Pol. J. Environ. Stud. Vol. 27, No. 4 (2018), 1541-1550
DOI: 10.15244/pjoes/76912 ONLINE PUBLICATION DATE: 2018-02-21

Original Research

Dynamics and Controls of Carbon Use Efficiency across China's Grasslands

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Received: 22 April 2017
Accepted: 10 September 2017

Abstract

China's grasslands play a significant role in the carbon cycle. Accurately evaluating carbon use efficiency (CUE) of grassland ecosystems is of great importance. Therefore, we adopted moderate resolution imaging spectroradiometer documents to explore dynamics and controls of CUE across grasslands of China from 2001 to 2010. Results demonstrated that CUE presented an increasing trend (0 to 0.0067 year^{-1}) in the most studies regions except for desert steppe (-0.0046 to 0 year^{-1}). At spatial scale, the precipitation, temperature, and aridity index significantly regulated the dynamics of CUE in alpine grasslands. Furthermore, the different mechanisms are explored at the transect scale, and CUE revealed the positive correlation with aridity index (R^2 = 0.92, P<0.0001) and precipitation (R^2 = 0.88, P<0.0001), but a negative correlation with temperature (R^2 = 0.92, P<0.0001) in alpine grasslands. However, in temperate grasslands, CUE exposed the negative correlation with aridity index (R^2 = 0.40, P<0.0001) and precipitation (R^2 = 0.54, P<0.0001), but a positive correlation with temperature (R^2 = 0.56, P<0.0001). Moreover, precipitation was decreasing with the increased temperature in the alpine grasslands (R^2 = 0.85, P<0.0001) and temperature of grasslands (R^2 = 0.19, P<0.0001). In conclusion, CUE had a slight increased trend across grasslands in China, with higher precipitation, aridity index, and lower temperature promoting CUE in the alpine region – nevertheless restraining the CUE variations in grassland temperature. The better heat and water conditions in temperate grasslands than in alpine grasslands resulted in higher CUE in temperate grasslands.

Keywords: carbon use efficiency, aridity index, precipitation, temperature, grassland ecosystems

Introduction

Understanding the responses of the terrestrial ecosystem carbon cycle and related vegetation growth to intensified global climate change, which has been reported widely, is of great significance [1-3]. For instance, more recent reports have documented that climate change regulates the carbon storage of Europe [4], with both precipitation and temperature affecting carbon storage of the Scots pine forest ecosystems of Poland [5], and the increasing temperature results in the reduction of

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carbon storage of the terrestrial ecosystem in Poland [6]. As a basic parameter of carbon cycling [1], carbon use efficiency (CUE) plays a vital control role in the carbon cycling of ecosystems [7]. CUE is also fundamental for better analyzing ecosystem carbon fluxes and carbon allocation patterns [8-9], and it can favor us to investigate mechanisms of terrestrial ecosystems' carbon dynamic and its sink-source relationship [10].

CUE is the proportion of gross primary production (GPP) invested into net primary production (NPP) [10-12]. GPP represents the total amount of carbon absorbed by photosynthesis, and NPP indicates the mass of carbon stored following the loss of carbon from GPP by autotrophic respiration [13]. Being a momentous parameter of CUE as well, respiration is separated into the two components by some scholars, i.e., preservation respiration and progress respiration [13-14]. They had elaborated preservation respiration as proportional to GPP with a variable CUE parameter and used a constant CUE parameter to model progress respiration as proportional to GPP [1, 14]. Many studies have used the fact that NPP comprised a constant proportion of GPP to assume a constant CUE [9]. The energy of respiration ultimately from photosynthesis, respiration has the linear relationship with GPP and results in a constant value of CUE [15-16]. Moderate resolution imaging spectroradiometer (MODIS) products of GPP are estimated with the special MODIS algorithm, which can divide the process to compute GPP and respiration. Meanwhile, the modelling of respiration does not influence the quality of GPP [13, 17]. MODIS of NPP is derived from the MODIS of GPP, and there is a difference in the annual estimates of maintenance respiration and growth respiration between MODIS GPP and MODIS NPP [13, 18]. The MODIS products have been well validated and used widely [13, 15-16], for instance, the CUE was calculated using the MODIS of GPP and NPP to explore the response of the CUE to climate change at global scale [10] and in the Tibet Plateau [2].

Understanding the variation of the CUE and the response of the CUE to climatic factors is vital to comprehending the carbon cycling and carbon storage of terrestrial ecosystems [19]. Previous studies explore the relationships of CUE with climate factors at the different spatial and temporal scales. At the global level, the CUE exhibited a decreasing trend from 2000 to 2010, the increased temperatures led to the lowered CUE, and the increased precipitation [13, 15-16] caused the higher CUE [1]. Most scholars also designated that there was a positive correlation between CUE and precipitation [1, 13, 18-19], but a negative correlation between CUE and precipitation was reported across the eastern USA [13]. It is worth noting that there is a lot of controversy about the effect of temperature on CUE, and global CUE decreased under the enhanced temperature from 2000 to 2009 [1]. In eastern North America the CUE also decreased with increasing temperature [20], but the CUE of forests in the eastern USA increased with enhanced temperature [13].

Consequently, it has been noticed that the aerobic respiration of plants requires water to dissolve a small amount of oxygen, so moderate precipitation may enhance respiration to reduce NPP. Thus, greater precipitation and aridity may lead to lower CUE. Temperatures falling into a certain range have a promoting effect on the CUE, and vice versa.

A grassland ecosystem is huge carbon storage, and it plays a momentous role to regulate the carbon cycle as well as the carbon balance of terrestrial ecosystem [2, 13, 18, 21]. China's grasslands – mainly across the Northeast Plain, the Inner Mongolian Plateau, the Tibetan Plateau, and the Xinjiang Mountains – account for about 40% of the national territorial area. Which plays a vital role in the carbon cycle of the terrestrial ecosystem [1]. The relationships between CUE and climatic factors also were detected on the Tibetan Plateau as various vegetation types exhibited different response magnitudes of CUE related to climatic change [3]. However, a few studies have systemically focused on comparison CUE and their interactions with multiple environmental factors across different grassland types in China. Specifically, in the current research we handled the MODIS NPP and GPP documents from 2001 to 2010 to explore the spatial pattern of CUE and its relationship with aridity index, precipitation, and temperature.

The aims of our study were to: 1) analyze spatial-temporal variations of climatic factors, NPP, GPP and CUE; 2) investigate the responses of CUE to climatic factors (precipitation, temperature, and aridity index) at the spatial and belt transect scale; and 3) explore the different controlled mechanisms of CUE in temperate and alpine grassland ecosystems.

Materials and Methods

Study Area

China's grasslands are mainly distributed across the 6 provinces of Inner Mongolia, Gansu, Ningxia, Xinjiang, Qinghai, and Tibet [22]. The grassland types contain temperate meadow, temperate typical steppe, temperate desert steppe, alpine meadow, and alpine steppe (Fig. 1). Where annual precipitation is less than 400 mm belongs to a sensitive arid and semi-arid region under climate change and anthropogenic activities.

Data Compilation

NPP, GPP, and CUE

Based on NASA's moderate resolution imaging spectroradiometer (MODIS) MOD17 product, the regional scale NPP and GPP were estimated. The MOD17 product provides continuous estimates of GPP/NPP across earth's entire vegetated land surface. The MOD17 product is used for global carbon cycle analysis. The MOD17 product is the first continuous satellite-driven dataset monitoring global vegetation productivity at a 1-km resolution [10] (modis.gsfc.nasa.gov/data/dataprod/mod17.php).

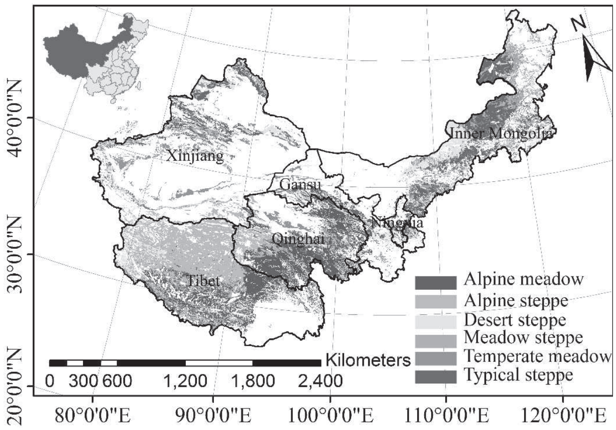

Fig. 1. The study area across China's grasslands, including the six provinces or autonomous regions of Inner Mongolia, Gansu, Ningxia, Xinjiang, Qinghai, and Tibet; the grasslands contain alpine meadow, alpine steppe, desert steppe, meadow steppe, temperate meadow, and typical steppe.

GPP is calculated as follows:

$$GPP = \epsilon_{max} \times 0.45 \times SWrad \times FPAR \times fVPD \times fT_{min} \tag{1}$$

…where ϵ_{max} is the max radiation use conversion efficiency of the vegetation; *SWrad* is short-wave downward solar radiation, and 45% of *SWrad* is photosynthetically active radiation (PAR); *FPAR* is absorbed by the plant canopy from PAR; and *fVPD* and fT_{min} are the reduction scalars from water stresses (high daily vapour pressure deficit) and low temperature (low daily minimum temperature Tmin), respectively. *FPAR* is estimated from satellite remote sensing; *PAR, SWrad, fVPD,* and *fT*minare derived from meteorological field data; and ϵ_{max} is determined based on the theory of Monteith (1972) for each biome. Some scholars had validated the GPP product by comparing with data from 250 global eddy flux towers, and gotten the results that there is a strong correlation between the modelled GPP and GPP data derived from the sites [23].

NPP is calculated as follows:

$$NPP = GPP - (R_{ml} + R_{mr} + R_{mw}) - \\ - (R_{gl} + R_{gr} + R_{gw} + R_{gd}) \tag{2}$$

…where R_{ml}, R_{mr}, and R_{mw} are maintenance respiration by leaves, fine roots, and livewood, respectively, and R_{gl}, R_{gr}, $R_{gw,}$ and R_{gd} are growth respiration (GR) for leaves, roots, livewood, and deadwood, respectively.

Some scholars had validated the NPP product and gotten the result that the modelled NPP results agree well withfield NPP data [23].

CUE is calculated as follows:

$$CUE = \frac{NPP}{GPP} \tag{3}$$

Carbon use efficiency (CUE) is the ratio of net primary productivity (NPP) to gross primary production (GPP) [24].

Precipitation, Temperature, and Aridity Index

Precipitation and temperature documents of 70 meteorological stations around the study area were obtained from the catalog of the China Meteorological Administration. We used the kriging method to interpolate the meteorological data from all 70 stations at 1 × 1 km resolution to create sequential data surfaces for precipitation and temperature factors.

Aridity index is calculated as follows [25]:

$$AI = \frac{P}{T + 10} \tag{4}$$

…where *AI* is the aridity index, *P* is the annual mean precipitation, and T is the annual mean temperature.

Data Analysis

We calculated the spatial change rate of CUE, aridity index, precipitation, and temperature calculated in ArcGIS (Formula 5), and calculated the spatial correlation between CUE and the environmental factors (aridity index, precipitation, and temperature) based on least squares (Formula 6) through the function of raster calculation in ArcGIS [26] as follows:

$$\beta = \frac{n\sum XY - \sum X \sum Y}{n\sum X^2 - \left(\sum X\right)^2} \tag{5}$$

$$r = \frac{n\sum_{i=1}^{n} x_i y_i - \sum_{i=1}^{n} x_i \sum_{i=1}^{n} y_i}{\sqrt{n\sum_{i=1}^{n} x_i^2 - \left(\sum_{i=1}^{n} x_i\right)^2} \times \sqrt{n\sum_{i=1}^{n} y_i^2 - \left(\sum_{i=1}^{n} y_i\right)^2}} \tag{6}$$

…where β is the change rate about *Y*, *n* is the total number of years of the study period, *X* is the year, *Y* is the CUE, *r* is the correlation coefficient between x_i and y_i, x_i is the aridity index, precipitation or temperature, and y_i is the CUE.

Finally, we used regression analysis to test the relationships between CUE and environmental factors (aridity index, precipitation, temperature) in different grassland ecosystems in SPSS (v. 21.0).

In addition, the study was carried out at the belt transect scale. In order to explore the different controlled mechanisms of temperate and alpine grassland ecosystems, two belt transects were chosen by the precipitation, temperature, and aridity index gradients.

Results and Discussion

Dynamics of Environmental Factors in Different Grassland Types

Fig. 2 presents the climate change spatially in the China's grasslands from 2001 to 2010. Although the spatial precipitation increased by 0 to 12 mm year^{1} in most regions of China's grasslands, the precipitation of the alpine grassland (alpine steppe, alpine meadow) of central Tibet and the desert steppe of Inner Mongolia and Xinjiang exhibited a decreasing trend at 0 to 5.57 mm year^{1} (Fig. 2a). Precipitation variation was comparable to the previous studies on the Tibetan Plateau and Inner Mongolia [3, 27]. Those findings indicated that most regions of China's grasslands were becoming wetter. The spatial temperature increased by 0 to 0.0885ºC year^{1} in the western area (Tibet, Xinjiang, Gansu, Qinghai, and Ningxia) of China's grasslands, particularly in the alpine grassland (alpine steppe and alpine meadow) of central Tibet, but the temperate grassland of Inner Mongolia decreased by 0 to 0.05ºC year^{1} (Fig. 2b). The warming of climate also was equal to previous investigations on the Tibetan Plateau [28]. In addition, aridity index represents the degree of a region's wetness, and we used it to explore the heat and water conditions of the different vegetation ecosystems [29-31]. The aridity index of most of China's grasslands presented an increasing trend, except for the alpine grassland (alpine steppe and alpine meadow) of the central Tibet and temperate grassland (desert steppe and meadow steppe) of Inner Mongolia, Ningxia, and Xinjiang (Fig. 2c), and the results are similar as a previous investigation on the Tibetan Plateau [2]. These results indicated that the climate presented a warming and drying trend across the alpine grassland (alpine steppe and alpine meadow) of central Tibet, and the temperate grassland (temperate meadow and typical steppe) of Inner Mongolia has become increasingly wetter.

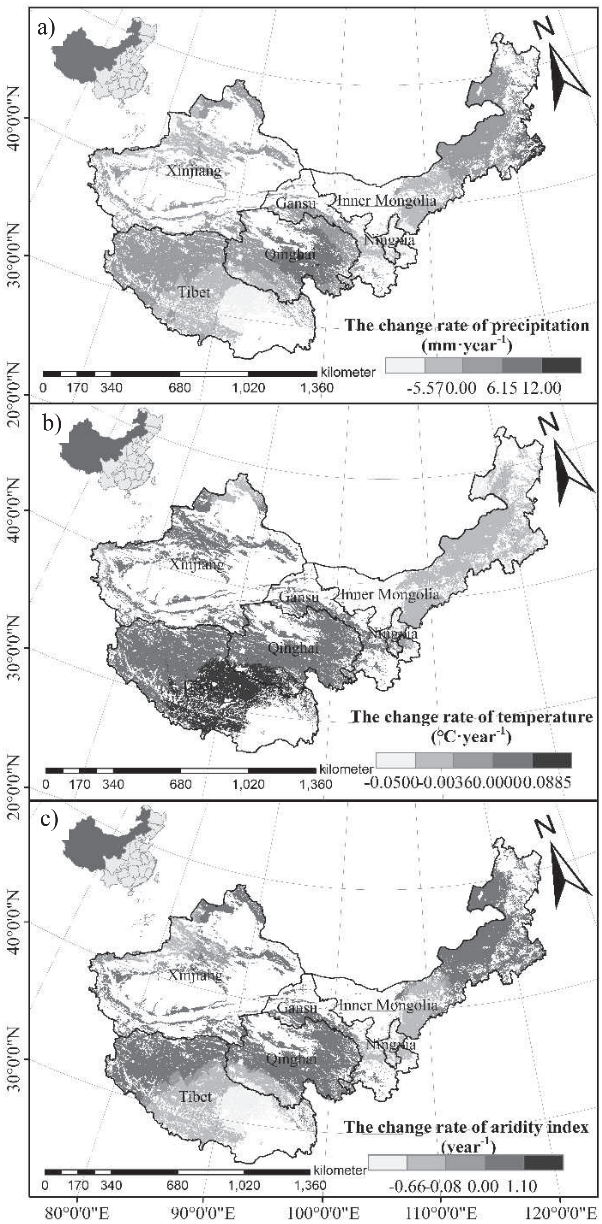

Fig. 2. Spatial distribution of change rate of precipitation, temperature, and aridity index across China' grasslands; graphs a), b), and c) represent the spatial distribution of change rate of precipitation, temperature, and aridity index, respectively.

Dynamics of NPP, GPP, and Carbon Use Efficiency in Different Grassland Types

Fig. 3 presents the dynamics spatially of NPP, GPP, and CUE in China's grassland from 2001 to 2010, with NPP and GPP as the main parameters of CUE, which principally influence the variation of CUE. The NPP of China's grasslands decreased by 0 to 40 g m^{-2} year^{1} spatially in most regions, while the NPP change rate of the alpine grassland (alpine steppe, alpine meadow) was less than the temperate grassland (typical steppe and temperature meadow) of Inner Mongolia and Xinjiang (Fig. 3a). Therefore, the carbon storage of China's grasslands was increasingly less, and the carbon storage of alpine grassland (alpine steppe and alpine meadow) of central Tibet was more efficient than the temperate grassland (typical steppe, temperate meadow, and desert steppe) of Inner Mongolia. In a comparison of previous research on the Tibetan Plateau and Inner Mongolia [3, 32], they learned that NPP increased linearly with greater mean annual temperature in dry and cold ecosystems [10, 33]. The decreasing NPP may be caused by the warming climate, which leads to much more maintenance respiration, and the different climate conditions of Tibet and Inner Mongolia resulted in the different change rate of the NPP. The GPP variation was different from the variation of the NPP. The area where the GPP increased by 0 to 5.4 g m^{-2} year^{-1} was larger than the area where the GPP decreased by 0 to 1.22 g m^{-2} year^{-1} (Fig. 3b). The GPP increased area mainly distributed in the alpine grassland (alpine steppe and alpine meadow) of the border of Tibet and Qinghai (Fig. 3b), which indicated that the efficiency of the photosynthesis was becoming higher in the alpine grassland. The GPP variation of China's grasslands was in agreement with previous research on Tibet [3]. The spatial CUE decreased by 0 to 0.0046 year^{-1} in most regions of China's grasslands (Fig. 3c). However, the CUE of the alpine grassland (alpine steppe and alpine meadow) of the border of Tibet and Qinghai presented an increasing trend at 0 to 0.0067 year^{-1}(Fig. 3c). Therefore, carbon storage of the alpine grassland (alpine steppe and alpine meadow) of the border of Tibet and Qinghai is becoming more efficient than most regions of China's grasslands. The finding presents the different change trends of CUE among the different ecosystems [1], and they were in line with a previous study in the Tibetan Plateau [19]. Evidence for the positive effect of climate warming on CUE has been extensively conveyed in permafrost regions [34-36]. Whereas climate warming promotes the photosynthesis process and respiration process of grass concurrently [36], so the changed trend of CUE was likely contributed to by the different sensitivities of NPP and GPP of the various grassland types to climate conditions [37].

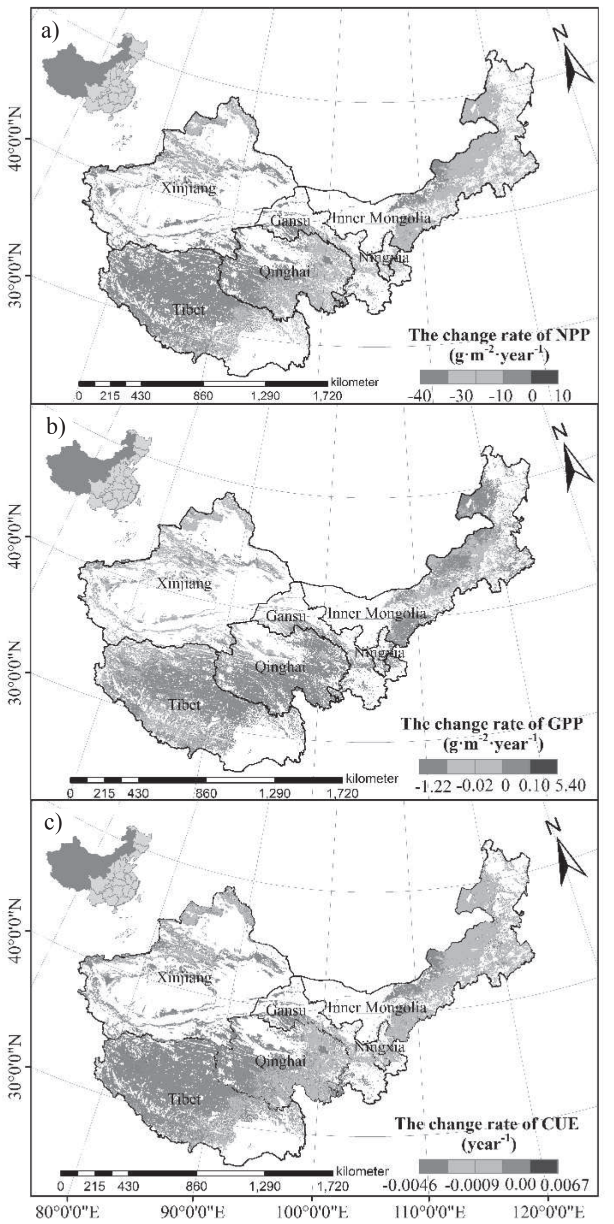

Fig. 3. Spatial distribution of change rate of NPP, GPP, and CUE across China's grasslands; graphs A, B, and C represent the spatial distribution of change rate of NPP, GPP, and CUE, respectively.

Responses of CUE to Variation of Environmental Factors in Different Grassland Types

The spatial correlations between CUE with climate factors (precipitation, temperature, and aridity index) and the significance analysis (Fig. 4) shows that climate factors play a remarkable role in the alpine grassland (alpine steppe and alpine meadow) of the border region between Tibet and Qinghai (Figs 4d-f). The findings indicated that precipitation, temperature, and aridity index promotes CUE of alpine grasslands [3], and the responses of CUE to these factors were different in the different grassland ecosystem [1, 3, 13, 38].

In order to explore the response mechanisms of CUE in different grassland ecosystems (temperate grassland and alpine grassland) to environmental variation, the three environmental gradients were set to explore the relationship with CUE (Figs 5a-c). There was a negative correlation between precipitation and CUE (R^2 = 0.54, P<0.0001) in the temperate grassland (typical steppe; Fig. 5 d); however, the CUE was increasing significant with increasing precipitation in the alpine grassland (alpine steppe) ecosystem (R^2 = 0.88, P<0.0001; Fig. 5e). Interestingly, CUE decreased with enhanced precipitation in the temperate grassland (typical steppe) belt transect of Inner Mongolia under 160 to 320 mm, but CUE increased with enhanced precipitation in the alpine steppe belt transect under the 300 to 500 mm rainfall gradient (Fig. 5e). The CUE decreased with enhanced precipitation in the areas where precipitation is in surplus [3, 10], and abundant precipitation is vital for grass in dry environments, but redundant precipitation leads to more energy expenditure, a lack of energy input, and the consequence of decreased CUE [10, 39-41]. In the eastern Amazon forest, similar results were obtained [42-43]. Specifically, enhanced precipitation reduces fine root production and brings a decreasing GPP in the alpine grassland ecosystem, increased respiration of leaf and root, and decreased NPP [38-39]. However, the correlation was not obvious in dry, cold areas and warm and humid areas [10, 24, 44]. The decrease of CUE with the increased precipitation could result in a lot of factors, e.g., increased cloudiness or a shortage of soil oxygen resulting in decreased nutrient supply [45].

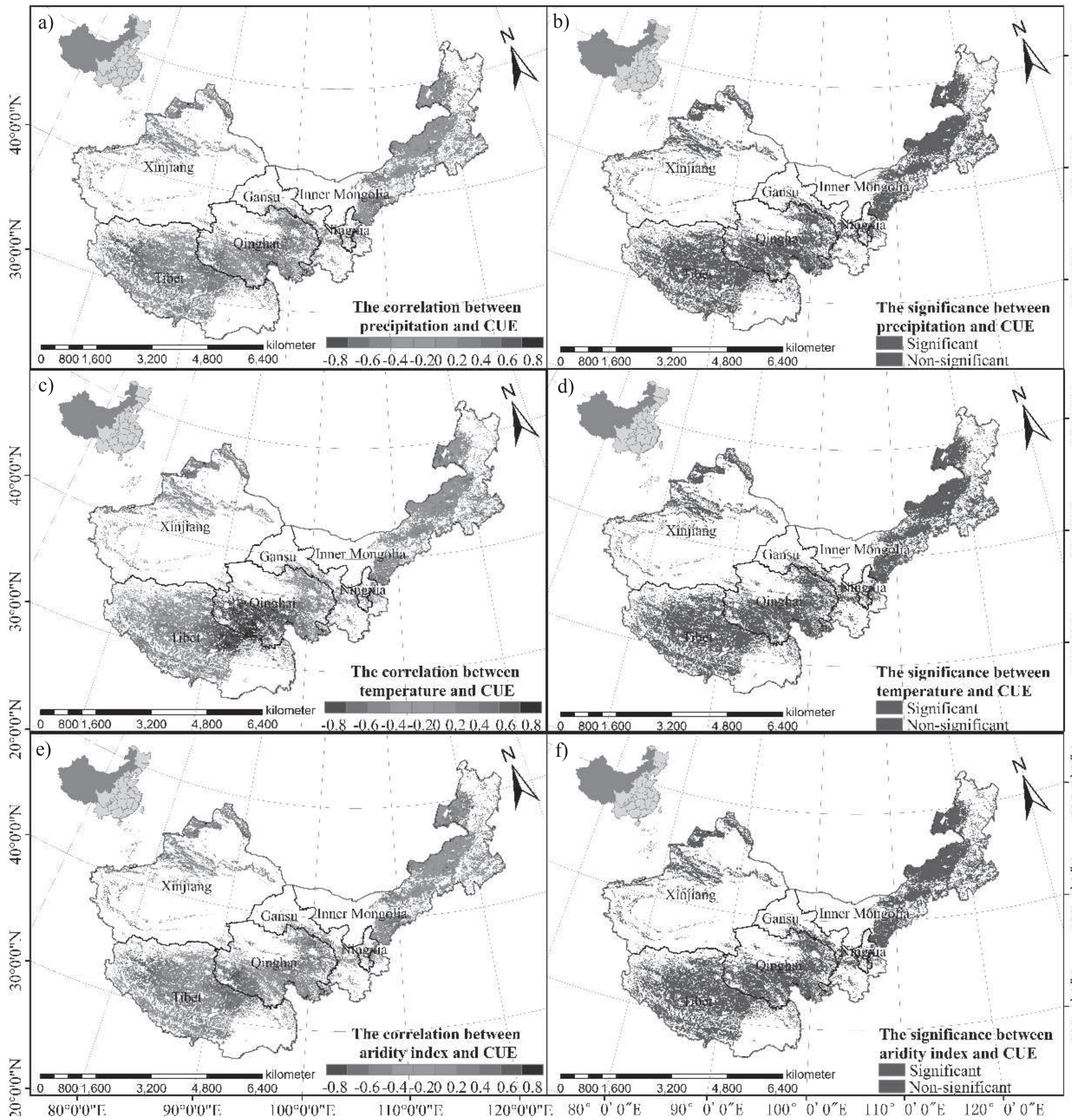

Fig. 4. Correlation and significant relationship between CUE and environmental factors (precipitation, temperature, and aridity index) across China's grasslands; graphs a), b), and c) represent the correlation between CUE and precipitation, temperature, and aridity index, respectively, while graphs d), e), and f) represent the significant relationship between CUE and precipitation, temperature, and aridity index.

According to Figs 5(f-g), the results showed that temperature has a totally opposite effect on CUE in comparison to precipitation. The positive effect of temperature on CUE (R^2 = 0.56, P<0.0001) in the temperate grassland (typical steppe) (Fig. 5f), nevertheless, the negative effect of temperature on CUE in the alpine grassland ecosystem (R^2 = 0.92, P<0.0001; Fig. 5g). Furthermore, CUE increased with enhanced temperature in the temperate grassland under 2.5-4.5ºC temperature gradient (Fig. 5f). Interestingly, CUE performed a significant negative correlation with temperature in the alpine grassland during the 0-5ºC temperature gradient (Fig. 5g). The correlation between temperature and CUE in the alpine steppe was similar to the CUE result of the eastern USA that declined with increasing temperature [13]. A study indicated that the CUE in eastern North America decreased with an increasing growth of temperature [20]. The temperature factor was important in regulating the CUE in the alpine steppe of China' grasslands [46-47]. The higher energy requirement to maintain a plant's growth with increased temperature results in increased respiration and decreased CUE [10, 13, 46].

Figs 5(h-i) showed that the aridity index has a similar effect on CUE in comparison to precipitation. The correlation of CUE with the aridity index in the temperate grassland (typical steppe) ecosystem existed in a significant negative correlation ($R^2 = 0.40$, $P<0.0001$; Fig. 5h), and the correlation of CUE with the aridity index was positive in the alpine grassland (alpine steppe) ecosystem ($R^2 = 0.92$, $P<0.0001$; Fig. 5i). Furthermore, there is a negative correlation between CUE and aridity index in the temperate grassland under the 12-22 aridity index gradient (Fig. 5h). Nevertheless, CUE increases with enhanced aridity index in the alpine grassland during the 20-25 aridity index gradient (Fig. 5i). Under slightly lower aridity index conditions, CUE decreased with the increased aridity index because of the decreased efficiency of photosynthesis and the increasing rate of respiration [10]. The main reason for this result was that the plants generally had more photosynthate in the dry regions for the conflict with water stress and to maintain

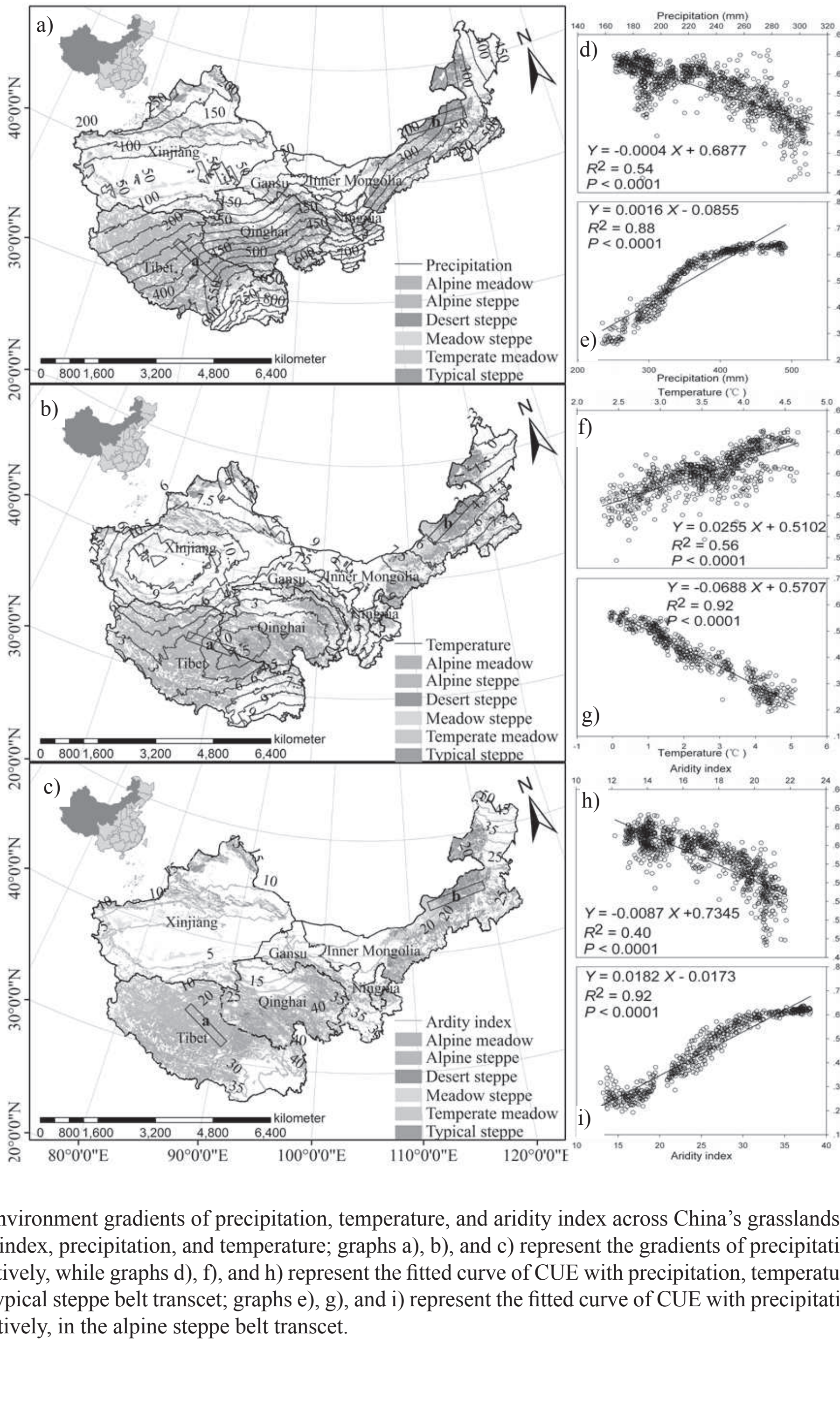

Fig. 5. The typical environment gradients of precipitation, temperature, and aridity index across China's grasslands, and the fitted curve of CUE with aridity index, precipitation, and temperature; graphs a), b), and c) represent the gradients of precipitation, temperature, and aridity index, respectively, while graphs d), f), and h) represent the fitted curve of CUE with precipitation, temperature, and aridity index, respectively, in the typical steppe belt transect; graphs e), g), and i) represent the fitted curve of CUE with precipitation, temperature, and aridity index, respectively, in the alpine steppe belt transect.

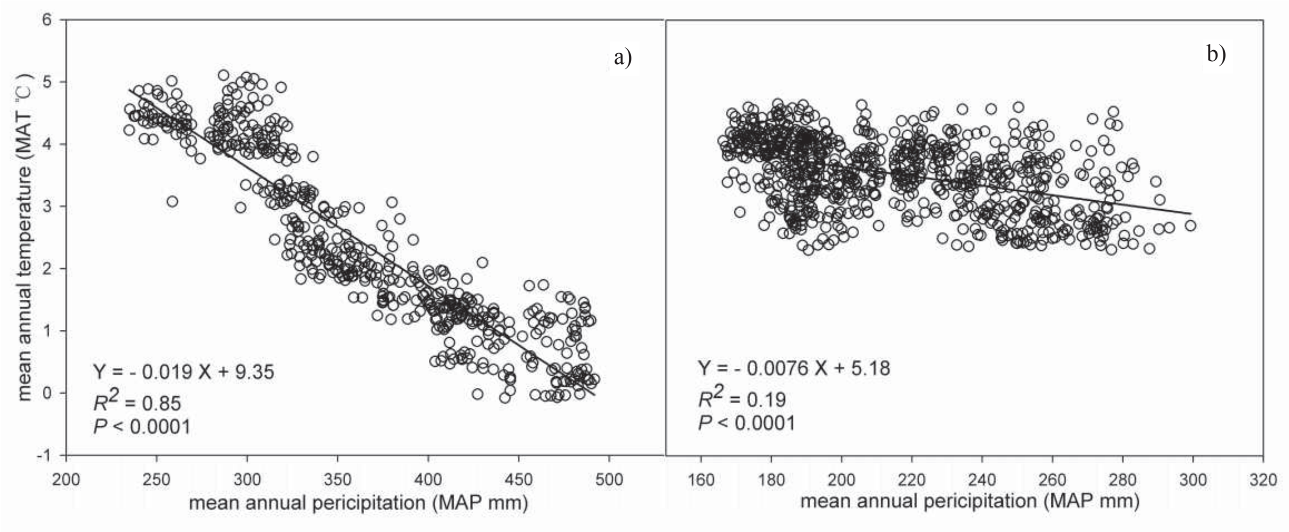

Fig. 6. Fitted curve between precipitation and temperature; graph a) presents the fitted curve in the alpine steppe belt transect while graph b) presents the fitted curve in a typical steppe belt transect.

their own growth [48]. However, higher carbon storage can be obtained by applying less energy on preservation respiration, and progress respiration, in a wet and warm environment [10]. Consequently, precipitation and temperature play a critical role in regulating the variations of CUE in temperate and alpine grasslands.

Heat and Water Condition Controls of Carbon Use Efficiency

Due to precipitation impressing the response of respiration and photosynthesis to temperature [38, 40] and affecting the dynamic of CUE, we explored heat and water conditions over the different grassland belt transects. In Fig. 6 we found that the temperature presented a decreasing trend with the increased precipitation in the alpine grassland (R^2 = 0.85, P<0.0001) and temperature grassland (R^2 = 0.19, P<0.0001) (Figs 6a-b). Nevertheless, the slope of the linear fitting equation is 0.0076 less in the temperate grassland than 0.019 in the alpine grassland. Therefore, the result suggested that the better heat and water conditions in the temperate grassland resulted in the different CUE.As we know that both precipitation and temperature of the growing period are closely related to plant growth, the rising temperature on the carbon assimilate will be simultaneously regulated by water availability in grassland ecosystems [26, 49].

Conclusions

In this study, the better heat and water conditions in temperate grassland compared to alpine grassland resulted in the higher CUE in temperate grasslands. The result highlighted that water and heat conditions play a critical role in regulating the variations of CUE, specifically the plants generally had more photosynthate in the dry regions for the conflict with water stress and to maintain their own growth, but higher storage of carbon by applying less energy on preservation respiration and progress respiration, in a wet and warm environment.

Acknowledgements

This research was supported by the State Key Research Development Program of China (grant Nos. 2016YFC0501802 and 2016YFC0501803), the National Natural Science Foundation of China (grant No. 41501057), the Construction Service Program for Cultivating Feature Institution of the Chinese Academy of Sciences (No. TSYJS05), and a Youth Innovation Research Team Project (No. LENOM2016Q0003).

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