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Inconsistent changes of biomass and species richness along a precipitation gradient in temperate steppe

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ABSTRACT

Biomass and species richness are two important indicators of ecosystem stability. The relationship between biomass and species richness along precipitation gradient in semi-arid regions is significant for prediction of ecosystem stability under the estimated climatic drying in the future. In this study, we investigated species richness, aboveground biomass and cover of temperate steppe along a mean annual precipitation (MAP) gradient in central Inner Mongolian of China. We also measured water use efficiency (WUE) of selected species and overall communities. Our results showed that biomass almost remained unchanged in the moist half of the gradient, but species richness decreased markedly with decreasing MAP. Species richness further showed a negligible decrease, whereas a much sharper drop was detected in biomass towards the arid end with decreasing MAP. Vegetation cover shared a similar pattern with biomass and dropped sharply towards the arid end, which may create a strong light and low competition environment favoring C_4 plants. The increment of C_4 species richness could prevent a more intensive decline of species richness under severe arid conditions by raising overall community water use efficiency. Thus, plant communities experiencing water deficiency could also maintain species richness with the occurrence of C_4 plants.

1. Introduction

Relationships between plant biomass and species richness of grasslands have interested ecologists for decades (Bai et al., 2007). A considerable amount of research has led to the hypothesis that species richness, as one of the most important ecosystem traits, has a positive relationship with plant biomass (Cardinale et al., 2006; Tilman et al., 2006; Van Ruijven and Berendse, 2010). For example, research has indicated that changed biomass may be stabilized by high species richness under severe environmental conditions (Hughes and Roughgarden, 2000). However, the above hypothesis has not yet been fully tested by field investigations and experiments (Bai et al., 2007; Gonzalez and Loreau, 2009; Campbell et al., 2011; Crawford and Rudgers, 2012). In addition, in natural environments, various stresses, such as soil moisture, may change the relationship between plant biomass and species richness (Fridley, 2002; Steudel et al., 2012).

Water availability is the most important limiting factor for grassland plants in arid and semiarid regions (Namgail et al., 2012). Plants may enhance their water use efficiency (WUE) as well as change the morphological features of organs to survive in harsh environmental conditions (Wang et al., 2013). A multitude of studies have demonstrated that both plant biomass and species richness decrease with an increase in drought (Rolim et al., 2005; Bai et al., 2008; Wang et al., 2013). However, ecosystems could still remain stable under drought stress because different functional groups have varied competitive abilities and can compensate for each other (Tilman et al., 2006; Gross et al., 2007; Volaire et al., 2009; Cadotte, 2011; McLaren and Turkington, 2011). Hence, focusing on the adaptive strategies that different plant functional groups display in response to drought may be the key to explain the relationships between plant biomass and species richness in grassland communities. Previous studies have found that water availability has a marked impact on plant functional groups as well as plant functional group traits in grasslands (Maseda and Fernández, 2006; Bai et al., 2008; Letts et al., 2010), but their results are widely disparate, and the underlying mechanism for the plant biomass–species richness relationship remains unclear.

C_3 and C_4 plants are two main functional groups with different photosynthetic pathways. C_4 carbon fixation improves photosynthetic efficiency under habitats of drought, strong light, high temperatures, and low atmospheric CO_2 (Buchmann et al., 1997;

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Spriggs et al., 2014). C_4 plants possess high photosynthetic efficiency, which leads to high WUE relative to C_3 plants under water stress (Ghannoum, 2009; Way et al., 2014). Thus to distinguish C_3 and C_4 photosynthetic functional groups in plant community could contribute to a better understanding of the plant biomass-species richness relationship (Qi and Redmann, 1993; Ward et al., 1999). We hypothesize that grassland community can maintain species richness under water stress through increase in richness of the C_4 plants with high WUE.

In order to explain the variance of community biomass and species richness, we analyzed the distribution patterns of C_3 and C_4 plants as well as their physiological traits along a precipitation gradient in the Inner Mongolian steppe of China. Particularly, we focused on: 1) detailing the different effects of drought on stand-level plant biomass (stand biomass) and species richness, and 2) explaining the effects through the distribution of C_3 and C_4 plants.

2. Study area

Our study area is located in the mid-east portion of the Inner Mongolia plateau, China (40°–50°N, 107°–125°E), with mean annual precipitation (MAP) of approximately 150 mm–450 mm. And mean annual temperature (MAT) of this area ranges from 0.1 °C to 4.9 °C. Following the MAP gradient, vegetation types change from meadow steppe, through typical steppe, to desert steppe. Steppe chestnuts soil is widely distributed in the study area and sandy soil also exists. The Palmer Drought Severity Index (PDSI) in this region has increased continuously during the last 70 years, especially after 1990s (Dai et al., 2004; Dai, 2011), and this trend could seriously threaten local ecosystems.

3. Methods

3.1. Data collection

We collected data on mean monthly temperature and mean monthly precipitation since the 1950s with 1 km × 1 km resolution data from the WorldCLIM dataset (http://www.worldclim.com/). MAT and MAP were calculated on the basis of monthly data over the past 50 years.

We systematically sampled 120 plots with different rainfall regimes in July and August, when vegetation growth is the most vigorous (Fig. 1). Size of each plot is 2 × 2 m^2. We firstly defined randomly sampling area along a rainfall gradient, then randomly set sampling sites on the mature grassland. We recorded the latitude, longitude, and altitude of plots. We also recorded plant species, as well as cover, abundance, and height of each species in each plot. Visual measurement was used for stands canopy coverage proportionally, and the aboveground biomass was harvested and weighed after 48 h storage in a consistent 65 °C drying oven. The mean dry mass of the harvested plants was used to estimate annual biomass production. For functional groups biomass, C_3 and C_4 plants were harvested and weighted respectively. For isotopic measurements, leaves of dominant species were sampled and kept in bags with silica-gel desiccant. A single 30 cm deep transect was sampled at each site and soil samples were collected every 10 cm. We used surface soil to measure total organic carbon (TOC) and total nitrogen (TN) using the Elementar Vario EL (Germany).

In the field investigations, we only picked mature and healthy leaves on 13 selected widespread species to find changes and tendency along the rainfall gradient. These species are dominant of each stands at temperate grassland in Inner Mongolia. Their cover accounts for 25% or more of total cover in 62.1% plots and 50% or more of total cover in 36.2% plots. Thus they are expected to play a central role in ecosystem functioning (Grime, 1998). In the lab, leaf samples had been dried under 48 °C for 70 h, then grinded into powder until they can through the 80-mesh sieve, and packaged into special tinfoil. The carbon isotope values of pretreated samples were measured by the CM-CRDS Isotopic Carbon Analyzer, produced by Picarro Inc (USA).

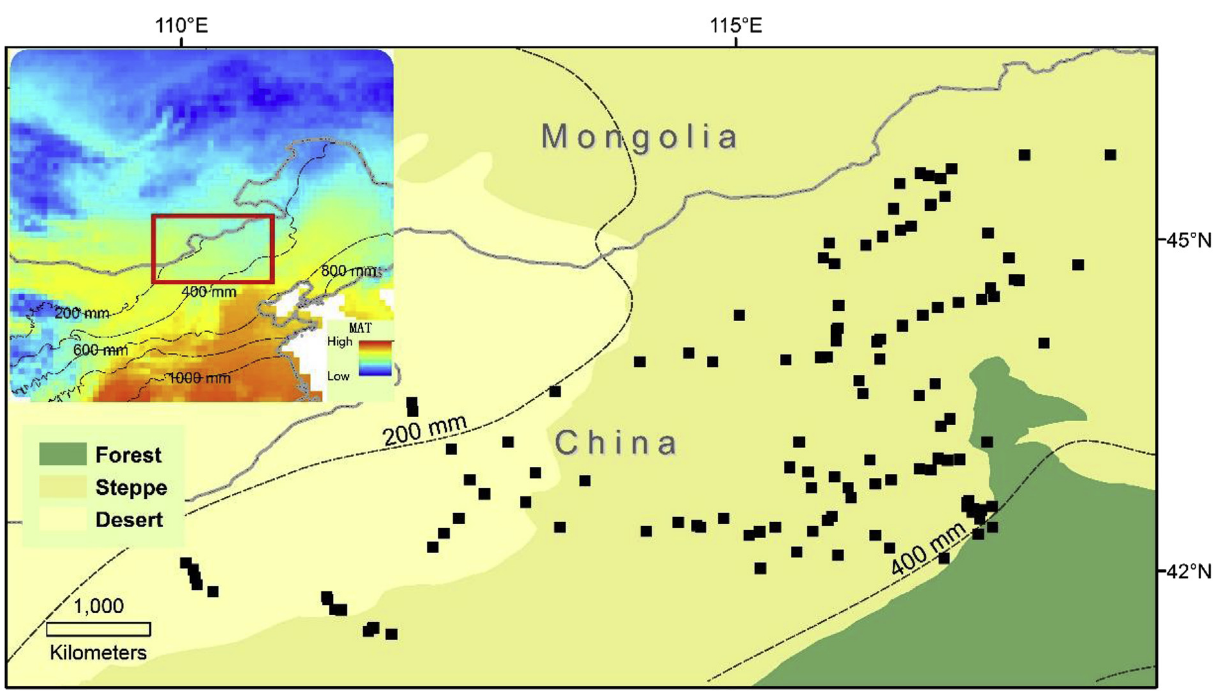

Fig. 1. Location of study area with sampling sites and vegetation types. Filled squares indicate sample sites. Light dark lines denote isohyets.