PLANT GROWTH AND FUNCTIONAL GROUP REGULATED ECOLOGICAL RESPONSE TO PRECIPITATION ALTERATION ON DESERT GRASSLAND

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Abstract. Precipitation alteration could profoundly affect the plant community structure and ecosystem function in desert grassland. However, the mechanism of ecological response driven by plant community during extreme changes in precipitation remains unclear. To address this uncertainty, we examined the responses of community composition, diversity and production in slope desert grassland of China to precipitation gradient experiment, which included five precipitation treatment levels (i.e., ambient precipitation as a control [0], ±20% and ±40% of ambient precipitation [-40%, -20%, +20% and +40%]). The extreme drought treatment (-40%) significantly reduced aboveground biomass (AGB) and plant growth (e.g. height, coverage and density) across three years, with no significant effect of increased precipitation treatments. This reduction in ecosystem function coincided with the reducing trend in productivity of forbs and grasses. The relative abundance of certain dominant species (*Ajania fruticulosa*) decreased, whereas the relative abundance of other dominant species (*Stipa breviflora*) increased; however, the reordering of species abundances under the extreme drought treatment was not confirmed. Meanwhile, species diversity did not change with precipitation treatments. Furthermore, species asynchrony was reduced by the extreme drought. Our results suggested that the decrease of ecosystem function indicated by AGB is mainly governed by plant growth and biomass of functional groups rather than community composition and diversity under precipitation alteration in the desert grassland.

Keywords: *aboveground net primary production, community composition, species diversity, plant functional groups, precipitation gradient experiment*

Introduction

Global warming may affect the continental hydrological cycle, including alterations in annual precipitation amount, more frequent extreme wet and dry years and increased interannual precipitation variability (IPCC, 2013; Prein et al., 2017; Lu et al., 2023). Precipitation is a paramount climatic factor controlling plant growth and distribution across most of the globe (Knapp et al., 2017), particularly in arid and semi-arid grasslands where water is the primary driver of community structure and ecosystem processes (Noy-Meir, 1973). Although there were many studies focused on the grasslands response to nominal (baseline or contemporary) precipitation variations (Knapp et al., 2002; Dukes et al., 2005; Hui and Jackson, 2006; Wu et al., 2011; Zhou et al., 2016), it is not clear how the ecosystem functions and processes respond to extreme precipitation variation.

Numerous studies found that above-ground net primary production (ANPP) increases linearly with increasing annual precipitation in temporal scale and nonlinearly to

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saturation across arid to extremely humid sites during the past few decades (Huxman et al., 2004; Yahdjian and Sala, 2006; Ponce-Campos et al., 2013; Wilcox et al., 2016). Furthermore, Knapp et al. (2017) framed a nonlinear double-asymmetry model to properly define the ANPP - precipitation relationship, that is, under normal precipitation ranges, ANPP was shown to be more sensitive to increased precipitation than decreased, whereas under extreme precipitation ranges, it was found to be more sensitive to decreased precipitation than increased precipitation. After testing the above double asymmetry model, Deng et al. (2017) found a single negative asymmetry response of switchgrass ANPP to the precipitation treatments, that is, only the extremely decreased precipitation significantly decreased ANPP. Ma et al. (2019) found a linear model was fitted better than nonlinear models for the ANPP - precipitation relationship, although extreme precipitation levels were included. Gherardi and Sala (2019) also indicated that environmental conditions such as historical precipitation should be considered in the production-precipitation relationship according to the global dryland synthesis. Thus, the patterns of productivity responding to a broad precipitation amount range (from extremely dry to extremely wet) are still unclear, particularly in semi-arid grasslands.

Biodiversity, particularly for plant species diversity, plays a critical role in ecosystem productivity and stability (Hautier et al., 2015; Anderegg et al., 2018) by increasing its resistance to climate change (Isbell et al., 2015). Global meta-analyses from Balvanera et al. (2006) and Cardinale et al. (2011) confirmed the reduction of plant productivity due to decreased plant diversity. Some precipitation manipulation experiments found that extreme drought decreases species diversity in semi-arid steppe (Zhong et al., 2019) and alpine meadow (Zhang et al., 2019a). Moreover, reduction in productivity resulted from drought-induced declines in species richness (Zhang et al., 2019a), forbs richness (Wellstein et al., 2017) and richness of annual forbs and exotic annual grasses (Copeland et al., 2016). While other studies reported that extreme drought (Hoover et al., 2014) or extreme wet (Zhong et al., 2019) had little effect on species richness. Thus, the response of species diversity to precipitation extremes and its corresponding effect on ecosystem function need further assessment.

Changes in community structure are predicted to be a critical mechanism driving ecological responses to climate extremes (Smith, 2011). The impacts of climate extremes at the species level such as mortality or significant loss in fitness of dominant species have the potential to affect ecosystem function through community-level responses including species reordering and composition changes. Even though species richness is stable, community composition was found to be altered due to species reordering and dominant species shift (Hoover et al., 2014; Griffin-Nolan et al., 2019; Ma et al., 2019), consequently impacting the response of ecosystem function (e.g. ANPP) to extreme drought or wet. On the other hand, Zhang et al. (2019a) found that asynchrony and species richness led to a significant reduction in productivity under the most extreme drought treatment. Thus, the contribution of dominant species to the effects of extreme precipitation on productivity is still not clear.

In this study, we conducted a three-year field precipitation manipulated experiment (i.e., ambient precipitation as a control, ±20% and ±40% of ambient precipitation) in a desert grassland of western Loess Plateau, China. Based on the previous study (Zhang et al., 2018), we further focus on the responses of ANPP in functional groups, community structure and asynchrony to precipitation alteration, and reveal the mechanism of ANPP responding to altered precipitation. The ±20% precipitation treatments representing nominal precipitation variations encompassed 73% of the inter-annual variation over the past 50 years in the study area, and the ±40% precipitation treatments representing precipitation extremes reached the highest and lowest historic values (355.6 mm and 157.5 mm, respectively). Our objectives were to test whether extreme precipitation was imposed by precipitation gradient experiment, observe the response of ecosystem to the mean annual precipitation alteration, and assess the proposed mechanisms underpinning ecosystem response to precipitation alteration. We hypothesized that (1) aboveground biomass (AGB) would be more sensitive to extreme drought (-40% precipitation treatment) than wet treatments (+20% and +40% precipitation treatments); (2) the responses of plant growth and functional group rather than species diversity and asynchrony would govern the responses of AGB to precipitation alteration.

Materials and methods

Site description and experimental design

The study was carried out at Gaolan Experiment Station for Ecology and Agriculture Research (36°13″N, 103°47″E, 1780 m a.s.l.), Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, desert grasslands in northwest of the Loess Plateau, China. The climate is a continental, semi-arid and drought-prone. The average annual precipitation since recent fifty years is 263 mm with 70% falling between May and September. The mean annual temperature is 8.4°C, with the maximum mean monthly temperature of 20.7°C (July) and the minimum mean monthly temperature of –9.1°C (January). Mean annual pan evaporation is 1786 mm (Zhang et al., 2018). The average soil organic carbon and total nitrogen are 0.75% and 0.1%, respectively; and pH is 8.52. The soil in this region is developed from wind-accumulated loess parent material, with a uniform silt loam texture and is classified as a *Haplic Calcisol* in the FAO/UNESCO classification system (Zhang et al., 2018). The site is covered with typical desert steppe vegetation, which is dominated by *Ajania fruticulosa* and *Stipa breviflora*. Accompanying species were *Peganum harmala*, *Zygophyllum mucronatum*, *Artemisia capillaris*, *Cleistogenes squarrosa* and *Salsola ruthenica*. The source for unified scientific nomenclature of plant taxa is official website for the electronic edition of Flora Republicae Popularis Sinicae (http://www.iplant.cn/frps).

The experiment used a randomized complete block design. According to the precipitation variability (from −41.1% to +39.2%) of the study area from 1966 to 2011, five treatments were set: the ambient precipitation amount as the precipitation control and reduced and increased precipitation by 40% and 20% relative to the ambient precipitation, marked here as −40%, −20%, CK, + 20% and +40% precipitation. Precipitation frequency and timing did not change within our treatments. Each treatment was replicated three times, and each replicate plot was 2.5 × 2.5 m^2. The rust-proof iron sheet was buried 35 cm deep around each plot and was exposed 15 cm to prevent the radial flow of surface water inside and outside the plot. The precipitation treatments were applied from May to September each year from 2013-2015.

For the drought treatments (−20%, −40%), the rainout shelters were used to intercept 20% and 40% of natural rainfall every time (Yahdjian and Sala, 2002). They were supported by a steel frame with transparent acrylic bands (V-shaped, 10 cm wide) above it that covered 20% and 40% of the experimental plots (Zhang et al., 2018). The height of the shelter was 0.50 m and it had a gutter on its lower side that channeled the intercepted water to an enclosed container. Compared with plastic or polyvinyl chloride

(PVC), the advantage of acrylic is that it has higher light transmittance and intercepts lower photosynthetic active radiation. The secondary microenvironmental effects may be minimized by opening shelter sides, such as maximizing air movement and minimizing temperature and relative humidity artifacts. Rainwater intercepted by the roof bands in the drought treatments was added to the corresponding wet treatment plots (+20% and +40%) manually within 8 h of each precipitation event.

Plant community investigation

Two frames (0.5 m × 0.5 m), each with 50 equally distributed grids, were placed above the canopy at the center of each plot and were used to measure plant species richness, density, height and coverage of each species once a month from late May to late September in 2013, 2014 and 2015. The Shannon’s diversity and Pielou’s evenness indices were calculated (Zhang et al., 2011). Aboveground biomass was assessed using a harvesting method at the time of peak biomass (early September). All plants were clipped to the soil surface by species in another two quadrats (0.5 m× 0.5 m) in each plot. After oven drying for 48 h at 65°C, the dry mass was weighed to determine the biomass (g m^{-2}) of each species. Community aboveground biomass (g m^{-2}) was estimated from the sum of all species’ aboveground biomass. All plant species were sorted into two plant functional groups: grass and forb (*Table A1*). The absolute and relative AGB of each functional group were calculated.

Species asynchrony was quantified as:

$$1\text{-}\varphi_b = 1\text{-}\sigma^2/(\textstyle\sum_{i=1}^{S}\sigma_{bi})^2 \qquad \text{(Eq.1)}$$

where φ_b is species synchrony, σ^2 is the variance of ecosystem ANPP and σ_{bi} is the standard deviation of ANPP of species *i* in a community with *S* species over the years 2013–2015 (Loreau and de Mazancourt, 2008).

Soil water content and soil temperature

Soil samples were collected from all 15 plots on August 15th of 2013, 2014 and 2015 and June 15th of 2014. Soil water content (SWC) at depths of 0–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–140, 140–160 and 160–180 cm in 2013, 0–5, 5–10, 10–20, 20–40 and 40–60 cm in 2014 and 0–5, 5–10, 10–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–140, 140–160 and 160–180 cm in 2015 were measured using the oven-drying method. In each plot, three soil cores at each depth were randomly taken using an auger and were mixed to obtain one composite sample per plot. Soil temperature (ST) at a 5 cm depth was determined using a thermocouple probe connected to the LI-6400-09 soil chamber (Li-Cor, Inc., Lincoln, NE, USA).

Statistical analysis

Precipitation amounts for every treatment were compared to estimated probability density functions (pdfs) of long-term (1966-2015) growing season precipitation in the study area. Values were considered extreme if they exceeded the 5th or 95th percentiles of the pdfs (Hoover et al., 2014).

The repeated-measure ANOVA analyses using a general linear model were used to examine the effects of precipitation variation, sampling year and their interactions on SWC, ST, AGB, absolute and relative AGB of grass and forb, plant growth (density, height and coverage) and diversity metrics. Moreover, multiple comparisons were used to determine the effects of the five precipitation treatments on each of these variables in each year. The effects of precipitation treatments on species asynchrony and plant growth were analyzed using one-way ANOVA. Correlation and regression analysis were used to examine the relationship between community AGB and plant growth, species diversity indices, relative abundance of dominant species, species asynchrony and AGB of functional groups. These analyses were performed using SPSS 20.0 (SPSS for Windows, Version 20.0).

Structural equation model (SEM) was used to analyze the effect path of precipitation change on community AGB in Amo (version 22.0, IBM, USA). A priori SEM was applied based on hypothesized causal relationships (*Fig. A1*). In the SEM analysis, the model is fitted using maximum likelihood estimation. The best-fitted model was selected by a non-significant χ^2 test, the root-mean-squared error of approximation (RMSEA) index and the goodness-of-fit (GIF) index.

Results

Changes in precipitation and soil moisture

Average growing season precipitation was 211.8 mm during the past 50 years, and was 235.0 mm, 252.7 mm and 152.5 mm in 2013, 2014 and 2015, respectively (*Fig. 1*). In 2013 and 2014, the growing season precipitation inputs were near the 5th percentile (130.3 mm) of the historical amounts under −40% precipitation treatment and exceeded the 95th percentile (276.0 mm) under +40% precipitation treatments (*Fig. 1*). In 2015, the growing season precipitation inputs were below the 5th percentile of the historical amounts under the decreased precipitation treatments and near the 50th percentile (226.5 mm) under +40% precipitation treatment (*Fig. 1*).

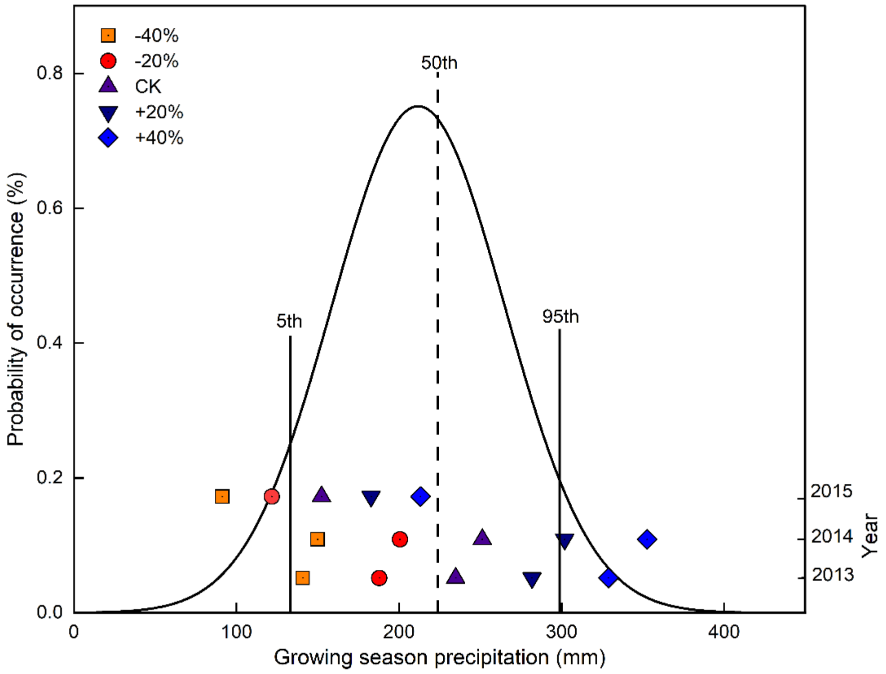

Figure 1. *The extremity of precipitation treatments based on the probability distribution of growing season precipitation during the past 50 years*

SWC in 0–20 cm depth was larger in the +40% precipitation treatment than that in the decreased precipitation treatments and control in 2014 and 2015 ($p < 0.01$; *Fig. 2; Table A2*). SWC at deeper depths did not vary along the precipitation gradient. Meanwhile, SWC varied with year ($p < 0.05$; *Table A2*). No significant effects of precipitation on soil temperature at the 5 cm depth were found while the effect of years was significant (*Table A2*).

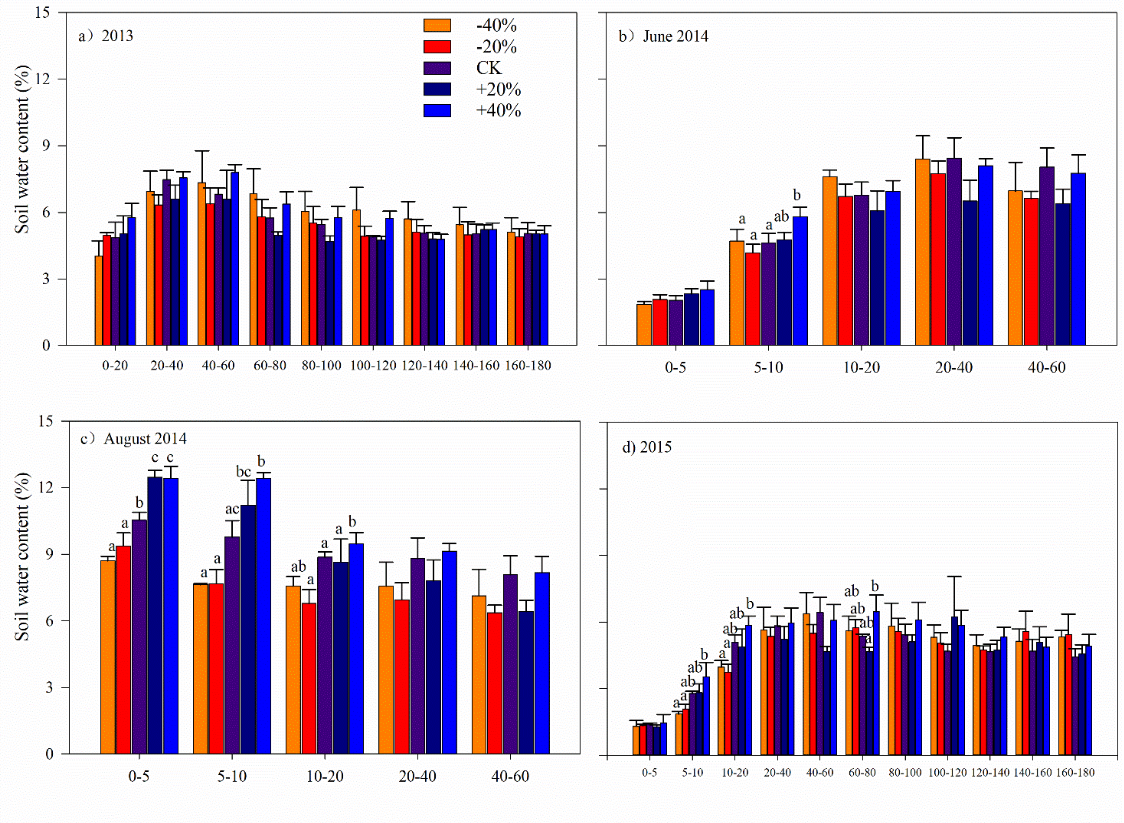

Figure 2. *The characteristics of soil water content under precipitation treatments in 2013 (a), June 2014 (b), August 2014 (c) and 2015 (d). The precipitation treatments include five levels, namely, −40%, −20%, CK, + 20% and +40% relative to the ambient precipitation amount, CK means ambient precipitation. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference between treatments at p < 0.05*

Changes in community AGB and diversity

There was significant effect of precipitation treatments on AGB across three years ($p < 0.01$, *Table 1; Fig. 3a*). The AGB-precipitation relationship was in a nonlinear and negative asymmetry under extreme precipitation (*Figs. 3a* and *4*). Compared with control (ambient precipitation level), the -40% treatment significantly decreased AGB in 2014 (by 52%) and 2015 (by 74%), while the wet treatment did not increase AGB (*Fig. A2*).

The density, coverage and height representing plant growth were lower under the -40% treatment than control and wet treatments across three years ($p < 0.05$, *Fig. 3b, c, d*), while they were not significantly different between wet treatments and control. The significant effects of precipitation treatments on plant species richness, Shannon's diversity and evenness were not found (*Table 1; Fig. 5*), while there was significant effect of year on species richness and Shannon's diversity ($p < 0.033$, $p < 0.002$, *Table 1*). The plant species richness and Shannon's diversity in the -20% precipitation treatment were lower compared with control in 2013 and compared with +40% precipitation treatment in 2015 (*Fig. A3*).

Table 1. *Repeated-measure ANOVA for the effects of precipitation variation (P) and sampling year (Y) and their interaction on components of AGB and species diversity metrics*

Effects	df	AGB		Absolute AGB				Relative AGB				Richness		Shannon diversity		Evenness	
				grass		forb		grass		forb							
		F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
P	4	5.784	0.011	0.746	0.582	1.595	0.25	0.867	0.516	0.867	0.516	1.449	0.288	1.276	0.253	1.187	0.374
Y	2	1.353	0.281	9.513	0.006	4.055	0.033	21.751	<0.001	21.751	<0.001	4.061	0.033	13.217	0.002	2.808	0.084
P × Y	8	1.088	0.41	0.491	0.848	0.859	0.565	1.333	0.284	1.333	0.284	0.859	0.565	1.526	0.21	1.076	0.418

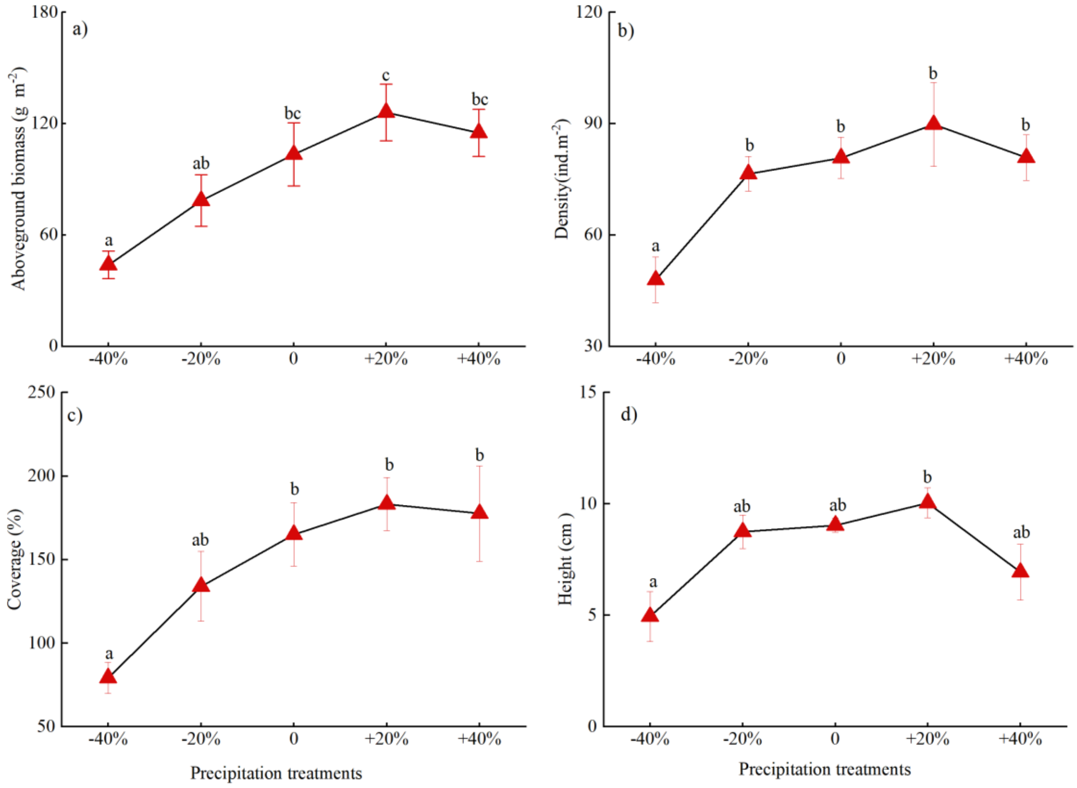

Figure 3. *The characteristics of AGB (a) and plant growth (density, b; coverage, c; height, d) under precipitation treatments across three years. The precipitation treatments include five levels, namely, −40%, −20%, 0, + 20% and +40% relative to the ambient precipitation amount, 0 means ambient precipitation. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference between treatments at* $p < 0.05$

Changes in AGB of the plant functional groups, dominant species and asynchrony

The precipitation treatments insignificantly impacted the AGB of two functional groups across three years (*Table 1*). The absolute AGB of grass and forb tended to be lower in the -40% treatment compared with control (*Fig. 6a, b*). Specifically, the absolute AGB of forb decreased by 56% in 2013, 60% in 2014 and 92% in 2015 under

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the -40% treatment compared with control (*Fig. A4b*), with the smaller amplitude for the absolute AGB of grass by 8%, 20% and 37% in 2013-2015, respectively (*Fig. A4a*). The Repeated-measure ANOVA also showed that the absolute AGB of forb and grass was different among years ($p < 0.006$, $p < 0.033$, *Table 1*).

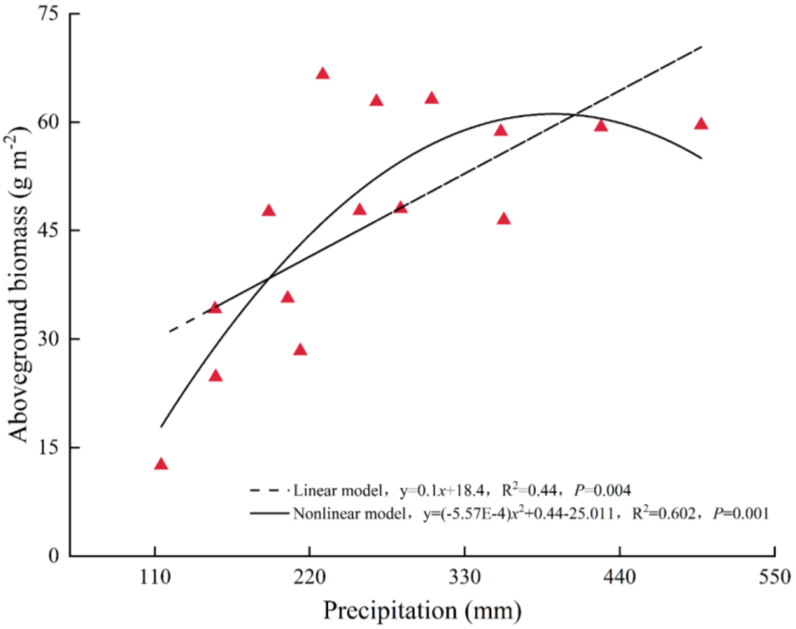

Figure 4. *Statistic relationship between AGB and precipitation amounts across three years*

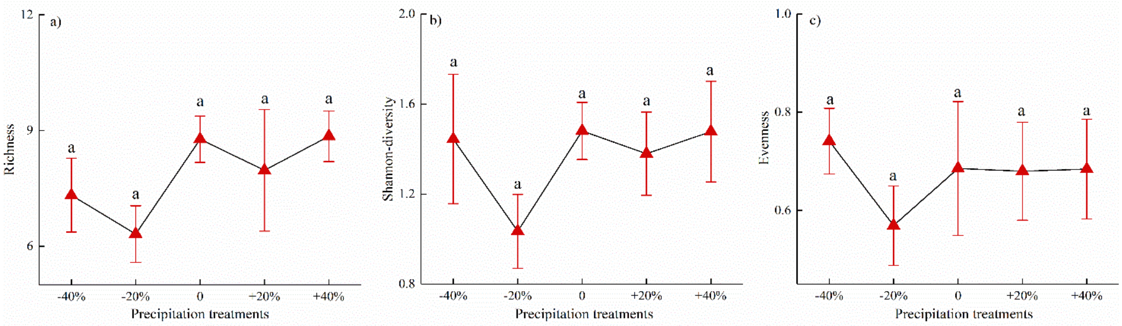

Figure 5. *The characteristics of plant community Richness (a), Shannon diversity (b) and Evenness metrics (c) under precipitation treatments across three years. The precipitation treatments include five levels, namely, −40%, −20%, 0, + 20% and +40% relative to the ambient precipitation amount, 0 means ambient precipitation. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference between treatments at p < 0.05*

The relative AGB of forb and grass were not found to be significantly affected by the precipitation treatment or its interaction with year (*Table 1*). Nevertheless, the relative AGB of grass tended to be higher under the -40% treatment, contrary to the relative AGB of forb (*Fig. 6c, d*). There was significant effect of year on the relative AGB of forb and grass ($p < 0.001$, *Table 1*). The relative AGB of grass was greater in 2015 than 2013 and 2014, particularly in the -40% treatment (*Fig. A4c, d*). The inter-annual variation of the relative AGB for forb was contrary to grass.

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Different from CK, the relative abundance of dominant grass *Stipa breviflora* under the -40% treatment increased evidently (from 27.7% in 2013 to 38.1% in 2014 and 55.5% in 2015), while the relative abundance of dominant forb *Ajania fruticulosa* under the -40% treatment decreased from 25.9% in 2013 to 16.6% in 2014 and 18.1% in 2015 (*Fig. 7*). Additionally, the relative abundance of perennial forb, *Linum nutans*, decreased by 72% under the -40% precipitation treatment across three years. In addition, the relative abundance of *Salsola ruthenica*, annual forb, was relatively high in 2013 and 2014, ranging from 5.8-15.8% and 12.9-23.8%, and was zero in 2015.

After 3 years of treatments, species asynchrony significantly decreased by 28.2% under the -40% treatment compared with control, while they were not different among other treatments (*Fig. 8*). Moreover, the species aboveground biomass usually decreased under extreme drought in three years, particularly in 2015 (*Fig. 9*).

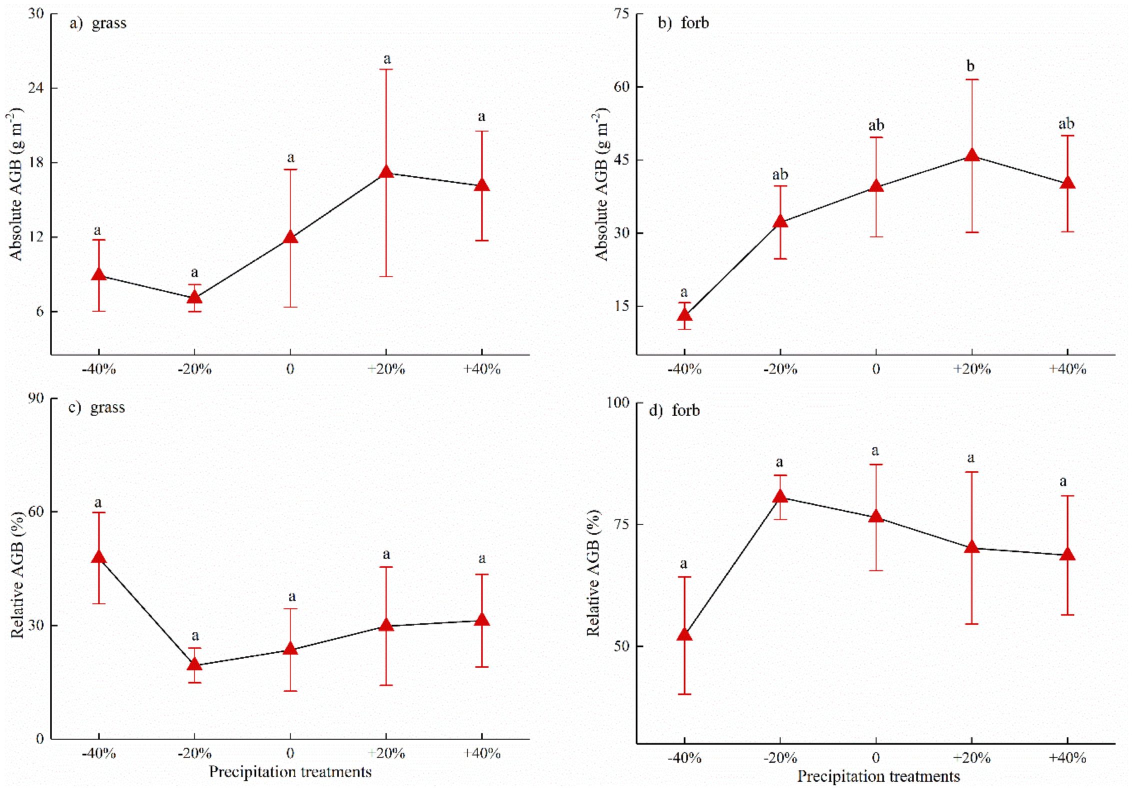

Figure 6. *The characteristics of absolute (a, b) and relative AGB (c, d) of forb and grass under precipitation treatments across three years. The precipitation treatments include five levels, namely, −40%, −20%, 0, + 20% and +40% relative to the ambient precipitation amount, 0 means ambient precipitation. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference between treatments at p < 0.05*

Main factors influencing AGB under precipitation alteration

Spearman’s correlation analysis showed that the community AGB was positively correlated with plant growth such as coverage, density and height and with absolute AGB of forb ($p < 0.05$, *Table 2*). Regression analysis also demonstrated the relationship between the community AGB and plant growth indices, AGB of functional groups ($p < 0.05$, *Fig. 10*). However, species diversity and asynchrony as well as relative abundance of dominant species did not display significant effects on the AGB. Moreover, using structure equation model (SEM) analysis, it was found that the direct effect of precipitation changes on AGB was fairly limited, while indirect shifts in plant growth (e.g. coverage, height and density) and the absolute AGB of functional group shrub (particularly for forbs) were the primary drivers of differences in community AGB in response to precipitation alteration (*Fig. 11*).

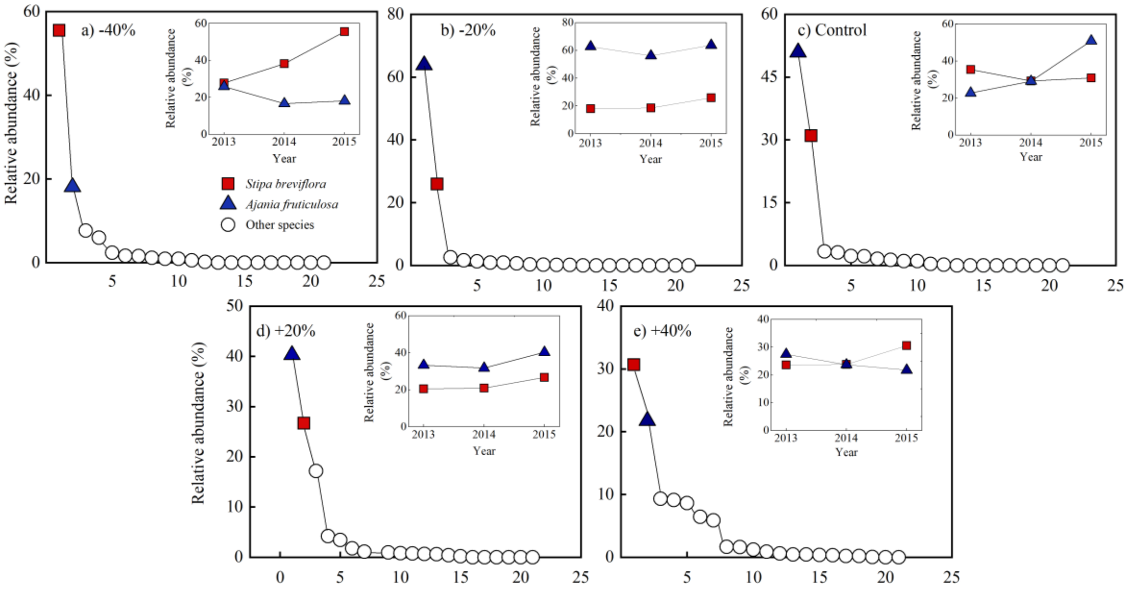

Figure 7. *Rank abundance curve of all species in -40% (a), -20% (b), control (c), + 20% (d) and +40% (e) precipitation treatments in 2015. Insets show relative abundance of the dominant grass (Stipa breviflora) and dominant forb (Ajania fruticulosa) during three years (2013-2015)*

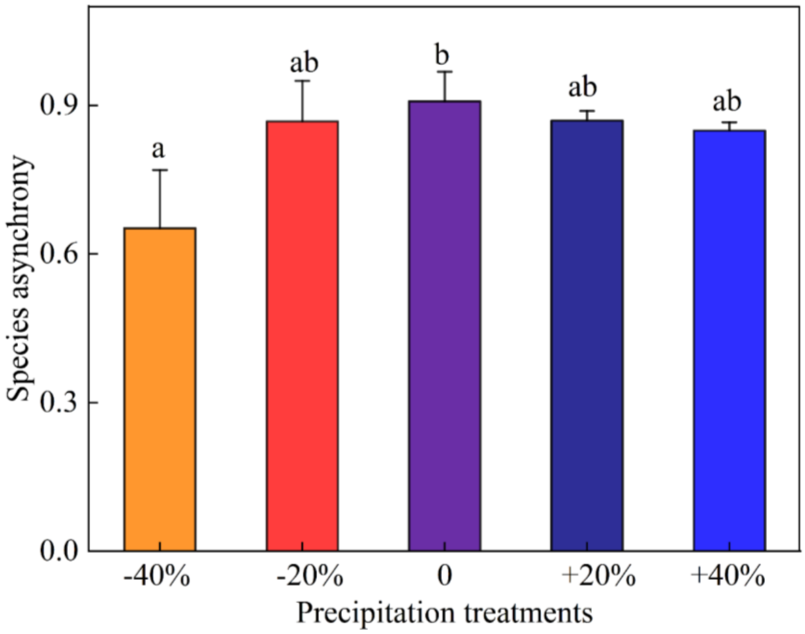

Figure 8. *Difference in species asynchrony under precipitation treatments across three years. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference between treatments at $p < 0.05$*

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Table 2. *Spearman's correlation coefficients (R) between species diversity indices (i.e., Richness, Shannon diversity, Evenness), plant growth characteristics (i.e., Coverage, Density, Height) and AGB (i.e., absolute and relative AGB of grass and forb)*

Variables	**R**	**H**	**E**	**Coverage**	**Density**	**Height**	**AGB**	**Asynchrony**	**Absolute AGB**		**Relative AGB**		**Relative abundance**	
									Grass	**Forb**	**Grass**	**Forb**	**Grass**	**Forb**
R	1													
H	**0.74****	1												
E	0.29	**0.85****	1											
Coverage	0.34	0.23	0.05	1										
Density	0.39	0.03	-0.25	**0.80****	1									
Height	-0.17	-0.47	**-0.53***	0.38	**0.62***	1								
AGB	0.08	-0.19	-0.31	**0.65****	**0.60***	**0.57***	1							
Asynchrony	0.04	-0.21	-0.23	**0.52***	**0.59***	**0.61***	0.45	1						
Absolute AGB of grass	**0.52***	**0.56***	0.41	**0.59***	0.49	-0.21	0.13	0.04	1					
Absolute AGB of forb	-0.18	-0.46	-0.49	0.34	0.35	**0.65****	**0.89****	0.45	-0.34	1				
Relative AGB of grass	0.23	**0.59***	**0.67****	-0.06	-0.20	**-0.69****	-0.48	-0.39	**0.71****	**-0.78****	1			
Relative AGB of forb	-0.23	**-0.59***	**-0.67****	0.06	0.20	**0.69****	0.48	0.39	**-0.71****	**0.78****	**-1.00****	1		
Relative abundance of grass	0.03	0.30	0.37	0.19	-0.04	-0.36	-0.08	0.22	0.49	-0.36	0.47	-0.47	1	
Relative abundance of forb	-0.37	**-0.73****	**-0.79****	-0.41	0.11	0.48	0.36	0.15	0.04	0.05	-0.39	0.39	-0.69**	1

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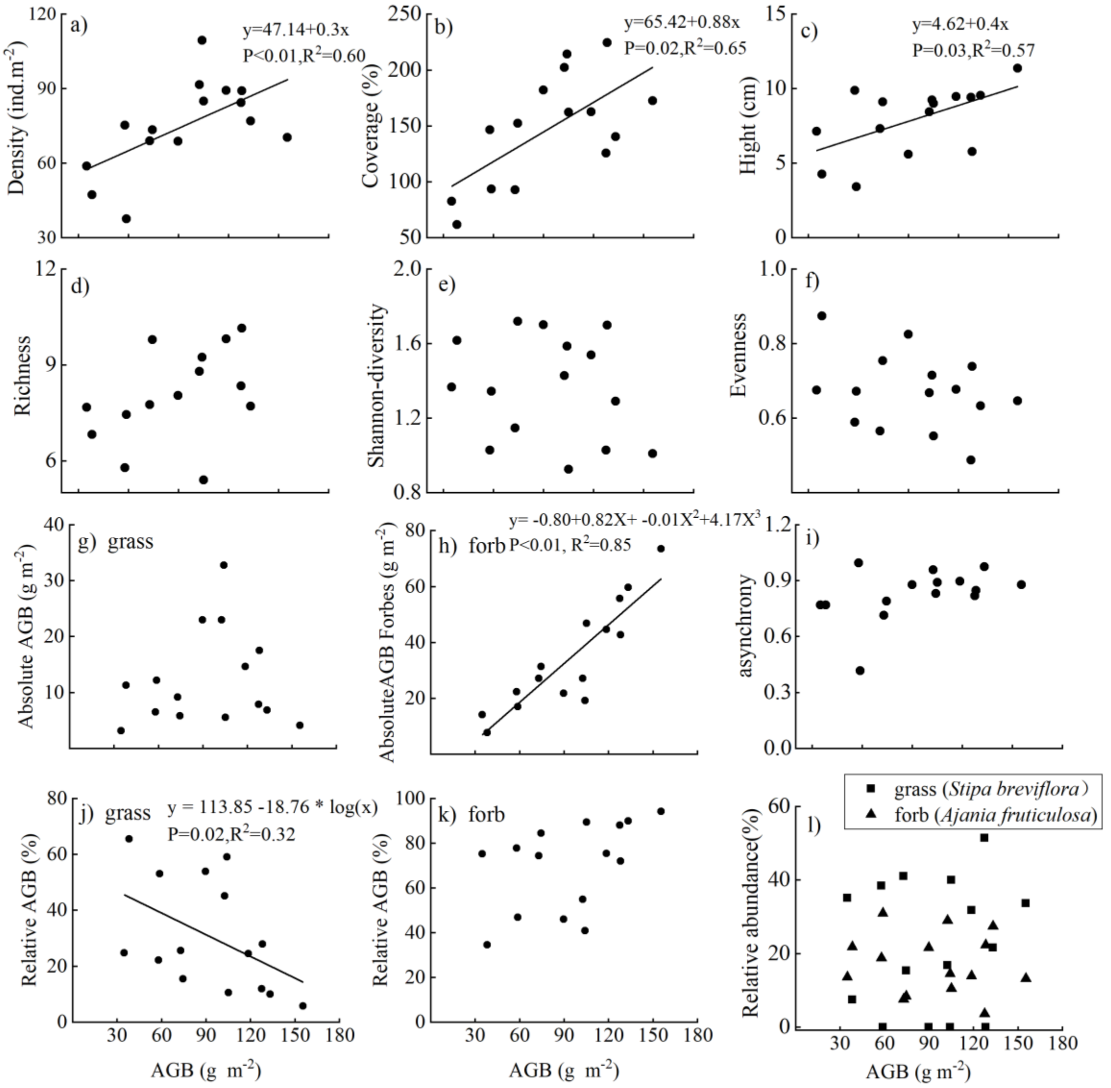

***Figure 9.** Relationships of AGB change to plant growth characteristics (density, a; coverage, b; height, c), species diversity indices (Richness, d; Shannon-diversity, e; Evenness, f), species asynchrony (i), AGB of functional groups (g, h, j, k) and the relative abundance of dominant species (l)*

Discussion

AGB responses to precipitation changes

In this study, the extreme dry treatment (-40%) significantly decreased AGB across three years' manipulated experiments, while increased precipitation treatments did not change AGB, which was consistent with our hypothesis. The AGB-precipitation relationship was in a nonlinear and negative asymmetry under extreme precipitation (*Fig. 3a* and *4*), which was consistent with Knapp's double-asymmetry model (Knapp et al., 2017). Generally, drought may suppress plant growth by exacerbating soil water limitation and even cause rapid mortality of populations or species, correspondingly the ANPP of a grassland decreases (Yahdjian and Sala, 2006; Zhang et al., 2019a). Through global satellite estimates of gross primary production (GPP) spanning 30 years and model intercomparisons, Zscheischler et al. (2014a,b) have revealed that negative impacts of extreme dry periods on GPP were much greater than positive effects of extreme wet periods. At the site level, empirical support for negative asymmetry is uncommon owing to rarity of extreme precipitation years as well as seldom encountering in long-term ANPP datasets (Smith, 2011). However, more evidence have been found at the site level through extreme precipitation manipulation experiments in several types of grasslands ranging from semiarid to mesic climate (Hoover et al., 2014; Deng et al., 2017; Stampfli et al., 2018; Zhang et al., 2019a,b). Generally, the constraints of plant physiological activity, leaf area, meristem and tiller density imposed by both dry and wet extremes could account for the double asymmetry model (Felton et al., 2019; Xu and Zhou, 2011; Yahdjian and Sala, 2006). Thus, a nonlinear and asymmetry relationship between precipitation and ANPP is more appropriate than a linear model when including extreme precipitation. Although Ma et al. (2019) found a linear model was fitted better than nonlinear models for the ANPP -precipitation relationship by two years' manipulation experiment, the magnitude, duration or timing of the extreme drought would also influence the fitted result.

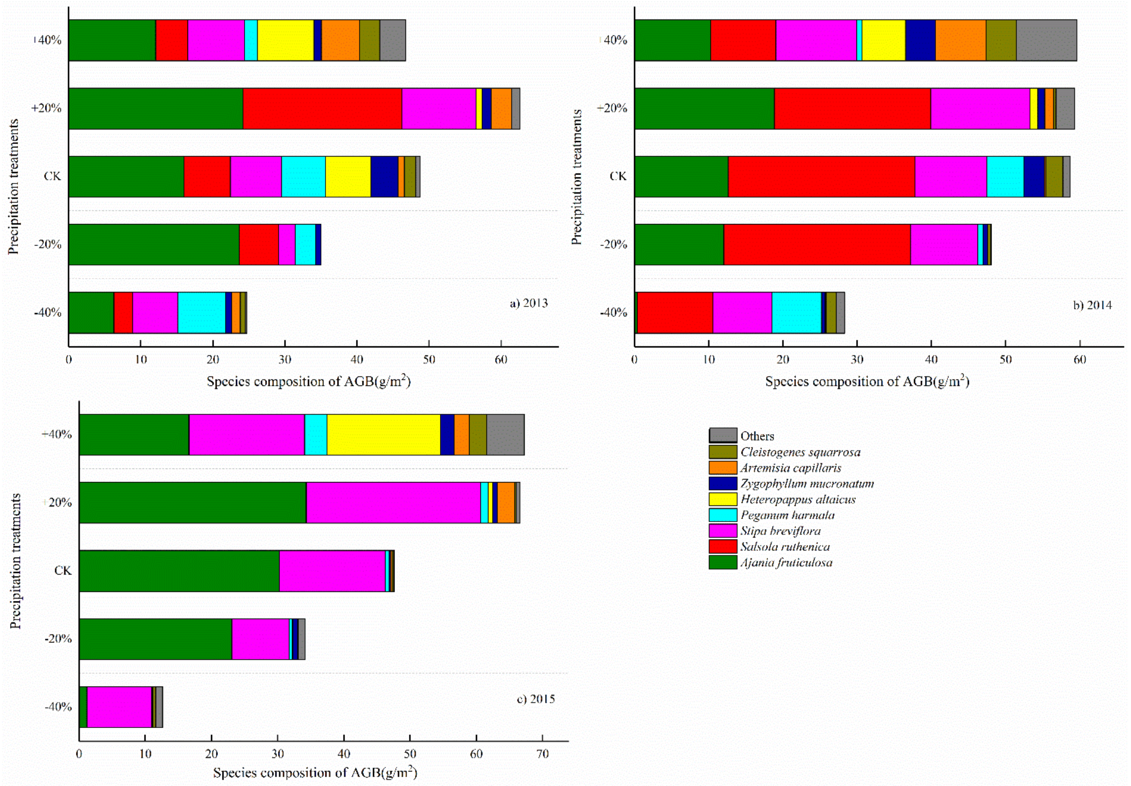

Figure 10. *Species composition of AGB under precipitation treatments during three years*

In this study, the not evident positive asymmetry (slight concave-up) for AGB - precipitation relationship under nominal precipitation, which was inconsistent with higher sensitivity of ANPP to the increased precipitation under normal precipitation ranges in Knapp's double-asymmetry model. It was possibly related to the increased runoff and nutrients leaching under the increased precipitation treatments. The slope terrain in the Loess Plateau may weaken the wet effect of increased precipitation and intensify the dry effect of decreased precipitation. The plant growth (eg. density, height and coverage) of three life forms (Wang et al., 2020) and the biomass of two function groups (grass and forb) (*Fig. 6*) were also found insignificantly impacted by the wet treatments. Thus, the response of ANPP to increased precipitation might be overestimated in the Loess Plateau and mountain areas particularly for the increased heavy precipitation.

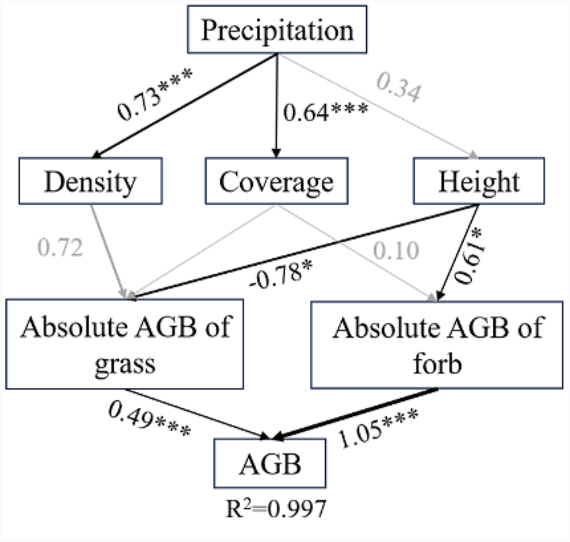

Figure 11. *Structure equation model (SEM) analysis of the effects of altered precipitation on AGB (χ2 = 4.105, df = 7, P = 0.796, GFI = 0.946, RMSEA < 0.001). Solid lines indicate significant path coefficients and gray lines indicate non-significant path coefficients. Line thickness is scaled according to magnitude of the path coefficient and the number adjacent to each line represents the standardized path coefficient. R^2 denotes the proportion of variance explained. GFI, goodness-of-fit; RMSEA, root mean square error of approximation. Significance levels: *p < 0.05; **p < 0.01; ***p < 0.001*

Community - driven mechanism for the response of AGB to precipitation change

In the present study, the positive correlation between plant growth, biomass of forbs function group and AGB under altered precipitation was found through spearman correlation and regression analysis as well as SEM. Much of the reduction in AGB under extreme drought was driven by reductions in forbs production by 56% in 2013, 60% in 2014 and 92% in 2015, respectively (*Fig. A4a, b*). It also agreed well with the result that reduced ANPP after extreme drought was a consequence of reduced productivity of both grasses and forbs (Hoover et al., 2014). Moreover, the dominant grass (*Stipa breviflora*) increased in dominance but the dominance of dominant species *Ajania fruticulosa* decreased under extreme drought treatment compared with control, both them still were the dominant species in the five precipitation treatments and thus precipitation alteration did not lead to species reordering (*Fig. 7a, c*). Our result was not consistent with the species reordering due to the dominant forb abundance decrease in mesic grassland after extreme drought (Hoover et al., 2014), species reordering due to increase in relative abundance of early-season annual species and shrubs after 4-year experimental drought (Griffin-Nolan et al., 2019) and community reorganization in upland grassland (Stampfli et al., 2018). Previous work in other ecosystems has shown that forbs rely on deep soil moisture to avoid water stress during dry periods, while grasses rely mostly on shallow soil moisture to tolerate dry periods (Nippert and Knapp, 2007). However, in this study, the differences in soil moisture at deeper soil layers were not found. But forbs have lower morphological plasticity compared to grasses during drought such as ability of rapid resprouting (Wellstein et al., 2017). Thus, in the present study, AGB decreased significantly following the biomass decrease of both grass and forb functional groups, while the dominant species did not change under extreme drought. The relative abundance of dominant species did not display evident relationship with AGB (*Table 2; Fig. 10*). It was inconsistent with our hypothesis that the responses of dominant species would govern the responses of ecological function to extreme precipitation, and was also inconsistent with several studies (Cavin et al., 2013; Hoover et al., 2014; Griffin-Nolan et al., 2019).

Consistent with our hypothesis, species diversity was not found to be different among precipitation treatments in this study, which was in accordance with the results that extreme drought (Hoover et al., 2014) or extreme wet (Zhong et al., 2019) had little effect on species richness. Moreover, species diversity was not the factor driving ANPP change through correlation and regression analysis during three years' precipitation manipulated experiment (*Table 2; Fig. 10*). However, decline of soil moisture with the decreased precipitation could suppress plant growth in the early years, led to reductions of plant density and coverage, and the consequent loss of plant species in long-term drought experiments (Storch et al., 2018). We found extreme drought (-40% precipitation treatment) reduced species density, coverage, height as well as biomass of forbs and grass during three years, while the responses of three species diversity indices to years were sensitive rather than precipitation treatments. It is necessary to detect the long-term change in species diversity as well as its relationship with the primary production.

In the present study, species asynchrony significantly decreased (by 28.2%) under the extreme drought treatment (*Fig. 8*). The study of Zhang et al. (2019a) also verified that large decrease in species asynchrony under most extreme drought contributed substantially to the reduction in ANPP. Through the increased niche partitioning or facilitation and alleviated fluctuation of summed community characteristics in response to precipitation change, asynchrony causes a high resistance of productivity to environmental precipitation variation (Xu et al., 2014). Our results suggest that significant reductions in species asynchrony can leave ecosystems more vulnerable to extreme drought. Therefore, three years' extreme drought did not significantly affect the species diversity and community composition based on the dominant species, but widely limited the plant growth in the individual or population level, consequently having the negative effect on the ecosystem function (i.e. productivity). In our study, the species aboveground biomass decreased under extreme drought in three years (*Fig. 9*). Under control, the reduction in biomass of *Salsola ruthenica* was compensated by biomass of *Stipa breviflora* and *Ajania fruticulosa* in dry year (2015), which resulted in species asynchrony of high degree. However, under extreme drought treatment, except *Stipa breviflora*, the biomass of other species (*Zygophyllum mucronatum, Halogeton arachnoideus* and so on) synchronously decreased and was not effectively compensated in 2015 (*Fig. 9*). As seen in our experiment, the significantly decreased AGB, plant growth indices and species asynchrony were found under extreme drought. Thus, although dominant species and species diversity did not change under three years' precipitation alteration, the plant growth and functional group biomass contributed majorly to AGB. However, species asynchrony did not drive AGB change under all the precipitation treatments (*Fig. 8; Table 2*). It was consistent with our hypothesis. The effects of extreme wet on the soil moisture, plant growth and species asynchrony might be weakened in some extent due to the runoff along the slope. Therefore, it is desirable to assess the species asynchrony to precipitation variation through long-term experiments as well as the relationship with AGB under extreme precipitation.

Conclusion

In this study, we used a field precipitation manipulation experiment to assess the potential mechanisms by which extreme precipitation changes can elicit a notable ecological response in semiarid grassland. We found that extreme drought decreased plant growth and AGB, increased precipitation did not significantly change AGB, coinciding with the nonlinear negative asymmetry under extreme precipitation of Knapp’s double-asymmetry model. It suggested the sensitivity of AGB to increased precipitation was less than decreased precipitation in the Loess Plateau. Furthermore, dominant species and species diversity did not change during three years’ precipitation alteration. The plant growth and functional group biomass contributed majorly to AGB along manipulated precipitation gradient. Declined species asynchrony responded sensitively to extreme drought rather than increased precipitation. The contribution of species asynchrony to AGB under precipitation extremes is necessary to detect for further research.

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Data accessibility statement. All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

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APPENDIX

Table A1. *The plant species sorted by different functional traits and functional groups (PFGs) in the experimental plots during the three years*

Species	Family	Life history	Life form	PFGs
Stipa breviflora	Gramineae	Perennial	Herb	Grass
Cleistogenes squarrosa	Gramineae	Perennial	Herb	Grass
Setaria viridis	Gramineae	Annual	Herb	Grass
Tragus racemosus	Gramineae	Annual	Herb	Grass
Mnesithea mollicoma	Gramineae	Perennial	Herb	Grass
Echinochloa crusgali	Gramineae	Annual	Herb	Grass
Ajania fruticulosa	Compositae	Perennial	Sub-shrub	Forb
Salsola ruthenica	Chenopodiaceae	Annual	Herb	Forb
Linum nutans	Linaceae	Perennial	Herb	Forb
Zygophyllum mucronatum	Zygophyllaceae	Perennial	Herb	Forb
Artemisia capillaris	Compositae	Perennial	Herb	Forb
Artemisia annua	Compositae	Annual	Herb	Forb
Heteropappus altaicus	Compositae	Perennial	Herb	Forb
Allium polyrhizum	Liliaceae	Perennial	Herb	Forb
Peganum harmala	Zygophyllaceae	Perennial	Herb	Forb
Euphorbia humifusa	Euphorbiaceae	Annual	Herb	Forb
Iris lactea	Iridaceae	Perennial	Herb	Forb
Convolvulus arvensis	Convolvulaceae	Perennial	Herb	Forb
Torularia humilis	Brassicaceae	Perennial	Herb	Forb
Asparagus gobicus	Liliaceae	Perennial	Sub-shrub	Forb
Lycium chinense	Solanaceae	Perennial	Shrub	Forb
Reaumuria soongarica	Tamaricaceae	Perennial	Sub-shrub	Forb
Plantago asiatica	Plantaginaceae	Perennial	Herb	Forb
Stragalus membranaceus	Leguminosae	Perennial	Herb	Forb
Halogeton arachnoideus	Chenopodiaceae	Annual	Herb	Forb

Table A2. *Repeated-measure ANOVA for the effects of year (Y), precipitation treatment (P) and their interactions (Y × P) on soil water content (SWC) and soil temperature (ST)*

Source of variation	**SWC**			**ST**		
	0-20 cm	**20-40 cm**	**40-60 cm**	**8:00**	**11:00**	**15:00**
Y	489.48***	85.71***	11.543***	17.94***	37.91***	46.84***
P	0.46	0.14	0.253	0.13	0.20	0.26
Y×P	5.923**	1.94	0.936	0.50	0.68	1.86

Significance levels: *P < 0.05, **P < 0.01, ***P < 0.001

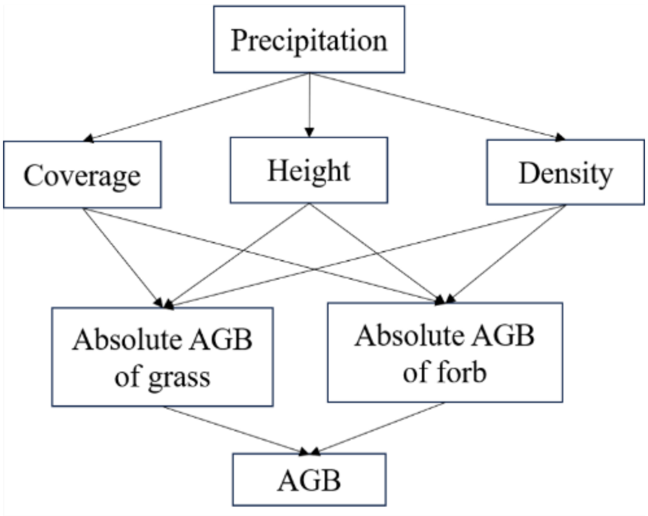

Figure A1. *A priori conceptual model of the precipitation, coverage, height, density on AGB*

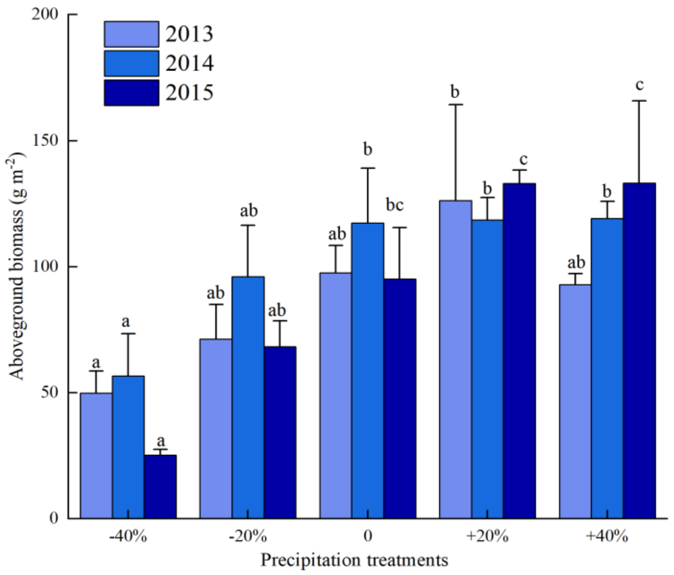

Figure A2. *The characteristics of aboveground biomass (AGB) under precipitation treatments during three years of experiment. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference among precipitation treatments in the same year at* $p < 0.05$

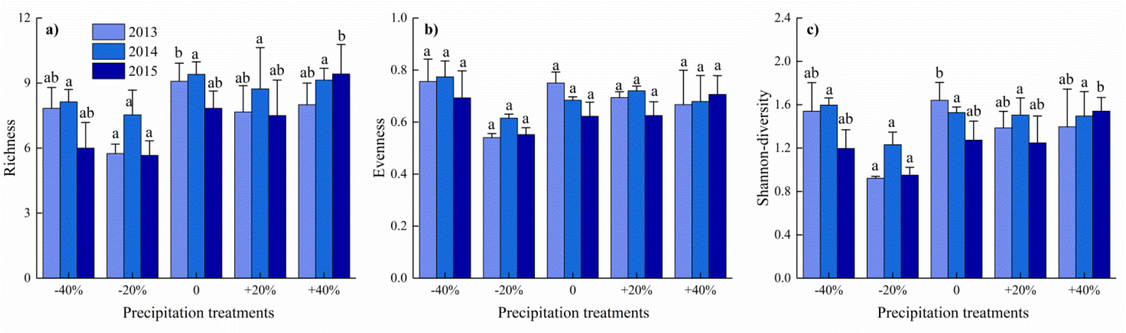

Figure A3. *The characteristics of community diversity metrics under precipitation treatments during three years of experiment. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference among precipitation treatments in the same year at* $p < 0.05$

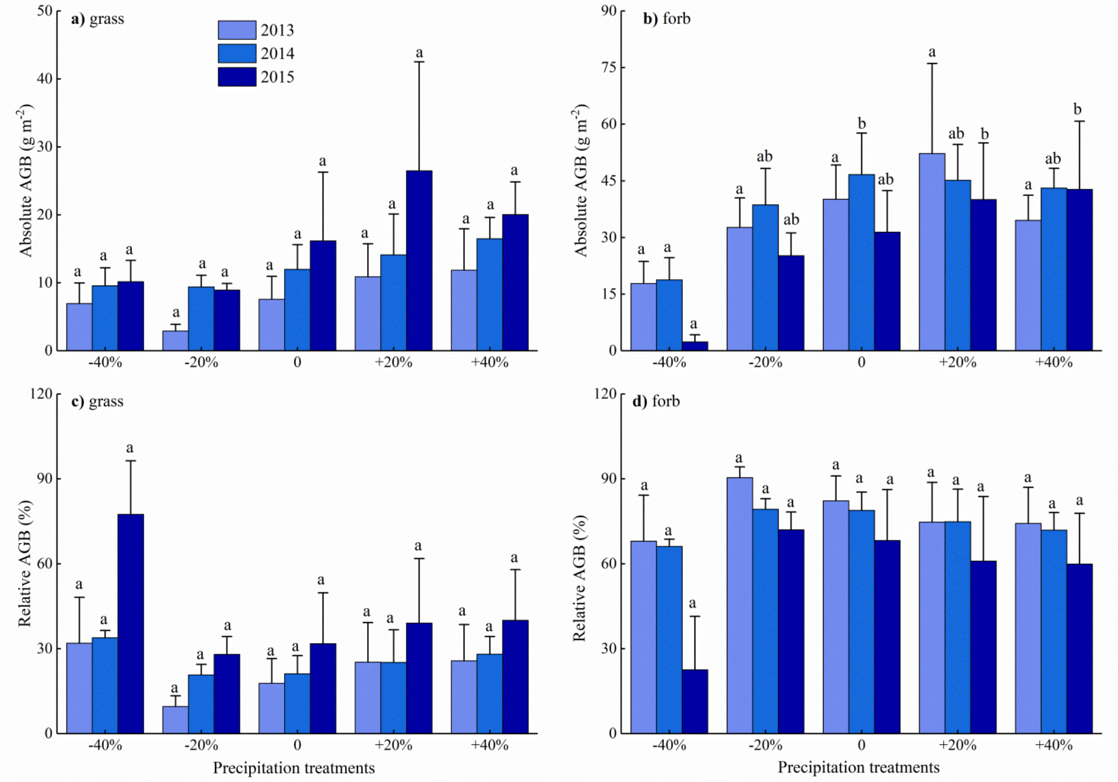

Figure A4. *The characteristics of absolute and relative AGB (aboveground biomass) of forb and grass under precipitation treatments during three years of experiment. Error bars indicate means ± SE (n = 3). Different letters indicate statistically significant difference among precipitation treatments in the same year at* $p < 0.05$

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