Front. Earth Sci. 2016, 10(4): 784–793
DOI 10.1007/s11707-016-0566-3

RESEARCH ARTICLE

Assessing spatio-temporal variations of precipitation-use efficiency over Tibetan grasslands using MODIS and *in-situ* observations

Zhengjia LIU[1,2], Mei HUANG (✉)[1]

1 Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
2 State Key Laboratory of Remote Sensing Science, Institute of Remote Sensing and Digital Earth, Chinese Academy of Sciences, Beijing 100101, China

Abstract Clarifying the spatial and temporal variations in precipitation-use efficiency (PUE) is helpful for advancing our knowledge of carbon and water cycles in Tibetan grassland ecosystems. Here we use an integrated remote sensing normalized difference vegetation index (NDVI) and *in-situ* above-ground net primary production (ANPP) measurements to establish an empirical exponential model to estimate spatial ANPP across the entire Tibetan Plateau. The spatial and temporal variations in PUE (the ratio of ANPP to mean annual precipitation (MAP)), as well as the relationships between PUE and other controls, were then investigated during the 2001–2012 study period. At a regional scale, PUE increased from west to east. PUE anomalies increased significantly (>0.1 $g\cdot m^{-2}\cdot mm^{-1}/10$ yr) in the southern areas of the Tibetan Plateau yet decreased (>0.02 $g\cdot m^{-2}\cdot mm^{-1}/10$ yr) in the northeastern areas. For alpine meadow, we obtained an obvious breaking point in trend of PUE against elevation gradients at 3600 m above the sea level, which showed a contrasting relationship. At the inter-annual scale, PUE anomalies were smaller in alpine steppe than in alpine meadow. The results show that PUE of Tibetan grasslands is generally high in dry years and low in wet years.

Keywords normalized difference vegetation index (NDVI), Tibetan Plateau, inter-annual variations, alpine grasslands, exponential model

Received May 5, 2015; accepted November 1, 2015

E-mail: huangm@igsnrr.ac.cn

1 Introduction

Precipitation is a crucial climate factor in controlling the carbon cycle of terrestrial ecosystems, especially that of grassland ecosystems (Bonan, 1997; Zhao et al., 2001; Fay et al., 2008). In recent decades, extreme precipitation and drought events have resulted in greater impacts on global grassland ecosystems (Zhao et al., 2001; Valladares and Pearcy, 2002). Climate change has caused significant variations in precipitation patterns, which have resulted in uncertain impacts on key processes that control ecosystem function and carbon cycling (Fay et al., 2008). Both instrumental observations and model simulations have identified amplified climate change in high mountain areas (Beniston et al., 1997; Findell et al., 2009), such as on the Tibetan Plateau (Baumann et al., 2009; Piao et al., 2011; Zhang et al., 2013). Alpine grasslands are the dominant vegetation types across the Tibetan Plateau, including alpine meadow and alpine steppe. It has been suggested that amplified climate change affects carbon and water cycling in Tibetan grassland ecosystems (Tao et al., 2014). Previous studies showed that annual variations in net primary production (NPP) on the Plateau were primarily controlled by changes in temperature and precipitation at the annual scale (Piao et al., 2006). In arid and semi-arid regions, precipitation is a limiting factor on biological diversity, plant growth, and NPP, and strongly determines above-ground biomass in Tibetan grasslands (Yang et al., 2008). Thus, precipitation is commonly used to account for spatial variations in vegetation productivity (Fensholt and Rasmussen 2011; Fensholt et al., 2013). Furthermore, precipitation amounts and patterns are especially important due to their association with soil water properties which are key controls of carbon exchange.

Precipitation-use efficiency (PUE), defined as the ratio of above-ground net primary production (ANPP) to mean annual precipitation (MAP), has been used as an indicator of the response of vegetation productivity to precipitation (Huxman et al., 2004; Bai et al., 2008). Although several field studies on PUE have been conducted on the Tibetan Plateau (Hu et al., 2010; Yang et al., 2010), they were restricted to point measurements at a limited number of field sites. For example, recent research reported that PUE in Tibetan grasslands showed a unimodal pattern across the precipitation gradients, with a temporally increasing trend in alpine steppe and a decreasing trend in alpine meadow (Yang et al., 2010). The field surveys and long-term *in-situ* observations were used for investigating the relationships between precipitation and PUE along a 4500 km long grassland transect (Hu et al., 2010). Both of the above studies were site-specific, and did not consider either long-term temporal changes or the spatial distribution in PUE over Tibetan grasslands. Thus, little is known about PUE in this area where key climate factors (e.g., precipitation and temperature) and PUEs are highly variable in both time and space. Given the sensitivity of grassland ecosystems to temporal and spatial variability in PUE, an investigation of these trends over a larger area and longer period would improve our understanding of the inherent variability and dynamics of alpine grasslands. This understanding would support the implementation of effective land management strategies and possibly sustain the development of the Tibetan Plateau. Understanding variations in PUE at different spatial and temporal scales and elevation gradients would also be helpful for forecasting the impacts of climate change on plant productivity.

Satellite remote sensing provides an opportunity to monitor changes in vegetation cover at regional and global scales, and therefore has the capability to upscale field observations. Although previous studies have employed linear regressions of Tibetan grassland above-ground biomass and vegetation indices to investigate primary productivity (Yang et al., 2009b), recent studies have shown that exponential equations are more effective in describing the relationship between ANPP and vegetation indices (Ma et al., 2010; Guo et al., 2012). Thus, we employed the exponential relationship between normalized difference vegetation index (NDVI) data and ground sampling observations to spatially upscale ANPP and then eventually calculate spatial distribution of PUE. We further investigated the spatial and temporal variations in PUE and the changes across elevation gradients. Specifically, this study aims to address the question of how the spatial and temporal distribution of PUE in alpine grasslands on the Tibetan Plateau is changing under global climatic warming.

2 Study area

The Tibetan Plateau is the highest, with an average elevation of more than 4000 m above sea level (ASL), and largest, with an area of 1.92×10^6 km^2 (Fig. 1), plateau on Earth. It is also referred to as the third pole, due to its dry and thin air, strong solar radiation, and low temperatures. The annual mean temperature is 0±5°C and annual precipitation is 250–550 mm. Alpine steppe and alpine meadow are the main grassland types, together covering 60% of the plateau (Yang et al., 2009a; Liu et al., 2015).

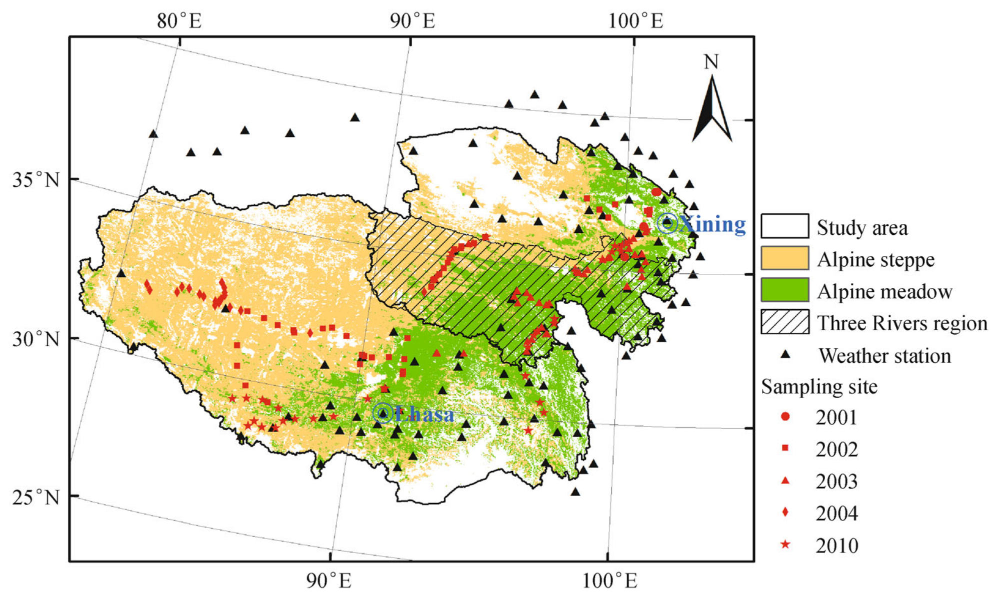

Fig. 1 Study area, locations of sampling sites and weather stations on the Tibetan Plateau. The base map is the 1:1,000,000 vegetation map of the Tibetan Plateau.

3 Materials and methods

3.1 ANPP data

In this study, ANPP data were obtained from two sources: 1) previously published summer (July and August) ANPP data at 112 sites from 2001–2004 (Yang et al., 2009a), and 2) the ANPP data collected during our survey in late July and early August 2010, at 34 sites (3 plots at each site). All sampling sites were located adjacent to homogeneous grasslands (at least 1 × 1 km). ANPP data from both sources were collected from a total of 146 sites (Fig. 1). Above-ground biomass was oven-dried to constant mass at 65°C and then weighed to an accuracy of 0.1 g. More information about sampling sites and protocols is available in the literature Hu et al. (2010) and Yang et al. (2010).

3.2 Remote sensing data and meteorological interpolation

The MODerate resolution Imaging Spectroradiometer (MODIS) NDVI products (MOD-13Q1) with a 250-m spatial resolution and a 16-day interval were obtained from the United States Geological Survey (USGS). The quality of the data was further improved by correcting for noise resulting from cloud contamination, atmospheric perturbations, and zenith angle changes. The maximum value composites (MVC) method (Holben, 1986) was used for obtaining maximum NDVI during the period 2001–2012.

The temperature and precipitation data from 71 meteorological stations across the Tibetan Plateau (Fig. 1) were obtained from the China Meteorological Administration (CMA). Annual mean precipitation was interpolated to a spatial resolution of 250 m using the Anusplin software package (Hutchinson et al., 2009; Liu et al., 2012; Yuan et al., 2014), which uses a thin plate smoothing spline method to interpolate spatially continuous climate data.

3.3 PUE calculation

LeHouerou (1984) originally introduced the rain-use efficiency (PUE in this study) concept. According to the definition, PUE in alpine grasslands was calculated as follows (Hu et al., 2010; Yang et al., 2010):

$$PUE = \frac{ANPP}{MAP}, \quad (1)$$

where PUE in $g \cdot m^{-2} \cdot mm^{-1}$; ANPP is above-ground net primary production ($g \cdot m^{-2}$) and MAP is the mean annual precipitation (mm).

3.4 Data analysis

We investigated the spatial and temporal distribution of PUE in alpine grasslands on the Tibetan Plateau using the following steps. Based on the geographical location information of sampling sites, we first extracted NDVI pixels (e.g., 3 × 3 homogeneous pixels) around the center of each site, and then averaged these values to obtain the mean NDVI of each site (Liu et al., 2014). Second, *in-situ* measured ANPP values were regressed against corresponding NDVI data (Guo et al., 2012). The relationship between measured ANPP and NDVI was used to produce a spatial ANPP inversion of alpine meadow and alpine steppe during the period 2001–2012. Third, we fitted linear regression trends to annual ANPP, PUE, and MAP using ordinary least squares regression (Wang et al., 2014), and then analyzed trends in the spatial and temporal variation of PUE over alpine grasslands. The Student t-test was applied to evaluate the null hypothesis that there was no overall trend. The following method was used for calculating the anomalies of ANPP or PUE.

$$\Delta X = X_i - \overline{X}, \quad (2)$$

where, X represents ANPP or PUE; ΔX is the anomaly; X_i is the i^{th} X; and $\overline{X}$ is the average of X. To analyze changes in PUE with increasing elevation, we calculated the average and standard deviation (SD) of PUE in alpine meadow and alpine steppe with altitude at 100-m intervals with a sample size of > 30,000 pixels.

4 Results

4.1 The ANPP model and spatial patterns of ANPP

The observed ANPP across all sites ranged from 7.0 to 347.5 $g \cdot m^{-2}$, with a mean value of 80.9 $g \cdot m^{-2}$. ANPP also varied across different grassland types. The mean ANPP was (120.9±70.8) $g \cdot m^{-2}$ for alpine meadow (58 sampling sites), which is significantly higher than the mean of (54.5±45.9) $g \cdot m^{-2}$ for alpine steppe (88 sampling sites). There was also a significant exponential relationship (R^2= 0.45, $P < 0.001$) between measured ANPP and the corresponding NDVI (Fig. 2):

$$ANPP = 21.41e^{2.424NDVI}. \quad (3)$$

Based on Eq. (3), spatial ANPP values of alpine meadow and alpine steppe for the entire region during 2001–2012 were estimated using NDVI data combined with a vegetation type map.

The spatial distribution of mean ANPP for 2001–2012 (see supplementary material, Fig. S1) reflects the southwest–northeast precipitation gradients across the study region. In the northeast (higher precipitation), most grassland ANPPs are > 150 $g \cdot m^{-2}$. However, in the northwest (lower precipitation), grassland ANPPs are typically much less than 50 $g \cdot m^{-2}$.

The mean ANPP for all alpine grasslands is 61.0 $g \cdot m^{-2}$

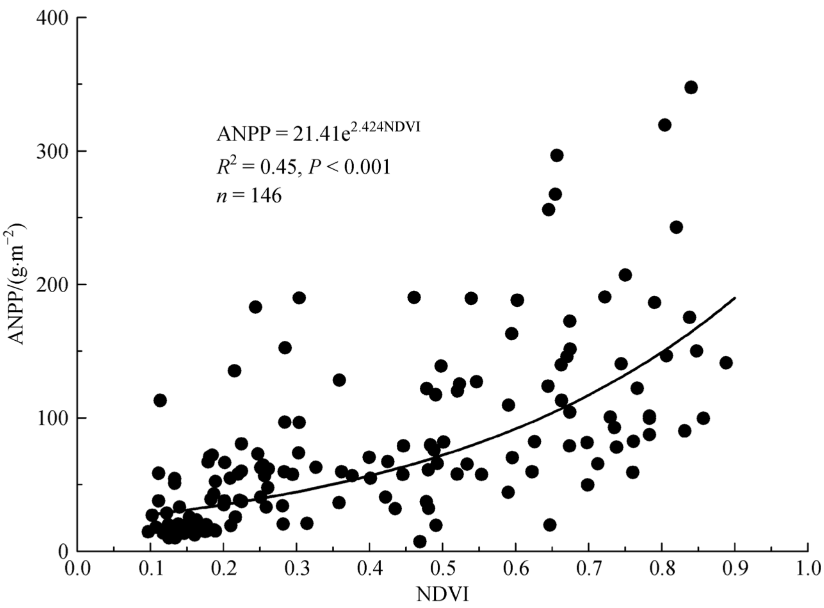

Fig. 2 Relationship between above-ground net primary production (ANPP) and Normalized Difference Vegetation Index (NDVI). The ANPP measured at sampling sites was used for developing the empirical function between measured ANPP and growing season NDVI to estimate ANPP at the regional scale.

Table 1 Statistical results of spatially averaged above-ground net primary production (ANPP) and precipitation-use efficiency (PUE) in alpine grasslands on the Tibetan Plateau during the period of 2001–2012

Grassland type	ANPP/($g \cdot m^{-2}$)				PUE/($g \cdot m^{-2} \cdot mm^{-1}$)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Alpine meadow	20.4	215.5	95.5	34.2	0.03	0.85	0.20	0.07
Alpine steppe	18.7	211.5	40.8	16.9	0.03	0.87	0.13	0.04
Total	18.7	215.5	61.0	36.2	0.03	0.87	0.16	0.06

(Table 1). Mean ANPP ((95.5±34.2) $g \cdot m^{-2}$) in alpine meadow is greater than that in alpine steppe ((40.8± 16.9) $g \cdot m^{-2}$). It seems that spatially-averaged ANPP values for alpine meadow and alpine steppe derived from MODIS NDVI are lower than the corresponding values from *in-situ* observations. This may be related to the different spatial resolutions of the datasets. Furthermore, our values for alpine meadow were higher and those for alpine steppe were lower than those previously observed, reporting ANPP values of 50.1 $g \cdot m^{-2}$ for alpine meadow and 90.8 $g \cdot m^{-2}$ for alpine steppe with an average of 68.8 g $\cdot m^{-2}$ for alpine grasslands (Yang et al., 2009b). The differences between the studies probably relate to remote sensing data and the ANPP equation. In this study, we used NDVI at a spatial resolution of 250 m rather than the MODIS-EVI data at 0.1° spatial resolution used by Yang et al. (2009b), and also an exponential rather than a linear equation to predict spatial ANPP.

4.2 Inter-annual variations in ANPP

The ANPP anomalies are much higher for alpine meadow than for alpine steppe in most years from 2001–2012 (see supplementary material, Fig. S2). The inter-annual ANPP anomalies in both areas have the same sign except during years 2001, 2009, and 2011. The anomalies in alpine steppe during 2001–2009 are negative or near zero, while those during 2010–2012 are consistently positive and larger in amplitude. The inter-annual variations of ANPP in alpine steppe show an increasing trend (slope = 0.108, R^2 = 0.490, $P < 0.05$). However, there is no statistically significant trend for alpine meadow over the study period.

4.3 The relationship between ANPP and MAP

Linear regression analysis of ANPP and MAP for the period 2000–2012 was used to explain precipitation effects on vegetation growth. A great spatial difference was observed (see supplementary material, Fig. S3), but ANPP and MAP were positively correlated in most alpine grassland regions. The correlation coefficients are greater than 0.68 ($P < 0.01$) in the northeast region and greater than 0.55 ($P < 0.05$) in the southern and most western regions of the Tibetan Plateau, implying that precipitation controls ANPP in these regions.

4.4 Spatial patterns and inter-annual variations in PUE

The averaged PUE over 2001–2012 for all alpine grasslands is 0.16 $g \cdot m^{-2} \cdot mm^{-1}$, as estimated from growing season MODIS NDVI observations (Table 1). The mean PUE is higher in alpine meadow ((0.20±0.07) $g \cdot m^{-2} \cdot mm^{-1}$) than in alpine steppe ((0.13±0.04) $g \cdot m^{-2} \cdot mm^{-1}$). The spatial distribution of annual mean PUE is shown in Fig. 3(a). PUE increases from west to east, reflecting spatial differences in NDVI. In the eastern region, PUE is typically > 0.3 $g \cdot m^{-2} \cdot mm^{-1}$. However, it is less than 0.2 $g \cdot m^{-2} \cdot mm^{-1}$ in the mid-western regions of the Plateau.

PUE shows a temporally decreasing trend (> 0.02 $g \cdot m^{-2} \cdot mm^{-1}$/10 yr) in the northeast regions (Fig. 3(b)), significant at the 95% confidence level (Fig. 3(c)). PUE is spatially homogeneous across the mid-west regions, except for some areas in the south where PUE has an increasing temporal trend (> 0.1 $g \cdot m^{-2} \cdot mm^{-1}$/10 yr), which is significant at the 95% confidence level in most areas (Fig. 3(c)).

Figure 4 shows average PUE (2001–2012) and its standard deviation as a function of altitude (in 100-m bands). There is no significant trend in PUE with increasing elevation for alpine steppe (R^2 = 0.13, P = 0.075). Many reports suggested a linear relationship between ANPP and MAP across environmental gradients (Lauenroth et al., 2000; Knapp et al., 2002), similar to the changes between ANPP and MAP for alpine steppe. For alpine meadow, we obtained different variation trends in PUE at 3600 m ASL. Above 3600 m ASL, PUE tends to gradually decrease with increasing elevation (R^2 = 0.98, $P < 0.001$), whereas it shows a weakly increasing trend (R^2 = 0.89, $P < 0.01$) below 3600 m ASL.

The spatially averaged PUE for alpine grasslands shows fluctuations with no significant inter-annual variations (for alpine meadow: slope = 0, $R^2 = 0.036$, $P = 0.553$; for alpine steppe: slope = 0, R^2 = 0.001, P = 0.919). Similar to the ANPP anomalies, we calculated PUE anomalies to study their inter-annual variability. PUE anomalies in alpine meadow and alpine steppe are of the same sign, except for 2002, 2003, and 2004 (Fig. 5). PUE anomalies are stronger in alpine meadow than in alpine steppe, except for 2004.

5 Discussion

5.1 Spatial variance analysis

Spatial variation trends in precipitation appear to be the principal driving factor for the observed trends in ANPP and PUE. Over the study period, precipitation shows a temporal increase in the northeastern regions of the Tibetan Plateau and a decreasing trend in the southern regions (see supplementary material, Fig. S4). Generally, precipitation is an important factor controlling changes in ANPP (Piao et al., 2006; Yang et al., 2010). Our investigations also support the idea that changes in precipitation determine the dynamics of spatial ANPP. Changes in ANPP in response to precipitation changes are opposite to those observed in PUE, as observed in the eastern and southern regions of the Tibetan Plateau (see supplementary material, Fig. S5(a) and Fig. 3(b)).

In the northeastern regions of the Plateau, characterized by higher precipitation, inter-annual ANPP variations show a significant positive trend at the 95% confidence level (Fig. S5(b)), especially in the Three Rivers region (Fig. 1). In this region, a series of ecological protection measures have been implemented during the past decade (Fan et al., 2010), such as artificial rainfall, the return of livestock pastures to natural grasslands, and the establishment of nature reserves. Since these measures have begun to take effect, ANPP in the Three Rivers region has increased significantly (95% confidence level). However, PUE trends presented here show a significant decrease, suggesting that arid regions with relatively high production potential are highly sensitive to variations in water availability (Huxman et al., 2004). In the Three Rivers region, increasing precipitation is conducive to vegetation growth; however, alpine grasslands do not utilize higher precipitation effectively. In these areas, it is likely that a larger fraction of total precipitation is lost to runoff or soil evaporation compared with vegetation transpiration (Hu et al., 2010). By analyzing observed runoff data from hydrological stations in the Three Rivers region, Huang et al. (2012) reported an increase at a rate of 1.949 $m^3 \cdot s^{-1} \cdot yr^{-1}$ at Tuotuo River station. In addition, water availability has an important effect on the cycling of nutrients, such as nitrogen and phosphorous, in arid climates (He et al., 2006). The change in nutrient cycling limits growth rates during anomalously wet periods (Huxman et al., 2004), potentially resulting in reduced PUE. In addition, PUE tends to be lower in regions below 3600 m ASL due to the influence of human activities, such as livestock grazing. Generally, grazing leads to degradation of grasslands (Fan et al., 2010), further resulting in a decline in soil nutrients.

In the southern parts of the Tibetan Plateau, ANPP decreased significantly (95% confidence level), while PUE increased significantly over the study period. Our results also indicate that the greatest changes in ANPP and precipitation generally occurred at the driest sites, while the smallest changes occurred at the most mesic sites (Huxman et al., 2004). In the southern regions, higher temperatures and reduced precipitation resulted in vegetation deterioration. Higher temperatures further exacerbated regional evaporation (Wang et al., 2007), especially soil moisture evaporation. However, PUE improved during

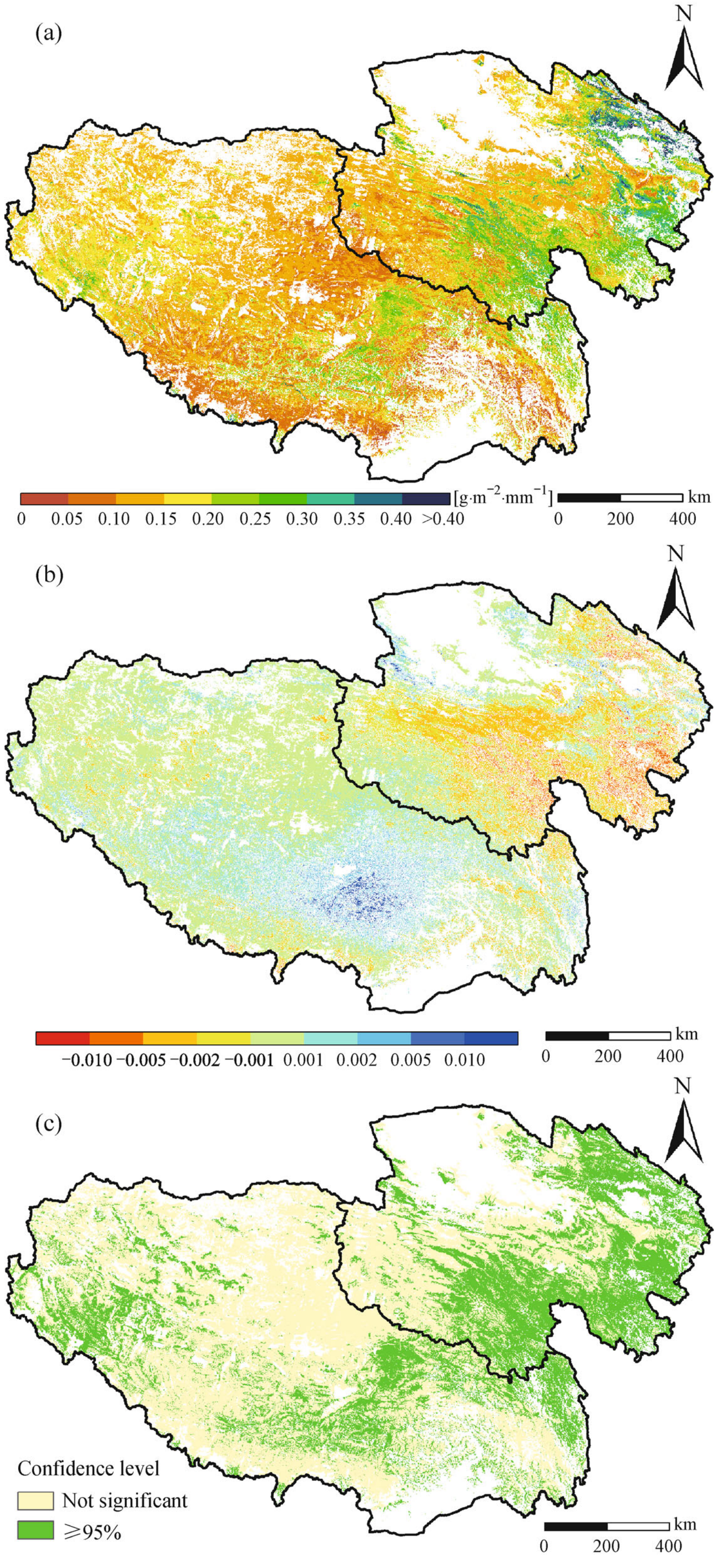

Fig. 3 (a) Spatial distribution of mean precipitation-use efficiency (PUE), (b) slope of inter-annual PUE, (c) and confidence level (t-test) in alpine grasslands on the Tibetan Plateau during the period 2001–2012.

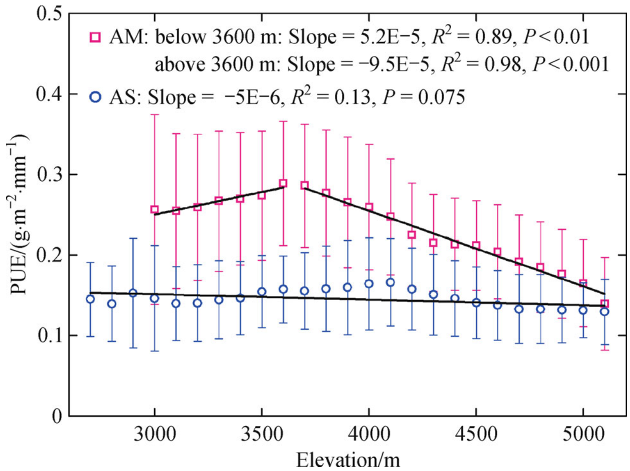

Fig. 4 Changes in precipitation-use efficiency (PUE) for alpine meadow (AM in pink color) and alpine steppe (AS in blue color) on the Tibetan Plateau with elevation. Error bars represent one standard deviation (SD) of pixels in each elevation interval with a sample size of > 30,000 pixels. The black solid lines are trend lines.

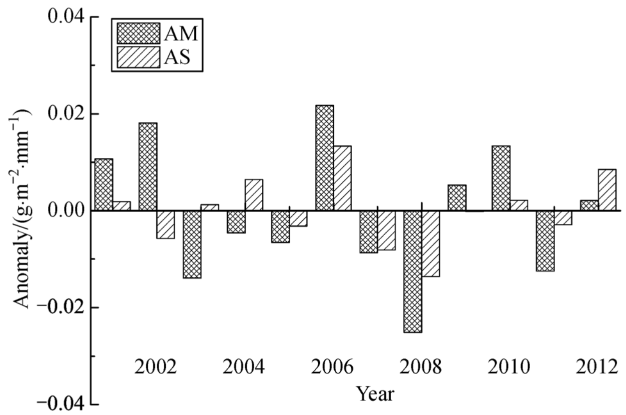

Fig. 5 Inter-annual variations in precipitation-use efficiency (PUE) anomalies (2001–2012) for alpine meadow (AM) and alpine steppe (AS).

periods of decreased precipitation and vegetation degeneration, owing to the fact that precipitation is utilized more efficiently in drier environments. Huxman et al. (2004) noted that strong water limitations on ANPP were linked to a common maximum PUE in all biomes at sites in the United States. In recent years, drying and warming climate trends in southern regions have influenced vegetation growth. The spatial correlation between ANPP and precipitation shows that MAP affects vegetation growth (see supplementary material, Fig. S3). Drought under global warming, with increased runoff and decreased precipitation (Fig. S4) intensified the severity of land degradation (Lotsch et al., 2005; Bunn and Goetz, 2006; Peng et al., 2011).

PUE shows almost no spatial variation across the entire mid-west Tibetan Plateau, suggesting that water-limited regions with low production potential are relatively insensitive to inter-annual variations in precipitation (Huxman et al., 2004).

5.2 Analysis of inter-annual variations in PUE

At the inter-annual scale, alpine meadow has higher PUE than alpine steppe. This is a result of adverse environmental conditions in alpine steppe, such as lower precipitation and lower temperatures with higher elevation. It is also related to differences in plant structure and function resulting from adaptation to a harsher living environment.

We analyzed the relationships between inter-annual variations in PUE, ANPP, and MAP from 2001 to 2012. No statistically significant correlation exists between PUE and ANPP (r = 0.542, P = 0.069 in alpine meadow; r = 0.051, P = 0.874 in alpine steppe) or between ANPP and MAP (r = −0.110, P = 0.734 in alpine meadow; r = 0.033, P = 0.919 in alpine steppe). However, comparison between PUE and MAP in alpine meadow and alpine steppe, using regional statistical methods, shows that PUE is significantly anti-correlated with MAP (for alpine meadow; r = −0.841, $P < 0.001$; for alpine steppe: r = −0.871, $P < 0.001$). Bai et al. (2008) reported similar results for temperate grasslands, finding that the temporal PUE correlated negatively with MAP. High vegetation cover would generally conserve more water and reduce runoff (O'Connor et al., 2001); however, climate change reduces the frequency of precipitation, which contributes to the under-utilization of precipitation by vegetation (Wu et al., 2012). Our results confirm the assumption that PUE is highest in the driest years and lowest in the wettest years, as also observed for Tibetan grasslands. Nitrogen availability and other factors have constrained the response of production potential to increased MAP, resulting in lower PUE in humid environments (Huxman et al., 2004; Bai et al., 2008; Yang et al., 2010). Generally, soil carbon content is positively related to soil nitrogen availability, and PUE is positively related to soil carbon content in grassland ecosystems (Yang et al., 2010).

Present results imply there may be a MAP threshold at which point minimum MAP exists to meet the requirement of maximum vegetation growth for each grassland type (alpine meadow (AM) or alpine steppe (AS)) at the inter-annual scale. When MAP is closer to the threshold, vegetation is supposed to have a higher PUE (Fig. 6). For example, although both MAP_{AM} and MAP_{AS} have their lowest values in 2006 (433.0 and 286.4 mm, respectively), PUE_{AM} and PUE_{AS} have their highest values during the same year (0.224 and 0.148 $g \cdot m^{-2} \cdot mm^{-1}$, respectively). However, MAP_{AM} and MAP_{AS} are both highest in 2008 (543.1 and 364.3 mm, respectively), when PUE_{AM} and

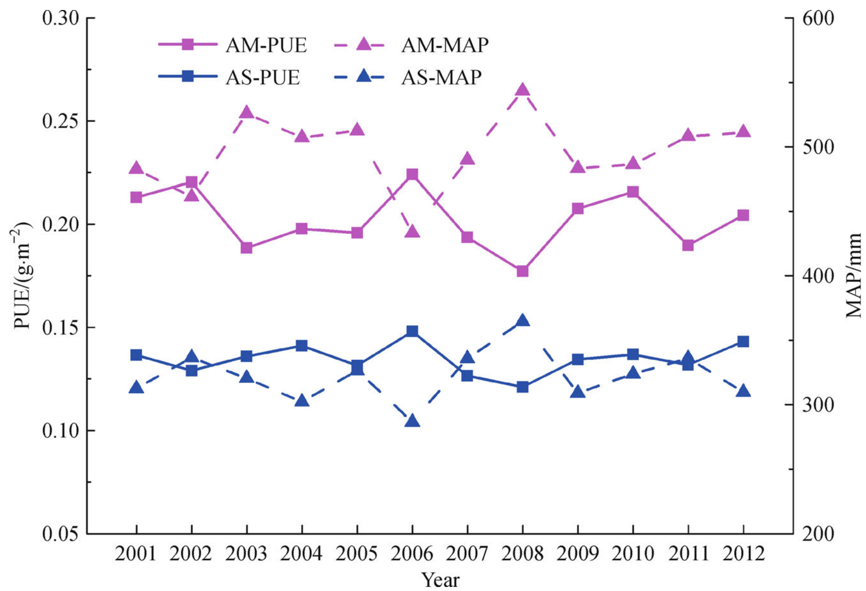

Fig. 6 Inter-annual variations in precipitation-use efficiency (PUE) and the mean annual precipitation (MAP) in alpine meadow (AM, pink) and alpine steppe (AS, blue) during the period of 2001–2012.

PUE_{AS} are both lowest (0.177 and 0.121 g·m^{-2}·mm^{-1}, respectively). The reliability of the assumption may need to be further validated combined with more measured data and other methods in the future.

6 Conclusions

By combining remote sensing data with *in-situ* observations, we greatly expanded the ANPP time series. This allowed us to exploit more spatial information to make up for deficiencies in *in-situ* observations, such as the limited number of observation years and non-uniform distribution of observation sites. This study presented an exponential model for estimating spatial ANPP. The spatial ANPP with MAP allowed us to better explore the spatial patterns of PUE. Alpine meadow had higher PUE than alpine steppe at the inter-annual scale. The inter-annual changes in PUE are negatively correlated with MAP for both alpine meadow ($r = -0.841$, $P < 0.001$) and alpine steppe ($r = -0.871$, $P < 0.001$). Changes in MAP likely acted as the major controlling factor of observed changes in PUE on the Tibetan Plateau. This study suggests that the relationship between MAP and PUE should be considered in ecological models to accurately reflect the effects of global climate change on carbon and water cycling across the Tibetan Plateau. At the regional scale, PUE increased from west to east. PUE anomalies in the southern regions of the Plateau increased significantly (>0.1 g·m^{-2}·mm^{-1}/10 yr), whereas those in the northeast decreased (>0.02 g·m^{-2}·mm^{-1}/10 yr), both at the 95% confidence level. No significant changes in PUE were observed in alpine steppe ($R^2 = 0.13$, $P = 0.075$) as a function of altitude. PUE in alpine meadow, along with elevation gradients, showed a breaking point in relationship at 3600 m ASL.

Acknowledgements We thank Hongsheng Liu, Xiujing Yang, Lei Li, Yibo Liu, Weiliang Fan, Hui Zhan and others for help with sampling. This study was supported by the National Natural Science Foundation of China (Grant Nos. 41271118, 41471227, and 41371013) and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA05050209). We are grateful to Yuanhe Yang and coauthors for sharing their *in-situ* data, and thank Drs. Muhammad Hasan Ali Baig and A. Gonsamo for providing valuable suggestions.

Supplementary material is available in the online version of this article at http://dx.doi.org/10.1007/s11707-016-0566-3 and is accessible for authorized users.

References

Bai Y, Wu J, Xing Q, Pan Q, Huang J, Yang D, Han X (2008). Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology, 89(8): 2140–2153

Baumann F, He J, Schmidt K, Kuhn P, Scholten T (2009). Pedogenesis, permafrost, and soil moisture as controlling factors for soil nitrogen and carbon contents across the Tibetan Plateau. Glob Change Biol, 15(12): 3001–3017

Beniston M, Diaz H, Bradley R (1997). Climatic change at high elevation sites: an overview. Clim Change, 36(3–4): 233–251

Bonan G B (1997). Effects of land use on the climate of the United States. Clim Change, 37(3): 449–486

Bunn A G, Goetz S J (2006). Trends in satellite-observed circumpolar photosynthetic activity from 1982 to 2003: the influence of seasonality, cover type, and vegetation density. Earth Interact, 10

(12): 1–19

Fan J, Shao Q, Liu J, Wang J, Harris W, Chen Z, Zhong H, Xu X, Liu R (2010). Assessment of effects of climate change and grazing activity on grassland yield in the Three Rivers Headwaters Region of Qinghai–Tibet Plateau, China. Environ Monit Assess, 170(1–4): 571–584

Fay P A, Kaufman D M, Nippert J B, Carlisle J D, Harper C W (2008). Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change. Glob Change Biol, 14(7): 1600–1608

Fensholt R, Rasmussen K (2011). Analysis of trends in the Sahelian 'rain-use efficiency' using GIMMS NDVI, RFE and GPCP rainfall data. Remote Sens Environ, 115(2): 438–451

Fensholt R, Rasmussen K, Kaspersen P, Huber S, Horion S, Swinnen E (2013). Assessing land degradation/recovery in the African Sahel from long-term earth observation based primary productivity and precipitation relationships. Remote Sens, 5(2): 664–686

Findell K L, Pitman A J, England M H, Pegion P J (2009). Regional and global impacts of land cover change and sea surface temperature anomalies. J Clim, 22(12): 3248–3269

Guo Q, Hu Z, Li S, Li X, Sun X, Yu G (2012). Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: effects of mean annual precipitation and its seasonal distribution. Glob Change Biol, 18(12): 3624–3631

He J, Fang J, Wang Z, Guo D, Flynn D F, Geng Z (2006). Stoichiometry and large-scale patterns of leaf carbon and nitrogen in the grassland biomes of China. Oecologia, 149(1): 115–122

Holben B N (1986). Characteristics of maximum-value composite images from temporal AVHRR data. Int J Remote Sens, 7(11): 1417–1434

Hu Z, Yu G, Fan J, Zhong H, Wang S, Li S (2010). Precipitation-use efficiency along a 4500-km grassland transect. Glob Ecol Biogeogr, 19(6): 842–851

Huang L, Shao Q, Liu J (2012). Forest restoration to achieve both ecological and economic progress, Poyang Lake basin, China. Ecol Eng, 44(3): 53–60

Hutchinson M F, McKenney D W, Lawrence K, Pedlar J H, Hopkinson R F, Milewska E, Papadopol P (2009). Development and testing of Canada-wide interpolated spatial models of daily minimum-maximum temperature and precipitation for 1961–2003. J Appl Meteorol Climatol, 48(4): 725–741

Huxman T E, Smith M D, Fay P A, Knapp A K, Shaw M R, Loik M E, Smith S D, Tissue D T, Zak J C, Weltzin J F (2004). Convergence across biomes to a common rain-use efficiency. Nature, 429(6992): 651–654

Knapp A K, Fay P A, Blair J M, Collins S L, Smith M D, Carlisle J D, Harper C W, Danner B T, Lett M S, McCarron J K (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science, 298(5601): 2202–2205

Lauenroth W K, Burke I C, Paruelo J M (2000). Patterns of production and precipitation-use efficiency of winter wheat and native grasslands in the central Great Plains of the United States. Ecosystems (N Y), 3 (4): 344–351

LeHouerou H N (1984). Rain use efficiency: a unifying concept in arid-land ecology. J Arid Environ, 7(3): 213–247

Liu Z, Shao Q, Wang S (2015). Variation of alpine grasslands and its response to climate warming in the Tibetan Plateau since the 21st Century. Arid Land Geography, 38(2): 275–282 (in Chinese)

Liu Z, Wang L, Wang S (2014). Comparison of different GPP Models in China using MODIS image and China FLUX Data. Remote Sens, 6 (10): 10215–10231

Liu Z, Yu X, Wang S, Shang G (2012). Comparative analysis of three covariates methods in thin-plate smoothing splines for interpolating precipitation. Progress in Geography, 31(1): 56–62 (in Chinese)

Lotsch A, Friedl M A, Anderson B T, Tucker C J (2005). Response of terrestrial ecosystems to recent Northern Hemispheric drought. Geophys Res Lett, 32(6): L06705

Ma W H, Fang J Y, Yang Y H, Mohammat A (2010). Biomass carbon stocks and their changes in northern China's grasslands during 1982–2006. Sci China Life Sci, 53(7): 841–850

O'Connor T, Haines L, Snyman H (2001). Influence of precipitation and species composition on phytomass of a semi-arid African grassland. J Ecol, 89(5): 850–860

Peng S, Chen A, Xu L, Cao C, Fang J, Myneni R B, Pinzon J E, Tucker C J, Piao S (2011). Recent change of vegetation growth trend in China. Environ Res Lett, 6(4): 044027

Piao S, Cui M, Chen A, Wang X, Ciais P, Liu J, Tang Y (2011). Altitude and temperature dependence of change in the spring vegetation green-up date from 1982 to 2006 in the Qinghai-Xizang Plateau. Agric For Meteorol, 151(12): 1599–1608

Piao S, Fang J, He J (2006). Variations in vegetation net primary production in the Qinghai-Xizang Plateau, China, from 1982 to 1999. Clim Change, 74(1–3): 253–267

Tao J, Zhang Y, Zhu J, Jiang Y, Zhang X, Zhang T, Xi Y (2014). Elevation-dependent temperature change in the Qinghai–Xizang Plateau grassland during the past decade. Theor Appl Climatol, 117 (1–2): 61–71

Valladares F, Pearcy R (2002). Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Niño year. Plant Cell Environ, 25 (6): 749–759

Wang K, Wang P, Li Z, Cribb M, Sparrow M (2007). A simple method to estimate actual evapotranspiration from a combination of net radiation, vegetation index, and temperature. J Geophys Res, 112 (D15): D15107

Wang S, Yu X, Liu Z (2014). Spatiotemporal patterns of NDVI and its responses to temperature and precipitation over Yimeng Mountainous Area. Remote Sensing Technology and Application, 29(1): 61–68 (in Chinese)

Wu C, Chen J M, Pumpanen J, Cescatti A, Marcolla B, Blanken P D, Ardö J, Tang Y, Magliulo V, Georgiadis T, Soegaard H, Cook D R, Harding R J (2012). An underestimated role of precipitation frequency in regulating summer soil moisture. Environ Res Lett, 7 (2): 024011

Yang Y, Fang J, Fay P A, Bell J E, Ji C (2010). Rain use efficiency across a precipitation gradient on the Tibetan Plateau. Geophys Res Lett, 37: L15702

Yang Y, Fang J, Ji C, Han W (2009a). Above- and below ground biomass allocation in Tibetan grasslands. J Veg Sci, 20(1): 177–184

Yang Y, Fang J, Ma W, Wang W (2008). Relationship between

variability in aboveground net primary production and precipitation in global grasslands. Geophys Res Lett, 35(23): L23710
Yang Y, Fang J, Pan Y, Ji C (2009b). Aboveground biomass in Tibetan grasslands. J Arid Environ, 73(1): 91–95
Yuan W, Xu B, Chen Z, Xia J, Xu W, Chen Y, Wu X, Fu Y (2014). Validation of China-wide interpolated daily climate variables from 1960 to 2011. Theor Appl Climatol, 119(3–4): 689–700
Zhang G, Zhang Y, Dong J, Xiao X (2013). Green-up dates in the Tibetan Plateau have continuously advanced from 1982 to 2011. Proc Natl Acad Sci USA, 110(11): 4309–4314
Zhao M, Pitman A, Chase T (2001). The impact of land cover change on the atmospheric circulation. Clim Dyn, 17(5–6): 467–477