International Journal of Remote Sensing

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tres20>

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Published online: 19 Aug 2013.

To cite this article: Huixia Li, Guohua Liu & Bojie Fu (2013) Spatial variations of rain-use efficiency along a climate gradient on the Tibetan Plateau: A satellite-based analysis, International Journal of Remote Sensing, 34:21, 7487-7503, DOI: [10.1080/01431161.2013.826839](https://doi.org/10.1080/01431161.2013.826839)

To link to this article: <http://dx.doi.org/10.1080/01431161.2013.826839>

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Spatial variations of rain-use efficiency along a climate gradient on the Tibetan Plateau: A satellite-based analysis

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(Received 22 November 2012; accepted 23 April 2013)

Understanding the spatial relationship between rain-use efficiency (RUE) and climate conditions is crucial for predicting the steady-state responses of an ecosystem to climate variations. We clarified the spatial variations of RUE in different ecosystems along both mean annual precipitation (MAP) and mean annual temperature (MAT) gradients in the Three-river Headwaters Region (THR) of China. RUE displayed a unimodal pattern along a MAP gradient across different ecosystems, with a higher value in forest, shrub, and less-arid alpine meadow than in alpine steppe, alpine talus vegetation, and more-arid alpine meadow. RUE followed an increasing trend along the MAT gradient both in a given ecosystem and across various ecosystems. The varying maximum RUE (RUE_{max}) with temperature suggested that no common spatial RUE_{max} existed across different ecosystems in the driest pixels. With the mutual interference between precipitation and temperature excluded, RUE increased both with precipitation at a given temperature level and with temperature at a given precipitation level in cold and dry ecosystems, while RUE probably decreased both with precipitation at a given temperature level and with temperature at a given precipitation level in warm and humid ecosystems. Our study illuminates the response of RUE to climate variations in alpine areas based on the spatial model, aiming to improve our understanding of the interactions between vegetation and climate conditions and the potential trade-offs between the ecosystem's carbon and water.

1. Introduction

Ecosystem structure and function are strongly controlled by climate conditions at the regional or global scale (Woodward 1987; Stephenson 1990; Gritti et al. 2010). Clarifying the relationship between productivity and precipitation is crucial to understanding the response of ecosystems to global change (Fang et al. 2001; Huxman et al. 2004; Yang et al. 2008). Rain-use efficiency (RUE), defined as the ratio of aboveground net primary productivity (ANPP) to precipitation, provides a simple but useful index to improve our knowledge of the interactions between vegetation and precipitation (Paruelo et al. 1999; Huxman et al. 2004; Bai et al. 2008), thus the potential trade-offs between an ecosystem's carbon and water. The spatial patterns of RUE based on average productivity and precipitation data set (Paruelo et al. 1999) can explicitly present the steady-state of ecosystem water use and thus ecosystem functioning. Furthermore, understanding the spatial variation in

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RUE is essential for decision-making and practices in ecosystem management (Prince, De Colstoun, and Kravitz 1998; Huxman et al. 2004; Bai et al. 2008; Hu et al. 2010).

As a typical alpine area, the Tibetan plateau is considered to be a natural barrier of the ecosystem of China. The degradation of the ecosystem is threatening the ecological security of China and beyond (Qian, Fu, and Pan 2010). Thus since 2005, China's government has invested RMB 7500 million (equal to about US\$1.176 billion) to protect and construct the ecosystem in the Three-river Headwaters Region (THR) of the Tibetan plateau. Meanwhile, many studies have been conducted to advance our understanding of the spatial pattern and temporal trend of vegetation on the Tibetan plateau (Yang and Piao 2006; Zhang et al. 2007; Liu, Xun, and Shao 2008; Li, Liu, and Fu 2011), but little attention has been paid to variations in RUE along a climatic gradient. Recently, Yang et al. (2010) examined RUE variations across a precipitation gradient on the Tibetan plateau, which provided the initial knowledge on the relationship between RUE and precipitation in the alpine grassland of China. However, their study discounted the impact of temperature that was recognized as another crucial climate factor for alpine vegetation (Yang and Piao 2006; Chen et al. 2010; Li, Liu, and Fu 2011). Additionally, Yang et al. (2010) described an RUE pattern based on sampling data at site scale, which unavoidably brought uncertainties in field measurements based on one or a few years. As the authors mentioned, the sample sites were along major roads due to the extreme climate conditions and sparse road networks on the Tibetan plateau (Yang et al. 2010), which would also weaken the reliability of the results due to human disturbance.

Much work has been done to address the relationship between RUE and precipitation at both temporal and spatial scales (Paruelo et al. 1999; Huxman et al. 2004; Bai et al. 2008; Hu et al. 2010). Existing studies have basically reached an agreement that RUE negatively correlates with precipitation based on a temporal model (Huxman et al. 2004; Bai et al. 2008; Hu et al. 2010), but a general pattern of RUE along a spatial gradient of precipitation is still unavailable (Yang et al. 2010). Sala et al. (1988), Lauenroth and Sala (1992), and Knapp and Smith (2001) reported a constant spatial RUE with increasing precipitation; however, Paruelo et al. (1999) and Yang et al. (2010) presented a unimodal pattern of RUE across the spatial gradient of precipitation. Nevertheless, Le Houérou (1984), Prince, De Colstoun, and Kravitz (1998), Bai et al. (2008), and Hu et al. (2010) detected an increase in RUE with annual precipitation, while Huxman et al. (2004) showed a decreased RUE in space caused by increased precipitation in North America. Furthermore, none of the above studies took temperature into account, which may mask the relationship between RUE and precipitation. As Chen et al. (2010) concluded, temperature is the dominant factor for vegetation change in alpine grassland. So one may ask what the relationship is between RUE and temperature, and further, how RUE responds to precipitation at a given temperature level. Therefore, illuminating the responses of RUE to variations in precipitation and temperature will achieve an important improvement in our understanding of the relationship between RUE and climate conditions and the trade-offs between carbon and water cycles of the ecosystem.

In this study, we examined variation in RUE along a precipitation gradient and a temperature gradient both across various ecosystems and within a given ecosystem in THR, using a *Système Pour l'Observation de la Terre Vegetation* (SPOT-VEG) normalized difference vegetation index (NDVI) data set (proxy for ANPP) from 1998 to 2010, vegetation maps at a scale of 1:1,000,000 and climate data obtained from 16 weather stations in or near to THR. Meanwhile, we fitted the RUE trend on wet edge and dry edge along a temperature gradient and on warm edge and cold edge along a precipitation gradient to investigate the responses of RUE to precipitation at a given temperature level and to temperature at a

given precipitation level. In addition, we examined whether there existed a common spatial maximum RUE (RUE_{max}) among different ecosystems in the driest pixels (dry edge) along the temperature gradient, based on the hypothesis proposed by Huxman et al. (2004) and Bai et al. (2008) that there is convergence to a common spatial RUE_{max} among various ecosystems during the driest year.

2. Materials and methods

2.1. Study area

This study was conducted in THR, which is located in the hinterland of the Tibetan plateau (Figure 1), with a mean elevation of 4000 m and an area of about 36×10^4 km² (Tang et al. 2007). THR is also known as ‘China’s water tower’ since three of China’s largest rivers, the Yangtze, Yellow, and Lancang, originate here. As an important part of the Tibetan plateau, this region is characterized by a sparse population with a population density below two per km² and an alpine climate that is warm and humid in summer and cold and dry in winter. Based on the interpolation results of meteorological data (1998–2010), the mean annual temperature (MAT) in this area ranges from -4.5°C to 6.2°C , with minimum mean monthly temperature in January and maximum in July, and mean annual precipitation (MAP) ranges from about 350 to 720 mm, more than 85% of which occurs during the short growing season from May to September in synchrony with peak temperature. The vegetation types are coniferous forest, shrub, alpine meadow, alpine steppe, and alpine talus vegetation from southeast to northwest with decreasing annual precipitation and annual temperature (Zhang et al. 2007), in which alpine meadow and alpine steppe is calculated at about 80% of the total land. Owing to the high elevation, the vegetation ecosystems in this area may be more frangible and sensitive to climate change, making it an important region for studying the response of vegetation to global change.

Figure 1. Location of the Three-river Headwaters Region.

2.2. Data collection

2.2.1. The NDVI data set

NDVI, which takes advantage of the spectral response difference of chlorophyll-loaded vegetal tissues between the red and infrared channels has been widely used to detect vegetation change in both productivity and density (Prince 1991a; Schmidt and Karnieli 2000; Wang et al. 2004; Li, Liu, and Fu 2011). For relatively homogeneous biomes in arid and semi-arid ecosystems such as the Tibetan plateau, a near-linear relation may be assumed to exist between primary productivity and NDVI (Prince 1991b; Du Plessis 1999; Wessels et al. 2004; Li and Liu 2007). Based on this theory, the use of seasonally or annually summed NDVI (Σ NDVI) as an appropriate proxy for ANPP is generally accepted (Prince, De Colstoun, and Kravitz 1998; Wessels et al. 2007; Bai and Dent 2009; Fabricante, Oosterheld, and Paruelo 2009; Fensholt and Rasmussen 2011), with the advantage that it may be directly monitored by Earth's observation (EO) methods (Prince, De Colstoun, and Kravitz 1998; Fensholt and Rasmussen 2011). The high elevation and harsh climate make it difficult to get long-term and large-area primary productivity data by field survey on the Tibetan plateau. Thus EO data sets have been widely used to estimate regional vegetation biomass or productivity in this region, with the advantage of high efficiency and low cost (Niu and Ni 2003; Zhang et al. 2010). Recently, Fensholt et al. (2006) found that EO-driven NPP products may introduce more noise compared with Σ NDVI when validated against *in situ* measured ANPP in semi-arid ecosystems. We thus calculated RUE as the ratio of growing season (from May to September) total NDVI (Σ NDVI-G) to precipitation in the same period ($\text{RUE} = \Sigma\text{NDVI-G}/\text{P}$).

SPOT-VEG 10 day composite NDVI images (S10 products) at 1 km² resolution, which are synthesized following a maximum value compositing (MVC) procedure as described by Holben (1986), and distributed by the Vlaamse Instelling Voor Technologisch Onderzoek (VITO; <http://www.vgt.vito.be/>), were used to calculate mean Σ NDVI-G (1998–2010) and thus mean RUE in this study. All NDVI images derived from primary SPOT-VGT products were corrected for surface reflectance, molecular and aerosol scattering, and water vapour, ozone, and other gas absorption following procedures described by Duchemin et al. (2002). NDVI values in S10 products are converted to a digital number in the range 0–255, so we calculated the real NDVI value based on the relation between digital number and real NDVI ($\text{DN} = (\text{NDVI} + 0.1)/0.004$).

2.2.2. Climate data

Monthly precipitation and monthly temperature data sets of 16 weather stations in or near to the THR from 1998 to 2010 were obtained from the China Meteorological Data Sharing Service System (<http://cdc.cma.gov.cn/index.jsp>). Then the point data were interpolated into raster in ArcMap using an inverse distance-weighted (IDW) method at 0.1° resolution. Three rasters were prepared using raster calculator, including mean precipitation in the growing season (May–September) (Chen et al. 2010) and MAP and MAT from 1998 to 2010. The reliability of the inverse distance-weighted method was estimated using cross-validation among the 16 weather stations. The mean absolute errors (MAEs) of mean growing season precipitation, MAP, and MAT are 34 mm, 49 mm, and 1.67°C, respectively. Accordingly, the root mean square errors (RMSEs) are 38 mm, 54 mm, and 1.95°C, respectively. Growing season precipitation was used to calculate RUE, while annual precipitation and annual temperature were used to analyse the variation of RUE along a climate gradient.

2.2.3. Vegetation map

A vegetation map at a scale of 1:1,000,000 available on the data sharing infrastructure of earth system science (<http://www.geodata.cn>) was adapted to analyse the RUE patterns of different vegetation types along a climate gradient. Based on the primary category legend, the vegetation types in the study area were classified into five types including forest, shrub, alpine meadow, alpine steppe, and alpine talus vegetation. A tiny minority of swamp meadow, desert steppe, and alpine cushion vegetation was categorized into alpine meadow, alpine steppe, and alpine talus vegetation, respectively.

2.3. Data analysis

Non-vegetation area was excluded based on the vegetation map before we analysed the spatial patterns of RUE and Σ NDVI-G. We normalized RUE and Σ NDVI-G to make them more comparable in a coordinate system ($\text{normalized RUE} = (\text{RUE}_i - \text{RUE}_{\min}) / (\text{RUE}_{\max} - \text{RUE}_{\min})$, $\text{normalized } \Sigma\text{NDVI-G} = (\Sigma\text{NDVI-G}_i - \Sigma\text{NDVI-G}_{\min}) / (\Sigma\text{NDVI-G}_{\max} - \Sigma\text{NDVI-G}_{\min})$). Then we compared the variations in RUE and Σ NDVI-G along a precipitation gradient at a regional scale using their cubic polynomial fitting curves of all vegetation pixels.

We also analysed the RUE variations in the vegetation area along a temperature gradient with MAT on the horizontal axis and RUE on the vertical axis. Then we compared the RUE trend among different ecosystems along a spatial gradient of precipitation or temperature using scatter plots and tried to answer the question of whether RUE variation along a precipitation or temperature gradient for a given ecosystem differs from that across different ecosystems.

To further understand the effect of precipitation (or temperature) on RUE under similar temperature (or precipitation) conditions, we divided temperature into 108 equals at intervals of 0.1°C (the subsequent results did not depend on this value) and calculated maximum RUE at a given temperature level ($\text{RUE}_{\max_t}$), mean RUE at a given temperature level ($\text{RUE}_{\text{mean}_t}$), RUE with maximum precipitation ($\text{RUE}_{\text{wetedge}}$), and RUE with minimum precipitation ($\text{RUE}_{\text{dryedge}}$) for each interval, then created a scatter plot with MAT on the horizontal axis and RUE on the vertical axis and fitted the variation trend of $\text{RUE}_{\max_t}$, $\text{RUE}_{\text{mean}_t}$, $\text{RUE}_{\text{wetedge}}$, and $\text{RUE}_{\text{dryedge}}$ along a temperature gradient using the cubic polynomial method. Similarly, we divided precipitation into 75 equals with an interval of 5 mm (the subsequent results did not depend on this value) and calculated maximum RUE at a given precipitation level ($\text{RUE}_{\max_p}$), mean RUE at a given precipitation level ($\text{RUE}_{\text{mean}_p}$), RUE with maximum temperature ($\text{RUE}_{\text{warmedge}}$), and RUE with minimum temperature ($\text{RUE}_{\text{coldedge}}$) for each interval, then created a scatter plot with MAP on the horizontal axis and RUE on the vertical axis and fitted the variation trend of $\text{RUE}_{\max_p}$, $\text{RUE}_{\text{mean}_p}$, $\text{RUE}_{\text{warmedge}}$, and $\text{RUE}_{\text{coldedge}}$ along a precipitation gradient using the cubic polynomial method.

3. Results

3.1. Spatial variation in RUE along a precipitation gradient

Average RUE decreased markedly from east to west and average Σ NDVI-G decreased from southeast to northwest (Figure 2). Along a precipitation gradient across various ecosystems, RUE exhibited a unimodal pattern with low values at both the dry and wet ends and peaked around 600 mm ($R^2 = 0.38$, $p < 0.001$), and Σ NDVI-G showed a similar pattern with a

Figure 2. Normalized RUE (a) and normalized Σ NDVI-G (b).

peak at 640 mm ($R^2 = 0.60$, $p < 0.001$) (Figure 3). In the areas where MAP was less than 600 mm, an increase in precipitation led to an increase in both RUE and Σ NDVI-G. Where MAP was between 600 and 640 mm, an increase in MAP caused an increase in Σ NDVI-G but a decrease in RUE. Where MAP was more than 640 mm, both RUE and Σ NDVI-G declined with increasing MAP.

Averaging RUE at vegetation-type level, this followed a descending order of forest, shrub, alpine meadow, alpine talus vegetation, and alpine steppe (Figure 4). The responses of RUE to MAP change varied among different vegetation types (Figure 5). The most marked increase in RUE along the MAP gradient was for alpine steppe ($R^2 = 0.71$, $p < 0.001$). RUE also increased with MAP in alpine talus vegetation, but the trend was not as steep as that of alpine steppe ($R^2 = 0.09$, $p > 0.05$). In contrast, RUE showed a non-significant declining trend with MAP in forest ($R^2 = 0.08$, $p > 0.05$) and shrub ($R^2 = 0.18$, $p > 0.05$). The spatial trend of RUE in alpine meadow was similar to that across different ecosystems, following a unimodal pattern with a peak around 600 mm ($R^2 = 0.83$, $p < 0.001$).

3.2. Spatial variation in RUE along a temperature gradient

From the scatter plot at the regional scale with MAT on the horizontal axis and RUE on the vertical axis (Figure 6), we determined that there was a marked correlation (positive) between RUE and MAT across various ecosystems with a correlation coefficient of 0.59 ($p < 0.001$). To investigate the correlation between RUE and MAT within a given ecosystem, we divided the MAT gradient at intervals of 0.1°C and calculated average RUE of each interval for each ecosystem (Figure 7). The scatter plot showed that RUE increased

Figure 3. Relationship between normalized RUE and normalized Σ NDVI-G.

Figure 4. RUE of different vegetation types.

significantly with increasing MAT for all vegetation types ($R^2 > 0.15$, $p < 0.001$), which indicates that the spatial trend of RUE along the MAT gradient within a given ecosystem was similar to that across different ecosystems. The increase in RUE with MAT was the most remarkable in alpine steppe ($R^2 = 0.58$, $p < 0.001$) and the least in shrub ($R^2 = 0.18$,

Figure 5. RUE trends of different vegetation types along MAP gradient.

Figure 6. RUE variation along MAT gradient.

$p < 0.001$) and alpine talus vegetation ($R^2 = 0.18$, $p < 0.001$). In conclusion, RUE was positively correlated with annual temperature both across different ecosystems and within a given ecosystem with the effect of precipitation included.

Figure 7. RUE trends of different vegetation types along MAT gradient.

3.3. RUE trends on wet edge and dry edge along a temperature gradient

To illuminate the effect of annual precipitation on RUE under a similar temperature condition, we fitted the spatial variation in RUE on wet edge and dry edge along the MAT gradient (Figure 8). The wet/dry edge is defined as the pixels with maximum/minimum MAP along the MAT gradient, that is, the relatively (not absolutely) wet/dry pixels under the same temperature condition. The trend curves show that RUE_{max_t} , RUE_{mean_t} , $RUE_{wetedge}$, and $RUE_{dryedge}$ varied markedly with annual temperature. RUE_{max_t} , RUE_{mean_t} , and $RUE_{dryedge}$ showed an obvious increasing trend ($R^2 > 0.50$, $p < 0.001$), but $RUE_{wetedge}$ showed a sigmoid pattern ($R^2 = 0.47$, $p < 0.001$). RUE_{max_t} occurred neither on dry edge nor on wet edge, but in areas where MAT was between -3.6°C and 0.5°C , $RUE_{wetedge}$ was very near to RUE_{max_t} . $RUE_{wetedge}$ was higher than $RUE_{dryedge}$ where MAT ranged from -4°C to 2°C , indicating a positive effect of precipitation on RUE under similar temperature conditions, especially where RUE_{mean_t} was between $RUE_{wetedge}$ and $RUE_{dryedge}$ ($r = 0.62$, $p < 0.001$). In contrast, $RUE_{wetedge}$ was lower than $RUE_{dryedge}$ where MAT ranged from 2.0°C to 5.6°C . Although both $RUE_{wetedge}$ and $RUE_{dryedge}$ were lower than RUE_{mean_t} in most cases, RUE still significantly correlated with MAP ($r = -0.25$, $p < 0.001$), implying a negative effect of precipitation on RUE without a change in temperature. $RUE_{wetedge}$ was close to $RUE_{dryedge}$ where MAT was around 2°C , probably implying a least impact of precipitation on RUE.

3.4. RUE trends on warm and cold edges along a precipitation gradient

Similarly, we fitted the spatial variation in RUE on warm and cold edges along the MAP gradient to illuminate the effect of annual temperature on RUE without a change in precipitation. The warm/cold edge is defined as the pixels with maximum/minimum mean annual temperature along the MAP gradient, that is, the relatively (not absolutely) warm/cold pixels under the same precipitation condition. The fitting curves show that

Figure 8. RUE trends on wet and dry edges along MAT gradient.

RUE_{max_p} , RUE_{mean_p} , $RUE_{warmedge}$, and $RUE_{coldedge}$ varied markedly along the MAP gradient. RUE_{max_p} occurred on neither the warm nor the cold edge, but the trend of $RUE_{warmedge}$ was remarkably similar to that of RUE_{max_p} ($r = 0.62$, $p < 0.001$), and the trend of $RUE_{coldedge}$ was similar to that of RUE_{mean_p} ($r = 0.85$, $p < 0.001$). $RUE_{warmedge}$ was higher than $RUE_{coldedge}$ along the MAP gradient from 350 to 540 mm but lower than $RUE_{coldedge}$ where MAP ranged from 540 to 720 mm. RUE_{mean_p} was between $RUE_{warmedge}$ and $RUE_{coldedge}$ in most cases along the MAP gradient. This indicates that under similar precipitation conditions, temperature had a positive effect on RUE where annual precipitation was between 350 and 540 mm ($r = 0.58$, $p < 0.001$), but a negative effect where MAP ranged from 540 to 720 mm ($r = -0.28$, $p < 0.001$). $RUE_{warmedge}$ was close to $RUE_{coldedge}$ where MAP was around 550–700 mm, probably indicating a least impact of temperature on RUE. Considering both precipitation and temperature, the maximum RUE for alpine ecosystems would probably occur in the areas where the annual precipitation is around 470 mm and the annual temperature is about 5.5°C.

4. Discussion

Our study investigated the spatial variation in RUE along precipitation and temperature gradients individually and in combination with THR of China. The results will advance our understanding of how the ecosystem's carbon and water cycles respond to the spatial variations in combination of precipitation and temperature. We compared our results with previous reports and explained how climate variation altered RUE to further illuminate our results.

4.1. RUE variation along a precipitation gradient

A generalized pattern of RUE along the precipitation gradient is still unavailable (Yang et al. 2010). Our study revealed that the spatial variation in RUE along a precipitation gradient (350–720 mm) across alpine ecosystems followed a unimodal distribution that peaked around 600 mm, with an increasing trend in the drier portion and a decreasing trend in the

wetter portion. This pattern is consistent with the results of Paruelo et al. (1999) conducted in typical grassland areas, in which RUE increased first and then decreased along a precipitation gradient (200–1200 mm) and peaked around 475 mm due to the relatively low levels of both vegetational and biogeochemical constraints at this level of resource availability. Our results also concur with those of Yang et al. (2010), who reported a unimodal pattern of RUE along a precipitation gradient (100–700 mm) in alpine grassland using actual measurements obtained from a regional survey.

According to the definition, RUE is determined by water-use efficiency (WUE) at leaf level (ANPP/transpiration) and the relative amount of precipitation used for plant growth (transpiration/precipitation) (Hu et al. 2010). By comparing variation in RUE and Σ NDVI-G along the precipitation gradient, we can infer that ecosystems located at the drier portion (350–600 mm) were water-limited ecosystems where vegetation productivity increased markedly with increasing precipitation. In these ecosystems, increased productivity caused by the precipitation increment was of a magnitude larger than the magnitude of change in precipitation due to the high WUE of plants adapted to a dry climate by using water in deeper soil layers (Jobbagy and Sala 2000). The productivity of the ecosystems located in the relative wetter portion of the gradient (600–640 mm) still increased with precipitation but at a magnitude smaller than the magnitude of increase in precipitation, most of which was lost directly via evaporation and run-off. Thus an increase in precipitation caused a decrease in RUE as a result of a decrease in the relative amount of water used for plant production. There was a negative relationship between NDVI and precipitation in ecosystems located at the wet end (640–720 mm), implying that the productivity of vegetation was not determined by precipitation. We interpreted the decrease in RUE across the spatial gradient towards the wet end as the result of a decrease in both WUE and the relative amount of water used for plant production. Increased precipitation resulted in large increases in run-off and evaporation, but small changes in transpiration (Bell, Weng, and Luo 2010). Meanwhile, for an ecosystem self-sufficient in water, a large increase in precipitation probably caused little change or even a decrease in vegetation productivity by cooling down the summer temperature, which is equally important for alpine vegetation (Yang and Piao 2006). As a consequence, RUE decreased in response to a decrease in both WUE and the ratio of transpiration to precipitation. Furthermore, in a humid environment, increase in water availability causes an increase in nitrogen-use efficiency (Vinton and Burke 1995), suggesting an increasing potential for nitrogen limitation (Vitousek 1982) and consequently an increase in biogeochemical constraints (Paruelo et al. 1999), likely resulting in decreased RUE.

However, our results disagree with many studies investigating the spatial relationship between ANPP and precipitation by a single straight line with a constant RUE (Sala et al. 1988; Lauenroth and Sala 1992; Lauenroth, Burke, and Paruelo 2000; Knapp and Smith 2001). Our results are also in disagreement with those of Le Hourou (1984), Prince, De Colstoun, and Kravitz (1998), Bai et al. (2008), and Hu et al. (2010), in which RUE increased with MAP. In contrast, Huxman et al. (2004) reported that RUE declined along the increasing MAP gradient across North America. We attributed the differences in study results to the spatial magnitude (Bai et al. 2008), MAP ranges (Hu et al. 2010), and ecosystem types (Hu et al. 2010) used by these studies. At the regional scale, when the MAP gradient narrowed towards the dry end (less than 600 mm) in arid ecosystems such as arid steppe, RUE exhibited an increasing trend with MAP as described in our study. When the MAP gradient extended to around 1500 mm in typical grassland ecosystems, RUE tended to be constant or showed a unimodal pattern depending on the number of sites selected and fitting methods (Sala et al. 1988; Paruelo et al. 1999). While at continental scale or

global scale with a broad MAP gradient (about 100–3000 mm) and diverse ecosystems, RUE probably showed a decreasing trend with MAP (Leith 1975; Hu et al. 2010).

At vegetation type level, both mean RUE and its spatial response to precipitation variation varied with ecosystem types. Focusing on the most widely distributed vegetation types including alpine meadow and alpine steppe on the Tibetan Plateau, RUE in alpine meadow was significantly higher than that in alpine steppe, possibly due to the trade-offs between relative growth rate and drought resistance in plants (Keddy 1992). Our results showed an increasing trend of RUE with MAP in alpine steppe and a unimodal trend in alpine meadow, which was similar but not identical to the results of Yang et al. (2010), in which RUE increased in alpine steppe but decreased in alpine meadow with increasing MAP. We ascribe this difference to the inadequacy of sampling sites, especially towards the dry end of the MAP gradient, and the uncertainties resulting from field measurements based on study durations of only one or two years. Apparently, when most sampling sites were located at the wet end of the precipitation gradient, RUE shows a declining rather than a unimodal trend.

4.2. RUE variation along a temperature gradient

Knowledge of the effect of temperature on RUE is crucial to understanding how climate warming alters the coupling of carbon and hydrologic cycles. Our study proved that at the spatial scale an increase in temperature caused an increase in RUE across various ecosystems or within a given ecosystem in the alpine area, which was supported by a modelling study in a tallgrass prairie (Bell, Weng, and Luo 2010). Some reports have come to a different conclusion, in that ecosystem WUE reduced under a warmer climate (Allen et al. 2003; de Boeck et al. 2006), possibly due to the lower carbon uptake rate resulting from stomatal regulation (Niu et al. 2008), which could be a water-saving adaptive mechanism to drier conditions (Niu et al. 2011). However, for alpine areas characterized by high elevation and low temperature, temperature was positively correlated with vegetation density (Li, Liu, and Fu 2011) and was considered the most important factor for vegetation growth (Chen et al. 2010). Moreover, the temperature changed synchronously with precipitation at the spatial scale in THR (Zhang et al. 2011). Thus, the amount of carbon uptake by plants per unit of water probably increased with temperature in most alpine ecosystems, implying an increase in RUE with MAT.

4.3. RUE trends on wet and dry edges

Huxman et al. (2004) and Bai et al. (2008) reported a common spatial RUE_{max} among various ecosystems during the driest year at site level. However, Hu et al. (2010) proved that RUE_{max} varied among ecosystems at site level and ascribed this discrepancy to the different method used to calculate RUE_{max}. Our study also showed that no common spatial RUE_{max} occurred on the dry or wet edges based on the spatial pattern of RUE. Apart from the different methods of calculating RUE_{max} (Hu et al. 2010), this difference may partly be due to the different scale used in analysis and variation in relationships between RUE and precipitation. Huxman et al. (2004) and Bai et al. (2008) estimated RUE_{max} as RUE occurring in driest year based on a temporal model at site scale, while we supposed that RUE_{max} might occur in the driest or wettest pixels based on a spatial model at regional scale. Variation in RUE between temporal and spatial models has been reported in detail by Paruelo et al. (1999). Generally, RUE tends to decrease temporally with increasing precipitation

(Huxman et al. 2004), but opinion is divided in regard to the spatial relationship between RUE and precipitation as discussed above. Our study showed a unimodal pattern in RUE along a spatial gradient of MAP which differed from the RUE trend in the temporal model, accounting for the absence of common RUE_{max} on dry or wet edges.

Previous studies on the relationship between RUE and precipitation (Paruelo et al. 1999; Huxman et al. 2004; Bai et al. 2008; Hu et al. 2010) were conducted under varying temperature conditions. Little is known about how RUE responds to precipitation variation at a given temperature level. Precipitation and temperature interact with each other, and thus the impact of temperature may mask the relationship between RUE and precipitation. The relationship between $RUE_{wetedge}$, $RUE_{dryedge}$, and RUE_{mean_t} can, at least to some extent, illustrate RUE response to precipitation at a given temperature level. Our results suggest that under similar temperature conditions, RUE positively correlates with annual precipitation in cold ecosystems (-4.0°C to -2.0°C) but negatively with annual precipitation in warm ecosystems (2.0 – 5.6°C), resulting partly from synchronized precipitation and temperature in space. The areas located in the colder portion, usually of high aridity, are covered by water-limited ecosystems with high plant-level WUE, in which vegetation productivity is decided by water availability. A small increase in precipitation would cause a marked increase in vegetation density, and thus productivity, at a magnitude greater than the magnitude of change in precipitation, implying an increase in RUE under similar temperature conditions. However, the areas located in the warmer portion with sufficient precipitation are usually nutrient limited. A large increase in precipitation, most of which is lost via runoff and evaporation, would cause little change or even a decrease in vegetation productivity, but an increase in biogeochemical constraints (Paruelo et al. 1999). This may probably cause a decrease in RUE at a given annual temperature level.

4.4. RUE trends on warm and cold edges

We hypothesized that maximum RUE would occur on warm edges based on spatial variation in RUE along the MAT gradient across THR. However, the scatter (Figure 9) shows that the trend of RUE_{max_p} was remarkably similar but not totally in agreement with $RUE_{warmedge}$ ($r = 0.62$, $p < 0.001$), and RUE_{mean_p} was between $RUE_{warmedge}$ and $RUE_{coldedge}$ in most cases. This suggested a complicated underlying mechanism for RUE involving interactions among climate, terrain, soil, and biotic factors. Notably, other environmental factors such as soil types, altitude, and topography may also have effects on spatial RUE. For example, soil texture and soil nutrients may largely impact RUE through their influence on water-holding capacity and plant productivity (Le Houérou 1984). Moreover, precipitation and temperature physically interact through the dependence of atmospheric moisture on temperature, and the link between the amount of precipitation and temperature is also influenced by other environmental factors such as altitude and topography. Therefore, future research should pay special attention to the relationship between climate index and RUE considering the interactions among climate, terrain, and soil in the study area.

The relationship between $RUE_{warmedge}$ and $RUE_{coldedge}$ indicated RUE positively correlates with annual temperature in dry ecosystems (350–540 mm) but negatively with annual temperature in humid ecosystems (540–720 mm) at a given precipitation level. In the dry ecosystems, synchronously low in temperature, appropriately increased temperature would cause little change in transpiration due to the sparse vegetation density but a rapid increase in productivity as a result of the increased energy used for photosynthesis and accordingly increased rate of photosynthesis. As a consequence, RUE increased with temperature with no change in precipitation. In warm and humid ecosystems, warming would cause an

Figure 9. RUE trends on warm and cold edges along MAP gradient.

increase in transpiration at a larger magnitude than that in productivity without a change in precipitation, leading to a decrease in plant WUE (Bell, Weng, Luo 2010) and probably in RUE.

5. Conclusions

The spatial pattern in RUE, which decreased from east to west, was similar but not identical to the NDVI pattern. RUE showed a unimodal pattern along a MAP gradient (350–720 mm) across different ecosystems, with an increasing trend in alpine steppe, alpine talus vegetation, and more-arid alpine meadow and a decreasing trend in forest, shrub, and less-arid alpine meadow. RUE exhibited an increasing trend along a MAT gradient (−4.5°C to −6.2°C) both within a given ecosystem and across various ecosystems. No common spatial RUE_{max} was found across various ecosystems in the driest pixels (dry edge) based on the spatial model at the regional scale, which was different to findings from previous studies based on a temporal model at site scale. Although RUE_{max} did not occur on dry or warm edges in most cases, the trend of RUE_{max} along the precipitation gradient was remarkably similar to that of the warm edge ($r = 0.624$, $p < 0.001$), implying a complicated underlying mechanism for RUE involving interactions among climate, terrain, soil, and biotic factors. Under the influence of precipitation and temperature, RUE of alpine ecosystems would probably peak at a MAP of about 470 mm and a MAT of about 5.5°C. Removing the mutual interference between precipitation and temperature, we found that RUE increased with both precipitation at a given temperature level and temperature at a given precipitation level in cold and dry ecosystems. In contrast, RUE probably decreased with both precipitation at a given temperature level and temperature at a given precipitation level in warm and humid ecosystems.

Acknowledgements

This research was carried out as part of the supporting programme of the ‘Chinese Academy of Sciences Western Action Plan’ (NO. KZCX2-XB3-10), Chinese Ministry of Education Layout

Foundation of Humanities and Social Sciences (NO. 13YJAZH041), 'Eleventh Five-year Plan' for Science and Technology Research of China (NO. 2009BAC61B02), and China Postdoctoral Science Foundation funded project (NO. 20100470561).

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