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Legacy effects of precipitation amount and frequency on the aboveground plant biomass of a semi-arid grassland

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Abstract

Precipitation is known to have a legacy effect on plant diversity and the production of many terrestrial ecosystems. Precipitation regimes are expected to become more variable with increasing extreme precipitation events. However, how previous-year precipitation regimes affect the current-year aboveground biomass (AGB) remains largely unknown. Here we measured long-term (2004-2017) AGB in semi-arid grassland of the Chinese Loess Plateau to evaluate the impact of previous-year precipitation amount on current-year AGB. Furthermore, to assess the response of current-year AGB to previous-year precipitation regimes, we conducted a field manipulation experiment that included three precipitation regimes during 2014-2017: (i) ambient precipitation, (ii) monthly added four 5 mm rain events, and (iii) monthly added one 20 mm event. Both the long-term (2004-2017) observations under ambient precipitation and short-term (2014-2017) measurements under manipulative treatments showed significant positive effects of previous-year precipitation on current-year AGB. Our path analysis suggested that previous-year precipitation frequency had negative effects on the current-year density and mean height of grass (*Leymus secalinus*) while had positive effects on forb (*Artemisia capillaris*). The forb had much smaller height and AGB (65% and 53% less, respectively) than the grass. Consequently, the AGB reduced in the weekly determining event treatment, causing the sensitivity to decrease. Therefore, our findings indicated that the impacts of precipitation regimes on plant community dynamics should be taken into consideration while assessing the precipitation legacy effect on ecosystem production.

Keywords: legacy effect, precipitation regime, extreme event, aboveground biomass, community composition, semi-arid grassland

1. Introduction

Precipitation input or soil water availability is the determining factor of aboveground net primary production (ANPP) of almost all terrestrial ecosystems, especially in arid and semiarid ecosystems where plant growth is limited by water scarcity (Huxman et al., 2004; Knapp et al., 2017; Noy-Meir, 1973; Ponce Campos et al., 2013; Sala et al., 1988; Ye et al., 2018b). Globally, arid and semi-arid grassland ecosystems account for about 19% of the Earth's surface excluding Antarctica and Greenland (White et al., 2000). Grassland ecosystems are known to be highly responsive to precipitation variability (Hawinkel et al., 2016; Knapp and Smith, 2001). Therefore, understanding the relationship between arid and semi-arid grassland ecosystems productivity and precipitation is of fundamental importance for more comprehensive management of rangelands and for better predicting their response to climate change.

Mounting evidence suggests that ANPP increases significantly with annual precipitation at a given site (Estiarte et al., 2016; Huxman et al., 2004; Knapp et al., 2017; Sala et al., 2012; Ye et al., 2018b). It is tempting to use such a relationship to predict the response of ANPP in an ecosystem to precipitation changes through time. However, in most sites, annual precipitation interprets only less than 50% of the interannual variability in ANPP (Estiarte et al., 2016; Sala et al., 2012). Sala et al. (2012) and Reichmann et al. (2013b) attribute this low explanatory power to the lagged response of ecosystems to changing precipitation and soil water availability. Indeed, previous-year precipitation had been found to drive the ecosystem process in current-year due to lagged/legacy effect across sites in the Patagonian steppe (Yahdjian and Sala, 2006), the Tallgrass Prairie in Oklahoma (Sherry et al., 2012; Sherry et al., 2008) and the grasslands in northern California valley (Dudney et al., 2017). These studies revealed a variety of causes of the lagged effect, for example, soil moisture, vegetation structure, seed production, and plant litter in the previous-year condition may affect current-year ANPP. Shen et al. (2016) conducted a modeling analysis and implied that growing season precipitation amount and the number of extreme precipitation events in previous-year were significantly and positively correlated with the quantified legacy effect (the difference in net ecosystem production between current-year after precipitation changes in the previous-year and that without precipitation changes in the previous-year). However, field study to address such potential cause is lacking.

Changes in precipitation regimes have been observed in many regions of the world. These include increases in the total precipitation amount and extreme precipitation events (Easterling et al., 2000; IPCC, 2013; Kharin et al., 2007). These changes are being observed currently (Fischer and Knutti, 2016; Min et al., 2011) and also projected to continue in the future by climate models (Ban et al., 2015; Bao et al., 2017; IPCC, 2013). The effects of precipitation regimes on grassland ecosystem has received much attention in recent decades. For example, Thomey et al. (2011) showed that the ANPP of dominant species in a Chihuahuan Desert grassland was significantly higher in the plots received monthly one large precipitation event compared with those received multiple small precipitation events. Knapp et al. (2002) demonstrated that more extreme precipitation patterns reduced ANPP in a native grassland ecosystem of northeast Kansas, USA. Heisler-White et al. (2009) suggested that the response of ANPP to more extreme precipitation regimes was contingent on the mean soil water content for each grassland type in three grasslands of the North American Central Plains Region. Although the effect of extreme precipitation patterns on ANPP vary among the three grassland ecosystems, the authors consistently attributed these results to variability in soil moisture. Moreover, different functional groups respond distinctively to extreme precipitation (Stampfli et al., 2018) and hence shifts of dominant species in the community have large effects on ANPP (Avolio et al., 2014; Knapp et al., 2012). In other words, apart from the direct effect of altered precipitation remiges, ANPP may be affected indirectly by shifts in functional groups caused by changes in precipitation regimes and soil moisture. Therefore, the community composition should be considered in predicting how the productivities of grassland ecosystems respond to future changes in precipitation regimes. However, previous studies have paid little attention to the impacts of community composition changes caused by extreme precipitation patterns on plant AGB.

To explore the impacts of precipitation amount and altered precipitation patterns (extreme events, event size, and frequency) on the plant production, we measured AGB since 2004 in a semi-arid grassland and experimentally altered precipitation frequency and size without changing the total addition precipitation since 2014. Our main objectives were to: (1) identify whether current-year AGB is affected by previous-year precipitation, and clarify the potential causes for such legacy effect, (2) evaluate whether changes in the precipitation amount and patterns alter the relationship between AGB and precipitation.

2. Materials and methods

2.1 Experimental site

We conducted a field manipulative study at a semi-arid grassland site in the Loess Plateau of China. The site locates within the Semi-arid Ecosystem Research Station of Lanzhou University (latitude 36°02′, longitude 104°25′, and elevation 2400 m). This site is characterized as a moderate temperate semi-arid climate, with a mean annual temperature of 6.5 °C and mean annual precipitation of 330 mm. The majority of rainfall events are concentrated in the growing season (1 May to 30 September), and extreme precipitation events often occur during this period. The mean annual evaporation is about 1300 mm (Zhang et al., 2019). The soil is classified as Heima according to Calcic Kastanozem, FAO Taxonomy, with a 1.22 g cm^{-3} bulk density, 9% clay, 13% sand and 78% silt in 0-20 cm soil profile (Fang et al., 2017). The site is representative for the semi-arid grassland in the area, as the two dominant species found at the site, a perennial grass (*Leymus secalinus*) and a perennial forb (*Artemisia capillaris*), which are also most abundant in many other semi-arid grassland ecosystems of the Loess Plateau (Zhu et al., 2016).

2.2 Experimental design

To achieve the objective of how changes in the precipitation amount and patterns affect the relationship between AGB and precipitation, we conducted a field manipulative experiment during the growing season of 2014-2017. We included three treatments: control and two treatments received the same rain amount but differing in frequencies and event sizes. In each month during the growing season of 2014, the "weekly small events" and "monthly heavy event" treatment plots additionally received four 2.5 mm rain events and one 10 mm event, respectively. The 10 mm rainfall is considered a heavy event, based on the Expert Team on Climate Change Detection and Indices (Sillmann and Roeckner, 2008; Ye et al., 2018a; Zhang et al., 2011). We improved the rain manipulation during the following three years, based on the probability density function of precipitation event size at the study site (Fig. S1). In each month during the growing season of 2015-2017, the "weekly small events" and "monthly heavy event" treatment plots additionally received four 5 mm rain events and one 20 mm event, respectively. The 5 mm is an average size event (between 10th to 90th percentiles) and 20 mm is an extreme event (above the 90th percentile, Fig. S1) at the study site. Ultimately, the annual precipitation under the rainfall addition treatments was 50 mm or 100 mm more than control from 2014 to 2017 (Fig. 1a). Annual precipitation in the rainfall addition treatments was classified as extreme annual precipitation (exceeding 90th percentile) based on the long-term distribution function at the study site (Fig. S1). These experimental designs allowed us to assess the impacts of both increasing total precipitation amount and altering rainfall regimes (event size and frequency).

The treatment plots were irrigated with a hand sprayer, using rainwater harvested at the research station. To minimize evaporation loss and aboveground lateral flow, we irrigated at a rate of 2.5 mm per hour during 5-6 pm for the average event treatment (5 mm-event), and during 5-8 pm and 6-9 am for the extreme event treatment (20 mm-event). We set up two blocks (7 m × 7 m) in an adjacent location to reduce the differences within a treatment. We used the Latin square design in each block, consequently, each block contained nine plots (1 m × 1 m). There are six replicates (i.e., plots) for each treatment.

2.3 Abiotic data

Ambient daily precipitation data acquired from the Semi-arid Ecosystem Research Station of Lanzhou University were combined with the added rainwater to calculate annual and daily precipitation for each treatment. Volumetric soil water content (SWC) and soil temperature (ST) for the top 5 cm soil layer were continuously measured with Watchdog 2000 Series Mini station-T/RH (Spectrum Technologies Inc., Aurora, IL, USA) at a 1-h interval since 1 May 2015. Each sensor was inserted at a 45° angle in the center of one randomly selected plot of each treatment.

We collected soil samples at the end of the growing season each year, about 15-day after the last rain addition. Soil cores of 2 cm diameter by 20 cm depth were used to measure inorganic nitrogen (NO_3^- and NH_4^+) within 24 hours of collection. A 20-g soil subsample through a 2-mm mesh was extracted in 100 mL of 2 mol/L KCl solution to determine the contents of NO_3^- and NH_4^+ of soil. Nitrate (NO_3^-) and ammonium (NH_4^+) concentration in the KCl extracts were analyzed using FIAstar

5000 Analyzer (Foss Tecator, Sweden).

2.4 Biotic data

We used a non-destructive sampling method to estimate the AGB in the rain manipulative experiment with three rainfall treatments (control, “weekly small events treatment” and “monthly heavy event treatment”) during 2014-2017. The method used vegetation height data and height-to-AGB regression equation of each species developed for the same study site (Fang et al., 2018). *Leymus secalinus* and *Artemisia capillaris* accounted for more than 95% of plant cover at the study site, we measured the height and density for the two species at the peak biomass period of each year. We defined the density of the dominant species as the number of each dominant species in each plot. In addition, we also measured annual AGB over the long-term (2004-2017) in ten randomly selected 1 m × 1 m plots with ambient precipitation adjacent to the manipulative experiment plots, using the harvesting method.

2.5 Statistical analyses

We built linear regression models between the average of total AGB of ten plots and the current-year total ambient precipitation (PPT_i) and/or previous-year total ambient precipitation (PPT_{i-1}), using the linear model (lm) function in R version 3.4.2 (R Core Team, 2019). We selected the best model based on the Akaike information criterion (AIC) (Burnham and Anderson, 2002). To assess the differences between these linear relationships under each treatment, we used covariance analysis to test the statistical difference in the slopes and intercepts of these linear fittings. We conducted a covariance analysis with the R package “HH” version 3.1-35 (Heiberger and Holland, 2004).

We used path analysis to evaluate the direct and indirect effects of precipitation regimes (amount and frequency) on plant height, density, and AGB. We conducted path analysis using the R package “lavaan” version 0.6-3 (Rosseel, 2012). A brief description of the path analysis is provide in supplementary section #2 of the supplementary material.

3. Result

3.1 Microclimate

Ambient annual precipitation amount varied during the period: 421 mm in 2014 (wet year), 294 mm in 2015 and 285 mm in 2016 (average years but lower than 50th percentile, and 350 mm in 2017 (average year but higher than 50th percentile) (Fig. S1). Approximately 78% of annual precipitation falls during the growing season (1 May to 30 September) (Fig. 2a). The weekly small events treatment and the monthly heavy event treatment had 20 and 5 more precipitation events than the control, respectively (Fig. 1b). The monthly heavy event treatment had five more precipitation extreme events than the weekly small events treatment and control in each year of 2015-2017. The extreme rainfall events in 2014 (an extreme wet year) had exceeded the average number of the region's historical record before the growing season began (Fig. 1c).

The effects of rainwater addition on monthly volumetric soil water contents (SWC) depended on the ambient rainfall. Paired t-test suggested that precipitation addition treatments significantly increased the average monthly SWC in the growing seasons of 2015 and 2016, and there was no significant difference between weekly small events and monthly was event treatments (Fig. 2b). The average monthly SWC in the non-growth season was not significantly different among treatments (Fig. 2b). However, in the growing season of 2017, monthly heavy rainfall addition treatment significantly increased the average monthly SWC compared with weekly small rainfall addition treatment and control. In addition, the mean monthly SWC in weekly small rainfall addition treatment was significantly higher than that in control (Fig. 2b). Rainfall addition treatments did not significantly affect mean monthly soil temperature (ST) (Fig. 2c).

3.2 Impact of precipitation legacy on AGB

The long-term (2004-2017) observations suggested that current-year AGB increased linearly with previous-year precipitation amount and previous-year precipitation best predicted current-year AGB at our study site (Fig. 3a and Table 1). Moreover, the short-term (2014-2017) measurements under different precipitation regimes presented a similar pattern (Fig. 3b). Therefore, there is a robust legacy effect of past precipitation on current-year AGB at our study site. In contrast, the linear regression model between current-year AGB and precipitation was not statistically significant (P>0.05) (Fig. S2).

The regression models between current-year AGB and previous-year precipitation under different precipitation regimes were significantly different (Fig. 3b, Table 2). The sensitivity of AGB to previous-year precipitation (i.e. the slope of liner model) in weekly small events treatment was significantly lower than that of the control and the monthly heavy event treatment. However, the sensitivities were not significantly different between the monthly heavy event treatment and control (Table 2). The intercept of the linear regression model was significantly higher in the weekly small event treatment compared to the control, but significantly lower in the monthly heavy event treatment than that of the control (Table 2).

3.3 Path analysis for the precipitation legacy effect on plant community and AGB

Path analysis showed that previous-year precipitation amount and frequency indirectly affected the current-year AGB by affecting the density and average height of the dominant species in the current-year (Fig. 4). The effects of previous-year precipitation amount or frequency on the quantitative characteristic of the two dominant species were opposite. With the increase of previous-year precipitation frequency, the density and the average height of forb (*A. capillaris*) increased, while these of grass (*L. secalinus*) decreased (Fig. 4 and Fig. 5). In contrast, increased previous-year precipitation amount had positive effects on the density of both species and the average height of the grass but a negative effect on the average height of forb (Fig. 4). Furthermore, the density and the average height of grass had significant direct effects on AGB, which were 350% stronger than the found for the average height of forb (Fig. 4). The density of forb had no significant direct effects on AGB.

4. Discussion

Both the long-term (2004-2017) observations under ambient precipitation and short-term (2014-2017) measurements under manipulated treatments show a positive linear association between current-year AGB and precipitation in the previous year, suggesting a significant legacy effect of antecedent precipitation (Fig. 3). However, there was no significant correlation between current-year AGB and precipitation (Fig. S2). Our result is not an exception. No significant relationship between current-year precipitation and plant productivity was found in some other ecosystems, as summarized by Sala et al. (2012). Our findings further suggested that weekly small event treatment significantly decreased the sensitivity of AGB to previous-year precipitation (Table 2). These results add to the growing evidence that previous-year precipitation impact current-year ecological processes (Dudney et al., 2017; Sala et al., 2012; Shen et al., 2016), and provide novel perspective about the potential influences of altered precipitation regimes on the AGB-precipitation relationship. Significantly, we found that the density of forb (*A. capillaris*) increased, but grass (*L. secalinus*) decreased under weekly small event treatment (Fig. 5). The two species vary in their contribution to the total primary productivity of an ecosystem. Thus, altered precipitation regimes changed the plant community and then indirectly affect AGB.

Three primary potential causes for the precipitation legacy effects had been proposed. First, the carry-over of soil moisture from one year to the next could lead to precipitation legacy (Sun et al., 2018). However, soil moisture carry-over did not occur in our study site because of high potential evapotranspiration. The potential evapotranspiration is about four times of the annual precipitation amount, resulting in the increasing SWC in the monthly heavy precipitation event treatment lasted only 5 days, and 2 days in the weekly small precipitation event (Fig. S3b). Additionally, the rainy growing seasons are separated by the dormant dry seasons, and there was no significant difference among treatments in SWC at the beginning of each growing season (Fig. 2b). Second, previous-year precipitation may influence microbial mineralization and immobilization, plant uptake and growth and N leaching, resulting in soil inorganic N pools accumulation or decrease (Evans and Burke, 2012; Giese et al., 2010; Shen et al., 2016; Yahdjian and Sala, 2010), thus promote or suppress current-year production. Nevertheless, our findings do not support the carry-over of soil inorganic N availability, because there was no significant difference in soil inorganic N among treatments (Fig. S4a-c). This may be attributed to the fact that soil inorganic N concentration is influenced by immediate soil water conditions (Giese et al. 2010), and the changes in N availability caused by precipitation may last only in the short-term (Yahdjian and Sala, 2010). Third, previous-year precipitation is known to have a significant effect on the density of plant tiller and stolon (Reichmann and Sala, 2014; Reichmann et al., 2013a), which are the controlling factors of aboveground net primary productivity (Reichmann et al., 2013a). Our result showed that previous-year precipitation characteristics influenced current-year AGB indirectly by affecting the density of the dominant species (Fig. 4). The direct effect of the previous-year precipitation characteristic on the current-year density of dominant species may be due to the fact that the dominant species are perennials at our research site. Similarly, Yahdjian and Sala (2006) reported that meristem (tillers, stolon, stems, etc.) density loss during extreme drought may constrain post-drought plant growth, even if precipitation are abundant after the drought event.

The sensitivity of AGB to previous-year precipitation decreased in weekly small event treatment but did not in monthly heavy event treatment, suggesting a significant impact of previous-year precipitation patterns. Previous studies reported that, in arid ecosystems, frequent but small precipitation events can only reach the shallow depths and promote shallow-rooted species, whereas larger events may effectively recharge deeper soil layer, favoring deeply rooted species (Knapp et al., 2008; Schwinning and Ehleringer, 2001; Schwinning and Sala, 2004; Thomey et al., 2011). Indeed, in our research site, the root length of the forb is only half of that of grass. The density of the forb was higher under the weekly small event treatment than the control and monthly heavy event treatment (Fig. 5). The average in all treatments height and AGB of the forb are 65% and 53% smaller than the grass, respectively. Consequently, the AGB reduced in the weekly small event treatment, causing the sensitivity of AGB to precipitation to decrease.

Our path analysis further verified the above findings. The precipitation frequency had positive effects on the forb but had negative effects on the grass (Fig. 4). The negative effects may be due to the increase in the density of the forb with the increase of precipitation frequency, which leads to the interspecific competition for resources. The path analysis also showed that precipitation amount increased the mean height and density of grass and thus increased AGB and sensitivity. However, in our experimental results, there is no significant difference in AGB and sensitivity in monthly heavy event treatment compared with control. This may result from the fact that the increase of precipitation amount is accompanied by the increase of precipitation frequency in monthly heavy precipitation event treatment, which leads to an offset between the positive effect of an increase in precipitation amount and negative effect of an increase in frequency on AGB.

Our findings suggest that the intercept of the relationship between AGB and precipitation may be impacted by the abundance and the relative proportion of species. The total AGB is mainly determined by *L. secalinus* (Fig. 4), thus it controls the relationship between AGB and precipitation. With the increase of precipitation frequency, the density and relative proportion of *A. capillaris* increased, while these of *L. secalinus* were opposite (Fig. 4, Fig. 5). Decreases of *L. secalinus* density and relative proportion lead to the reduction of AGB, and then alter the slope and intercept of this relationship. Compared with the control, the intercept increased and slope decreased significantly in the weekly small event treatment with the most precipitation frequency (Fig. 1b), and only the intercept decreased significantly under the monthly heavy event treatment with slight increase in precipitation frequency (Fig. 1b), (Table 2). Changes in the intercept and slope of a linear regression between biological responses and environmental drivers indicated an ecosystem state change, such as abundance or biomass of individual species (Bestelmeyer et al., 2011) .

5. Conclusion

Together, our study demonstrated that the previous-year precipitation regimes have significant impacts on the current-year AGB in semi-arid grassland of the Chinese Loess Plateau. This finding highlights the necessary to account for not only the previous-year precipitation amount but also precipitation frequency and size, in order to predict the response of the AGB in the ecosystem. Our results implied that precipitation regime shift with ongoing climate change may indirectly affect the AGB of the grassland ecosystem by altering the plant community. Therefore, the vegetation structure is also essential for predicting the response of grassland ecosystem productivity.

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article.

Table 1 Linear regression between current-year total aboveground biomass (AGB_i) from 2004 to 2017 and current-year total ambient precipitation (PPT_i), previous-year total ambient precipitation (PPT_{i-1}) or both. *P*, *P* values of the model; R^2, *R* squared values of the model; *F*, *F* values of the model; AIC, Akaike information criterion of the models. The best model with the lowest AIC value is in bold.

Model	*F*	*P*	R^2	AIC
AGB_i=157.33-0.08PPT_i	0.11	0.74	0.01	155.11
AGB_i=-61.56+0.63PPT_{i-1}	17.82	0.00	0.56	**142.50**
AGB_i=-53.33-0.02PPT_i+0.63PPT_{i-1}	8.20	0.01	0.53	144.47

Table 2 Slopes and intercepts of linear regressions between current-year aboveground biomass and previous-year precipitation for control (Control), weekly small events (4 × 5 mm) and monthly heavy event (1 × 20 mm) treatments. Different letters among treatments are statistically significant at $P<0.05$.

	slope	intercept
Control	0.95a	-133.36b
4 × 5 mm	0.26b	21.44a
1 × 20 mm	0.98a	-220.89c

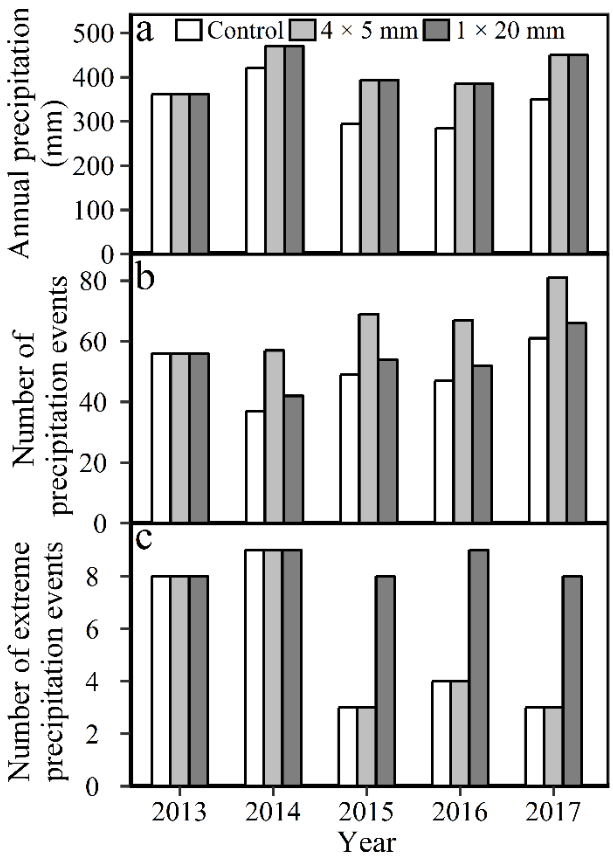


Fig. 1 (a) Annual precipitation amount, (b) number of precipitation events above 1 mm, (c) number of extreme precipitation events exceeding the 90th percentile (i.e. 14.5 mm) from 2013 to 2017 for control (Control), weekly small events (4 × 5 mm) and monthly heavy event (1 × 20 mm) treatments.

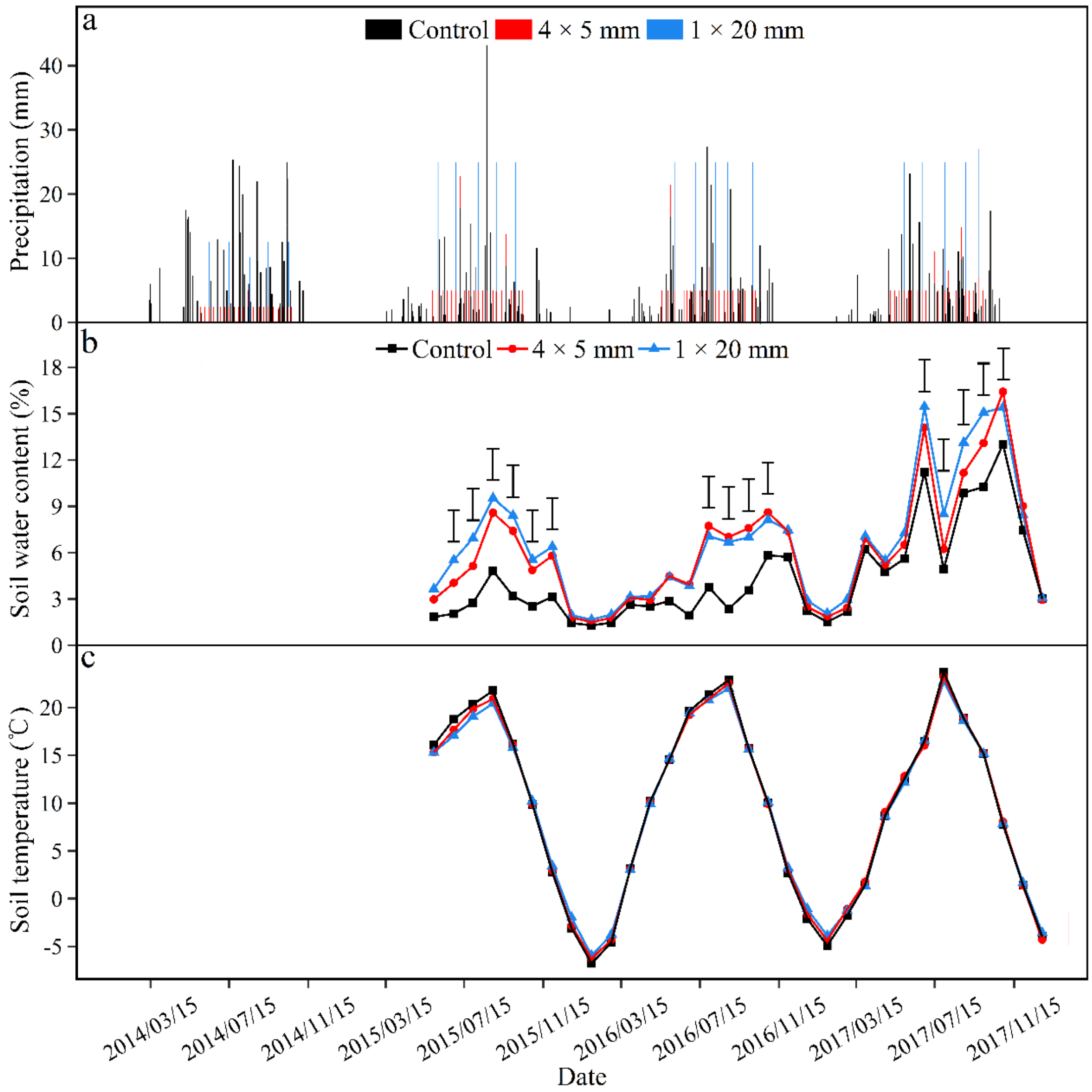


Fig. 2 (a) Daily precipitation from January 2014 to December 2017, (b) monthly volumetric soil water content and (c) soil temperature from May 2015 to December 2017, for the control (Control), weekly small events (4 × 5 mm), and monthly heavy event (1 × 20 mm) treatments. The error bars of the monthly volumetric soil water content (b) are t values for a degree of freedom of 30 and statistical significance at *P*= 0.05 level.

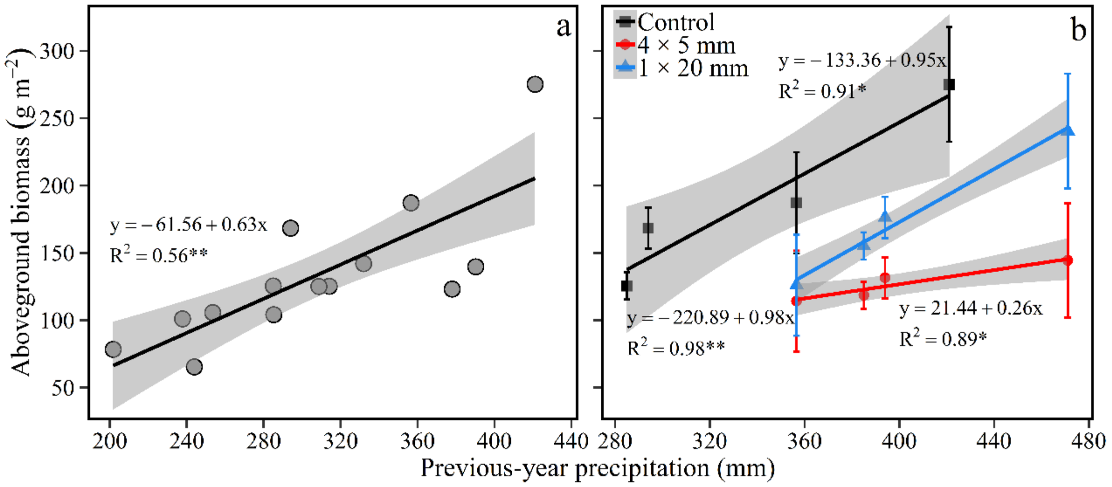


Fig. 3 (a) Linear regressions between current-year (2004-2017) total aboveground biomass (AGB) and previous-year (2003–2016) total ambient precipitation amount. Points are a mean of 10 sample plots. (b) Relationships between current-year total AGB and previous-year total precipitation for control (Control), weekly small events (4 × 5 mm) and monthly heavy event (1 × 20 mm) of the treatment years (2014–2017). Points are an AGB mean ± standard error (n=6) in each treatment for a year. Gray shaded areas indicate a 95% confidence interval. Significance level **, *P*<0.01; *, *P*<0.05.

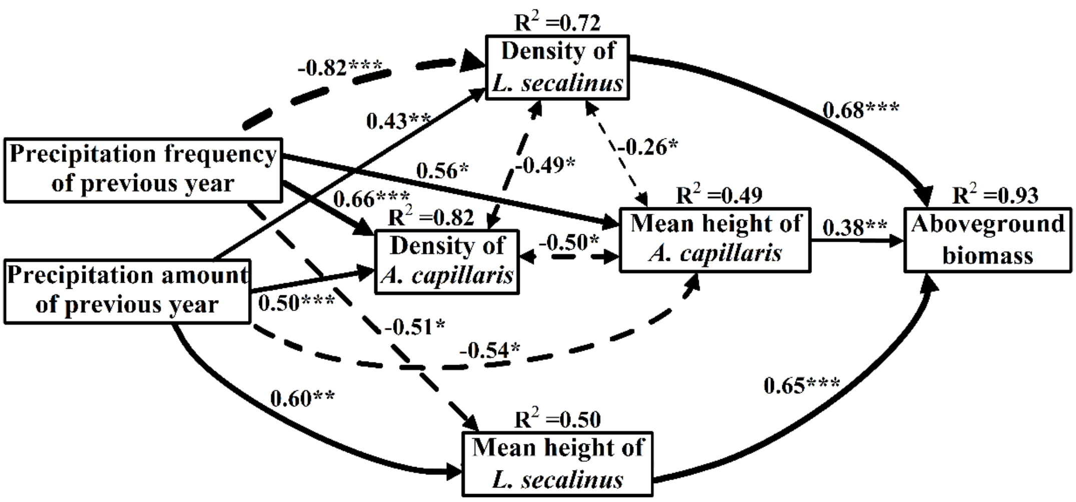


Fig. 4 Path diagrams showing the direct and indirect effects of precipitation frequency and amount on aboveground biomass. Only the significant paths are shown in the diagram, non-significant paths were removed to simplify the path diagram. The value adjacent to each arrow indicates the standardized path coefficient. Significance code: *** 0.001, ** 0.01 and * 0.05. Solid and dashed arrows represent positive and negative effects, respectively. A single-headed arrow indicates causal relationships of one variable on another, and double-headed arrows indicate a covariance between variables. Arrow widths denote proportionally to path coefficients.

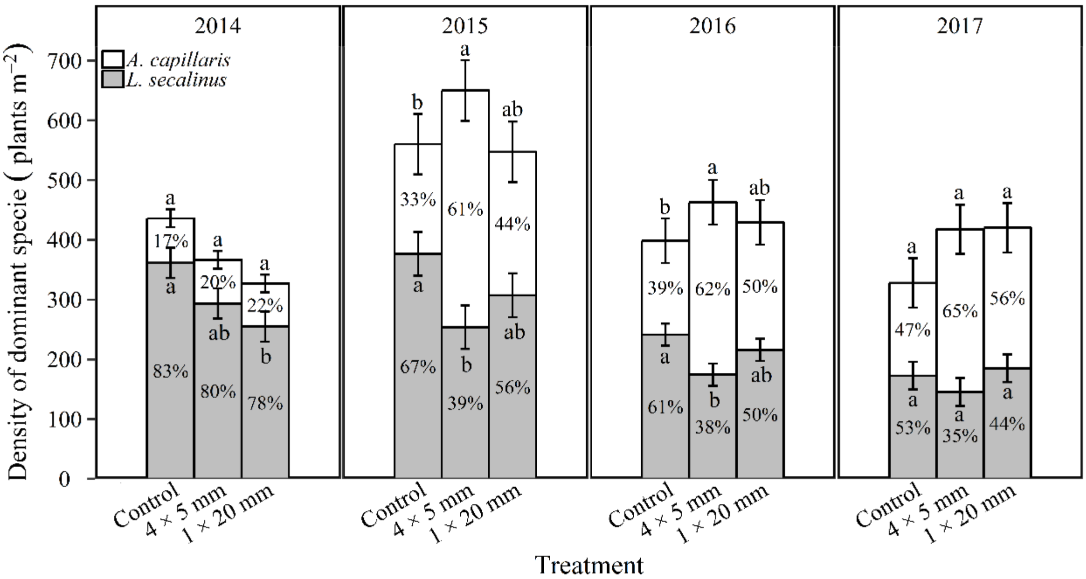
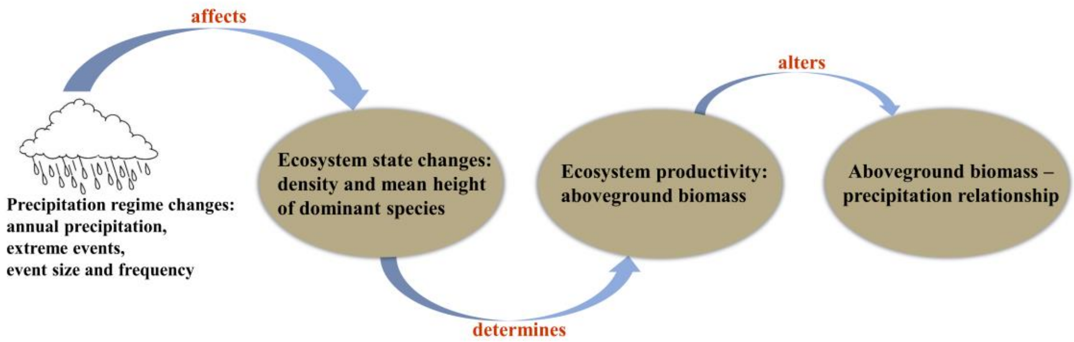


Fig. 5 The contribution of *Leymus secalinus* (grass) and *Artemisia capillaris* (forb) to dominant species density from 2014 to 2017 under control (Control), weekly small events (4 × 5 mm) and monthly heavy events (1 × 20 mm). The dominant species density is the sum of *L. secalimus* and *A. capillaris*. Statistically significant differences at *P*<0.05 are represented by different letters. Data are means ± standard deviation (n=6).

Declaration of interest Statement

All of the co-authors have read and approved the submitted version of the manuscript, and all the persons entitled to authorship have been so named. The authors declared that they have no conflicts of interest to this work. We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted. This manuscript has not been published or presented elsewhere in part or in entirety, and is not under consideration by another journal.

Graphical abstract



Highlights

- Current-year aboveground biomass (AGB) increased linearly with previous-year precipitation.
- Precipitation frequency negatively affects the sensitivity of AGB to precipitation.
- Previous-year precipitation amount increases the current-year grass density.
- Previous-year precipitation frequency increases the current-year forb density.