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► **To cite this version:**

Tianyou Zhang, Zhi Chen, Weikang Zhang, Cuicui Jiao, Meng Yang, et al.. Long-term trend and interannual variability of precipitation-use efficiency in Eurasian grasslands. *Ecological Indicators*, 2021, 130, pp.108091. 10.1016/j.ecolind.2021.108091 . hal-03320237

HAL Id: hal-03320237

<https://hal.science/hal-03320237>

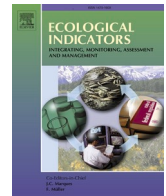
Submitted on 27 Aug 2021

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Original Articles

Long-term trend and interannual variability of precipitation-use efficiency in Eurasian grasslands

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ARTICLE INFO

Keywords:

Precipitation-use efficiency
Trend
Climate change
Interannual variation
Eurasian grasslands

ABSTRACT

Precipitation-use efficiency (PUE) is an important ecosystem indicator of the efficiency of carbon–water conversion. The trend and interannual variation of precipitation-use efficiency (PUE) response to climatic factors provide a theoretical foundation for understanding how Eurasian grasslands adapt to climate change. However, the long-term trends and regulating factors of PUE in Eurasian grasslands at the continental scale are still unclear. Here, we integrated long-term Global Inventory Monitoring and Modeling System (GIMMS) Normalized Difference Vegetation Index (NDVI), field surveys of aboveground net primary production (ANPP) and meteorological datasets during 1982–2015 to reveal the temporal variations and controls of PUE in Eurasian grasslands. We found that there was an overall uptrend of PUE ($3 \times 10^{-3} \text{ g C m}^{-2} \text{ mm}^{-1}/10 \text{ yr}$) in Eurasian grasslands. The greatest increasing trends of PUE was found in forest steppe at the rate of $13 \times 10^{-3} \text{ g C m}^{-2} \text{ mm}^{-1}/10 \text{ yr}$, while greatest decreasing trend presented in alpine steppe at the rate of $-2.6 \times 10^{-3} \text{ g C m}^{-2} \text{ mm}^{-1}/10 \text{ yr}$. The PUE showed linearly decreasing patterns with precipitation at the biome and continental scales, while it was uncorrelated with temperature at the continental scale and showed diverse patterns of linear increase, concave-down and no correlation with temperature for different biomes. The temporal variation of PUE was mainly controlled by precipitation in Eurasian grasslands. This result further revealed that climatic factors shaped the temporal pattern of PUE by the cascading effects networks of climatic factors (precipitation and temperature) – vapor pressure deficit (VPD) – leaf area index (LAI) – ANPP – PUE (CVLP-CENet). This study identified the long-term trends, interannual variations and controls of PUE in Eurasian grasslands over the past three decades, and provided crucial insights into understanding grassland ecosystems dynamics and response to climate change.

1. Introduction

With continued warming, climate is becoming increasingly variable and models predict that this trend will continue in the future (Diffenbaugh et al., 2008; Wuebbles et al., 2014). Under climate change, increased drought intensity will have far-reaching implications for the structure and functioning of ecosystems, particularly in arid areas (Berdugo et al., 2020; Maurer et al., 2020). It has been reported that dryland grassland ecosystems were most sensitive to climate change

(Maurer et al., 2020), and have controlled the trend and variability of the global carbon budget over the past few decades (Ahlstrom et al., 2015; Poulter et al., 2014). As the main ecosystem type in arid and semi-arid areas, grassland ecosystems serve as habitat for various plants and animals and provide numerous benefits to human development, particularly in developing countries (Berdugo et al., 2020; Middleton and Sternberg, 2013). Therefore, it is critical to recognize how the resource utilization strategy of grassland ecosystems adapt to a changing climate, as this will help predict future changes in grassland ecosystem

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<https://doi.org/10.1016/j.ecolind.2021.108091>

Received 1 December 2020; Received in revised form 6 August 2021; Accepted 7 August 2021

Available online 9 August 2021

1470-160X/© 2021 The Authors.

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services in arid and semi-arid areas.

Precipitation is one of the most important limiting factors in regulating the structure and function of grassland ecosystems (Hu et al., 2008; Huxman et al., 2004). Exploring the relationship between vegetation productivity and precipitation is the key to understanding the formation of ecosystem productivity. Precipitation-use efficiency (PUE), the ratio of vegetation aboveground net primary production (ANPP) to annual precipitation, is an indicator of the efficiency of carbon–water conversion in ecosystems (Gamoun, 2016; Hu et al., 2010; Lehouerou, 1984). Meanwhile, as an important ecosystem functional trait, it can be used to measure the strategic change of precipitation when an ecosystem adapts to environmental changes (He et al., 2019). The increase in PUE indicates an increase in the efficiency of carbon–water conversion in ecosystems. Studying the dynamic change in carbon–water conversion efficiency in grassland ecosystems can more accurately predict the impact of changes in precipitation resources on productivity. Experimental warming enhanced PUE in most years, with larger positive effects in normal and wet than dry hydrological years in tallgrass prairie site study (Yan et al., 2014). The increase in PUE has been substantial in the Sahelian zone during 1982–2011 (Fensholt and Rasmussen, 2011; Gamoun, 2016). Although prior studies have analyzed the interannual dynamics of PUE, the long-term adaptation of ecosystems to climate change is often difficult to capture at short-time scales.

Previous studies of changes in precipitation utilization strategy in response to climate in grassland ecosystems have conducted using isolated ground-based observations in temperate and desert grasslands and experimental manipulations in tallgrass prairie (Bai et al., 2008; Liu et al., 2012; Yan et al., 2014). Bai et al. (2008) found that the temporal PUE negatively correlated with annual precipitation at the study site. Hu et al. (2010) study used 23 data sites, which concluded that inter-annual variations in precipitation and PUE was no significant relationship within given ecosystems along the China Grassland Transect (CGT). Most studies elucidated the physiological processes of using precipitation resources and the effects of surface transport on PUE for different grassland ecosystem types in arid areas (Guo et al., 2015; Huang et al., 2015; Liu et al., 2012). These efforts were valuable and provided a theoretical basis for understanding the changes in grassland ecosystem PUE in response to climate at the biome scale.

Eurasian grasslands, located in arid and semi-arid areas, are an important component of global grasslands (Jiao et al., 2017) and highly sensitive to climate change (Hu et al., 2018; Zhang et al., 2016). With their large and continuous spatial distribution, diverse vegetation types, complex topography and a wide range of climate gradients, Eurasian grasslands serve as an indispensable and exemplary macrosystem for conducting the continental scale analysis to understand the temporal variation and controls of PUE. However, previous studies of Eurasian grasslands were mostly focused on subregions (eg. Mongolian plateau, Tibet plateau) and at short-term observation scales that found PUE exhibited linear increases, decreases, or unrelated variation patterns with temperature and precipitation (Bai et al., 2008; Hu et al., 2010; Sun and Du, 2017). At present, at the continental scales, there is still a lack of holistic understanding of the long-term temporal patterns and controls of PUE in Eurasian grasslands.

In this study, we integrated field-observed aboveground net primary production (ANPP), long-term Global Inventory Monitoring and Modeling System (GIMMS) Normalized Difference Vegetation Index (NDVI), and meteorological datasets to calculate PUE in Eurasian grasslands from 1982 to 2015, aiming to answer the following questions: (1) What was the trend and spatial distribution of PUE in Eurasian grasslands during the period of 1982–2015? (2) What was the temporal variation pattern of PUE response to climate changes? (3) What were the main controls of temporal variation patterns of PUE in Eurasian grasslands? Addressing these questions would be of great importance for improving the understanding and predictions of productivity in Eurasian grasslands under the future precipitation resources changes.

2. Material and methods

2.1. Data collection

2.1.1. ANPP field observation data

Field-observed ANPP datasets were collected from three resources: (a) publications, from which 1015 field-observed ANPP datasets were extracted from the tables or figures of 206 publications in the Web of Science (<https://apps.webofknowledge.com>) and China National Knowledge Infrastructure (<https://www.cnki.net/>); (b) seven field-observed ANPP datasets from the Oak Ridge National Laboratory (https://daac.ornl.gov/cgi-bin/datasetlist.pl?p=13#grassland_anchor); and (c) 809 field-observed ANPP datasets were obtained directly from field surveys by the researchers of this study. To ensure data quality, we excluded datasets with ANPP outliers (observations falling outside the range of the mean \pm 3 standard deviations) and those that did not belong to grassland ecosystems in the Moderate Resolution Imaging Spectroradiometer Land cover product (MCD12C1) according to the vegetation classification scheme of the International Geosphere-Biosphere Programme (IGBP). Finally, 1539 field survey and observation ANPP datasets in total were used in this study. ANPP was estimated as the peak above-ground biomass (including live biomass as well as standing dead biomass produced in the current year) during the growing seasons (from April to October of the year). Detailed descriptions of these ANPP datasets are available in Jiao et al. (2017).

2.1.2. Long term GIMMS NDVI and LAI data

The full-year coverage of GIMMS NDVI (1982–2015) remote sensing datasets was obtained from Advanced Very High Resolution Radiometer (AVHRR) sensors (<https://www.ncei.noaa.gov/data/avhrr-land-normalized-difference-vegetationindex/access/>). The AVHRR reflectance data were from NASA's Land Long-Term Data Record (LTDR) project, with a spatial resolution of 0.05° and a daily temporal sampling period, and used a geographic latitude/longitude projection. The maximum-value composite (MVC) approach was used to composite the daily AVHRR surface reflectance data into eight-day temporal resolution time series (Holben, 1986; Tucker et al., 2005). Data were corrected for sensor degradation, cloud cover, the solar zenith angle, and the viewing angle effects of the satellite as well as the presence of volcanic aerosols. The Global Land Surface Satellite (GLASS) leaf area index (LAI) product had a temporal resolution of eight-day and spans from 1982 to 2015. For the period of 1982–2015, the LAI product was generated from LTDR AVHRR reflectance data. It was provided in a geographic latitude/longitude projection with a spatial resolution of 0.05°, and eight-day temporal resolution. The GLASS LAI product version 3.0 was obtained from the National Earth System Science Data Center, National Science & Technology Infrastructure of China (<http://www.geodata.cn>). These data have been widely used to monitor long-term vegetation activation trends (Chen et al., 2019; Fensholt and Rasmussen, 2011; Piao et al., 2015).

2.1.3. CRU climate data

Meteorological data were derived from the Climate Research Unit 4.05 (CRU) dataset available from University of East Anglia Climate Research Unit (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.05/cruts.2103051243.v4.05/) (Harris et al., 2020), which had a spatial resolution of 0.5°. The climate variables included temperature, precipitation, vapor pressure and shortwave radiation from 1982 to 2015. The climate anomaly method (CAM) was used to identify and remove outliers of precipitation and air temperature values beyond \pm three times the standard deviations (four times for precipitation) (Peterson et al., 1998). Annual temperature and precipitation were calculated from the monthly temperature and precipitation datasets, respectively. Annual shortwave radiation was calculated from the six-hourly shortwave radiation datasets. Vapor pressure deficit (VPD) was calculated from the

actual vapor pressure (AVP) and temperature datasets, according to follow equation (Buck, 1981; Yuan et al., 2019):

$$VPD = SVP - AVP \quad (1)$$

$$SVP = 6.112 \times e^{\frac{17.67 \times AT}{AT - 243.5}} \quad (2)$$

Where SVP and AVP are saturated vapor pressure and actual vapor pressure (kPa), Ta is the land air temperature (°C). We used a simple regression model to analyze those climate factors (temperature and precipitation) changes of long-term trends, and applied the Structural equation modeling (SEM) to clarify their influences on the PUE during 1982 to 2015 in Eurasian grasslands.

2.1.4. ENSO data

The El Niño/Southern Oscillation (ENSO) variability was evaluated using a revised Multivariate ENSO Index (MEI) (<https://www.psl.noaa.gov/enso/mei/>), which based on five variables: sea level pressure (SLP), SSTs, 10-m zonal wind (U), 10-m meridional wind (V), and outgoing longwave radiation (OLR). A principal-component (i.e., Empirical Orthogonal Function (EOF)) analysis is performed upon an array composed of column vectors of the standardized anomalies of SLP, SST, U, V, and OLR (Wolter and Timlin, 2011). November-December MEI for the labeled year organized by El Niño and La Niña events. El Niño and La Niña events based on a threshold of ± 1 . MEI > 1 indicates particularly strong El Niño event. MEI < 1 reveals the particularly strong La Niña events that related ocean conditions exert on the tropical Pacific atmosphere (Zhang et al., 2019).

2.2. Data post-processing and methodology

2.2.1. ANPP estimation from GIMMS NDVI

Field-observed ANPP and GIMMS NDVI were used to construct 52 regression models, including linear, exponential, power, and logarithmic models, and the optimization model was assessed by the maximum R-squared (R^2 , Equation 3) and the minimum root mean square error (RMSE, Equation 4) of these regression models:

$$R^2 = \frac{\left(\sum_{t=1}^n ((ANPP_{obs})_t - (\overline{ANPP_{obs}})) ((ANPP_{mod})_t - (\overline{ANPP_{mod}})) \right)^2}{\sum_{t=1}^n ((ANPP_{obs})_t - (\overline{ANPP_{obs}}))^2 \sum_{t=1}^n ((ANPP_{mod})_t - (\overline{ANPP_{mod}}))^2} \quad (3)$$

$$RMSE = \sqrt{\frac{\sum_{t=1}^n ((ANPP_{obs})_t - (ANPP_{mod})_t)^2}{n}} \quad (4)$$

where R^2 explains the strength of the relationship between field-observed ANPP ($ANPP_{obs}$) and modeled ANPP data ($ANPP_{mod}$), RMSE was the root mean square error between $ANPP_{obs}$ and $ANPP_{mod}$, n was the number of field-observed ANPP for model validation.

As stated above, the model with the highest R^2 (0.68) and lowest RMSE (14.76 g C m⁻²) of these 52 regression models was identified as the optimal model for estimating the ANPP in Eurasian grasslands. Approximately 75% of the field-observed ANPP data were randomly selected to develop the ANPP estimation model, and the remaining 25% were used to validate the model. Detailed information about the development of the empirical ANPP-NDVI model was available in Jiao et al. (2017). To match the CRU climatic dataset, the ANPP gridded dataset was scaled to a resolution of 0.5° by bilinear interpolation resampling (Parker et al., 1983).

2.2.2. PUE calculation

The PUE in this study was calculated as the ratio of ANPP to the corresponding annual precipitation (AP) at each pixel from 1982 to 2015 (Knapp and Smith, 2001; Lehouerou, 1984), according to Equation (5):

$$PUE_{yr(i,j)} = \frac{ANPP_{yr(i,j)}}{AP_{yr(i,j)}} \quad (5)$$

where PUE was the precipitation-use efficiency (g C m⁻² mm⁻¹), ANPP was the aboveground net primary productivity (g C m⁻² yr⁻¹), and AP was the annual precipitation (mm). yr was long term time series, corresponding with grid cell (i, j) for each year from 1982 to 2015.

2.3. Data analysis

2.3.1. Trend of PUE and climate

PUE, temperature and precipitation time series trends during 1982–2015 were analyzed using a simple regression model:

$$y = \alpha + \beta t + \xi \quad (6)$$

where t was the year of time series from 1982 to 2015. y was PUE, temperature and precipitation per year. $\hat{\alpha}$ was intercept, and β was slope, and ξ was the residual of the fit. A statistical probability of $P < 0.1$ determined significance. We used Kolmogorov-Smirnov parameters to test the normality of PUE, AP and AT data series. The results of Kolmogorov-Smirnov parameters analysis showed that the PUE (0.07 > 0.05), AP (0.11 > 0.05), AT (0.20 > 0.05) data series all conform to normal distribution.

2.3.2. Contribution of grassland types to Eurasian grasslands PUE

The partitioning of the trend to grassland types followed the definition of Equation (7). For the entire PUE, the contribution of the trend of grassland types j (alpine meadow, alpine steppe, arid steppe, desert steppe, forest steppe and typical steppe) to the Eurasian grasslands PUE trend was defined as (Ahlstrom et al., 2015):

$$f_j = \frac{\sum_t x_{jt} |X_t|}{\sum_t |X_t|} \quad (7)$$

where x_{jt} was the PUE long-term interannual dynamic for grassland type j at time t (years), and X_t was the entire Eurasian grasslands PUE, so that $X_t = \sum_j x_{jt}$. By this definition f_j was the contribution of j grassland type to the entire Eurasian grasslands PUE.

2.3.3. Z-score of PUE and climatic factors

In order to explore the synergy between annual temperature and annual precipitation on temporal variations of PUE, we applied the z-score methods to normalize annual temperature, precipitation, and PUE from 1982 to 2015 (Ahlstrom et al., 2015; Poulter et al., 2014), according to Equation (8):

$$Z_{(i,j)} = \frac{X_{(i,j)} - \bar{X}_{1982-2015, (i,j)}}{\sigma X_{1982-2015, (i,j)}} \quad (8)$$

where $Z(i, j)$ was the z score of annual temperature, annual precipitation and PUE for grid cell (i, j) in each year (1982–2015). X was the temperature, precipitation, and PUE values for each grid cell (i, j) in each year (1982–2015). \bar{X} was the average value of temperature, precipitation, and PUE for each grid cell (i, j) from 1982 to 2015. σ was the standard deviation of temperature, precipitation, and PUE for each grid cell (i, j) from 1982 to 2015.

2.3.4. Cascading effects networks

SEM is a methodology for representing a theoretical network of linear relations between variables (Gefen et al., 2011). We performed

SEM to construct the cascading effects networks of climatic factors (precipitation and temperature) – VPD – LAI – PUE (CVLP-CENet), and explore how climate factors controlled the temporal variation of PUE. Optimal model was determined by the standard of the χ^2 -test ($P > 0.05$), the comparative fit index (CFI) (> 0.9) (Bentler, 1990), and low RMSEA (< 0.08). SEM was conducted in the AMOS 18.0 software (IBM, Chicago, IL, USA). Further statistical analyses were conducted in SPSS 13.0 (IBM).

3. Results

3.1. Temporal dynamics of PUE in Eurasian grasslands

The PUE showed a significant uptrend from 1982 to 2015 over the Eurasian grasslands ($P < 0.1$) (Fig. 1a). The PUE fluctuated from 0.13 to 0.16 $\text{g C m}^{-2} \text{mm}^{-1}$, with fluctuation of 20.4% of the 34 years average value ($0.15 \pm 0.01 \text{ g C m}^{-2} \text{mm}^{-1}$). The PUE increased at an average rate of $3 \times 10^{-3} \text{ g C m}^{-2} \text{mm}^{-1}/10 \text{ yr}$, which implied that the efficiency of carbon–water conversion of Eurasian grassland ecosystems slightly increased over the past three decades.

The mean annual temperature in Eurasian grasslands fluctuated from -1.78 to $3.9 \text{ }^\circ\text{C}$, with an average temperature of $0.31 \text{ }^\circ\text{C}$. There was a significant increase of temperature at a rate of $0.3 \text{ }^\circ\text{C}/10 \text{ yr}$ from 1982 to 2015 in Eurasian grasslands ($P < 0.1$) (Fig. 1b). By contrast, over the period of 1982–2015, the change in annual precipitation was relatively stable with no significant trend changes ($P > 0.1$) (Fig. 1b). The annual precipitation fluctuated from 285.20 to 358.67 mm.

The MEI represents ENSO events, which indicated warm and dry years in El Niño and cold and rainy years in La Niña. However, our result showed that temperature and precipitation in Eurasian grasslands did not correspond to the expected El Niño and La Niña event (Fig. 1b). The result suggested that the ENSO event had no significant direct effects on the interannual dynamic changes of the PUE in Eurasian grasslands.

3.2. PUE trends and contribution of different grassland types

The PUE trend of Eurasian grasslands varied greatly at geographic

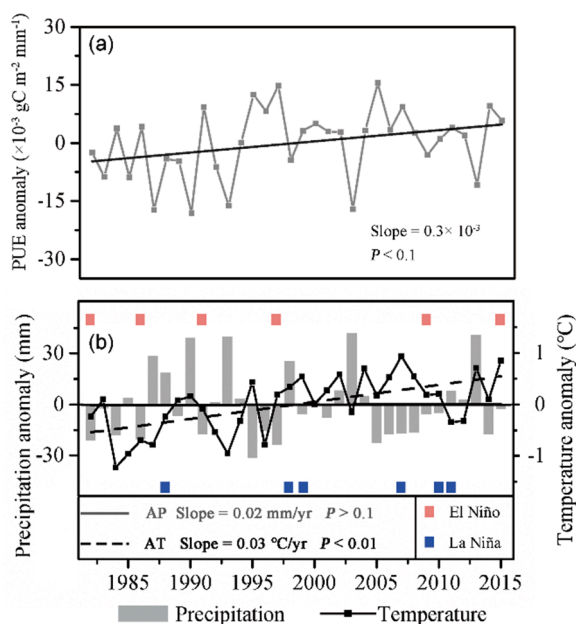


Fig. 1. Interannual dynamics of PUE (a), annual precipitation and annual temperature (b) in the whole Eurasian grasslands during 1982–2015. The slope of PUE, annual precipitation and annual temperature were shown in each subplot. The red and blue squares represented El Niño and La Niña events, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

distribution. The result showed that the PUE trend varied from -25×10^{-3} to $45 \times 10^{-3} \text{ g C m}^{-2} \text{mm}^{-1}/10 \text{ yr}$ at grids, with an average of $2.6 \times 10^{-3} \text{ g C m}^{-2} \text{mm}^{-1}/10 \text{ yr}$. The PUE increasing trends were found in 54.3% of the total area (Fig. 2b). PUE significantly increased in the eastern region of the Eurasian grasslands, while it decreased in the central and western regions (Fig. 2a).

The trend of PUE also varied greatly among different grassland types (Fig. 2c, d, e, f, g, h). The PUE in alpine meadow, alpine steppe, desert steppe and typical steppe showed decreasing trend, with the mean rate of -0.2×10^{-3} , -2.6×10^{-3} , -0.03×10^{-3} , and $-0.9 \times 10^{-3} \text{ g C m}^{-2} \text{mm}^{-1}/10 \text{ yr}$, respectively (Fig. 2c, d, f, h). On the contrary, the PUE in arid and forest steppe were in increasing trend. The PUE in forest steppe showed the greatest increasing trend ($13 \times 10^{-3} \text{ g C m}^{-2} \text{mm}^{-1}/10 \text{ yr}$), and the areas with growing trend accounted for 95% of the total area of forest steppe (Fig. 2g).

The PUE trends of different grassland types played different roles in the overall trend of PUE in Eurasian grasslands (Fig. 2c, d, e, f, g, h). Forest steppe contributed the most to PUE trend of Eurasian grassland, at 31.42% (Fig. 2g). The following contribution was arid steppe (25.31%) (Fig. 2e), while the alpine grasslands contributed the least to the trend of Eurasian grassland (1.90%). The contribution of alpine meadow, typical steppe and desert steppe to the trend of the Eurasian grassland were 9.94%, 11.90% and 19.52%, respectively (Fig. 2a, f, h).

3.3. Relationships between the temporal variations of PUE and climatic factors

We analyzed the effects of temperature, precipitation and radiation variables on the temporal variation of PUE (Fig. 3). On the continental scale, the PUE was not significantly correlated with temperature ($P > 0.05$, Fig. 3a), but it showed a linear decrease pattern with precipitation ($P < 0.01$, Fig. 3b), and exhibited a secondary concave function with radiation pattern ($P < 0.01$, Fig. 3c). Among the climatic factors, precipitation shown as the main factor affecting the interannual variation of PUE at the continental scale in Eurasian grasslands.

The synthetic effects of temperature and precipitation on PUE were further analyzed by using the normalized z-score of annual precipitation and temperature (Fig. 4). We found that PUE had a decreasing trend along the increase of precipitation, but no significant trend with the increase of temperature (Fig. 4a). It further demonstrated that the interannual variation of PUE was mainly affected by precipitation, showing PUE being smaller in wet years and larger in dry years.

We then used a linear regression model to analyze how the PUE response to temperature and precipitation in different grassland types (Fig. 4b, c, d, e, f, g). The result showed that the interannual variation of PUE response to precipitation had similar linear decreasing patterns for all grassland types. By comparison, the PUE in forest steppe was most sensitive to precipitation change ($5 \times 10^{-4} \text{ g C m}^{-2} \text{mm}^{-2}$) (Fig. 4f), while in alpine steppe and alpine meadow remained a slight decrease with precipitation (Fig. 4b, c).

The PUE showed various patterns with temperature in different grassland types. In alpine meadow, arid steppe and forest steppe, the PUE exhibited a linear increase pattern with temperature ($P < 0.05$, Fig. 4b, d, f). In typical steppe, the PUE showed a significant concave-down pattern with temperature ($P < 0.05$, Fig. 4g). However, there were no significant relationships between PUE and temperature in alpine steppe and desert steppe ($P > 0.05$, Fig. 4c, e).

4. Discussion

4.1. Long-term trend and interannual variations of PUE in Eurasian grasslands

We integrated long-term observations during 1982–2015 to identify the trend of PUE at the continental scale in Eurasian grasslands. We found that PUE showed an uptrend in Eurasian grasslands over the past

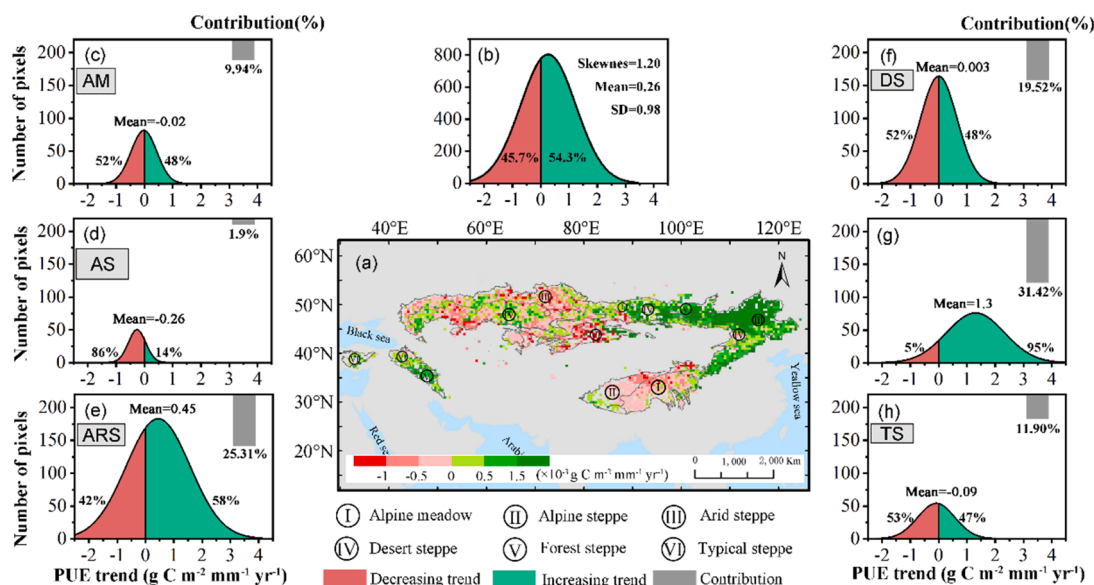


Fig. 2. Spatial distribution of the trends of precipitation-use efficiency (PUE) in Eurasian grasslands during 1982–2015 (a), and frequency distribution and contribution of PUE trends in Eurasian grasslands (b), alpine meadow, AM (c), alpine steppe, AS (d), arid steppe, ARS (e), desert steppe, DS (f), forest steppe, FS (g) and typical steppe, TS (h). Red color represents a decreasing trend, green color represents an increasing trend, and grey color represents the contribution of different grassland types to the Eurasian grasslands PUE trend (1982–2015) (c–h). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

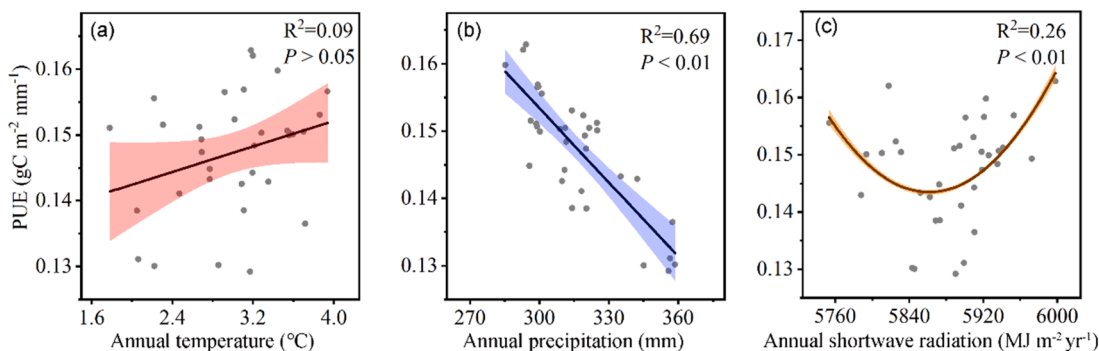


Fig. 3. Interannual variation of precipitation-use efficiency (PUE) with annual temperature (a), annual precipitation (b), and annual shortwave radiation (c) at continental scale in Eurasian grasslands. The thick lines were the regression curves. A statistical probability of $P < 0.05$ determined significance. The shading represented the regression analysis confidence range (5th and 95th percentiles).

three decades. This increase in PUE suggested an increase in the efficiency of carbon–water conversion in Eurasian grasslands, which was consistent with the results of increased vegetation productivity observed in this region (Jiao et al., 2017). Previous studies in Sahelian similarly found that PUE displayed significant increase during 1982–2007 (Fensholt and Rasmussen, 2011). However, in Tunisia rangeland and Northwestern China grasslands, the PUE were shown in decreasing trend and no trend, respectively (Chang et al., 2018; Gamoun, 2016).

We found that the Eurasian grasslands consist of various types exhibited different PUE trends. The PUE in arid and forest steppe had an increasing trend, of which forest steppe showed the largest growth rate. It would be attributed to that forest grasslands are mainly distributed in the East Asian monsoon region, where sufficient hydrothermal resources and nitrogen deposition greatly facilitate the fastest growth of productivity and PUE (Fang et al., 2014; Palpurina et al., 2019; Yu et al., 2014). On the contrary, the PUE in alpine meadow, alpine steppe, desert steppe and typical steppe showed decreasing trend, of which the decrease rate of PUE in alpine steppe was maximal. Previous study shown that nutrients were main factor in limiting the growth of vegetation in alpine steppe (Kou et al., 2020). In addition, increased precipitation is liable to

lost as runoff (Hu et al., 2010; Lehouerou, 1984), which likely increases the loss of soil nutrients, limits vegetation productivity and thus results in the decline of PUE (Yang et al., 2010; Zhang et al., 2017). The decreasing trend of PUE generally indicates that the stability and productivity potential of grassland ecosystems tend to decrease (Gamoun, 2016; Huxman et al., 2004). Therefore, the maintenance of these grassland ecosystems with decreasing trend of PUE needs to be paid more attention by grassland managers.

4.2. Climate controls on the interannual variation of PUE

Climate variations are important factors in regulating the structure and function of grassland ecosystems in arid and semi-arid areas (Huxman et al., 2004; Zhao et al., 2020). We found that the interannual variation of PUE was mainly regulated by precipitation at the continental and biome scales, and the PUE showed a linearly decreasing trend with the increase of precipitation (Fig. 3b). Previous local studies in North America and Inner Mongolian grasslands similarly indicated that the temporal pattern of PUE showed significant decreasing trends with precipitation (Bai et al., 2008; Huxman et al., 2004). At the regional

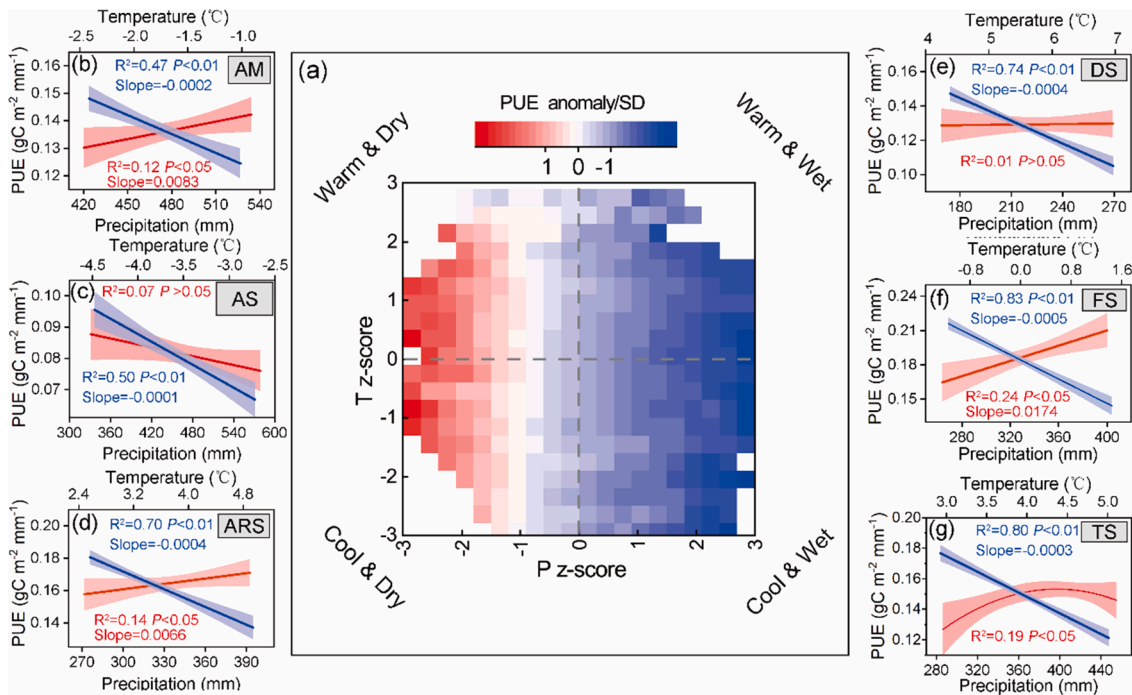


Fig. 4. The influence of the covariance of precipitation and temperature on interannual variations of precipitation-use efficiency (PUE) in Eurasian grasslands. Distribution of normalized PUE with precipitation and temperature z-score in Eurasian grasslands (a), and temporal variation patterns of PUE with precipitation and temperature in alpine meadow, AM (b), alpine steppe, AS (c), arid steppe, ARS (d), desert steppe, DS (e), forest steppe, FS (f) and typical steppe, TS (g). The thick lines were the regression curves. Blue and red colors represent precipitation and temperature, respectively (b-g). A statistical probability of $P < 0.05$ determined significance. The shading represented the regression analysis confidence range (5th and 95th percentiles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

scale, the consistent decreasing patterns were reported in alpine grassland in the Tibetan Plateau (Sun and Du, 2017). This is likely because the proportion of runoff and soil evaporation loss (ineffective precipitation) increased overwhelms the proportion of vegetation absorption and utilization (effective precipitation) with the increase of precipitation (Lehouerou, 1984; Yan et al., 2014). For example, in desert and arid steppe with low precipitation, low vegetation cover usually causes increased precipitation to be lost by soil evaporation (Gaitan et al., 2014). In alpine grasslands with more precipitation, while temperature and nutrients limit the absorption and utilization of water, resulting in increased precipitation likely being lost by runoff (Lehouerou, 1984).

Compared to precipitation, temperature played relatively minor effects on the temporal variation of PUE in Eurasian grasslands. We found that the interannual variation of PUE at the whole continental scale was not significantly correlated with temperature, but showed diverse patterns for different biomes scale that explained the weak relations at continental (Fig. 3a). We found that in alpine meadow, arid steppe and forest steppe, the PUE showed linear increase patterns with temperature, but a first increase and then decrease pattern with temperature in typical steppe (Fig. 4 b, d, f). Increases of temperature facilitate vegetation optimal photosynthesis and promote the PUE in low temperature regions (Xu et al., 2012). Continuously rising temperatures could also accelerate soil moisture loss, which lead to droughts with a negative effect on PUE (Liu et al., 2012).

The PUE are closely related to carbon uptake and multiple water cycling processes which with complicated regulating components. Hydrothermal conditions are found to be the most important influence factors for the temporal variations of PUE. We then built the cascading effects networks to further reveal the underlying mechanism of interannual variations of PUE (Fig. 5). We found that precipitation had direct negative effect on PUE, and indirect positive effect on PUE through its positive effects on LAI and ANPP. However, the direct negative effect (-0.92) of precipitation was overwhelmingly stronger than that indirect

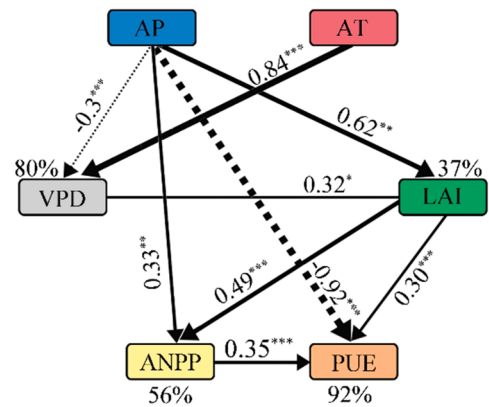


Fig. 5. Structural equation models of climatic factors (annual temperature, AT; annual precipitation, AP), atmospheric vapor pressure deficit (VPD), leaf area index (LAI) and aboveground net primary production (ANPP) with precipitation-use efficiency (PUE) in Eurasian grasslands. Solid and dashed arrows represented the positive or negative effects in fitted structural equation models, respectively. The widths of arrows indicated the strength of the relationships. The percentage (R^2) indicated the degrees of explanation of variables, and *, ** and *** represented a significant relationship at $P = 0.05$, $P = 0.01$ and $P = 0.001$ level, respectively.

positive effect (0.41) on PUE. Temperature had no direct effect on PUE, while have indirect positive effect though its positive effects on VPD, LAI and ANPP. LAI, shaped by the climate pattern, as an important ecosystem trait directly affects PUE (Konings et al., 2017; Niu et al., 2011). The increase of LAI is beneficial to plant photosynthesis, and meanwhile reduces water dissipation by intercepting soil moisture evaporation thus improves the efficiency of precipitation conversion into biomass (Tao et al., 2020). The direct effect of precipitation and

temperature and their indirect effects on VPD, LAI and ANPP together determined 92% of the temporal variations of PUE in Eurasian grasslands. These results clarified the underlying processes that climate factors shaped the PUE temporal pattern by the cascading effects networks of precipitation and temperature – VPD – LAI – ANPP – PUE (CVLP-CENet).

5. Conclusions

We analyzed a long-term dynamic PUE and clarified the trend and temporal variations of PUE in response to climatic factors at the biome and continental scales in Eurasian grasslands. Our results showed that, overall, the PUE in Eurasian grasslands increased from 1982 to 2015, implying that the efficiency of water-carbon conversion was gradually increasing. In forest steppe the PUE was fastest increased, while in alpine steppe the PUE was fastest decreased. Our results indicated that precipitation was the dominant factor to control the temporal variation of PUE, and PUE exhibited consistent linear decreasing response to precipitation at the biome and continental scale. The PUE had hardly relationship with temperature at the continental scale, but showed linear increase, concave-down and no correlation with temperature for different biomes. Climatic factors shaped the temporal variations of PUE through the underlying cascading effects networks of precipitation and temperature – VPD – LAI – ANPP – PUE (CVLP-CENet) in Eurasian grasslands. Our study identified the long-term trends, interannual variations and controls of PUE responses to climate change and would be helpful for understanding the mechanisms and predicting future grassland ecosystems dynamics.

6. Data availability statement

The data that support the findings of this study are available on request from the corresponding author.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was supported by National Key Research and Development Program of China (No. 2016YFA0600104), National Natural Science Foundation of China (No. 41991234, 31800406), and International Partnership Program of Chinese Academy of Sciences (No. 121311KYSB20170004).

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