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Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: effects of mean annual precipitation and its seasonal distribution

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Abstract

Concomitant changes of annual precipitation and its seasonal distribution within the context of global climate change have dramatic impacts on aboveground net primary productivity (ANPP) of grassland ecosystems. In this study, combining remote sensing products with *in situ* measurements of ANPP, we quantified the effects of mean annual precipitation (MAP) and precipitation seasonal distribution (PSD) on the spatial variations in ANPP along a climate gradient in Eurasian temperate grassland. Our results indicated that ANPP increased exponentially with MAP for the entire temperate grassland, but linearly for a specific grassland type, i.e. the desert steppe, typical steppe, and meadow steppe from arid to humid regions. The slope of the linear relationship appeared to be steeper in the more humid meadow steppe than that in the drier typical and desert steppes. PSD also had significant effect on the spatial variations in ANPP. It explained 39.4% of the spatial ANPP for the entire grassland investigated, being comparable with the explanatory power of MAP (40.0%). On the other hand, the relative contribution of PSD and MAP is grassland type specific. MAP exhibited a much stronger explanatory power than PSD for the desert steppe and the meadow steppe at the dry and wet end, respectively. However, PSD was the dominant factor affecting the spatial variation in ANPP for the median typical steppe. Our results imply that altered pattern of PSD due to climate change may be as important as the total amount in terms of effects on ANPP in Eurasian temperate grassland.

Keywords: aboveground net primary productivity, climate change, mean annual precipitation, precipitation seasonal distribution, temperate grassland

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Introduction

Climate change is predicted to cause dramatic variability in precipitation regime not only in terms of change in annual precipitation amount, but also in precipitation seasonal distribution (PSD), which combined to influence various processes of terrestrial ecosystems (Easterling *et al*., 2000; Meehl *et al*., 2007). Among terrestrial ecosystems, grassland in arid and semiarid regions is one of the most sensitive ecosystems to changes in precipitation (Noy-Meir, 1973; Knapp & Smith, 2001). In addition, grassland comprises ca. 40% of the world land cover, and thus its responses to altered rainfall pattern may have significant and widespread consequences for global carbon balance, hydrological cycle, and even the livestock development under future climate change scenarios (Reynolds *et al*., 2005). As one of the most important processes for grassland ecosystem (even for all terrestrial ecosystems), aboveground net primary productivity (ANPP) is closely linked to nutrient cycle, energy flow, and carbon cycles (McNaughton *et al*., 1989; Chase *et al*., 2000). The ANPP–precipitation relationship is always a scientific focus in ecology during the past decades (Noy-Meir, 1973; Cable, 1975; Webb *et al*., 1978; Lehouerou, 1984; Fang *et al*., 2001; Knapp & Smith, 2001; Huxman *et al*., 2004), while there is a growing interest on this topic more recently under the context of global climate change (Weltzin & Mcpherson, 2003; Schwinning & Sala, 2004; Craine *et al*., 2012). Many methods, such as the environmentally controlled field experiments, long-term monitoring, and ecological modeling, have been employed to explore the responses of ANPP to altered rainfall patterns (Lauenroth & Sala, 1992; Knapp *et al*.,

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2008; Heisler-White *et al.*, 2009). Notably, exploring the ANPP–precipitation relationship along a climate gradient is a critical approach to understand how altered rainfall regime may affect ecosystem processes, which has been widely studied to date (Paruelo *et al.*, 1999; Vermeire *et al.*, 2009; Hu *et al.*, 2010).

Many studies have presented a positive correlation between mean annual precipitation (MAP) and ANPP (Lehouerou *et al.*, 1988; Sala *et al.*, 1988; Briggs & Knapp, 1995). However, the shape of the relationship varies among different studies. In most cases, simple linear relationships were found between ANPP and MAP (Briggs & Knapp, 1995; Paruelo *et al.*, 1999; O'connor *et al.*, 2001; Bai *et al.*, 2008; Fan *et al.*, 2009). However, some recent studies have demonstrated that this linearity is likely to be not universal. For example, exponential relationships have been reported for the temperate grasslands in China (Hu *et al.*, 2007, 2010; Ma *et al.*, 2008). Meanwhile, some other studies showed that the increasing trend of ANPP with precipitation leveled off in humid regions (Huxman *et al.*, 2004; Yang *et al.*, 2008). There was also a study finding ANPP peaked in the median MAP region (Kanniah *et al.*, 2011). The underlying mechanisms of the varied shapes of MAP–ANPP relationship are yet to be fully understood. Studies at site scale illustrated that plant composition played an important role in the precipitation–ANPP relationship (Jobbágy & Sala, 2000; Swemmer *et al.*, 2007). For example, in the grasslands of Argentina, contrary to the remarkable positive correlation between shrub ANPP and annual precipitation, herbaceous ANPP illustrates no significant correlation with annual precipitation (Jobbágy & Sala, 2000). Therefore, we are wondering whether the plant composition also play some role in the shape of MAP–ANPP relationship along climate gradients? Are the shapes and slopes of the MAP–ANPP relationship for inter and intragrassland types along a climate gradient coherent? If not, how does this relationship vary with grassland types?

Precipitation seasonal distribution, as another important aspect of rainfall pattern, also has significant impacts on grassland ANPP (Potts *et al.*, 2006; Knapp *et al.*, 2008; Hao *et al.*, 2010). PSD in this study is defined as a measure of the evenness of distribution of monthly precipitation amount within the growing season. Studies demonstrated that precipitation distribution remarkably influenced interannual variations in ANPP at site scale. For example, it was reported that more concentrated precipitation distribution (i.e. large, infrequent rainfall events) attenuated water stress, which in turn resulted in improved ANPP in Kansas steppe and Chihuahuan desert (Heisler-White *et al.*, 2008, 2009; Thomey *et al.*, 2011). However, an opposite pattern was found in Kansas tallgrass prairie that more even precipitation distribution would favor higher ANPP (Knapp *et al.*, 2002; Fay *et al.*, 2003; Harper *et al.*, 2005; Heisler-White *et al.*, 2009). Recent researches infer that site-specific climate characteristics are likely responsible for the distinct patterns. In humid ecosystems, where soil water content is usually high, the increase in large, infrequent precipitation events may lengthen the interval between the two events, thereby increase the risk of water shortage or drought stress. In contrast, in arid and semiarid ecosystems, where soil moisture is chronically low, the increase in large, infrequent precipitation events can charge deeper soil profiles, relatively reduces or avoids evaporation water loss and thus improve the moisture conditions (Knapp *et al.*, 2008). Previous studies on the PSD–ANPP relationship are mostly conducted at site scale; however, little is known whether the PSD will affect the spatial variations in ANPP, and whether the effect is positive or negative.

In this study, we examined the spatial variations in ANPP and the effects of MAP and PSD on these variations along a precipitation gradient in the temperate grassland in Inner Mongolia, China, which is located in the eastern Eurasian grassland. Along the gradient, there are distributed three main grassland types: the desert steppe at the dry end, the typical steppe at the middle part, and the meadow steppe at the wet end. These distinct grassland types facilitated us to address the precipitation–ANPP relationship in terms of plant composition along the climate gradient. To bridge the knowledge gap mentioned above, this study attempts to address the following questions: (1) What is the shape of the MAP–ANPP relationship in this region? Are there any differences in this relationship among different grassland types? (2) Does the seasonal distribution of precipitation in the growing season affect the spatial variations in ANPP? If so, whether the effect is positive or negative? And to what degree it will affect the spatial ANPP in comparison with MAP?

Materials and methods

Study region

The study region is the temperate grassland in Inner Mongolia, China, which covers 66% of the total land area of Inner Mongolia Autonomous Region (ca. 1.18 million km^2). Inner Mongolia temperate grassland belongs to the Eurasian grassland. The study region is strongly influenced by Asian monsoon climate, with which most rainfall coincides with high temperature in summer season. Mean annual temperature ranges from −3 to 9 °C. There is a *ca*. 400 mm gradient of MAP from northeast (440 mm) to southwest (35 mm). Along this MAP gradient, three grassland types are distributed: meadow steppe at the east end (MAP > 230 mm), typical steppe in the middle (MAP ranging from 180 to 420 mm), and desert steppe at the dry end (MAP < 260 mm) (Fig. 1). The soil shifts from chernozems, chestnut, and meadow soil to calcic brown and desert soils from the wet northeast to the dry southwest along the gradient (Hu *et al*., 2007). The meadow steppe has the highest plant biodiversity, with dominant species of *Stipa baicalensis*, *Leymus chinensis*, *Filifolium sibiricum*, and *Stipa grandis*. The typical steppe has moderate plant biodiversity and is dominated by *S. grandis*, *L. chinensis*, *S. krylovi*i, *Cleistogenes squarrosa*, *Agropyron cristatum*, *Artemisia frigida*, and *Caragana microphylla*. The desert steppe has the lowest plant biodiversity and is dominated by *Stipa klemenzii*, *Agropyron desertorum*, *Stipa gobica*, *Cleistogenes songorica*, *A. frigida*, and *Salsola collina*.

In situ ANPP measurements and regional ANPP estimation

To estimate the multiyear ANPP of the whole region, we used a conventional approach by establishing an empirical relationship between *in situ* measured ANPP and remotely sensed vegetation index (Paruelo *et al*., 1997; Ma *et al*., 2010). The *in situ* measured ANPP was evaluated by harvesting peak aboveground biomass accumulated during the growing season (including live biomass as well as standing dead biomass produced in the current year), which has been widely used previously to estimate ANPP of grassland (Scurlock *et al*., 2002). Field survey was conducted in 2003–2006, when the standing biomass reached its maximum (exactly at the middle of August). The sampling sites were selected along a survey route with intervals of ca. 50–100 km across the entire Inner Mongolia temperate grassland and sampling plots were fenced from herbivore grazing. At each site, aboveground biomass was measured in three to five independent 1 × 1 m quadrats. The sampled biomass was dried in an oven at 65 °C for 48 h and weighed. For the sites with shrub species, the biomass of current-year twigs was not measured, and thus we could not estimate ANPP. For that reason, we rejected sites with shrub species. Finally, we obtained ANPP data from 111 sites, which covers all the three grassland types in this region, with a variation ranged from 9.5 to 358.4 g m^{-2} yr^{-1} (Fig. 1). Statistical analysis indicated that the standard deviations of ANPP for the replicates, at 86% of the total sites, were less than 20% of the mean values, and the site-to-site differences were extremely significant (ANOVA, $P < 0.0001$). This illustrates that the heterogeneity at each site can be ignored when addressing the spatial pattern of ANPP (Hu *et al*., 2010). More information about the samples sites and sampling protocol is available in Ma *et al*. (2008), Hu *et al*. (2010), and Yang *et al*. (2010).

The peak monthly Normalized Difference Vegetation Index (NDVI), i.e. the monthly NDVI of August, in 1998–2007 was used to establish the relationship between *in situ* measured ANPP and NDVI and then to estimate ANPP for each pixel of the whole region. The NDVI data (1 × 1 km^2) were derived from the VEGETATION sensor on the board of the SPOT satellite platforms. The data of 10-day composition NDVI (S10 product) were obtained from Technologisch Onderzock (VITO) Image Processing centre (Mol, Belgium) (http://www.vgt.vito.be), and were corrected to reduce the effects of cloud contamination, atmospheric perturbations, and variable illumination and viewing geometry (Telesca & Lasaponara, 2006). The three 10-day NDVI compositions in August were averaged to represent the monthly NDVI of August.

A significant exponential relationship between measured ANPP and the corresponding NDVI in August was derived as $\mathrm{ANPP} = 20.04e^{3.75\mathrm{NDVI}}$($R^2 = 0.74$, $n = 111$, $P < 0.001$). With this

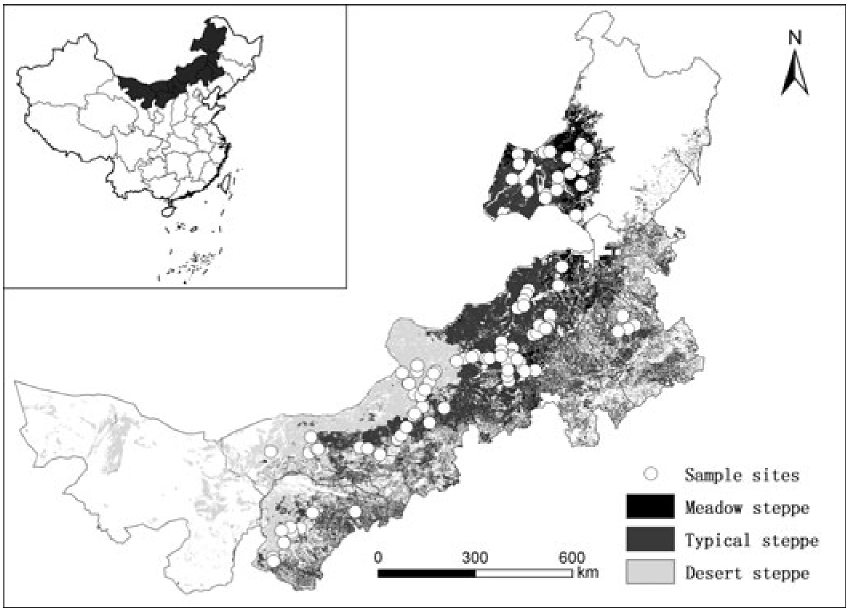

Fig. 1 Distribution of the 111 sampling sites for *in situ* measurements of aboveground net primary productivity (ANPP) in the study region. The measured ANPP at these sites was used to develop the empirical function between ANPP and Normalized Difference Vegetation Index for estimating ANPP at the regional scale.

relationship, ANPP for the entire region during 1998–2007 was estimated based on NDVI data of August. Using another dataset based on long-term *in situ* measurements at 20 sites (121 site-year) in 1990–1999 (shrub species existed at six sites and ANPP was measured by sampling and weighing the current-year twigs and leaves), we also yielded an exponential relationship between ANPP and NDVI from Advanced Very High Resolution Radiometer, Global Inventory Modeling and Mapping Studies (AVHRR GIMMS, 8 × 8 km^2 in resolution) (ANPP = $11.59e^{5.47\mathrm{NDVI}}$, $R^2 = 0.79$, $n = 121$, $P < 0.001$). With these two functions, we obtained similar results as illustrated in the following sections of the study. Considering the finer resolution, we choose the SPOT-VEG NDVI data and the former function to estimate regional ANPP and make analysis in this study.

Precipitation interpolation

Precipitation data at nearly 750 meteorological stations around the country were acquired from the database of China Meteorological Administration. We used the Anusplin software package (Hutchinson, 2004) to interpolate and derive spatially continuous climate data with thin plate smoothing spline interpolation method (1 × 1 km in resolution). A test of the accuracy of the interpolation method in our study region indicated a relative error of <7% for precipitation (Yu *et al.*, 2004). The MAP in 1998–2007 is quite similar to that of the long-term climate condition (1980–2010) for the study region (mean difference is 6%, $\mathrm{MAP}_{1998\text{–}2007} = 0.92\mathrm{MAP}_{1980\text{–}2010}$, $R^2 = 0.98$, $P < 0.001$). This indicates that the weather in 1998–2007 can in general represent the long-term climate of the past 30 years.

Data analysis

As precipitation after the end of growing season (August in our study) has little impact on current year's ANPP, we defined a water year (WY) herein as the period from 1 September to 31 August of the following year, and then, we yielded mean values of WY from 1998 to 2007 as MAP. Averaged values of ANPP in 1998–2007 for each pixel were calculated to describe the spatial variations in ANPP.

To the best of our knowledge, there is not an explicit index to quantify PSD. In this study, monthly mean precipitation for each pixel during the growing season (May to August) was obtained by averaging the monthly data from 1998 to 2007. Then, the coefficient of variance for the monthly precipitation ($\mathrm{CV_{mp}}$) in each pixel was calculated to quantify PSD:

$$\mathrm{CV_{mp}} = \frac{\sqrt{\frac{1}{4}\sum_{i=5}^{8}\left(M_i - \overline{M}\right)^2}}{\overline{M}}, \tag{1}$$

$$\overline{M} = \frac{1}{4}\sum_{i=5}^{8}(M_i), \tag{2}$$

where M_i is the averaged precipitation of month i (i from May to August) of 10 years (1998–2007), and $\overline{M}$ is the mean precipitation of the 4 months (May to August). A high $\mathrm{CV_{mp}}$ indicates that the growing season precipitation is highly concentrated. On the contrary, a low $\mathrm{CV_{mp}}$ indicates that precipitation is evenly distributed in the growing season. For example, if the 4 months experienced the same amount of rainfall, the $\mathrm{CV_{mp}}$ would be zero, implying a completely even distribution.

To qualify the effects of MAP and PSD on spatial variations in ANPP along the climate gradient, we randomly selected 500, 700, and 500 sites for the desert steppe, the typical steppe, and the meadow steppe, respectively, according to the area of each grassland type, and all the subsequent analyses were based on the data from these sites. Before sampling the sites, the data of Land Use and Cover of China (1 × 1 km^2, available at http://www.geodata.cn) developed by the Chinese Academy of Sciences was used to eliminate the nongrassland pixels. Mean values of ANPP, MAP, and $\mathrm{CV_{mp}}$ for the selected 1700 sites of the entire grassland were 119.66 ± 78.17 g m^{-2}, 269.33 ± 83.71 mm, and 0.36 ± 0.09, respectively, which were quite close to that of all sites (501294 pixels, ANPP, MAP and $\mathrm{CV_{mp}}$ were 104.19 ± 72.28 g m^{-2}, 259.34 ± 78.07 mm, and 0.35 ± 0.09, respectively). All statistical analyses were performed using the R software package (version 2.15.0).

Results

Relationship between MAP and ANPP

The ANPP of the entire temperate grassland in Inner Mongolia increased exponentially with increasing MAP along the precipitation gradient (Fig. 2, ANPP = $13.17e^{0.0075\mathrm{MAP}}$, $n = 1700$; $R^2 = 0.65$, $F = 4348$, $P < 0.001$). However, as Fig. 2 illustrates, the relationship was linear for each grassland type. Note that although a linear function could also be used to fit the MAP–ANPP relation of the entire grassland ($P < 0.01$), but the R^2 (0.55) and F value (2668) was obviously lower than that of the exponential function. MAP accounted for the spatial

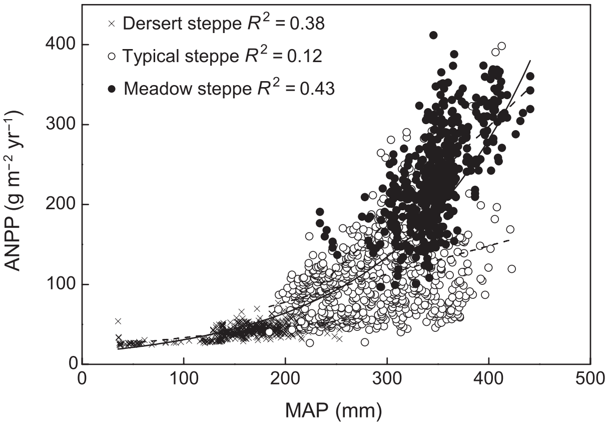

Fig. 2 Relationships between mean annual precipitation (MAP) and aboveground net primary productivity (ANPP) for the entire grassland and for each grassland type. Each data point in the figure represents a 10 year averaged value in 1998–2007. R^2 is the determinant coefficient of the linear functions between MAP and ANPP for each grassland type.

variations in ANPP more in meadow steppe (43%, i.e. the R^2) than in desert steppe (38%) and typical steppe (12%). The explanatory ability of MAP on variations in ANPP for each grassland type was substantially weaker than that for the entire temperate grassland (65%), which implies that the effects of MAP on ANPP increased with spatial scales. The sampling size may confound the comparisons of R^2 among the grassland types and the entire grassland. We further took a subset of the typical grassland (originally 700 sites) and the entire grassland (originally 1700 sites) to make comparison in the condition that the sampling size is similar (500 sites, all randomly selected). The result was consistent with the previous, with only a slight decrease in R^2 for the entire grassland from 0.65 to 0.62. The slope of MAP–ANPP relationship for the meadow steppe (1.02 ± 0.054) was significantly steeper than those for the typical steppe (0.31 ± 0.031) and desert steppe (0.12 ± 0.007) ($P < 0.001$), suggesting that ANPP was likely to be more sensitive to MAP as the climate tended to be more humid.

Relationship between PSD and ANPP

There was also a significant positive relationship between ANPP and CV_{mp} ($ANPP = 7.398e^{7.09CV_{mp}}$, $n = 1700$; $R^2 = 0.6$, $P < 0.001$), which implies a strong impact of PSD on the spatial variations in ANPP (Fig. 3). This positive relationship still held true for each grassland type, but with different R^2 ($P < 0.01$). According to the regression analysis, CV_{mp} accounted for more spatial variations of ANPP in the median typical steppe (24%) than in the dry desert steppe (14%) and the humid meadow steppe (7%). Meanwhile, the slope of the relationship (68.63 ± 7.43, 325.82 ± 21.55, 471.69 ± 75.65 for the desert steppe, typical steppe, and meadow steppe, respectively) became steeper as climate shift from arid to humid and illustrated a significant difference ($P < 0.001$), implying a promoted sensitivity of ANPP to PSD. Note that MAP and CV_{mp} were correlated in Inner Mongolian temperate grasslands ($R^2 = 0.62$, $P < 0.001$). To exclude the compounding effect of MAP on evaluating the influences of CV_{mp} on ANPP, we grouped all the sites into eight MAP groups with a bin width of 50 mm. Similarly, a significant positive CV_{mp}–ANPP relationship was obtained for each MAP group (Fig. 4). Apparently, the slope was increasing with the MAP groups moving from the dry area to the wet area, being in consistent with the grassland type-based pattern (Fig. 3).

To quantify the relative contribution of MAP and PSD to the spatial variations in ANPP, the general linear model analysis was employed. The results indicated that PSD was as important as MAP in affecting the spatial variations in ANPP for the entire temperate grassland, with the contribution of 39.4% and 40% for PSD and MAP, respectively (Table 1). However, the relative contribution of PSD and MAP differed remarkably among the grassland types. In the typical steppe, spatial ANPP was more affected by PSD (35.88%) than MAP (15.53%). However, an opposite pattern was found in meadow and desert steppes, implying that ANPP was more affected by MAP (ca. 35%) than PSD (lower than 10%).

Discussion

Effects of MAP on spatial variations in ANPP

A positive MAP–ANPP relationship was found in Inner Mongolia temperate grassland. This is consistent with

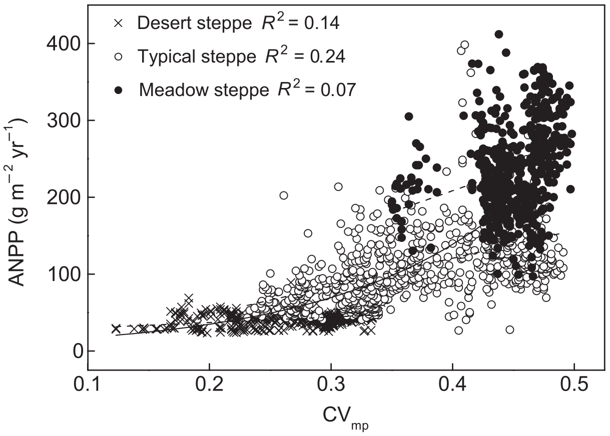

Fig. 3 Relationships between precipitation seasonal distribution (PSD, quantified herein with CV_{mp}) and aboveground net primary productivity (ANPP) for the entire grassland and for each grassland type.

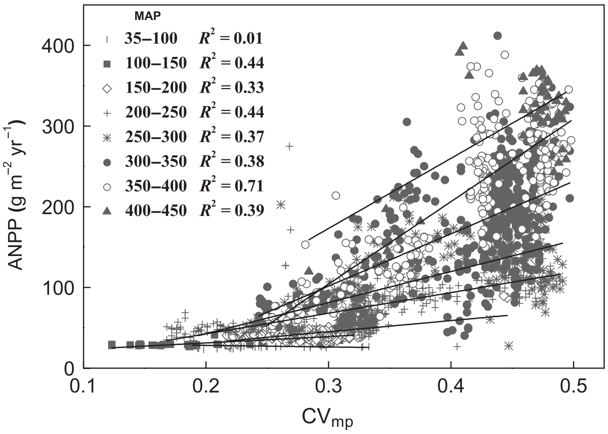

Fig. 4 Relationships between CV_{mp} and aboveground net primary productivity (ANPP) in different mean annual precipitation (MAP) groups. The whole MAP range was divided into eight groups with an interval of 50 mm.

Table 1 Contributions of precipitation seasonal distribution (PSD, quantified herein with CV_{mp}) and mean annual precipitation (MAP) to spatial variations in aboveground net primary productivity (ANPP)

Grassland type		MAP (SS%)	CV_{mp} (SS%)	Residual (SS%)	VIF	*P*
Desert steppe	Model 1*	36.6	6.9	56.4	1.01	<0.001
	Model 2	32.4	11.1	56.4		<0.001
	Average	34.5	9.0	56.4		
Typical steppe	Model 1	20.1	31.3	48.6	1.04	<0.001
	Model 2	10.9	40.5	48.6		<0.001
	Average	15.5	35.9	48.6		
Meadow steppe	Model 1	34.4	5.7	59.9	1.03	<0.001
	Model 2	38.1	2.0	59.9		<0.001
	Average	36.3	3.8	59.9		
Entire temperate grassland	Model 1	15.8	63.6	20.6	1.54	<0.001
	Model 2	63.0	16.4	20.6		<0.001
	Average	39.4	40.0	20.6		

VIF, variance inflation factor.

*Different sequences of the variables in the general linear model may result in different results. We thus averaged the contribution of each variable with different sequences as the final evaluation. 'Model 1' represents that CV_{mp} was at the first order and MAP at the second; 'Model 2' represents that MAP was at the first order and CV_{mp} at the second; 'Average' is the averaged value of results of model 1 and model 2.

most previous studies (Lehouerou *et al.*, 1988; Sala *et al.*, 1988; Briggs & Knapp, 1995). We also found that the explanatory power of MAP on the spatial variations in ANPP for each grassland type was weaker than that across the grassland types. This is in accordance with previous studies in which ANPP was significantly related to precipitation at the regional scale, but such relationship was weaken or disappeared at a site scale (Lauenroth & Sala, 1992; Hu *et al.*, 2010).

We found that the MAP–ANPP relationship was exponential for the entire temperate grassland, which agree with previous reports in Inner Mongolia temperate grassland (Ma *et al.*, 2008; Hu *et al.*, 2010). For the grasslands in other regions of the world, however, linearity was the mostly common shape of this relationship (Sala *et al.*, 1988; Briggs & Knapp, 1995; Paruelo *et al.*, 1999). Hu *et al.* (2010) inferred that this disagreement may be due to insufficient sampling sites in the arid regions in previous study. Our results support this assumption. With the data from sufficient randomly sampled sites, we found a linear MAP–ANPP relationship for a given grassland type; however, the function turned out to be exponential when combining all the sites of the three grassland types together. The main reason may be due to the differences in plant functional types and their sensitivities to changes in precipitation (Paruelo *et al.*, 1999; O'connor *et al.*, 2001; Huxman *et al.*, 2004).

The slope of the MAP–ANPP relationship increased as the climate shifted from the arid (desert steppe) to the humid (meadow steppe). This finding is consistent with previous reports in Inner Mongolia grasslands and other arid regions, in which sensitivity of ANPP to precipitation increased with MAP before MAP was less than 500 mm (Bai *et al.*, 2008; Hu *et al.*, 2010; Hsu *et al.*, 2012). However, the mechanism behind this pattern remains unclear, and additional studies are warranted to address this issue. We assume that the distinct spatial sensitivity of ANPP to MAP among the grassland types may be mainly due to the different composition of plant functional types for three reasons. First, the plants at the dry end (e.g., the desert steppe) generally have conservative water use strategies and plants' photosynthate is consumed mostly for the resistance to water stress and for the growth maintenance (Paruelo *et al.*, 1999). In this case, ANPP would be insensitive to changes in precipitation. On the other hand, ANPP in humid environment would be sensitive to changes in precipitation due to their open water use strategy (Webb *et al.*, 1978). Second, at the community level, the plant community in humid environment has relatively high plant biodiversity, which is superior in ANPP's response to increasing precipitation due to the compensatory effects among species (Bai *et al.*, 2004). Third, with the increase in MAP, the rainfall could be used more efficiently for primary production owing to the increased leaf area index and vegetation cover, and this will be advantageous to steeper MAP–ANPP slope (Hu *et al.*, 2008, 2010). It is noteworthy that some other abiotic factors may also have some influences. For example, it is found that soil nitrogen content increases with MAP in Inner Mongolia grasslands (Evans *et al.*, 2011). Thus, ANPP in the wetter area would benefit from the more fertile soil conditions (e.g., increase in soil N content and N deposition) and the slope would be steeper (Bai *et al*., 2010; Li *et al*., 2010). In addition, the study region is characterized with warmer climate in the dry desert steppe and cooler climate in the wetter meadow steppe. Our previous study indicated that using aridity index could explain ANPP spatial variations better than MAP alone (Hu *et al*., 2007). Therefore, higher precipitation together with lower temperature, and hence, lower potential evapotranspiration rates in meadow steppe would favor higher ANPP and precipitation-use efficiency (Hu *et al*., 2010).

Effects of PSD on spatial variations in ANPP

Significant effects of PSD on spatial variations in ANPP in Inner Mongolia temperate grassland was found in this study, implying that more concentrated precipitation distribution pattern favors higher ANPP (Fig. 3). Some site scale-based studies in arid regions indicated that infrequent, but large rainfall events could attenuate water stress and result in improved ANPP (Heisler-White *et al*., 2008, 2009; Thomey *et al*., 2011).

We expected that effects of PSD on the spatial variations in ANPP in our study can be interpreted by the mechanism at the site scale. Inner Mongolia grassland belongs to the arid and semiarid region, which is under the control of Asia monsoon climate. Concentrated PSD could let precipitation water infiltrate into deeper soil layers, lower the water loss by soil evaporation, and hence, increase soil water content during the growing season, making plants maintaining a high level of photosynthetic rate (Heisler-White *et al*., 2008, 2009; Thomey *et al*., 2011). In addition, the concentrated PSD can promote ANPP through increased recruitment and growth of annual plants, which can complete their life history in short time period during the relatively high soil moisture (Zhang *et al*., 2004). Although the concentrated PSD decreased soil water content of other periods, high stress tolerance of plants in arid and semiarid regions allow them to be less sensitive to the decline of water availability (Sala *et al*., 1992; Knapp & Smith, 2001).

It is noteworthy that the precipitation in July is most important among the 4 months of the growing season in our study area. CV_{mp} (the index of PSD) was positively related with the ratio of July precipitation to annual precipitation, and also a significant positive correlation was found between the ratio and ANPP ($P < 0.01$). However, our further analysis indicated that CV_{mp} showed overwhelming effects on the spatial ANPP over the July to annual precipitation ratio (data not shown).

Precipitation seasonal distribution and MAP contributed almost equally (both were ca. 40% in terms of the determination coefficient) to the spatial variations in ANPP for the entire temperate grassland in Inner Mongolia, reflecting a stronger significance of PSD than our expectation. The relative contribution of PSD and MAP heavily relied on the grassland type. PSD was the dominant factor of spatial variations in ANPP in the typical steppe, but MAP was more important in the desert steppe and meadow steppe. This difference may also be related to the different compositions of plant functional types in different grassland types. Higher soil water content in some periods as the result of higher CV_{mp} is at the cost of more severe water stress in other periods. Therefore, to what degree ANPP can benefit from high CV_{mp} would be highly depend on the plants' tolerance to water stress. From this perspective, the contribution of PSD would increase from the humid area (e.g., meadow steppe) to the arid area (e.g., desert steppe). However, the importance of PSD becomes again less important than MAP in the desert steppe due to the extremely low annual precipitation in this area (mostly lower than 180 mm).

In this study, we quantified the effects of MAP and its seasonal distribution, PSD, on the spatial variations in ANPP of Inner Mongolia temperate grassland. We conclude that it was an exponential relationship between MAP and ANPP for the entire Inner Mongolia temperate grassland, whereas linear relationship was found for a given grassland type. PSD contributed equally with MAP to the spatial variations in ANPP. This implies that changes in seasonal distribution of rainfall due to climate change would cause commensurate consequences as the total amount of annual precipitation, which has not been paid sufficient attention or even ignored in the past.

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