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Research paper

Plant coverage is more sensitive than species diversity in indicating the dynamics of the above-ground biomass along a precipitation gradient on the Tibetan Plateau

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ABSTRACT

Species diversity (SD) and total plant coverage (PC) are commonly used predictors of primary productivity (i.e., above ground biomass (ABG)). PC is a characteristic frequently used in remote sensing to assess land cover, land use, and vegetative condition, while species diversity serves as a measure of the existence and utilization of ecological niches. Both SD and PC are thought to be positively related to primary productivity, with SD further contributing to community stability. We investigate the effects of SD and PC on ABG under different mean annual precipitation (MAP) levels. The influences of SD and PC on community stability and biomass allocation were analyzed using redundancy analysis (RDA), correlation analysis (CA), and generalized linear models (GLM). Significantly positive relationships between precipitation and above-ground biomass, species diversity, and plant coverage occurred in the low rainfall gradient (100–400 mm/y) in the alpine steppes, while these relationships appeared in the high rainfall gradient (500–700 mm/y) in alpine meadow ecosystems. Second, we determined that plant coverage (r^2 = 0.88, $P < 0.001$) provided a better explanation for above-ground biomass than species diversity (r^2 = 0.67, $P < 0.001$). Moreover, we found that the relationships between SD and AGB and PC and AGB (r^2 = 0.52, $P < 0.001$, and r^2 = 0.85, $P < 0.001$, respectively) were more positive in the alpine steppes than in the alpine meadows (r^2 = 0.41, $P < 0.001$, and r^2 = 0.77, $P < 0.001$, respectively). Third, at the different precipitation gradients, especially at the 400–500 mm/y and > 600 mm/y ranges, the PC continued to increase, while SD decreased with increasing AGB. Moreover, SD was more sensitive to community stability and reproduction allocation than PC. Overall, plant coverage is better than species diversity in indicating the dynamics of above-ground biomass along a precipitation gradient.

1. Introduction

As an important part of terrestrial ecosystems (Nakano and Shinoda, 2014), grasslands account for 24% of the total land area and provide 6.8×10^9 t of organic matter every year, which is equal to 13.82% of the organic matter provided by terrestrial ecosystems (Zhou et al., 2014). Grasslands are vital for the total carbon circulation in ecosystems because of their photosynthesis and respiratory processes (Dhital et al., 2010). Furthermore, the carbon content in the biomass is crucial for regulating the earth's temperature (Aguirre-Salado et al., 2012) as evidenced by the global climate warming in recent years (Shen et al., 2015).

The grasslands on the Tibetan Plateau represent approximately half (44%) of China's grasslands and 6% of the world's grasslands (Piao et al., 2012). Considering the special alpine climate and complex terrain, the biomass of the Tibetan Plateau has been used as an indicator of global climate changes (Ni, 2000), with the evolution and development of species and ecosystems being both dynamic and varied in this region (Luo et al., 2002). There is no doubt that exploring the productivity of grasslands on the Tibetan Plateau is crucial to global ecosystems (Sun and Wang, 2016).

In general, net primary productivity (NPP) has been estimated by the peak biomass affected by various factors representing vegetation growth (Hirota et al., 2007). To date, most analyses have concentrated on the responses of above-ground biomass to temperature and precipitation (Gao et al., 2013a; Han et al., 2013; Ye et al., 2013; Zhao

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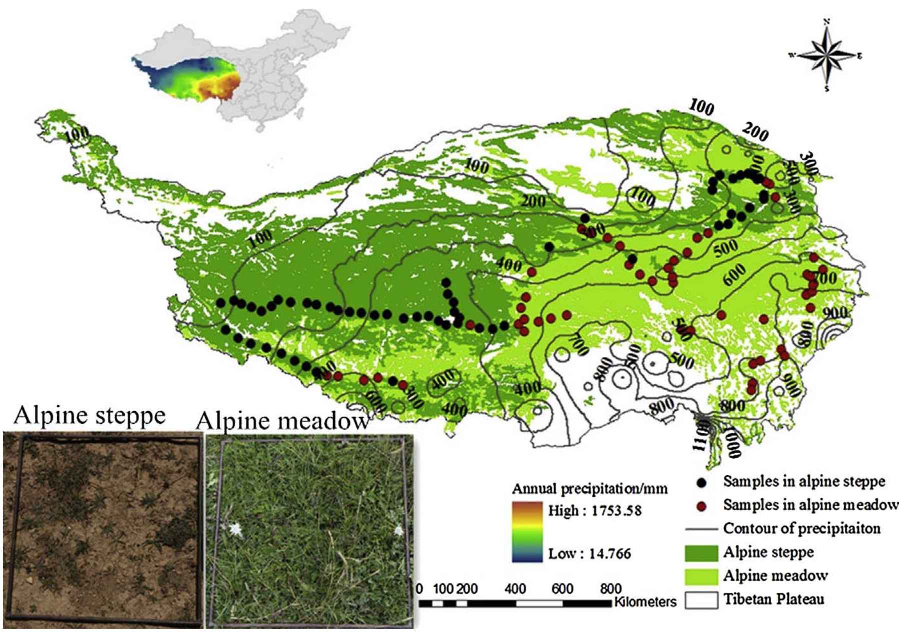

Fig. 1. Distribution of 112 sample sites across Tibetan Plateau.

et al., 2013). Most analyses have found that warming has a positive effect on the productivity of grasslands (Yang et al., 2009; Wu et al., 2010; Gao et al., 2013a; Yuan et al., 2014; Sun et al., 2016). However, a weakly negative relationship between precipitation changes and NPP has been found, as precipitation increases soil erosion and decreases soil organic matter content and therefore reduces productivity (Gao et al., 2013b). The interannual variability of NPP has been found to increase with the interannual variability of precipitation (Ye et al., 2013), and the annual precipitation has been found to be positively correlated with NPP (Piao et al., 2006). The rain use efficiency across the biomass decreases, especially during heavy rainfall events and long dry intervals (Liu et al., 2015). However, a previous study has shown that water-use efficiency in grasslands decreases with elevation due to the sharp changes in canopy cover (Han et al., 2013).

At the same time, similar influences of the species richness on the above-ground biomass have been found (Thein et al., 2008). The classical theory states that the species richness and primary productivity relationship exhibits a unimodal ("hump-shaped") pattern (Psomas et al., 2011; Sa et al., 2012), which means that the areas with the highest species richness often have intermediate productivity (Schumacher and Roscher, 2009). That unimodal relationship is the accumulated result, including positive, negative and non-existent patterns (Guo and Berry, 1998a), and the relationship patterns have been found to be dependent on geographical scales (Mittelbach et al., 2001). As species richness increases, the ability of the vegetation to capture natural resources improves (Adler et al., 2011; Wang et al., 2016). However, the total species richness has been found to be limited by competitive exclusions, such as succession time and productivity increases (Nylen and Luoto, 2015).

Cover depends on horizontal space occupation and is the projection of plants onto the land (Lavorel et al., 2008). In conservation reserve programme fields, basal plant cover has been found to have positive effects on the above-ground NPP (Munson and Lauenroth, 2014). Relative to temperature and precipitation, the basal cover was found to be the primary mechanism responsible for total phytomass production (Wiegand et al., 2004), which may be because plants can help maintain soil moisture through shading and litter deposition (McHugh and Schwartz, 2015). Moreover, the leaf area index has been found to be logistically correlated with both climatic and soil variables (Luo et al., 2004), and plant species with different growth strategies are conducive to achieving higher community coverage (Ji et al., 2009). Therefore, canopy cover has previously been used to characterize the dynamics of above-ground biomass on the Tibetan Plateau (Chen et al., 2009). Thus, the plant cover was regarded as an effective predictor for above-ground biomass by a model in arid ecosystems (Flombaum and Sala, 2009).

A previous analysis showed that plant coverage has a more significant impact than species richness on above-ground biomass in grasslands of northern China (Ji et al., 2009); these results are from artificial control experiments. Interpreted generally, competition for light is a factor that determines species composition in alpine communities (Grytnes 2000), as reducing the cover of dominant species has been found to enhance diversity (McCain et al., 2010). However, it is not clear if the internal mechanism of this interaction affects both the plant coverage and species richness of the above-ground biomass in a mature grassland.

Considering that species diversity involves the quantity of every species, it is better to investigate competition rather than species richness during the evolutionary process. Therefore, in this paper, we hypothesize that the above-ground biomass will show a better relationship with plant coverage than species diversity in alpine grasslands. A series of studies was conducted as follows: (1) the patterns of SD (species diversity) and PC (plant coverage) along precipitation gradients in the alpine grassland ecosystem were identified, and (2) the response of the above-ground biomass to species diversity and plant coverage at different precipitation levels was investigated.

2. Materials and methods

2.1. Study area

The Tibetan Plateau (80°–105°E, 27°–37°N) occupies approximately $2.3 \times 106\ km^2$ of land (Kramer et al., 2010). Western China has an alpine climate, with an annual mean temperature of 4 °C and a mean altitude of over 4000 m (Sun et al., 2013). The annual mean precipitation on the Tibetan Plateau is 400 mm, and it falls mainly in June-September, which is considered the rainy season. A significantly increasing gradient from the northwest to the southeast has been verified and is accompanied by a precipitation increase in most areas of the Tibetan Plateau (Tan et al., 2010). Furthermore, alpine steppes and meadows are the most widely distributed ecosystems on the Tibetan Plateau (Fig. 1) (Wu et al., 2011). Resistance to cold and drought is a characteristic of the alpine steppes, but most species of the alpine