

Response of net primary productivity to precipitation exclusion in a savanna ecosystem



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ABSTRACT

Declines in precipitation are expected to affect plant performance and ecosystem carbon uptake. The response of ecosystem productivity to declines in precipitation and potential underlying mechanisms have been well studied in many biomes; however, little is known about the role of declines in precipitation and the involved mechanisms in savanna ecosystems. In a 4-year field precipitation manipulation experiment, we simulated four levels of precipitation exclusion (control, 30%, 50% and 70%) to assess the effects of declines in precipitation on net primary productivity (NPP) in a savanna ecosystem in southwestern China. NPP was strongly correlated with soil water content during the experimental period. Precipitation exclusion significantly decreased the NPP of the entire vegetation including trees, shrubs, perennials and litterfall but significantly increased the NPP of annuals. Our results suggested that precipitation exclusion can reduce the productivity of savannas and that plant functional types differ in sensitivity to precipitation exclusion. These findings imply that future declines in precipitation in savanna regions may negatively impact carbon accumulation and may induce shifts in plant functional types to buffer the effects of declines in precipitation on productivity and stabilize ecosystem function in savannas.

1. Introduction

Savannas are a crucial terrestrial biome, covering 20% of the global land surface and supporting one-fifth of the global population (Beerling and Osborne, 2006). They contribute to approximately 30% of the global net primary production (Grace et al., 2006) and therefore play a vital role in global carbon budgets. Precipitation is one of the major driving factors for savanna ecosystems, and changes in precipitation may alter ecological processes and impact ecosystem carbon balance (Strickland et al., 2016; van der Molen et al., 2011). Savannas are now at risk due to increasing drought-induced mortality (Fensham et al., 2015). Savannas are typically more sensitive to changes in precipitation than other biomes (Berry and Kulmatiski, 2017; Gang et al., 2016); therefore, declines in precipitation are expected to impact their carbon sequestration ability. Savannas in China, which are mainly distributed in valleys across the southern regions (Jin and Ou, 2000), are also suffering due to declines in precipitation (Fei et al., 2017). Particularly during 2009–2012, intense drought events (i.e., declines in

precipitation) in these regions have caused large-scale plant mortality and weakened their carbon sequestration capacity; this poses a challenge to the local forest management and conservation (e.g., for maintaining the productivity and biodiversity). To date, no studies have assessed the effects of declines in precipitation on the productivity of savannas in China. Therefore, quantifying the variation in productivity under declines in precipitation in savannas is critical.

Net primary productivity (NPP) is used to quantify the health and carbon cycling of any ecosystem. NPP is influenced by different factors such as fire, herbivory, land use and precipitation (Beerling and Osborne, 2006; Frank et al., 2015). It is often treated as the most important measure of ecosystem functions and services (Stampfli et al., 2018). Most existing studies on productivity responses to declines in precipitation have mainly focused on grasslands, forests and shrubland ecosystems across spatial (e.g., natural precipitation gradients) and temporal gradients (e.g., site-specific precipitation manipulation experiments) (Liu et al., 2015; Wilcox et al., 2017; Wu et al., 2011; Zhang et al., 2013; Zhou et al., 2009). NPP responses to declines in

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precipitation vary across biomes due to differences in ecosystem attributes (e.g., vegetation structure and species composition) (Knapp et al., 2017; Liu et al., 2018; Stuart-Haëntjens et al., 2018). A growing body of evidence has revealed that declines in precipitation induce a linear reduction in ecosystem productivity (Knapp et al., 2015; Peñuelas et al., 2007; Xu et al., 2013; Zhang et al., 2013), but some studies have shown little effect (Arredondo et al., 2016; Deng et al., 2017) or nonlinear effects on ecosystem productivity (Gherardi and Sala, 2015a, 2015b; Zhu et al., 2016). Several studies have reported variation in productivity responses to declines in precipitation along spatial gradients in savannas (Ansley et al., 2013; Moore et al., 2018b; Pandey and Singh, 1992), but these studies neglected the differences in species composition and the effects of other factors (e.g., soil and topography) on productivity at different spatial gradients. Productivity responses to declines in precipitation do not always coincide across different spatial and temporal scales (Liu et al., 2015). A knowledge gap therefore remains regarding how the productivity of an individual savanna ecosystem responds to declines in precipitation across temporal gradients.

In addition, productivity responses to declines in precipitation vary among plant functional types within an ecosystem (Chelli et al., 2016; Yang et al., 2011a, 2011b). How the productivity of savannas responds to declines in precipitation and whether responses of different plant functional types are similar in savannas remains unclear. Ecosystem can utilize different mechanisms (e.g., reduction in plant growth, alterations in community structure) to respond and acclimate to declines in precipitation and stabilize ecosystem function (Liu et al., 2018; Wagg et al., 2017); however, the responsive mechanisms of ecosystems and plant functional types levels in savanna regions are still unsatisfactory. Therefore, a more complete understanding of the effects of declines in precipitation on the productivity of different plant functional types and their response mechanisms in savannas is needed.

To disentangle the effects of declines in precipitation on the productivity of savanna ecosystems, we performed a field precipitation manipulation experiment. A 4-year dataset was used to explore the response of NPP to precipitation exclusion (PE) across different plant functional types. We aimed to answer the following questions: (1) how do the declines in precipitation affect the NPP in savannas, and (2) do different plant functional types exhibit similar responses to declines in precipitation? We hypothesized that PE would lead to a decrease in NPP of savannas. On the other hand, plant functional types show different sensitivities to water stress (Chelli et al., 2016); therefore, we predicted that the response of different plant functional types to PE would vary.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted at the Yuanjiang Savanna Ecosystem Research Station (23°27'N, 102°10'E, and 551 m above sea level) of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, in Yunnan province of southwestern China. The soil in the region is classified as ferralic cambisol according to the FAO classification (Jin et al., 2018). Dominant species in this savanna are *Lannea coromandelica*, *Polyalthia cerasoides*, *Campylotropis delavayi* and *Heteropogon contortus* (Jin and Ou, 2000). The height of the canopy is approximately 6 m. The climate is dry and hot, the long-term (over the last 36 years) mean annual temperature and is 24.0 °C, and the long-term mean annual precipitation is 786.6 mm (Fei et al., 2017). Approximately 81.0% of the total precipitation occurs from May to October.

This experiment was established in March 2014 and used a randomized block design with four precipitation treatments: ambient precipitation (CK), 30% PE (PE30, covering 30% of the plot area), 50% PE (PE50, covering 50% of the plot area), 70% PE (PE70, covering 70% of the plot area). The four precipitation treatments were randomly distributed within three replicate blocks with a total of 12 experimental

plots. The 10 m × 10-m experimental plots were separated by 1-m walkways. PE treatments were achieved using a 7-m height rainout shelters above the canopy. All intercepted precipitation was drained using a polyvinyl chloride pipe system. Rainout shelters were fenced to exclude grazing (Fig. S1). More details on the precipitation manipulation experiment are available in Jin et al. (2018).

We measured soil water content (SWC) and soil temperature in the top 10 cm of the soil profile every 30 min in three replicates of each treatment using CS616 probes (Campbell Scientific, Logan, UT, USA) starting in June 2014. Data were logged onto a CR800 datalogger (Campbell Scientific, Logan, UT, USA).

2.2. Vegetation data

Vegetation sampling in each of experimental plots was conducted based on different vegetation layers: trees (> 3 m), shrubs, herbs and litterfall. Five vegetation surveys were conducted in March 2014 (pre-treatment, excluding shrubs) and in October 2014–2017.

In March 2014, the diameter at breast height (DBH, cm) and height (m) of all trees in in each 100-m² experimental plot were recorded. To minimize measurement error, the position of DBH was marked with red paint. We estimated the total biomass (t ha⁻¹) of trees (W_t) with an allometric equation (Jin et al., 2017),

$$W_t = 0.155 * (D^2 H)^{0.841}, \quad (1)$$

where D is the DBH of trees (cm) and H is the height of trees (m). Although biomass allocation of trees under water stress may support the optimal partitioning theory rather than the allometric partitioning theory (Poorter et al., 2012), this allometric equation was only used to estimate changes in the NPP of trees under PE. Biomasses of all trees in each experimental plot were summed as the total biomass of the tree layer (t ha⁻¹).

For shrubs, three permanent shrub quadrats (2 m × 2 m) were established along the diagonal of each experimental plot in October 2014. The percentage cover (%), average height (m) and average basal diameter (cm) of each shrub in the quadrats were measured once a year in late October from 2014 to 2017. We quantified shrub volume as average basal diameter squared times average height as a parameter to develop a multi-species shrub allometric equation (Flombaum and Sala, 2007; Gherardi and Sala, 2015b). To avoid disrupting the long-term experiment, a nondestructive method was used to estimate the biomass of the shrubs. We measured the average basal diameter (cm), percentage cover (%) and average height (m) of 59 shrubs, which were adjacent to the rainout shelters and encompassed different classes of basal area and species height. These shrubs were then harvested, dried and weighed. The optimal regression model was fitted as total shrub biomass (W_s) against shrub volume (V) and expressed as $W_s = 0.173V + 0.688$ ($R^2 = 0.81$, $P < 0.001$). Individual shrub biomasses were summed to obtain the total biomass of the shrub layer (t ha⁻¹).

Herbs were sorted into two functional types—perennials and annuals. The abundance (number of rooted individuals), average height (cm) and percentage cover (%) for each herb species were recorded in three 1-m² herb quadrats randomly placed in the each of experimental plots. Overstory coverage (trees and shrubs) was estimated for each herb quadrat. Aboveground and belowground biomass of herbs was harvested in three 0.25 m × 0.25-m sub-quadrates in the lower left corner of each herb quadrat. Herb biomass samples were oven-dried for 48 h at 70 °C and weighed. In March 2014, the pre-treatment herb biomass of each plot was recorded. Herb biomass (t ha⁻¹) was collected once a year in late October from 2014 to 2017. Litterfall (t ha⁻¹) was collected monthly starting in March 2014 using three mesh traps (0.5 m × 0.5 m) placed 0.5 m above the ground and arranged as a triangle in each experimental plot. Litterfall materials were oven-dried for 48 h at 70 °C and weighed.

Total NPP (t ha⁻¹ yr⁻¹) was calculated as the sum of increments in

live biomass (including trees, shrubs, perennials and annuals) and litterfall mass in each year of the study (2014–2017). The NPP of trees, shrubs and perennials was calculated as the difference in the total biomass between two consecutive sampling dates. The NPP of annuals was estimated using the current year's biomass. The mass of litterfall was calculated as the total litterfall each year (January–December).

Leaf area index (LAI) of each experimental plot was indirectly estimated monthly basis starting in March 2014 on a systematic grid (nine points in each plot) using a plant canopy analyzer (LAI-2200c, LI-COR Inc., Lincoln, NE, USA). Data from the growing season (May–October) were used for the analysis.

Shrub stems with a basal diameter > 1 cm in experimental plots were labeled with iron cards in March 2014. We labeled a total 273 stems (totaling 90 in control plots and 183 in PE plots) across the four treatments. Stem survival was assessed once a year in late December from 2014 to 2017.

To assess the dominance of different functional types in the herb layer, we calculated the importance value of perennials and annuals by summing their relative abundance, relative height and relative cover divided by 3 (Moore and Chapman, 1986).

2.3. Statistical analyses

Linear mixed-effects models (LMM) with repeated measures were used to respectively assess the effects of precipitation treatments, year and their interactions on environmental factors (SWC and soil temperature), LAI, total NPP, NPP of trees, shrubs, perennials, annuals and litterfall layers, in which precipitation treatments, year were treated as fixed factors, and block was treated as a random factor. Overstory cover was considered as a fixed factor in our analysis for perennials, annuals and litterfall. Multiple comparisons were tested with Tukey's Honest Significant Difference test at the $P < 0.05$ significance level. Pearson correlation was used to assess the correlations between SWC and the different measures of NPP. All variables were log-transformed to meet normality criteria where necessary. All statistical analyses were conducted in R platform version 3.1.3 (R Core Team, 2015), with the *nlme* package (Pinheiro et al., 2015) for LMM and the *lsmeans* package (Lenth, 2015) for Tukey's Honest Significant Difference test.

3. Results

3.1. Precipitation, SWC and soil temperature

Total annual precipitation was 662.7 mm in 2014, 798.2 mm in 2015, 754.9 mm in 2016 and 839.3 mm in 2017 (Fig. 1a). SWC was lower in the PE plots than in the control plots throughout the experimental period. Soil temperature in the PE plots was higher than that in the control plots (Fig. 1b and c; Table 1). Compared with the average SWC values in the control plots (17.39%), the average SWC across all experimental periods was slightly lower in the PE30 treatment (15.17%; $P = 0.09$) and significantly lower in the PE50 treatment (12.45%; $P < 0.001$) and the PE70 treatment (11.36%; $P < 0.001$). Compared with the control plots, soil temperature elevated by 0.16 °C, 0.74 °C and 1.17 °C in PE30 ($P = 0.86$), PE50 ($P < 0.01$) and PE70 ($P < 0.001$), respectively.

3.2. LAI

LAI varied significantly with year ($P < 0.001$) and precipitation treatment ($P = 0.01$) but remained by their interaction ($P > 0.05$) (Fig. 2; Table 1). Overall, PE treatment significantly reduced LAI across the 4 years. Compared with the control plots, LAI was slightly reduced by 8.4% in the PE30 plots ($P = 0.58$) and by 14.4% in the PE50 plots ($P = 0.16$) and significantly decreased by 23.6% in the PE70 plots ($P < 0.01$) across the 4-year period.

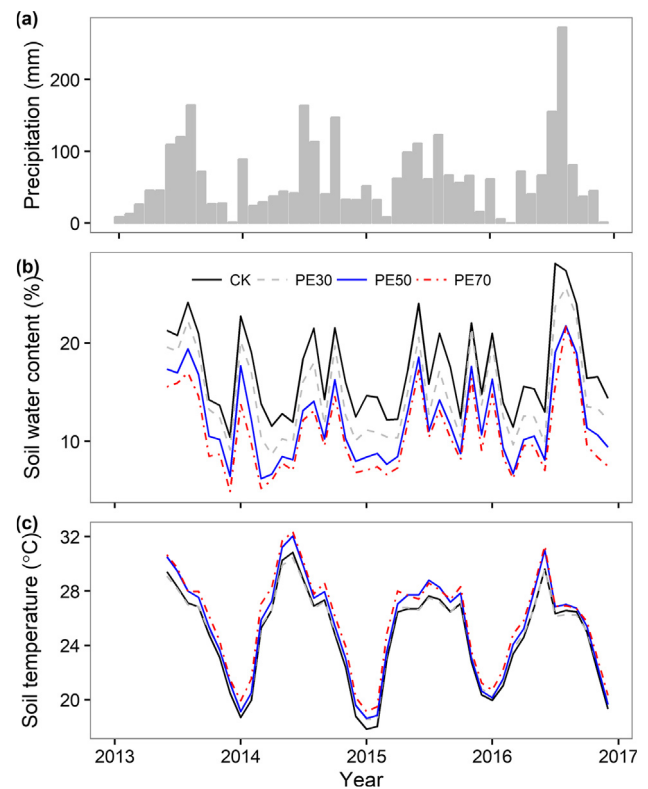


Fig. 1. Meteorological and environmental conditions across the study period (2014–2017) at the study site. Shown are (a) precipitation; (b) soil water content (v/v, %) and (c) soil temperature (°C) at a depth of 10 cm under precipitation exclusion (CK, control; PE30, 30% precipitation exclusion; PE50, 50% precipitation exclusion; PE70, 70% precipitation exclusion).

3.3. NPP

With an exception of year on total NPP ($P = 0.07$), total NPP and NPP of different layers (trees, shrubs, perennials, annuals and litterfall) changed significantly with year and precipitation treatment over the 4-year study period ($P < 0.05$; Table 1, Fig. 3).

On the whole, PE had negative effects on total NPP (reductions of 36.8% in PE30, 41.1% in PE50 and 45.5% in PE70; all $P < 0.001$), NPP of trees (reductions of 51.9%, 56.2% and 35.4% among respective treatments; all $P < 0.01$), shrubs (reductions of 36.0%, 45.0% and 55.0% among treatments; all $P < 0.001$), perennials (reductions of 93.9%, 91.9% and 96.3% among treatments; all $P < 0.001$) and litterfall (reductions of 16.1%, 20.1% and 36.6% among treatments; $P = 0.24$ under PE30, $P = 0.10$ under PE50 and $P < 0.001$ under PE70). Conversely, PE showed a positive effect on the NPP of annuals, resulting in an increase of 61.4% in PE30 ($P = 0.02$), 32.7% in PE50 ($P = 0.83$) and 44.6% in PE70 ($P = 0.56$).

Interaction effects between year and precipitation treatment were observed for shrubs and perennials ($P < 0.001$; Table 1). Specifically, NPP significantly decreased under PE70 for shrubs in 2015 ($P < 0.05$; Fig. 3c) and decreased after PE for perennials in 2014 ($P < 0.01$; Fig. 3d). Overstory cover did not affect the NPP of perennials, annuals and litterfall ($P > 0.05$; Table 1).

3.4. Relationship between SWC and NPP

Total NPP ($R = 0.54$, $P < 0.001$; Fig. 4a) and NPP of trees ($R = 0.28$, $P = 0.052$; Fig. 4b), shrubs ($R = 0.53$, $P < 0.001$; Fig. 4c), perennials ($R = 0.63$, $P < 0.001$; Fig. 4d) and litterfall ($R = 0.53$, $P < 0.001$; Fig. 4f) were significantly positively correlated with SWC. In contrast, the NPP of annuals showed a weak negative correlation

Table 1

Results (*F*-value) of linear mixed-effects models testing the effects of year (Y), precipitation treatment (P), overstory coverage (C) and their interactions on soil water content (SWC), soil temperature (ST), Leaf area index (LAI); net primary productivity (NPP) of totals, trees, shrubs, perennials, annuals and litterfall. Significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Factors	SWC	ST	LAI	Totals	Trees	Shrubs	Perennials	Annuals	Litterfall
Y	3.8*	18.6***	22.8***	2.6	7.6***	10.1***	14.6***	14.0***	5.2*
P	17.6***	15.7***	4.4*	48.1***	13.0***	28.4***	55.2***	4.4*	23.0***
C	–	–	–	–	–	–	0.1	2.2	< 0.1
Y*P	0.1	1.0	0.9	1.6	1.0	8.2***	15.0***	2.0	0.7
Y*C	–	–	–	–	–	–	1.0	1.7	6.0
C*P	–	–	–	–	–	–	1.4	3.6	0.3
Y*C*P	–	–	–	–	–	–	0.3	0.9	1.3

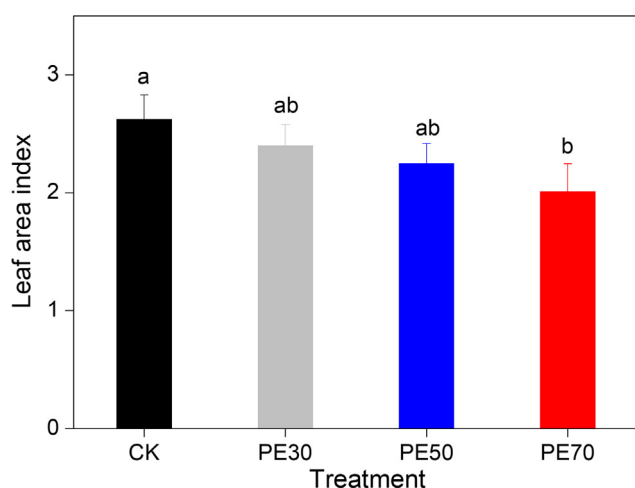


Fig. 2. Changes in leaf area index under precipitation exclusion (CK, control; PE30, 30% precipitation exclusion; PE50, 50% precipitation exclusion; PE70, 70% precipitation exclusion) across the study period (2014–2017) in a savanna ecosystem. Bars represent means $\pm$ SE ($n = 3$). The lowercase letters above the bars indicate significant differences among the treatments ($P < 0.05$).

with SWC ($R = 0.28$, $P = 0.05$; Fig. 4e).

4. Discussion

4.1. Inter-annual variation of NPP

In this study, a marked inter-annual variation of NPP was observed in the savanna ecosystem (Fig. 3) consistent with the findings from other savannas (Moore et al., 2018a; Räsänen et al., 2017) and biomes (Knapp and Smith, 2001; Yang et al., 2011a). These results suggest that carbon accumulation fluctuates with annual precipitation. This inter-annual fluctuation can be explained by difference in soil water supply in various years. Annual precipitation in this study varied over the 4-year experimental period from a minimum of 662.1 mm in 2014 to a maximum of 839.3 mm in 2017 (Fig. 1a), which would result in varying water availability for plant growth and varying effects on NPP among years. Previous studies have also revealed that NPP is more sensitive to wet years than to dry years (Hanson et al., 2001; Knapp and Smith, 2001). Intra-annual variation in precipitation may also contribute to fluctuations in NPP (Hsu et al., 2012; Knapp et al., 2002; Madrigal-González and Zavala, 2014). Large precipitation events or increases in non-growing season precipitation can enhance NPP and positively affect carbon accumulation, particularly in water-limited ecosystems (Heisler-White et al., 2008; McAbee et al., 2017; Swemmer et al., 2007; Zhang et al., 2012). In our study region, the variation in large precipitation events and the differential non-growing season precipitation (18%–32% of annual precipitation occurring during the non-growing season) were remarkable over the experimental period and this could impact carbon accumulation in savannas. Notably, our data also

showed that the NPP of perennials in the control plots was much higher in 2014 than in the other years (Fig. 3d), which is primarily ascribed to succession dynamics. Based on our vegetation survey, the perennials dominated in 2014 (percentage cover > 96%) in the control plots relative to pre-treatment due to the elimination of grazing, which promotes ability of carbon accumulation, leading to a higher NPP value. However, with prolonged drought, the high NPP of perennials may not be maintained in a limited niche because of increasing intraspecific competition and constrained ability of the meristem (Ogaya and Peñuelas, 2006; Stampfli et al., 2018). These findings highlight that the effects of inter-annual fluctuations should be considered when evaluating ecosystem carbon accumulation in response to changes in precipitation.

4.2. Effect of PE on NPP

As expected, the total NPP and NPP of different layers decreased under PE in the Yuanjiang savanna over the experimental period, which support our hypothesis that carbon accumulation would be negatively affected by declines in precipitation. Additionally, our experimental results demonstrated a significant linear correlation between the total NPP and SWC across the 4-year period (Fig. 4), suggesting that NPP may gradually decrease in parallel with intensified precipitation exclusion strengths. These results confirm conclusions derived from studies on other savannas across spatial precipitation gradients (Ansley et al., 2013; Moore et al., 2018b; Pandey and Singh, 1992) and various biomes (e.g., grasslands, forests and shrublands) across spatial and temporal gradients (Estiarte et al., 2016; Fay et al., 2000; Liu et al., 2015; Ma et al., 2017; Wilcox et al., 2017; Wu et al., 2011; Yahdjian and Sala, 2006; Zhang et al., 2013). Several mechanisms may contribute to reduced carbon accumulation under declines in precipitation. The primary reason is that plant growth is constrained under water stress (Fay et al., 2003; Knapp et al., 2017). Plant traits associated with drought sensitivity (e.g., cover, height, radial growth and leaf area) would weaken under water and nutrient stress. The growth rate of dominant species from the three layers (trees, shrubs and herbs) in this savanna significantly decreased under declines in precipitation. In particular, woody species demonstrated a substantial reduction in growth under PE70, resulting in a marked decrease in productivity (Jin et al., 2018). The tree canopy is more sensitive to declines in precipitation (Xu et al., 2018) which directly affect canopy photosynthetic rate and amount of litterfall. Litterfall and LAI over the 4-year experimental period significantly decreased with PE (Figs. 2 and 3f). Canopy development is depressed by declines in precipitation, leading to declines in productivity (Deng et al., 2017; Nepstad et al., 2002). This process of canopy thinning constitutes a conservative strategy where plants can reduce leaf area and leaf number to reduce transpiration and maintain hydraulic conductance under water stress (Brando et al., 2008). Variation in growing season duration may affect productivity (Nogueira et al., 2017; Wan et al., 2005). The leaves of the dominant species (*Lannea coromandelica*) in the tree layer of this savanna showed advanced yellowing (i.e., reduce the life span of leaves) with PE (Jin et al.,

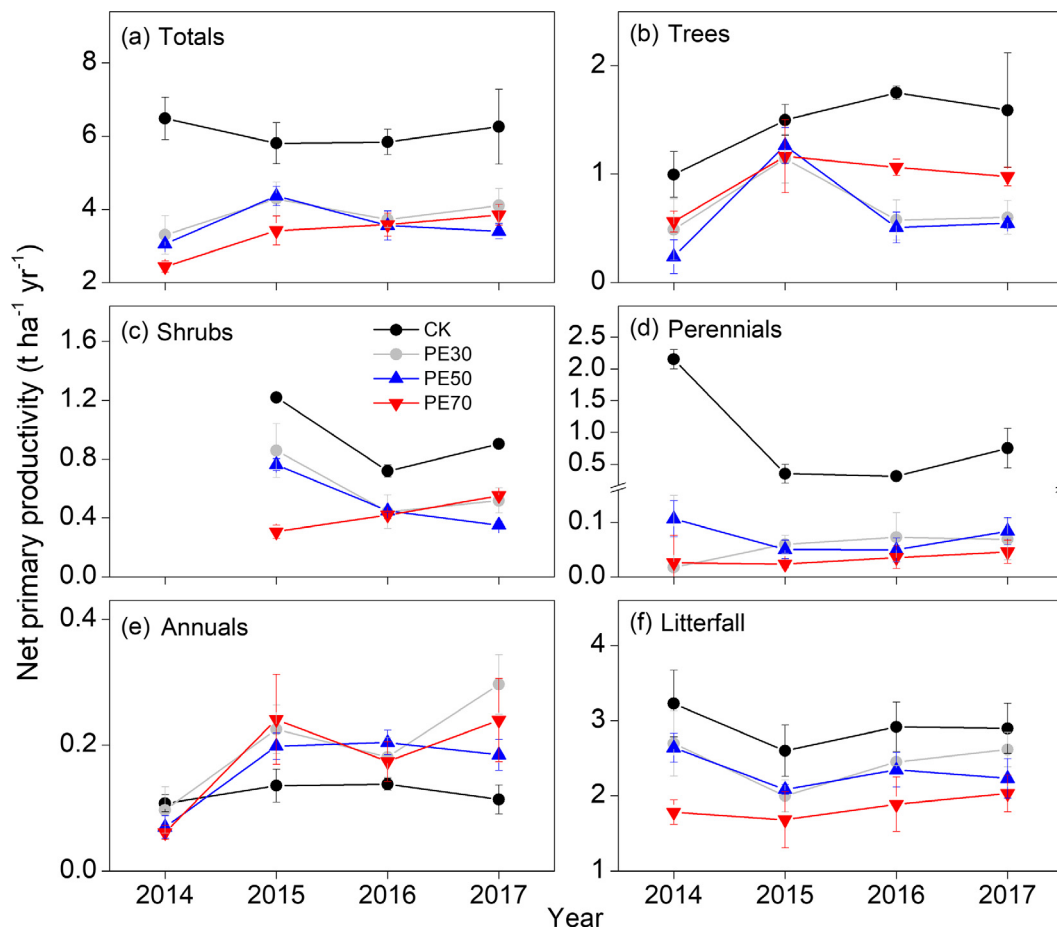


Fig. 3. Changes in net primary productivity ($\text{t ha}^{-1} \text{yr}^{-1}$) under precipitation exclusion (CK, control; PE30, 30% precipitation exclusion; PE50, 50% precipitation exclusion; PE70, 70% precipitation exclusion) during the study period (2014–2017) for: (a) totals (all vegetation), (b) trees, (c) shrubs, (d) perennials, (e) annuals and (f) litterfall. Bars represented means $\pm$ SE ($n = 3$).

2018), resulting in a shortened growing season and further declines in productivity. Reduction in productivity under declines in precipitation may also be linked to constraints in the meristem (e.g., tillering and budding) (Ogaya and Peñuelas, 2006). The budding and tillering of plants are inhibited under water stress, leading to reduction in leaf numbers and the ensuing effects on carbon accumulation. Drought can alter seedling recruitment and mortality to impact ecosystem productivity (Dietrich and Smith, 2016; Phillips et al., 2018; Wang et al., 2018). In particular for shrubs, PE slightly elevated stem mean mortality rates (3.8% and 5.8% in the control and PE plots, respectively), indicating that plant density may substantially constrain carbon accumulation. Yahdjian and Sala (2006) also noted that ecosystem productivity was constrained by vegetation structure in a steppe. The loss of production would also increase due to increased insect attack under declines in precipitation (Burkepile et al., 2017). These findings indicate that declines in precipitation can directly or indirectly impact ecosystem productivity, and the ability of carbon sequence will be weakened with the aggravation of drought stress. However, the response of ecosystem productivity to changes in precipitation is not always linear at different timescales (Gherardi and Sala, 2015b; Zhu et al., 2016), and long-term research on savanna ecosystems is needed.

4.3. Differential response of NPP between perennials and annuals

We found that the NPP of perennials decreased but increased for annuals with decreasing precipitation (Fig. 4d and e), indicating that the productivity of different plant functional types varies in response to declines in precipitation. This contrasting response echoes results from

studies on a desert grassland (Gherardi and Sala, 2015a, b), sub-Mediterranean grassland (Chelli et al., 2016) and peatland (Radu and Duval, 2018). This differential response is mainly driven by shifts in community composition (Dreesen et al., 2012). The dominance (importance value) of perennials in this savanna decreased with PE, whereas the dominance of annuals increased. Therefore, divergent vegetation composition and plant density induced a differential response in productivity. Different plant functional groups show different mechanisms under water stress. Annuals are more drought-tolerant and are favored under water stress due to their shorter lifespan compared with perennials. The annuals in our study site had obvious taproots, which helped them to acquire water from much deeper soil under water stress than the fibrous-rooted perennials. Furthermore, owing to their lower water and nutrition (e.g., nitrogen) requirements relative to the perennials, annuals may be better able to acclimate to declines in precipitation (Stampfli et al., 2018). These adaptive traits and strategies increase the capacity of annuals to occupy niches and enhance their carbon accumulation capacity. Overall, increased productivity of annuals could compensate for drought-induced carbon loss and buffer the negative effects of declines in precipitation on other groups (Gherardi and Sala, 2015a) and further stabilize ecosystem function (Liu et al., 2018; Wagg et al., 2017). Our findings provide further evidence that the ability of carbon accumulation differs among plant functional types under declines in precipitation in savanna ecosystems and that functional diversity can mitigate the negative effects of declines in precipitation.

Moreover, due to this compensatory mechanism in the herb layer, the perennials were lost and replaced by the annuals, implying that the

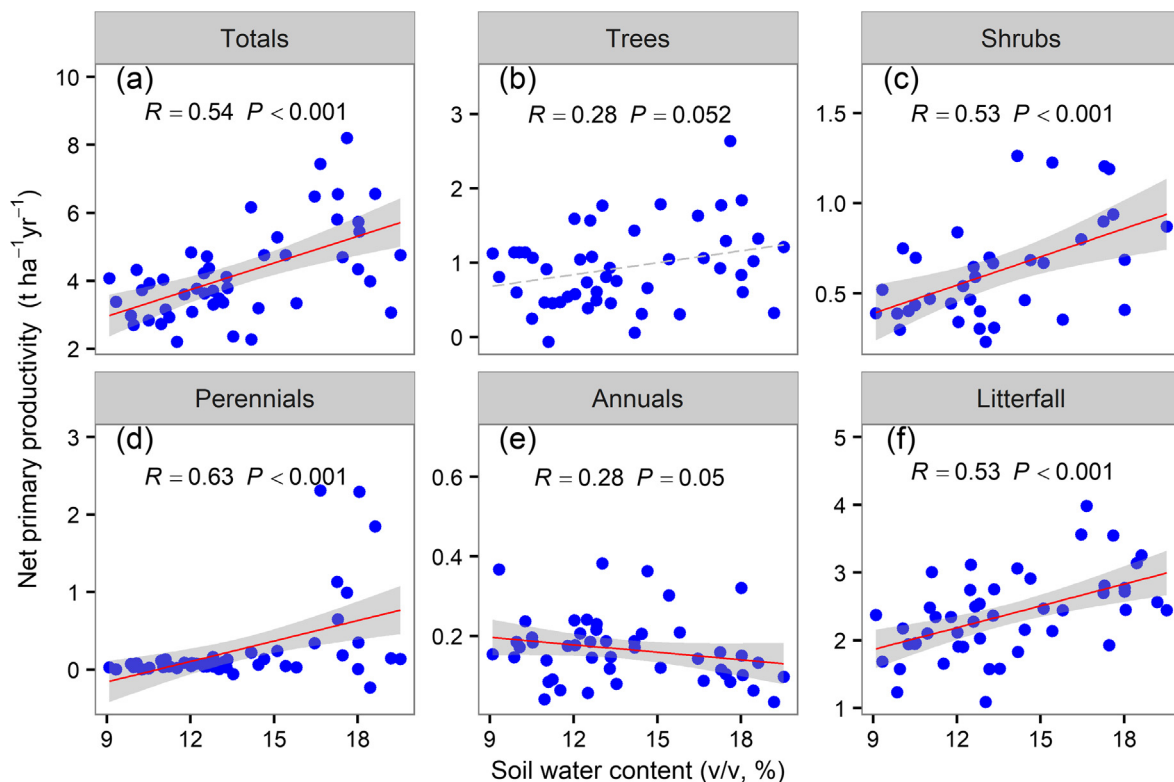


Fig. 4. Relationships between soil water content and net primary productivity of different community layers: (a) totals (all vegetation), (b) trees, (c) shrubs, (d) perennials, (e) annuals and (f) litterfall. Each black point represents an experimental plot ($n = 48$; $n = 36$ for shrubs) over the 4-year experimental period. Shaded areas represented 95% confidence intervals. The red solid lines indicate significant regression lines and the gray dashed line indicates the nonsignificant regression line for trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

herb community may be more resilient to the negative impacts of precipitation exclusion than the woody community (trees and shrubs), which is supported by a recent study (Stuart-Haëntjens et al., 2018). Therefore, as precipitation continues to decline in savanna regions, annuals may strengthen the resilience of the herb community.

5. Conclusions

This study provides new insights into the effects of declines in precipitation on productivity and carbon accumulation in savannas. Our results showed that PE significantly reduced the total NPP and NPP of trees, shrubs and litterfall in the savanna ecosystem, indicating that declines in precipitation can affect the productivity of savannas. We observed contrasting NPP responses to declines in precipitation between the perennials and the annuals, with a decrease in the NPP of the perennials and an increase in that of the annuals. In our 4-year study, declines in precipitation affected plant growth and caused shifts in community dynamics, both of which are involved in the variation of ecosystem productivity under declines in precipitation. These results suggest that the effects of declines in precipitation in savannas are complex across functional groups and this should be considered when assessing and predicting the effect of climate change on ecosystem productivity. Our findings have a crucial implication that ongoing climate change and especially declines in precipitation will accelerate the loss of production, drive changes in carbon accumulation, and substantially alter ecosystem functions and services in savannas worldwide. Under climate change scenarios, coupling effects of precipitation and indirect factors (e.g., grazing, insect attacks and land use) in savanna regions will persist and constrain carbon accumulation, potentially creating new issues for sustainable forest management and conservation. Interactions among direct and indirect factors should therefore be considered in future studies of savannas.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.07.007>.

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