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PAPER

## Precipitation-use efficiency along a 4500-km grassland transect

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### ABSTRACT

**Aims** Clarifying the spatiotemporal variations in precipitation-use efficiency (PUE), the ratio of vegetation above-ground productivity to annual precipitation, will advance our understanding of how ecosystems' carbon and water cycles respond to climate change. Our goal is to investigate the variations in PUE at both regional and site scales along a 4500-km climate-related grassland transect.

**Location** The Inner Mongolian Plateau in northern China and the Qinghai-Tibetan Plateau.

**Methods** We collected data on 580 sites from four data sources. The data were acquired through field surveys and long-term *in situ* observations. We investigated the relationships between precipitation and PUE at both regional and site scales, and we evaluated the effects of the main biotic and climatic factors on PUE at both spatial scales.

**Results** PUE decreased with decreasing mean annual precipitation (MAP), except for a slight rise toward the dry end of the gradient. The maximum PUE showed large site-to-site variation along the transect. Vegetation cover significantly affected the spatial variations in PUE, and this probably accounts for the positive relationship between PUE and MAP. However, there was no significant relationship between inter-annual variations in precipitation or vegetation cover and PUE within given ecosystems along the transect.

**Conclusions** The findings of this research contradict the prevailing view that a convergent maximum PUE exists among diverse ecosystems, as presented in previous reports. Our findings also suggest the action of distinct mechanisms in controlling PUE at different spatial scales. We propose the use of a conceptual model for predicting vegetation productivity at continental and global scales with a sigmoid function, which illustrates an increasing PUE with MAP in arid regions. Our approach may represent an improvement over use of the popular Miami model.

### Keywords

Alpine grasslands, China Grassland Transect (CGT), leaf area index, precipitation-use efficiency, rain-use efficiency, temperate grasslands, vegetation cover.

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### INTRODUCTION

Precipitation is a key climatic factor controlling primary productivity for most of the world's grassland ecosystems. Clarifying how precipitation affects productivity in grasslands is critical for predicting the impact of global climate change on the functioning of these ecosystems (Knapp *et al.* 2002; Weltzin *et al.*

2003; Huxman *et al.* 2004). Precipitation-use efficiency (PUE), or rainfall-use efficiency (RUE), which calculates the ratio of above-ground net primary productivity (ANPP) to precipitation, provides a useful index for improved understanding of the relationship between precipitation and vegetation productivity, as well as for evaluating the degradation of grasslands (Le Houérou, 1984; Justice *et al.* 1991; Prince *et al.* 1998). Examining

the spatiotemporal variations in PUE across a climate gradient is useful for predicting the effects of climate change on vegetation productivity. Further, the results of such examination are helpful in shaping and implementing effective land-management strategies (Prince *et al.* 1998; Huxman *et al.* 2004; Bai *et al.* 2008).

China has the second largest area of grassland in the world; indeed, grassland covers nearly 40% of the country (Fan *et al.* 2008). Much research has sought to improve our knowledge of the structure and function of China's grasslands (Ni, 2004; Bai *et al.* 2004; Hu *et al.* 2007; Fan *et al.* 2008, 2009), but very few reports have documented the spatial and temporal variations in PUE. Recently, Bai *et al.* (2008) described the spatial pattern of PUE along a precipitation gradient in the steppe region of Inner Mongolia. This study improved our knowledge of the relationship between climate and vegetation productivity in China's temperate grasslands. However, their study focused only on Chinese temperate grasslands; the alpine grasslands on the Qinghai-Tibetan Plateau, the highest plateau in the world, were not included. Consequently, the difference in PUE of the two contrasting grassland types remains unclear. In addition, Bai *et al.* (2008) used only 21 sites to assess the spatial variations in PUE, and the researchers used only one site to address the temporal variations in PUE. As the authors acknowledge, more data are needed to clarify the spatiotemporal patterns of PUE as well as the underlying mechanisms.

Indeed, although some researchers have sought to address the spatiotemporal patterns of PUE, few have documented or explained the underlying mechanisms (Huxman *et al.* 2004; Bai *et al.* 2008). According to the definition, PUE can be expressed as

$$\text{PUE} = \frac{\text{ANPP}}{\text{PPT}} = \frac{\text{ANPP}}{T} \times \frac{T}{\text{PPT}} \quad (1)$$

where  $T$  is plant transpiration and PPT is annual precipitation. In the equation, ANPP/ $T$  is similar to water-use efficiency (WUE) at the leaf level, which is closely linked to plant physiological characteristics and the vapour pressure deficit (VPD) in the air (Scanlon & Albertson, 2004; Xu & Hsiao, 2004; Ponton *et al.* 2006).  $T/\text{PPT}$  describes how much precipitation is used for plant growth, which is jointly influenced by plant physiological processes and the physical processes affecting water loss within the ecosystem (O'Connor *et al.* 2001; Scanlon & Albertson, 2004; Xu & Hsiao, 2004; Hu *et al.* 2008). Since ANPP/ $T$  and  $T/\text{PPT}$  are controlled by different physiological and physical processes, large uncertainty may exist in the spatiotemporal variations in PUE. For example, in arid climates high WUE allows individual plants to survive, resulting in high ANPP/ $T$  (Scanlon & Albertson, 2004). Much of the precipitation input, however, might be lost directly via soil-water evaporation and runoff caused by the sparse vegetation conditions or by the conservative water-use strategies of the plants (Paruelo *et al.* 1999; Hu *et al.* 2008). This reduces  $T/\text{PPT}$  and may result in low PUE. Conversely, in humid climates individual plants are likely to have low WUE, but much of the precipitation can be used for plant productivity and lost via transpiration due to dense canopies and high plant growth rates (Yahdjian & Sala, 2006; Hu *et al.* 2008). For these reasons, efforts to clarify the mechanisms controlling the spatiotemporal

dynamics of PUE should simultaneously investigate the main factors affecting both ANPP/ $T$  and  $T/\text{PPT}$ .

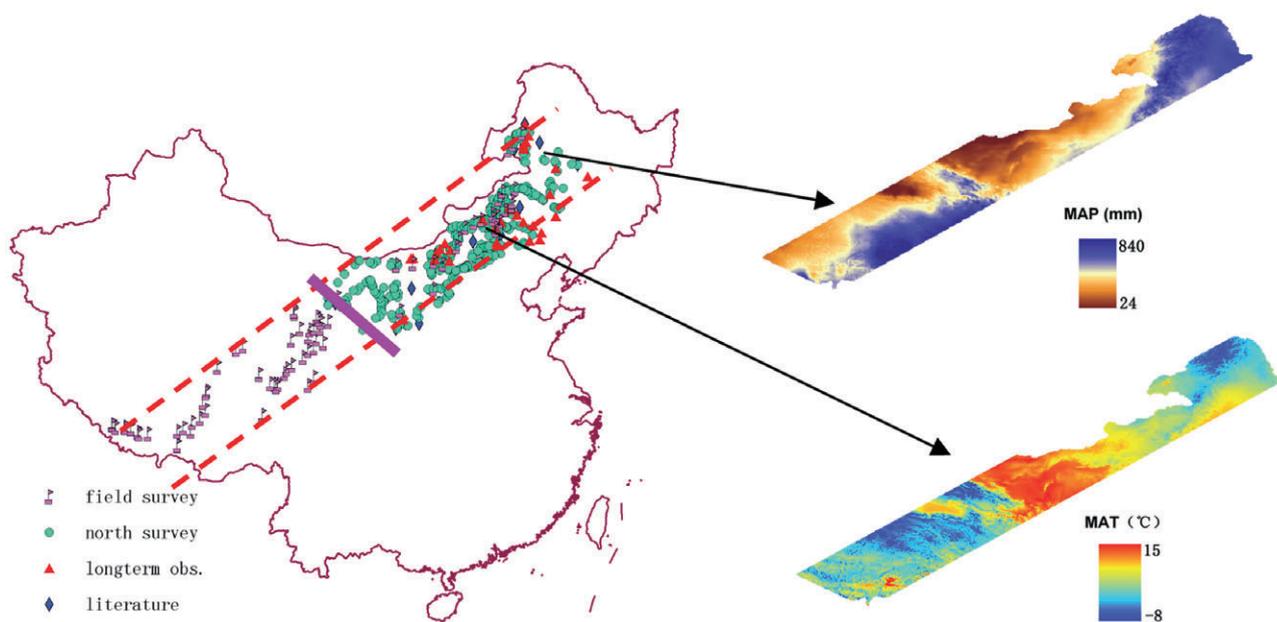
By taking the slopes of the relationship between ANPP and annual precipitation (PPT) as PUE, Huxman *et al.* (2004) investigated the spatial variations in PUE across 14 terrestrial ecosystems in nine biomes located throughout North and South America. They found that all sites converged to a common maximum PUE during the driest years. Using a similar approach, Bai *et al.* (2008) also determined a common maximum PUE, as well as a minimum PUE, for Chinese temperate grasslands. This work contributes to a deeper understanding of the relationship between vegetation productivity and precipitation. However, in their studies, the convergent maximum (or minimum) PUE was derived through the spatial relationship between ANPP and PPT (i.e. the slope) at the sites in the driest years, rather than from a direct calculation of the ratios of ANPP to PPT. In some cases, this approach might be problematic because of the different meanings of 'slope' and 'resource-use efficiency' (Verón *et al.* 2005). Furthermore, the 'slope' method is based on an assumption that PUE is highest in the driest year and lowest in the wettest year. One may wonder if, with direct calculation of the maximum PUEs (i.e. the maximum ratio of ANPP to annual precipitation), a common maximum PUE exists across ecosystems and, further, whether the maximum PUE does in fact occur in the driest year and the minimum PUE in the wettest year.

In this study, using data from 580 sites, we addressed the spatiotemporal variations in ANPP and PUE along the China Grassland Transect (CGT), a climate-related transect covering most of China's temperate and alpine grassland types. We investigated the main biotic and abiotic factors (e.g. leaf area index, vegetation cover and VPD) that may affect PUE through their influences on ANPP/ $T$  and  $T/\text{PPT}$ . In addition to testing the maximum PUE hypothesis presented in previous reports, we sought to answer the following questions: (1) Does PUE increase or decrease with precipitation along the precipitation gradient of the CGT? (2) Are the temporal responses of PUE to inter-annual variations in precipitation at given sites similar to the spatial responses? (3) Does PUE in the alpine grasslands differ from that in the temperate grasslands under similar conditions of precipitation? We hypothesized that ANPP as well as PUE would increase with mean annual precipitation (MAP) along this transect. We arrived at this hypothesis based on the likelihood that in sites in arid environments, only a small fraction of precipitation could be used for plant growth and, further, that much precipitation would be lost directly via soil evaporation and runoff. With increased MAP, vegetation canopies grow closer and plants have higher growth rates. In these conditions, more precipitation would be used for plant productivity and lost in the form of transpiration.

## MATERIALS AND METHODS

### Study area

The China Grassland Transect (CGT) is a c. 4500-km transect extending from Hailaer (122.4° E, 46.6° N, 500–700 m a.s.l.) on



**Figure 1** Range of the China Grassland Transect (CGT), gradients of related climate factors and distribution of sampling sites. The left legend indicates four data sources for above-ground net primary productivity (ANPP) and relevant biological variables. The bold line illustrates the boundary between the east and west sections of the CGT. MAP, mean annual precipitation; MAT, mean annual temperature.

the Inner Mongolia Plateau in north-eastern China to Pulan (81.0° E, 30.3° N, 3800–5000 m a.s.l.) in the south-western region of the Tibet Plateau (Fig. 1). The transect covers most of China's grassland types and can be divided into eastern and western sections, based on climate and geographic conditions. The eastern section is located mainly on the Inner Mongolia Plateau in northern China. This area belongs biogeographically to the Eurasia Steppe region, where precipitation is the principal climatic factor limiting plant growth. Five temperate grassland types are included in this section: meadow steppe, typical steppe, desert steppe, steppe desert and desert, which are characterized by decreasing precipitation as one moves from east to west. MAP in this section ranges from about 100 to 600 mm, and mean annual temperature (MAT) ranges from  $-3$  to  $9$  °C. The soils in this section are chernozems, chestnut, calcic brown and desert soils. More information about the eastern section of the CGT is available in Hu *et al.* (2007). The western section of the CGT is located on the Qinghai-Tibetan Plateau, which is characterized by high altitude (most of the area is above 4000 m a.s.l.) and an alpine climate. The climate in this section is warm and humid in summer and cold and dry in winter. MAP ranges from about 100 to 800 mm, and MAT ranges from  $-5.8$  to  $3.7$  °C. The main grassland types (and corresponding soil types) are alpine meadow, alpine steppe and alpine desert (DAHV and CISNR, 1996).

### Data collection

In this study, ANPP was estimated as the peak above-ground biomass (including live biomass as well as standing dead biomass produced in the current year) during the growing

seasons. This is a popular method for estimating grassland ANPP (Long *et al.* 1992; Scurlock *et al.* 2002). We measured vegetation cover before sampling above-ground biomass, and the replicate measures were the same as that of ANPP. We estimated vegetation cover through use of an empirical method: three or more persons independently visually estimated the vegetation cover for each quadrat. The mean of these visual estimates was used to establish the vegetation cover for the quadrat. To maximize the representativeness of the data used, we collected data on ANPP and relevant biological variables from diverse sources. We collected data on a total of 580 sites using the following four sources (Fig. 1).

### Field survey

During the peak growing seasons of 2003–2006, when vegetation reached its maximum above-ground biomass, we conducted field surveys along the CGT to sample the above-ground biomass. The sampling sites were selected at intervals of *c.* 50 km, and all were protected from herbivore grazing through use of fencing. Above-ground biomass in three independent  $1 \times 1$  m quadrats was harvested at each site. The sampled biomass was weighed after 48 h of drying in an oven set at  $65$  °C. 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 containing shrub species. We collected data on 81 sites, 47 of them alpine grasslands and 34 of them temperate grasslands. Statistical analysis indicated that the standard deviations of ANPP for the three replicates, at 86% of the total sites, were less than 20% of the mean values, and the site-to-site differences were extremely significant (one-way

ANOVA,  $P < 0.0001$ ). This illustrates that the heterogeneity at each site could be ignored when addressing the pattern of ANPP at the regional scale. This dataset was used to describe the spatial variations in PUE.

#### North survey

Supported by the Ministry of Agriculture of China, a background survey was conducted in the peak growing seasons of 1990–1999 to study the forage yield of the temperate grasslands in northern China. Through continuous 10-year field surveys, data from several hundred sites (also protected from grazing) were collected. These data include geographic coordinates, vegetation type, peak above-ground biomass, vegetation cover, etc. (available at: <http://www.grassland.net.cn>). During the surveys, the current-year twigs and leaves of shrub species from three or more separate quadrats were sampled and weighed. This enabled us to estimate the ANPP of the grassland types with shrub species (i.e. temperate desert steppe, temperate steppe desert and temperate desert). We selected sites located on or adjacent to the CGT and rejected sites with non-zonal vegetation. A total of 443 data sites were selected from this source, which was used to describe the spatial variations in PUE.

#### Long-term observations

To monitor the seasonal and inter-annual dynamics of grassland forage yield in Inner Mongolia, local governments established permanent study plots for continuous measurement of above-ground biomass, community composition, vegetation cover, etc. These plots were fenced to prevent grazing and to protect the plant communities from other disturbances. Five or more quadrats were used as the replicates for the measurements. For this dataset (also available at: <http://www.grassland.net.cn>), we took the peak above-ground standing biomass in each growing season as ANPP and rejected sites with non-zonal vegetation. This dataset enabled us to investigate both the spatial and temporal variations in PUE along the precipitation gradient. A total of 23 data sites were selected, and the average duration of the measurements was 7 years.

#### Literature

Ni (2004) collected ANPP data on grasslands in northern China from published articles, books and reports. In all cases, ANPP was estimated through measurement of biomass. For our study, we selected data based on long-term measurement (3 years and more). We rejected the sites whose geographic locations overlapped with those in the data source (three sites). We also excluded sites with non-zonal vegetation and not located in or proximate to the CGT. Using this method, 33 data sites were selected to describe the spatial variations in PUE.

We acquired annual precipitation, annual mean temperature and annual mean VPD for 1970–2000 from the public database of the Chinese National Bureau of Meteorology. We interpolated the station-specific data using three-dimensional second-order

trend surface analysis ( $1 \times 1$  km in resolution). A test of the accuracy of the interpolation method in the western regions of China, where the CGT is located, indicated a relative error of 3% for annual temperature, 7% for annual precipitation and 5% for VPD (Yu *et al.* 2004). This illustrates that the interpolated MAP and VPD used in this study are reliable. Leaf area index (LAI) may also have an important effect on PUE. We acquired LAI data from the MODIS LAI product ( $1 \times 1$  km; <http://lpdaac.usgs.gov>). We calculated the mean LAI in the peak growing season (July and August) during 2003–2005 as the mean maximum LAI for each site.

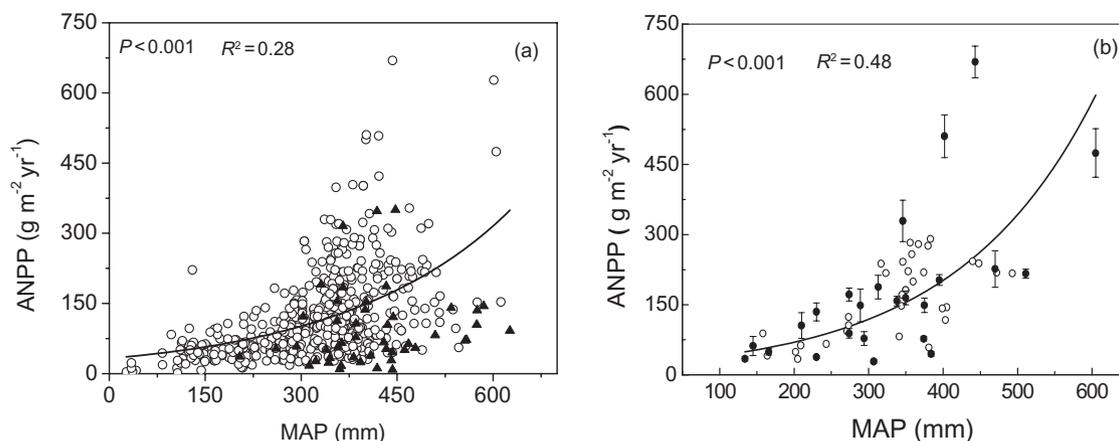
## RESULTS

### Variations in ANPP and PUE along the transect

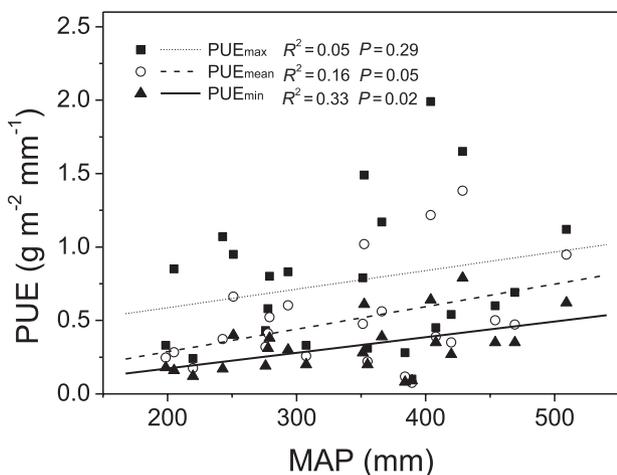
To maximize the reliability of our results, we used two datasets with different data numbers and qualities to examine the relationship between ANPP and MAP: the first represented the total data from the 580 sites, and the second reflected data from the 56 sites acquired through long-term measurement (i.e. data sources 3 and 4). Both datasets indicated that ANPP was positively correlated with MAP and that it increased exponentially with MAP ( $P < 0.001$ ), implying an increasing PUE with increasing MAP (Fig. 2). The temperate grasslands showed higher ANPP than the alpine grasslands at the same level of MAP, indicating that the temperate grasslands had higher PUE than the alpine grasslands.

Using the records derived from long-term observation (data source 3), we investigated the spatial variations in the maximum, mean and minimum PUE ( $PUE_{\max}$ ,  $PUE_{\text{mean}}$  and  $PUE_{\min}$ , respectively) along the precipitation gradient. There were distinctive spatial variations in the three PUE measurements. Specifically,  $PUE_{\max}$  had the widest range of variation ( $0.10$ – $1.99$  g m<sup>-2</sup> mm<sup>-1</sup>), followed by  $PUE_{\text{mean}}$  ( $0.07$ – $1.22$  g m<sup>-2</sup> mm<sup>-1</sup>) and  $PUE_{\min}$  ( $0.08$ – $0.79$  g m<sup>-2</sup> mm<sup>-1</sup>). These findings revealed no common  $PUE_{\max}$  or  $PUE_{\min}$ , as had been previously proposed (Huxman *et al.* 2004; Bai *et al.* 2008). The results also indicated that  $PUE_{\text{mean}}$  and  $PUE_{\min}$  were positively correlated with MAP ( $P \leq 0.05$ ), while  $PUE_{\max}$  was not significantly correlated with MAP. The different variations in the three PUE measurements resulted in a trend in which the significance of the relationships between MAP and the PUE measurements increased from  $PUE_{\max}$  ( $P = 0.29$ ,  $R^2 = 0.05$ ) to  $PUE_{\text{mean}}$  ( $P = 0.05$ ,  $R^2 = 0.16$ ) and to  $PUE_{\min}$  ( $P = 0.02$ ,  $R^2 = 0.33$ ) (Fig. 3).

At each section of the CGT, both ANPP and PUE decreased with the increase in aridity (ANOVA,  $P < 0.05$ , Fig. 4). It is worth noting that the alpine grasslands on the Tibetan Plateau had lower ANPP and PUE than the temperate grasslands under similar amounts of precipitation (*t*-test,  $P < 0.05$ , Fig. 4). For example, at a similar level of MAP, ANPP and PUE of the alpine meadow ( $141$  g m<sup>-2</sup> year<sup>-1</sup>,  $0.33$  g m<sup>-2</sup> mm<sup>-1</sup>) were much lower than those of the temperate meadow steppe ( $271$  g m<sup>-2</sup> year<sup>-1</sup>,  $0.64$  g m<sup>-2</sup> mm<sup>-1</sup>). Although PUE also decreased with MAP in the temperate grasslands, the trend was not as steep as that for ANPP. At the driest end (i.e. the temperate desert), there was a



**Figure 2** Relationship between mean annual precipitation (MAP) and above-ground net primary productivity (ANPP). In (a) all the 580 sites were included ( $ANPP = 22.53e^{0.004MAP}$ ). The triangles represent the sites of alpine grasslands and the circles represent the sites of temperate grasslands. In (b) only the 56 sites with long-term measurements (data source 3 (dots with SE) and 4 (circles)) were included ( $ANPP = 24.47e^{0.005MAP}$ , Hu *et al.* 2007).



**Figure 3** Relationships between mean annual precipitation (MAP) and three measurements of precipitation use efficiency (PUE):  $PUE_{max}$ , maximum PUE;  $PUE_{mean}$ , mean PUE;  $PUE_{min}$ , minimum PUE.

slight increase of PUE (Fig. 4b). This implies that PUE is more conservative than ANPP for the ecosystems in this study.

Using the long-term observation data (data source 3), we also investigated the temporal relationship between PUE and annual precipitation within given ecosystems on the CGT. The results indicated that PUE was only slightly correlated (negatively) with annual precipitation ( $P < 0.05$ ,  $R^2 < 0.06$ ) at only 2 of the 23 sites, which differs from the results at the transect scale. This indicates that increased annual precipitation has little impact on the temporal PUE for most ecosystems along this transect.

### Factors affecting the spatiotemporal variations in PUE

Spatially, the climatic and biotic factors showed significant correlation with each other, owing to the combined effects of lon-

gitude (precipitation gradient), latitude (temperature gradient) and elevation (Table 1). As MAP increased, MAT and VPD decreased, while LAI and vegetation cover increased. And, as expected, LAI and vegetation cover were significantly correlated with each other ( $P < 0.001$ ).

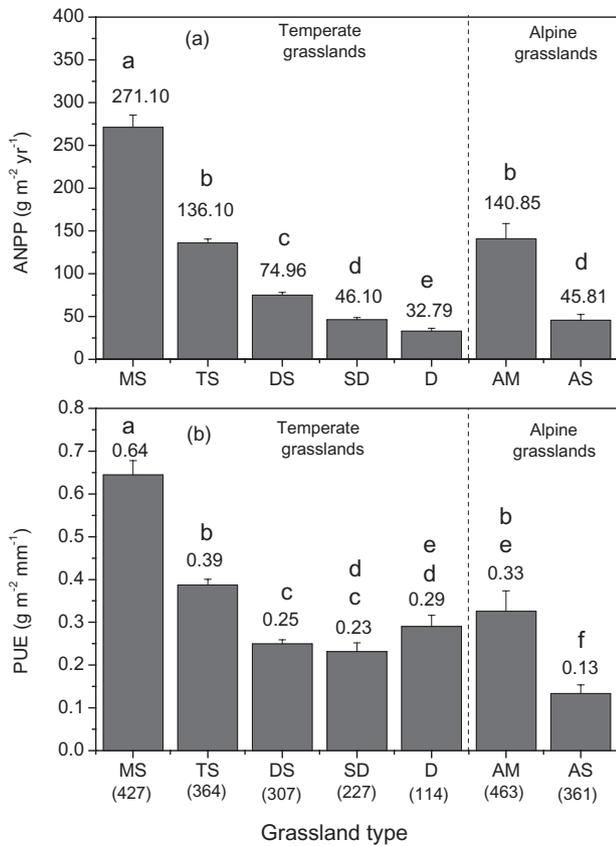
We conducted correlation and regression analysis to investigate the effects of the climatic and biotic factors on the spatial variations in PUE. The results indicated that both vegetation cover and LAI were linearly correlated with PUE ( $P < 0.001$ , Fig. 5). But the explanatory ability of LAI ( $R^2 = 0.07$ ) was much weaker than that of vegetation cover ( $R^2 = 0.20$ ). Besides, no significant relationship was found between PUE and VPD ( $P > 0.05$ ).

In contrast to the results at the transect scale, vegetation cover, as well as the other factors mentioned above, were not significantly correlated with PUE at the site scale (Fig. 6). This means that the inter-annual variations in vegetation cover did not have significant impacts on PUE within given ecosystems on the CGT.

## DISCUSSION

### Spatial variations in PUE

The PUE values of typical Chinese grasslands ( $0.13\text{--}0.64\text{ g m}^{-2}\text{ mm}^{-1}$ , Fig. 4b) are within the range ( $0.05\text{--}1.81\text{ g m}^{-2}\text{ mm}^{-1}$ ) reported by Le Houérou *et al.* (1988) for the rest of the world's grassland ecosystems in arid regions. Our values of PUE for China's temperate grasslands are also close to those of Bai *et al.* (2008). Furthermore, this study indicates that the alpine grasslands had lower PUE than the temperate grasslands at similar levels of precipitation. This is probably due to the adverse environmental conditions in alpine regions (e.g. low temperature and short growing season, heavy winds, strong solar radiation, etc.). It is noteworthy that there was a slight increase in PUE at the dry end of the



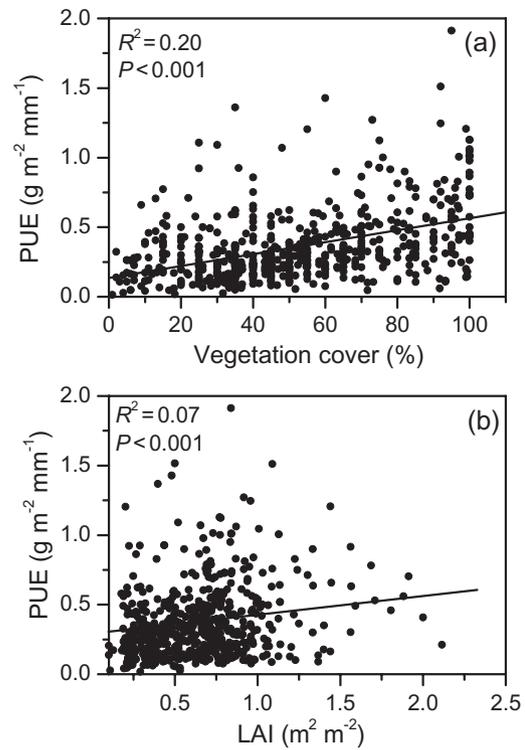
**Figure 4** Mean values of above-ground net primary productivity (ANPP) (a) and precipitation use efficiency (PUE) (b) for the following grassland types: MS, meadow steppe ( $n = 65$ ); TS, typical steppe ( $n = 208$ ); DS, desert steppe ( $n = 164$ ); SD, steppe desert ( $n = 59$ ); D, desert ( $n = 37$ ); AM, alpine meadow ( $n = 24$ ); AS, alpine steppe ( $n = 23$ ). The error bars depict standard errors. The letters above the error bars indicate significant differences between the grassland types. Bars that do not have a common letter are significantly different at  $P \leq 0.05$  ( $t$ -test). The numbers in brackets ( $x$ -axis) are the average mean annual precipitation (MAP) for the grassland types.

**Table 1** Pearson's correlations among main climatic and biotic variables.

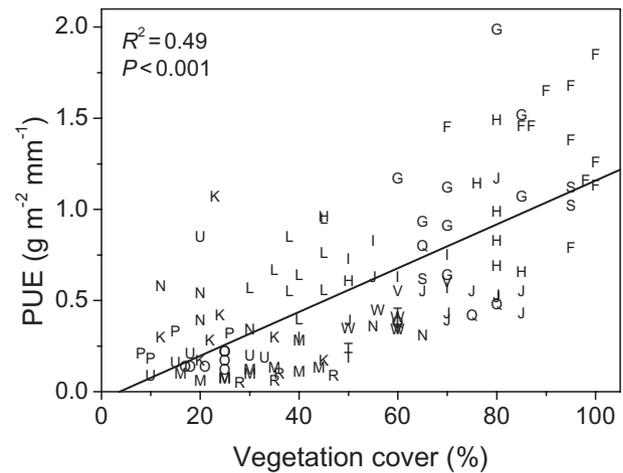
	MAT	VPD	VC	LAI
MAP	-0.527	-0.780	0.597	0.722
MAT		0.910	-0.611	-0.310
VPD			-0.672	-0.488
VC				0.454

MAP, mean annual precipitation; MAT, mean annual temperature; VPD, vapour pressure deficit; VC, vegetation cover; LAI, leaf area index.  $P < 0.01$  for all correlations.

eastern section of the CGT (Fig. 4). This might be related to the fact that desert plants have adapted to an extremely dry climate by using water held in deeper soil layers (Jobbagy & Sala, 2000).



**Figure 5** Spatial correlations between precipitation use efficiency (PUE) and (a) vegetation cover, (b) leaf area index (LAI).

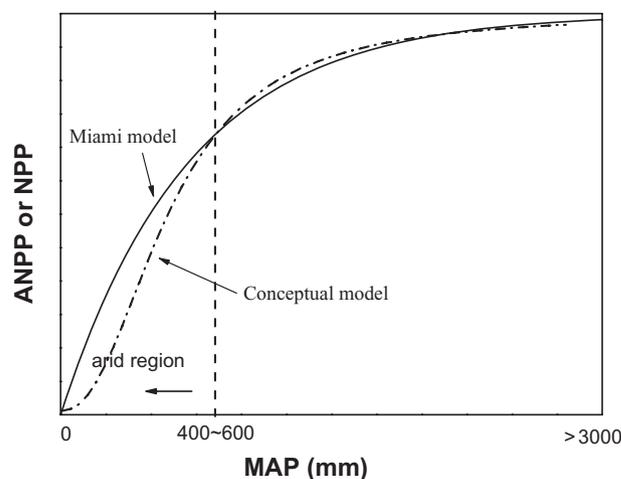


**Figure 6** Relationship between vegetation cover and annual precipitation use efficiency (PUE) at the site scale (data source 3). Each letter represents observations of PUE and vegetation cover in different years at a given site. The fit line and statistical notes indicate the cross-sites relationship between vegetation cover and PUE.

The results of this study, which are consistent with our hypothesis, illustrate an increased PUE with increasing MAP along the CGT, except in alpine grasslands where there was no obvious increase of PUE with MAP (Fig. 2a). We ascribe this to the uncertainties resulting from the measurements of the field survey, which were based on only a single year. When averaging

PUE at the grassland-type level, through which such uncertainties can be largely reduced, one sees obvious differences in the PUEs of the wetter alpine meadow and the drier alpine steppe (Fig. 4b). Our results agree with the results of Le Houérou (1984), Prince *et al.* (1998) and Bai *et al.* (2008), in which PUE increased with MAP. However, many previous reports showed linear relationships between MAP and ANPP along environmental gradients, suggesting constant spatial PUEs (Sala *et al.* 1988; Lauenroth & Sala, 1992; Lauenroth *et al.* 2000; Knapp & Smith, 2001). By contrast, Huxman *et al.* (2004) found that PUE decreased with the increase of MAP across North America. Similarly, Leith (1975) investigated the relationship between net primary productivity (NPP) and MAP at the global scale and developed the widely used Miami model to predict NPP with MAP. By comparing these results, one can conclude that the MAP ranges and ecosystem types involved in each work are different. In the studies showing increased PUE with MAP, the MAP was typically less than 600 mm and the ecosystems were deserts or grasslands in arid regions. In the studies suggesting near constant PUEs, the MAP was typically less than 1500 mm and the ecosystems were mainly grasslands with a few dry forests. Meanwhile, in the studies finding that PUE decreased with MAP, the MAP ranged from the dry end (less than 100 mm) to the wet end (more than 3000 mm) and diverse biomes were included (e.g. Leith, 1975; Huxman *et al.* 2004). Apparently, when the range of MAP and the ecosystem types were narrowed toward the dry end, the spatial variation in PUE would shift from a decrease to an increase with increasing MAP. Further, Paruelo *et al.* (1999) investigated the spatial variation in PUE (estimated as the slope of the relationship between ANPP and precipitation) across a precipitation gradient (200–1200 mm). They found that PUE was low at both the dry and wet ends and peaked around 475 mm, which is quite close to the wet end of this study. Based on our review of the work mentioned above, we suggested that PUE would increase at first and then decrease with increasing MAP at continental and global scales. We further proposed a conceptual model describing the relationship between ANPP (or NPP) and MAP, with a sigmoid function at the scales of the continent and above (Fig. 7). In comparing the conceptual model with the Miami model, it is likely that the Miami model overestimates NPP for ecosystems in arid and semi-arid regions. Further study based on sound datasets is needed to test this conceptual model.

Our data illustrate that both  $PUE_{max}$  and  $PUE_{min}$  varied greatly across the sites along the CGT. This runs counter to the research of Huxman *et al.* (2004) and Bai *et al.* (2008), which concluded a common spatial  $PUE_{max}$ . We ascribe this discrepancy to the different methods used to calculate  $PUE_{max}$ . In the work of Huxman *et al.* (2004) and Bai *et al.* (2008), the 'common spatial  $PUE_{max}$ ' was estimated as the slope of the relationship between annual precipitation and ANPP in the driest year, rather than the maximum value of the ratio of ANPP to annual precipitation. Actually, the slope indicates the sensitivity of ANPP to changes in annual precipitation, which may lead to incorrect conclusions when it is used as PUE (Verón *et al.* 2005). Furthermore, the 'slope' approach is based on the assumption



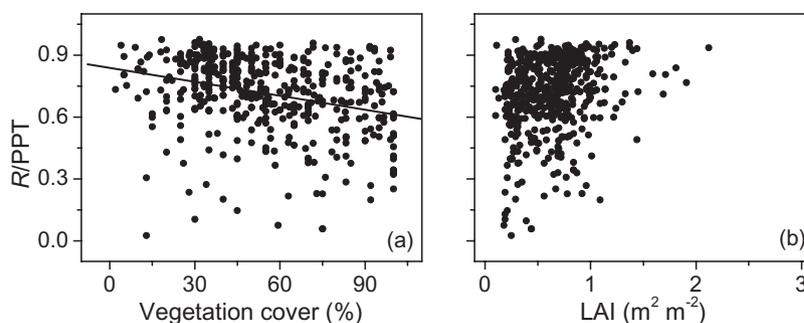
**Figure 7** A conceptual model (dashed line) describing the relationship between mean annual precipitation (MAP) and above-ground net primary productivity (ANPP) (or NPP) at continental and above scales. The solid line illustrates the Miami model (Leith, 1975). Changes of the slope of the relationship curve reflect the spatial variations in precipitation use efficiency (PUE) with MAP. Referring to the results of Paruelo *et al.* (1999) and this study, the broken line illustrates that the 'turning point' may change in a MAP range of 400–600 mm due to the effects of climate and soil conditions in different regions.

that PUE is highest in the driest year and lowest in the wettest year. Our data showed that this assumption is faulty in most cases. Thus, one should regard with caution the view that a common  $PUE_{max}$  or  $PUE_{min}$  exists among ecosystems.

Notably, the temporal variations in PUE decreased from  $PUE_{max}$  to  $PUE_{min}$ , resulting in a gradual increase in the significance between MAP and the three PUE measurements (Fig. 3). While we failed to identify the underlying mechanism, this result may have important implications regarding the water-use strategy of vegetation amid fluctuating climatic conditions.

### Factors affecting variations in PUE

We found a significant correlation between vegetation cover, an index of vegetation constraints (Yahdjian & Sala, 2006) and PUE along the climate gradient. This is consistent with the hypothesis of Paruelo *et al.* (1999), who proposed that vegetation constraints may result in a low PUE in dry areas. Further, the research of O'Connor *et al.* (2001) indicated that high vegetation cover would greatly reduce runoff and help conserve more water in the soil for plant growth. It is surprising that LAI, another measure of vegetation constraints, had only a minor effect on PUE, despite the fact that LAI plays a key role in determining ecosystem-level WUE for the grasslands of the CGT (Hu *et al.* 2008). To compare the effects of vegetation cover and LAI on PUE – assuming a balance between water input (precipitation) and output (evapotranspiration and runoff), with an omission of the downward infiltration of precipitation – we re-expressed equation 1 as



**Figure 8** Relationships between estimated ratio of runoff to precipitation ( $R/PPT$ ) and (a) vegetation cover, (b) Leaf area Index (LAI).

$$PUE = \frac{ANPP}{ET} \times \frac{ET}{PPT} = \frac{ANPP}{ET} \times \left(1 - \frac{R}{PPT}\right) \quad (2)$$

where  $ET$  is evapotranspiration and  $R$  is runoff. Assuming a fixed ratio of GPP to ANPP,  $a$ , equation 2 can be re-expressed as

$$PUE = \frac{aGPP}{ET} \times \left(1 - \frac{R}{PPT}\right) = aWUE \times \left(1 - \frac{R}{PPT}\right). \quad (3)$$

Based on the established relationship between LAI and ecosystem WUE ( $WUE = 0.459 \times LAI + 0.128$ ) (Hu *et al.* 2008), we estimated ecosystem WUE in equation 3 using LAI data. By setting a minimum of  $R/PPT$  as zero (i.e. all precipitation was lost via evapotranspiration), we estimated  $a$  as approximately 3, and then  $R/PPT$ . The result indicated that the estimated  $R/PPT$  was significantly correlated with PUE and vegetation cover ( $P < 0.001$ ) but not with LAI (Fig. 8), implying that LAI had much less impact on runoff, and hence on PUE, than vegetation cover.

This study found no significant relationship between PUE and VPD, suggesting that the mechanisms affecting WUE would shift from the leaf level to ecosystem level and, further, that it might be questionable to predict the response of ecosystem productivity to climate based merely on knowledge derived at the leaf level. Notably, soil texture and soil nutrients may also have some effects on spatial PUE through their influence on water-holding capacity and plant productivity (Le Houérou, 1984). Future research should pay special attention to the relationship between soil types and PUE in the study area.

Unlike results at the transect scale, the inter-annual variations in PUE at most of the sites were not correlated with annual precipitation. Further, vegetation cover also showed no significant effect on temporal PUE, reflecting distinct mechanisms controlling PUE at local and regional scales (Fig. 6). Bai *et al.* (2008) also found distinct patterns of between-site and between-year variations in PUE. They found that the temporal PUE negatively correlated with annual precipitation at the study site. In our study, however, PUE was negatively correlated with annual precipitation at only 2 of the 23 sites, indicating that, for most of China's temperate grasslands, increased annual precipitation would not reduce or improve PUE within given ecosystems. We speculate that distinct patterns of PUE at site and regional scales may be relevant to the varying importance of precipitation. At the regional scale, precipitation, beyond its direct impact, could improve ANPP and hence PUE through its

indirect effects on the composition and species diversity of plant communities (Paruelo *et al.* 1999; Yahdjian & Sala, 2006). At the site scale, however, without the greater range of biotic response provided by distinctive plant communities, the response of ANPP to annual precipitation would be greatly reduced (Lauenroth & Sala, 1992; Paruelo *et al.* 1999; Yahdjian & Sala, 2006). Furthermore, other factors beyond the total amount of annual precipitation affect the inter-annual variations in ANPP, including the seasonal distribution of precipitation, along with air temperature and the productivity of the previous year (Jobbagy & Sala, 2000; O'Connor *et al.* 2001; Oesterheld *et al.* 2001; Knapp *et al.* 2002). The effects of these factors may weaken the site-scale relationship between annual precipitation and ANPP and PUE.

The results of this study were derived from the sites where grazing activities had been largely excluded. This begs the question: how would the PUE pattern differ for most of the world's grasslands that experiencing regular grazing? Generally, grazing leads to some degree of degradation of grasslands. Such degradation is likely to cause a decline in PUE through changes in vegetation cover as well as soil structure and nutrient conditions (Le Houérou, 1984). As a result, the pattern of PUE for grasslands used for grazing would, to a large degree, be determined by the extent of the grazing pressure.

## CONCLUSIONS

Our study illustrates that the maximum PUE varied greatly across sites along the CGT, which runs counter to the prevailing view that a common maximum PUE exists across the ecosystems situated along a precipitation gradient. Vegetation cover was significantly correlated with the spatial variations in PUE, which was probably the main reason for the positive correlation between PUE and MAP. At the site scale, however, most ecosystems showed no significant correlation between annual precipitation and PUE, and higher vegetation cover did not significantly increase annual PUE. Based on the results of our study, as well as those of previous reports, we proposed a conceptual model to describe the relationship between MAP and ANPP (or NPP), with a sigmoid function. This approach might mark an improvement over reliance on the Miami model. In addition, our work highlights the importance of further studies to clarify the distinct mechanisms at work in controlling PUE at local and regional scales.

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