual variation of MAP (measured as the coefficient of variation; CV_{map}) and interannual variation of ANPP (measured as the coefficient of variation; CV_{anpp}) among the 12 grassland ecosystems. Productivity, productivity sensitivity, and RUE at spatial and temporal scales within and outside of China were compared to test whether the main findings in Chinese grasslands were similar to grasslands globally. All statistical analyses were conducted using SAS (SAS Institute Inc., Cary, NC).

3 | RESULTS

3.1 | Spatial and temporal patterns of primary productivity

Mean ANPP increased linearly with increasing MAP across all 32 sites (linear model AIC 387.9; logarithmic model AIC 405.1; exponential model AIC 390.2; unimodal model AIC 387.9) (Mean ANPP = 0.7 (MAP)-41.7; r^2 = 0.72, p < .001; Figure 2a). At the local scale, there was substantial variability in the ANPP-annual precipitation relationship: 20 out of the 32 sites showed a positive relationship between ANPP and annual precipitation, 11 had no relationship, and one in the typical steppe in Xiwu County, Inner Mongolia, China had a negative relationship (Figure 2b). Mean ANPP along the precipitation gradient in China was similar to grasslands on other continents, both linearly increased with MAP (China: linear model AIC 199.8; logarithmic model AIC 208.0; exponential model AIC 199.5; unimodal model AIC 199.8; Outside China: linear model AIC 181.4; logarithmic model AIC 184.3; exponential model AIC 183.2; unimodal model AIC 181.4; Figure 2a). Among Chinese grasslands, average ANPP was highest in Alpine meadow in Haibei, Qinghai (374.3 g m^{-2} yr^{-1}) and lowest in the desert in Alashan County, Inner Mongolia (13.0 g m^{-2} yr^{-1};

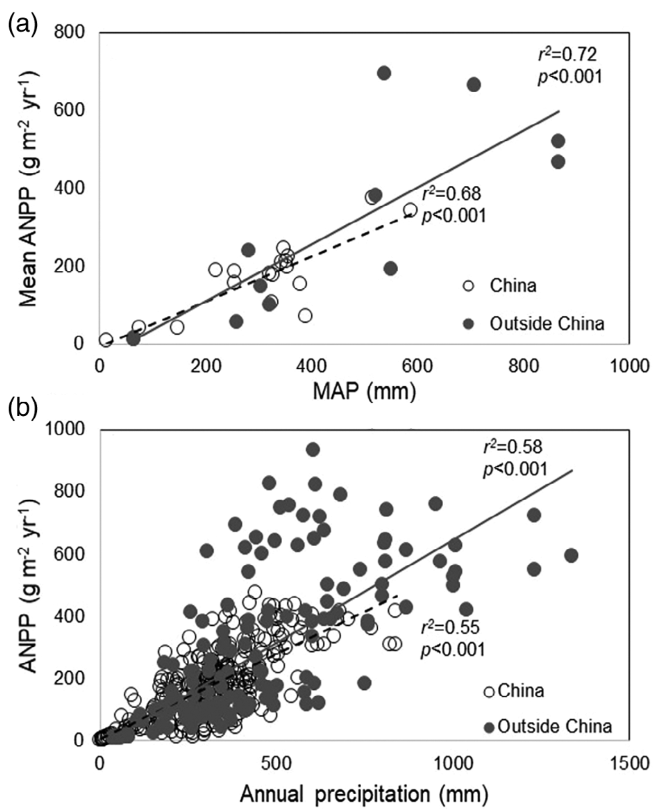

FIGURE 2 Effect of precipitation on annual net primary productivity (ANPP) along a precipitation gradient. (a) mean ANPP versus MAP for all 32 sites; (b) ANPP versus annual precipitation in each of the 32 sites (one was negative, 11 had no relationship and 20 were positive)

Figure 2b). Among grasslands outside of China, tallgrass prairie in Konza, United States had the highest average ANPP (692.7 g m^{-2} yr^{-1}) whereas desert steppes (HK) in Elouara, Tunisia had the lowest average ANPP (10.8 g m^{-2} yr^{-1}; Figure 2b). Across all grasslands, desert vegetation in Alashan County, China exhibited the highest CV_{anpp} and CV_{ap}, whereas Mediterranean grassland in United States and Israel had the lowest CV_{anpp} and CV_{ap}, respectively (Figure S2).

3.2 | Spatial and temporal patterns of ANPP sensitivity to precipitation changes

In China grasslands, maximum sensitivity of ANPP was found in desert grassland in Damao County, Inner Mongolia, China (slope = 1.41), whereas the lowest sensitivity occurred in the typical steppe in Xiwu County, Inner Mongolia, China (slope = –0.38). Overall, mean sensitivity was slope = 0.33 ± 0.05 *SD*. Ourside of China, maximum sensitivity of mean ANPP was found in plains grasslands in Wyoming, United States (slope = 0.63), and minimum sensitivity occurred the Mediterranean grassland, in Israel (slope = –0.26). Mean ANPP sensitivity to changing precipitation showed no relationship with MAP at 18 sites in China, 14 sites outside of China, and all 32 sites combined (Figure 3). As for temporal patterns, relative ANPP pulse/decline increases linearly with relative precipitation maxima/minima for the 18 sites in China and for all 32 sites combined, whereas no correlations were found for ANPP pulse/decline with relative precipitation maxima/minima at the 14 sites on other continents (Figure 4). Also, a positive correlation occurred between relative ANPP pulse and relative ANPP decline among all 32 grassland sites (Figure 5). However, the patterns were highly heterogeneous, and 20 out of 32 sites showed that ANPP pulses in the wet years were much stronger than ANPP declines in dry years (what we refer to here as positive asymmetry, Figure 5). In contrast, negative asymmetry characterized the responses at the remaining 12 sites (Figure 5).

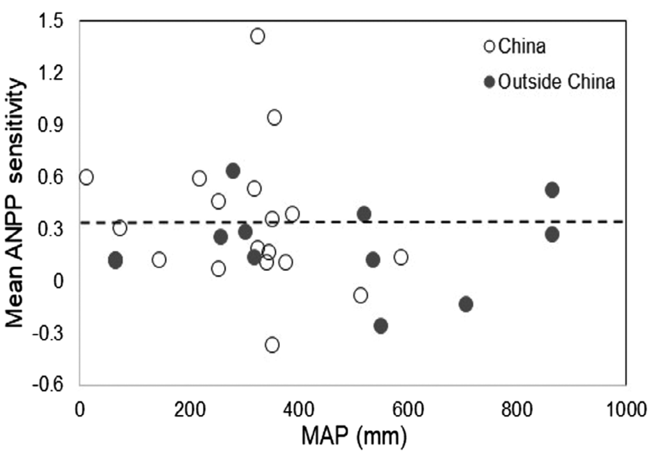

FIGURE 3 Mean annual net primary productivity (ANPP) sensitivity to mean annual precipitation (MAP)

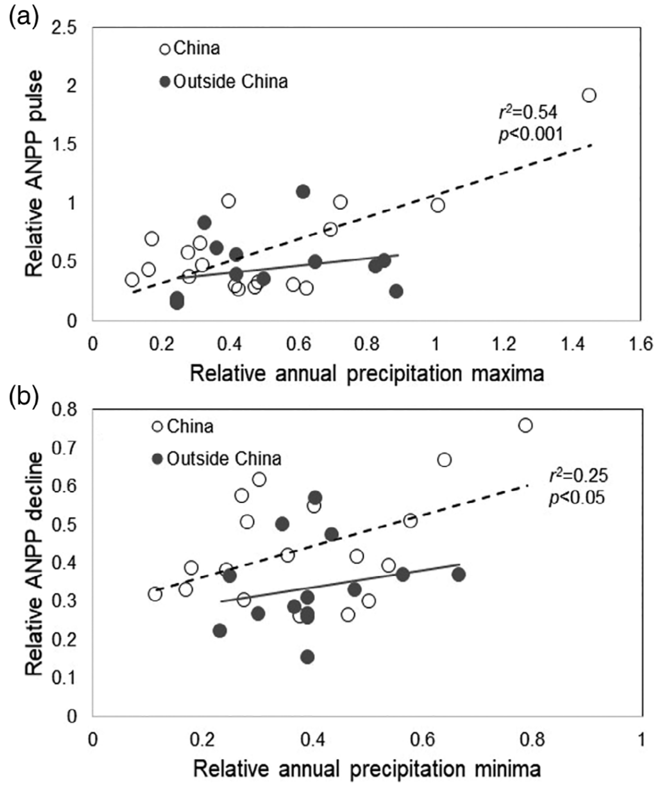

FIGURE 4 The relationship between (a) relative annual precipitation maxima and relative annual net primary productivity (ANPP) increase for the wettest year, and (b) the relationship between relative annual precipitation minima and relative ANPP decline for the driest year

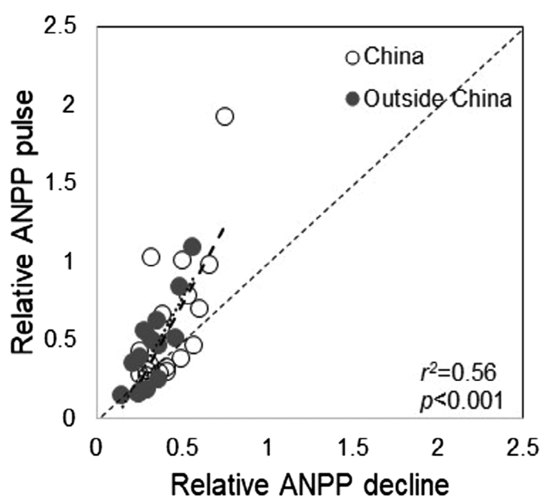

FIGURE 5 Relative annual net primary productivity (ANPP) increase and decline are positively correlated across the 32 sites. The dashed line represents a hypothetical 1:1 relationship between the variables

3.3 | Spatial and temporal patterns of RUE

RUE_{mean} (linear model AIC was equal to quadratic model AIC, 397.8), RUE_{max} (linear model AIC was equal to quadratic model AIC, 410.7), and RUE_{min} (linear model AIC was equal to quadratic model AIC, 397.3) increased linearly with increasing MAP across the 32 grassland sites (Figure 6a). The highest RUE (1.32 g m^{-2} mm^{-1}) were found in tallgrass prairie, Konza, United States, and the lowest RUE (0.11 g m^{-2} mm^{-1}) occurred in the desert steppes, in Damao County, China. The overall average RUE_{mean} was 0.53 g m^{-2} mm^{-1} across sites. This RUE was within the broad range of RUE values reported for arid and semi-arid ecosystems (0.05–1.81 g^{-2} mm^{-1}), but with a wider range than the mean RUE for Inner Mongolia steppes (0.51-–1.08 g^{-2} mm^{-1}) and North American grasslands (0.73–0.82 g^{-2} mm^{-1}). We found positive linear relationships of RUE_{mean} (linear model AIC was equal to quadratic model AIC, 176.5), RUE_{max} (linear model AIC was equal to quadratic model AIC, 184.6), and RUE_{min} (linear model AIC was equal to quadratic model AIC, 181.4) with MAP in the 14 grasslands outside of China, whereas RUE_{mean}, RUE_{max}, and RUE_{min} in 18 China sites showed no relationship with MAP (Figure 6a).

Temporal RUE showed different patterns compared to spatial RUE. Specifically, RUE decreased over time with increasing MAP in 19 out of the 32 grassland sites, whereas three sites showed positive and 10 sites showed no relationship between RUE and MAP (Figure 6b). The lower slope of the temporal annual precipitation-ANPP relationship compared with the slope of the spatial MAP-mean ANPP resulted in slightly lower temporal compared to spatial RUE (Figure S3).

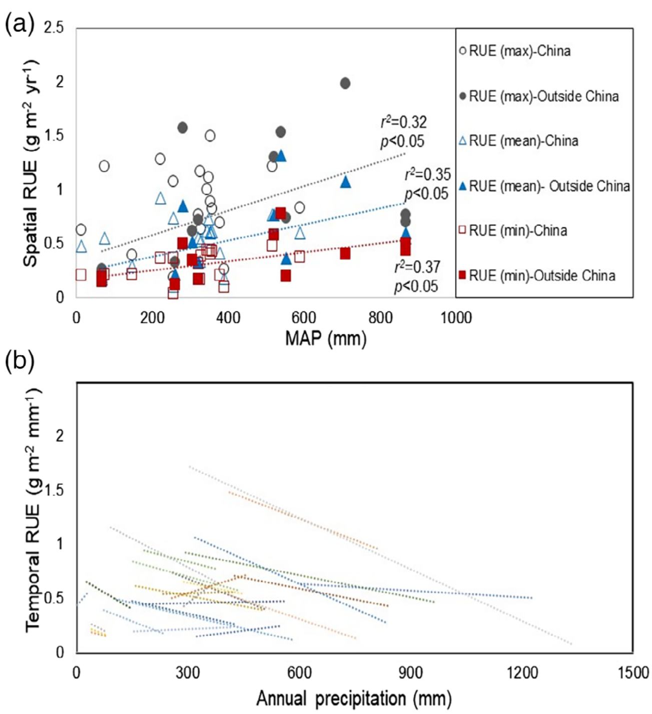

FIGURE 6 Variation in mean, maximum, and minimum rain-use efficiency (RUEmean, RUEmax, RUEmin, respectively) across the 32 sites; (b) Temporal RUE in each of the 32 sites [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Convergence across grassland ecosystems to a common RUE

By regressing ANPP against historical minimum and maximum annual precipitation, we found a common maximum RUE value in the 18 China sites (RUE_{max} of 0.60 g^{-2} mm^{-1}; r^2 = 0.68, p < .001), and the 14 sites outside of China (RUE_{max} of 0.82 g^{-2} mm^{-1}; r^2 = 0.56, p < .001), as well as for all 32 sites (RUE_{max} of 0.78 g^{-2} mm^{-1}; r^2 = 0.50, p < .001) during the driest years. In addition, we found a common minimum RUE value in the 18 China sites (RUE_{max} of 0.43 g^{-2} mm^{-1}; r^2 = 0.57, p < .001), and 14 sites outside of China (RUE_{max} of 0.53 g^{-2} mm^{-1}; r^2 = 0.81, p < .001), as well as for all 32 sites (0.51 g^{-2} mm^{-1}, r^2 = 0.77, p < .001) during the wettest years (Figure 7). The increase in ANPP with an increase of 1 mm precipitation in the wettest year across the 32 sites is 0.2 g m^{-2} more than the decrease in ANPP with a decrease of 1 mm precipitation in the driest year (Figure 7). The common maximum RUE in 14 non-China grasslands was greater than the 18 China sites during the driest years, whereas we found no difference in the common minimum RUE between sites in and outside of China (Figure 7).

4 | DISCUSSION

Relationships of primary productivity and RUE with precipitation are fundamental to understanding differential sensitivities of grassland ecosystems to climate variability. By synthesizing data from 32 terrestrial sites in 12 grassland ecosystems, we observed a well-known positive relationship between annual precipitation and ANPP, even when partitioned between wetter and drier sites. In addition, we found that

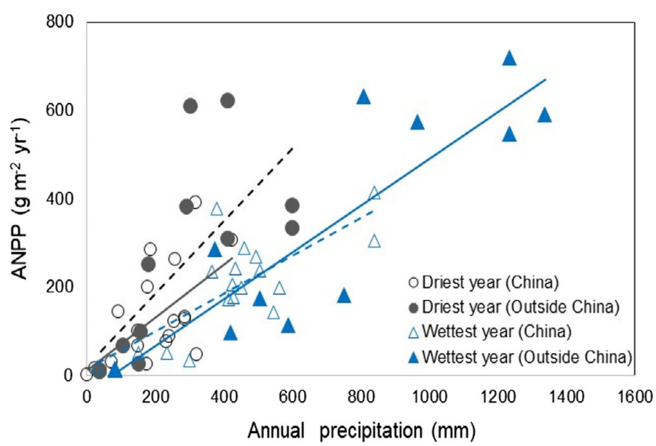

FIGURE 7 The relationship between annual net primary productivity (ANPP) and annual precipitation in the driest (open circles) and wettest (filled circles) years at all sites. The slopes of the two regression lines represent the overall RUEmax in the driest years (maximum rain-use efficiency) and RUEmin in the wettest years (minimum rain-use efficiency) for the 32 sites [Colour figure can be viewed at wileyonlinelibrary.com]

ANPP increased more in extreme wet years than it declined during extreme dry years. Our study also found that RUE increased with MAP across sites, whereas RUE decreased with annual precipitation within most individual sites. The contrasting patterns of temporal RUE within a site and spatial RUE across sites demonstrate the importance of considering both spatial and temporal relationships when assessing mechanisms driving aspects of primary productivity in grassland ecosystems.

4.1 | Spatial and temporal ANPP sensitivity to precipitation

Theory predicts that ANPP sensitivity to changing precipitation should be constant if mean ANPP is related linearly to MAP across sites (Bai et al., 2008; Huxman et al., 2004; Petrie et al., 2018). Consistent with this prediction, we found that mean ANPP increased linearly with MAP across all 32 sites as well as for the 18 sites in China, and the average slope of the relationship between productivity and inter-annual variation in precipitation (e.g., sensitivity) was 0.33 ± 0.05 across the precipitation gradient. Del Grosso et al. (2008) demonstrated that shrub and grass ANPP increased with increasing MAP, whereas tree ANPP increased initially with increasing MAP before leveling off at MAP ≥3,000 mm yr^{-1}. A possible reason for the linear increase of mean ANPP with increasing MAP may be that the maximum MAP (1,339 mm yr^{-1}) does not reach the MAP threshold that is associated with a decline in productivity sensitivity (i.e., in those systems where water is one of the major limiting factors of plant growth). However, in the 14 sites outside of China and 18 sites within China, no correlation between productivity sensitivity and MAP was detected. This may be caused by the negative relationship between ANPP and annual precipitation in the Mediterranean grasslands and Alpine meadows (Figure S4).

The relative ANPP maxima increased significantly with relative MAP maxima. Similarly, the relative ANPP minima showed a positive correlation with the relative MAP minima. The former is in agreement with Knapp and Smith (2001), whereas the latter exhibits the opposite pattern. The inconsistencies may be due to differences in the studied ecosystem. Knapp and Smith (2001) included grassland and forest ecosystems when our study mainly focuses on grasslands. The positive relationship between the relative magnitude of ANPP and MAP can be attributed to the importance of water availability for grassland productivity (Deng, Wang, Li, Zhao, & Shangguan, 2016; Fang et al., 2005; Jobbagy, Sala, & Paruelo, 2002; Lauenroth & Sala, 1992; Liang, Xia, Liu, & Wan, 2013; Sagar, Li, Singh, & Wan, 2017; Sala, Parton, Joyce, & Lauenroth, 1988; Yahdjian & Sala, 2006). Available water content can directly influence plant production by changing leaf area development, overall leaf-level photosynthetic capacity, tillering, and root characteristics in grassland ecosystems (De Micco & Aronne, 2012; Huang et al., 2018), and indirectly by affecting soil nutrient supply and plant species composition (Huxman et al., 2004).

For temporal data, we found a positive correlation between relative ANPP pulses and ANPP declines, and most sites showed larger increases in ANPP compared to declines. These results suggest that grassland production responds most strongly in wet years (Hoover et al., 2014; Luo et al., 2008; Wilcox, Shi, Gherardi, & Lemoine, 2017; Wu et al., 2018). A number of potential mechanisms may explain the positive asymmetric responses in ANPP to annual precipitation. First, many species in dry environments are adapted to droughts and have high-stress tolerance (i.e., small leaf surface area, high leaf water content, and deep root systems; Sala, Lauenroth, & Parton, 1992), and therefore are less sensitive to periods with lower precipitation. Second, hydraulic lift through deep-rooted species transfers water into the top soil, benefiting neighboring plants, ameliorating negative effects of low levels of precipitation on ANPP (Kong et al., 2017, 2019; Miao et al., 2019; Yang et al., 2019). Third, increased precipitation is often accompanied by more frequent extreme precipitation events (Knapp et al., 2015), and these events can disproportionately increase ANPP, particularly in arid ecosystems (Heisler-White, Blair, Kelly, Harmoney, & Knapp, 2009; Miao, Qiu, Guo, Alamusa, & Jiang, 2016).

4.2 | Spatial and temporal RUE

RUE serves as an integrated measure for evaluating responses of primary productivity to precipitation changes (Bai et al., 2008; Huxman et al., 2004; Knapp & Smith, 2001). Across the entire data set, we found that RUE increases linearly with increasing MAP. This finding is consistent with other studies that reported an increase in RUE with increasing MAP at the low end of a MAP gradient (Bai et al., 2008; Hu et al., 2010). It is inconsistent, however, with most other studies that reported RUE decreased with increasing MAP (Heisler-White et al., 2009; Huxman et al., 2004; Knapp et al., 2015; Lin, Xia, & Wan, 2010; Petrie et al., 2018; Prince, De Colstoun, & Kravitz, 1998), and also conflicts with results showing that RUE is low at both the dry and wet ends of the annual precipitation gradient with a peak at moderate MAP (Hein & de Ridder, 2006). The different ranges of precipitation gradients may explain some of the inconsistency of these results. For example, Zhao et al. (2019) reported that when MAP was <400 mm, RUE decreased with an increase in MAP, but when MAP was >400 mm, RUE increased with an increase in MAP. Moreover, overland flow, controlled by topography, has a clear effect on vegetation productivity and RUE (Del Grosso et al., 2008; Sun et al., 2018; Huang et al., 2020). For example, annual precipitation in alpine meadow is nearly 600 mm, but RUE is approximately 0.6 due to steep slopes and high runoff, leading to no significant correlation between RUE and MAP across sites in China.

Within sites, temporal analyses showed that RUE decreased with increasing annual precipitation, a pattern that contrasts with what we identified for spatially-based RUE trends. Spatial relationships reflect long-term, equilibrium conditions, whereas temporal relationships reflect more dynamic local variation. Spatially-based RUE patterns are reflected over a wide range of precipitation (Figure S2) and nutrient levels, as well as a greater range of biological responses associated with distinct plant communities. In contrast, temporal RUE for a given site is influenced mainly by relatively small differences in water and nutrient availability among years, which is particularly important when vegetation change is further constrained by other factors (Bai et al., 2008). Our results show a common maximum RUE, supporting Huxman et al. (2004) that all biomes in North and South America converge to a common maximum RUE during the driest years. However, we also report a common minimum RUE during the wettest years. These values of RUE_{max} and RUE_{min} may result in divergent relationships of biomass production with water availability, meaning that the mean RUE will generally overestimate ecosystem productivity in the wettest years and underestimate it in the driest years.

5 | CONCLUSIONS

Our study demonstrated general patterns of ANPP, ANPP sensitivity to changing precipitation, and RUE along precipitation gradients. ANPP increased linearly with increasing precipitation over space, while ANPP sensitivity to changing precipitation within a site over time remained stable. Moreover, we also find that spatial RUE patterns increased with increasing MAP, whereas temporal RUE patterns decreased with increasing annual precipitation. The results further describe intrinsic links between the primary productivity-precipitation relationship, ANPP sensitivity, and RUE. The differences in spatial- and temporal patterns of ANPP, ANPP sensitivity, and RUE along precipitation gradients indicate biome-specific importance of precipitation as a driver of ecosystem processes.

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AUTHOR CONTRIBUTIONS

Zhongling Yang proposed the scientific hypotheses and supervised the study. Dong Wang and Rui Xiao collected data and performed data analyses, Zhongling Yang wrote the draft of the manuscript, and Scott L. Collins and Rebecca J. Bixby contributed substantially to paper revisions.

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