



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

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