https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

Carbon–Water Flux Coupling Characteristics and Driving Factors at Multi-temporal Scales in an Alpine Meadow Ecosystem on the Tibetan Plateau

Yerong Gao[1, 2, 3], Suosuo Li[1, 2], Haipeng Yu[1], Shaoying Wang[1], Yongjie Pan[1, 2], Zongming Li [1, 2, 3]

[1]Northwest Institute of Ecological Environment and Resources, Chinese Academy of Sciences/ Key Laboratory of Cryospheric Science and Frozen Soil Engineering, Lanzhou, 730000, Gansu, China

[2]Comprehensive Observation and Research Station for Qinghai Lake, Chinese Academy of Sciences, Gangcha, 812300, Qinhai, China

[3]University of Chinese Academy of Science, Beijing, 100049, China

Correspondence to: Suosuo Li (liss@lzb.ac.cn)

Abstract. Alpine meadow ecosystems play a crucial role in the global carbon and water cycles, with water use efficiency (WUE) serving as a key indicator of carbon-water coupling. Investigating the characteristics of carbon and water fluxes and WUE in alpine meadows on the Tibetan Plateau (TP) is essential for accurately assessing carbon budget, water cycling, and carbon–water interactions under climate change. This study utilized eddy covariance observations from 2012 to 2017 in an alpine meadow of the eastern TP to analyze the temporal dynamics of carbon fluxes (net ecosystem carbon exchange, NEE; ecosystem respiration, Re; gross primary productivity, GPP), water flux (evapotranspiration, ET), and WUE across daily, monthly to seasonal, and inter-annual timescales. Ridge regression was applied to identify the main drivers of carbon and water fluxes and WUE at different time-scale. The results indicate that: (1) the alpine meadow acted as a carbon sink, with a multi-year average NEE of 109.7 gC $m^{-2}y^{-1}$, and carbon and water fluxes as well as WUE exhibited pronounced temporal variations across daily, monthly to seasonal, and inter-annual timescales; (2) daily and monthly to seasonal variations of carbon fluxes were primarily driven by soil temperature (Ts), while ET was mainly controlled by radiation. At the inter-annual timescale, precipitation (PRE) and leaf area index (LAI) were the dominant factors influencing carbon and water fluxes; (3) Ts regulated WUE at daily, monthly to seasonal scales, whereas PRE was the key factor controlling carbon–water coupling at the inter-annual timescale. These findings enhance our understanding of the coupling characteristics and driving mechanisms of carbon

and water fluxes in alpine meadows, providing a scientific basis for predicting the responses of grassland ecosystems on the TP to future climate change.

Key Words: Tibetan Plateau, Alpine meadow ecosystem, Carbon and water fluxes, Water use efficiency (WUE), Environmental drivers

1 Introduction

The carbon and water cycles of terrestrial ecosystems are two fundamental biogeochemical processes at the land surface and serve as key pathways for energy transfer and water movement (Baldocchi et al., 2004; Luo, 2007; Melillo et al., 2017; IPCC, 2023). Under the ongoing context of global warming, these cycles exert significant impacts on regional and global climate (Zhou et al., 2004). Carbon and water cycles are closely linked and often vary synchronously, being tightly coupled through a series of transformations along the soil–vegetation–atmosphere continuum (Monson et al., 2010; Yu et al., 2013). Understanding the mechanisms of this coupling is therefore essential for advancing research on the carbon cycle (Hu et al., 2008; Zhang et al., 2018).

Grassland ecosystems are an important component of terrestrial ecosystems and play a key role in the carbon and water cycles of the land surface, serving as significant ecological carbon reservoirs (Liang et al., 2017; Schuman et al., 2002). Compared with other terrestrial ecosystems, grasslands exhibit higher sensitivity and vulnerability to climate change and human activities (Ahlstrom et al., 2015; Campos et al., 2013). The Tibetan Plateau (TP), known as the “Asian Water Tower” and the “Roof of the World,” not only plays a critical role in regional carbon and water cycling but also is highly sensitive to climate change. Grasslands cover more than 60% of the TP, with alpine steppe and alpine meadow being the dominant vegetation types, accounting for 34% and 27% of the total area, respectively (Liu et al., 2018; Miehe et al., 2019). The study area is an alpine meadow ecosystem, and investigating its carbon and water cycles and their coupling processes is of great significance for understanding carbon dynamics in terrestrial ecosystems.

A large number of studies have investigated the temporal dynamics of grassland carbon fluxes on the TP (Sun et al., 2019; Li et al., 2019; Wang et al., 2020, 2021; Li et al., 2021; Wang et al., 2022; Tao et al., 2023), and the mechanisms driving carbon fluxes have been comprehensively explored. Research across ten alpine grassland sites on the TP indicates that soil temperature (Ts), soil moisture (SW), and vapor pressure deficit (VPD) jointly regulate the intensity of seasonal and inter-annual carbon flux variations (Wang et al., 2021). Studies at seven sites in the Inner Mongolian grasslands have shown that growing-season precipitation (PRE) and leaf area index (LAI) are the most important drivers of inter-annual carbon fluxes. Eddy covariance measurements demonstrate that water availability significantly influences gross primary productivity (GPP) and can potentially shift ecosystems from carbon sinks to carbon sources in North American prairies (Fischer et al., 2012). European grassland studies emphasize that the same environmental factors can affect GPP at both daily and inter-annual timescale (Bahn et al., 2008). Analyses of the daily variation of net ecosystem carbon exchange (NEE) reveal that aridity and temperature regulate carbon fluxes at daily and seasonal scales in the sandy grasslands of Inner Mongolia (Niu et al., 2020). While the dominant drivers differ among grasslands in various climatic regions of the TP, most studies indicate that water availability and temperature condition are the primary factors influencing carbon flux dynamics. Although these studies have characterized carbon fluxes at the grassland surface and explored their driving mechanisms, most have focused on single time-scale. Comparative studies of carbon fluxes across multiple temporal scales in alpine grasslands remain limited, and research on the drivers and mechanisms of carbon flux variations across multiple timescales is still relatively scarce.

Evapotranspiration (ET) exhibits strong spatial and temporal heterogeneity and pronounced seasonality on the TP (Han et al., 2021), with higher ET in humid regions such as wetlands and alpine meadows, and lower ET in arid, high-elevation desert areas. The main factors driving ET include net radiation and energy supply, air and soil temperature, VPD, soil moisture, PREand groundwater levels, vegetation cover and phenology, as well as freeze–thaw and ice-phase dynamics (Shen et al., 2015; Wang et al., 2020; Chang et al., 2023). Studies based on remote sensing, reanalysis data, and eddy covariance observations have gradually revealed thatET over the past decade has shown an increasing or initially rising and then stabilizing trend in most humid regions of the eastern and central TP (Chen et al., 2024), with enhanced radiation and vegetation recovery contributing to increased ET. In some arid areas, water limitations also significantly affect ET variability. Most existing studies have focused on large-scale regional trends, and when exploring driving mechanisms, analyses are often restricted to a single

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

temporal scale or the inter-annual timescale. Consequently, a systematic understanding of ET variations and their coupling with driving factors across multiple time-scale remains limited.

Water use efficiency (WUE) typically defined as the ratio of ecosystem carbon assimilation to water consumption and is a key parameter for investigating carbon–water coupling processes and a core indicator for understanding ecosystem metabolism and climate response mechanisms (Cai et al., 2021; Hu et al., 2024). In recent years, researchers have examined the temporal dynamics and controlling factors of carbon and water fluxes and WUE on the TP, highlighting the synergistic effects of vegetation, soil, and atmospheric factors in regulating the carbon–water coupling of terrestrial ecosystems (Chen et al., 2004; Hu et al., 2009; Zhao and Yu, 2008). The high spatial heterogeneity of multiple environmental variables also contributes to differences in flux exchanges across regions (Sun et al., 2019). At the daily scale, VPD has been identified as the dominant factor influencing WUE across all seasons (Wu et al., 2019). At monthly to seasonal scales, soil water content (SWC) has been shown to be a key determinant of WUE in the Mongolian grasslands (Li et al., 2008). Seasonal dynamics studies across typical Chinese ecosystems indicate that temperature and LAI regulate WUE mainly by affecting the proportion of transpiration in ET (T/ET) (Zhu et al., 2014). At the inter-annual timescale, NDVI, temperature, and atmospheric CO_2 concentration are important drivers of WUE variability across mainland China (Sun et al., 2021). These findings suggest that the dominant drivers of WUE differ across time-scale, and that single-timescale studies limit both intra-regional comparisons across scales and inter-regional comparisons.

Based on observational data, this study analyzed the temporal dynamics of carbon and water fluxes and WUE in an alpine meadow ecosystem at daily, monthly to seasonal, and inter-annual timescales. Ridge regression was applied to identify the key drivers of carbon and water fluxes and WUE across these time-scale. The results provide insights into the carbon–water cycling and its controlling mechanisms in alpine meadow ecosystems of the TP.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

2 Materials and methods

2.1 Study area

This study was conducted in an alpine meadow at Maqu observation site (33.89 °N, 102.14 °E, 3423 m a.s.l.) on the Zoige Plateau, located in the upper reaches of the Yellow River on the eastern Tibet Plateau (Figure 1). The site lies in a seasonally frozen ground region within the sub-frigid humid zone and is characterized by a typical continental climate. The underlying surface is a representative alpine meadow dominated by Kobresia tibetica, Potentilla anserina, and Kobresia humilis, with a vegetation cover of approximately 92% (Wang et al., 2012).

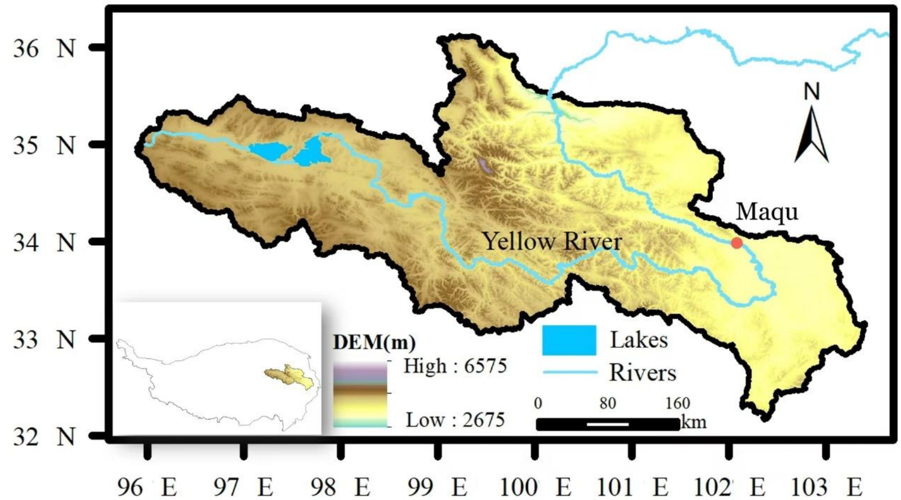


Figure 1: The location of the study area on the source of the Yellow River on the Qinghai-Tibet Plateau

2.2 Data collection and processing

At the Maqu observation site, an eddy covariance system and a micrometeorological observation system were currently installed. In this study, we used six years of continuous observations from 1 January 2012 to 31 December 2017. The variables analyzed include evapotranspiration (ET) (calculated from the latent heat flux), NEE, air temperature (Ta), relative humidity (RH), photosynthetically active radiation (PAR), Ts at four depths (5, 10, 20, and 40 cm), and SWC at the same depths as Ts. All data were recorded at a 30 min temporal resolution.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

LE and NEE were derived from 10 Hz raw turbulence data using EddyPro 6.1 (https://www.licor.com). The processing steps included spike removal, coordinate rotation, air density correction, virtual temperature correction, and frequency response correction. In addition, since daytime NEE values occasionally indicated unrealistically negative fluxes (i.e., apparent CO_2 uptake) during the non-growing season, these data were excluded (S. Wang et al., 2020).

VPD was calculated using standard formulas (Seager et al., 2015). Leaf area index (LAI) was obtained from the MODIS Land Product, Collection 6 (MOD15A2H; https://modis.ornl.gov/cgi-bin/MODIS/global/subset.pl), with a spatial resolution of 500 m and a temporal resolution of 8 days. PRE data were derived from the Maqu National Meteorological Station.

The carbon fluxes analyzed in this study included net ecosystem CO_2 exchange (NEE), ecosystem respiration (Re), and GPP. NEE was directly obtained from eddy covariance observations, whereas Re was modeled as a function of Ts and SWC using a composite model. GPP was then calculated as the difference between NEE and Re (Guan et al., 2009; Huang et al., 2008)：

$$R_e = R_{10} e^{E_0\left(\frac{1}{T_{ref}-T_0}-\frac{1}{T-T_0}\right)} e^{(d \cdot SWC + f \cdot SWC^2)} \qquad (1)$$

GPP was then calculated as the difference between NEE and Re:

$$GPP = -(NEE - Re) \qquad (2)$$

Evapotranspiration (ET) was estimated from the latent heat flux (LE, W m^{-2}) obtained by the eddy covariance measurements:

$$ET = LE/\lambda \qquad (3)$$

Where λ is the latent heat of vaporization ($J \cdot kg^{-1}$). In the Maqu alpine meadow on the eastern Qinghai–Tibet Plateau, λ was assigned an empirical value of 2.501×10^6 J kg^{-1}.

The calculation methods of ecosystem WUE (gC kg^{-1}) at daily, monthly, and inter-annual timescales were as follows:

$$\begin{cases} WUE_d = \frac{GPP_d}{ET_d} \\ WUE_m = \frac{GPP_m}{ET_m} \\ WUE_y = \frac{GPP_y}{ET_y} \end{cases} \qquad (4)$$

The growing and non-growing seasons were defined based on NEE dynamics (Körner et al., 2023). At the daily timescale, the onset and end of the growing season were determined by the net daily NEE. At the monthly to seasonal scale, the growing and non-growing seasons were simply defined as May–October and April–November, respectively. Carbon fluxes and environmental variables at different time-scale were aggregated either by summation or averaging, depending on the variable.

2.3 Method

In this study, carbon fluxes (NEE, Re, and GPP), water flux (ET), and WUE were treated as dependent variables, while environmental factors including Ta, soil temperature at 5 cm depth (Ts), PRE, SWC, VPD, PAR and LAI were considered as independent variables to identify the major drivers of the dependent variables.

Ridge regression was employed as the primary regression method. As an improved linear regression technique, ridge regression introduces an L2 regularization term into the loss function, which effectively addresses multicollinearity problems (Walker and Birch, 1988). Its mathematical expression is as follows:

$$Y = X\mathrm{B} + \varepsilon \quad (5)$$

Here, Y represents the response variable, X is the matrix of independent variables, B denotes the regression coefficients, and ε is the error term. The objective of ridge regression is to minimize the following loss function:

$$\mathrm{Loss}(\beta) = \frac{1}{2N}\sum_{i=1}^{N}(y_i - X_i\beta)^2 + \alpha\sum_{j=1}^{p}\beta_j^2 \quad (6)$$

The first summation term represents the ordinary least squares loss function, while the second summation term introduces the ridge regression regularization (L2 regularization). $\alpha$is the regularization parameter, and β_j is the regression coefficient of feature j. The regularization term is added to prevent overfitting by penalizing large coefficients, thereby reducing model complexity, lowering the risk of overfitting, and improving model stability. In this study, the ridge regression coefficients are interpreted as the relative contributions of the independent variables to the dependent variable.

When the sample size is limited, Pearson correlation coefficients were used to quantify the linear relationships between variables. The coefficient of determination (R^2) was employed to describe the strength and direction of these relationships. Pearson correlation coefficients range from -1 to 1, where -1 indicates a perfect negative correlation, 0 indicates no correlation, and 1 indicates a perfect positive correlation. Confidence interval (CI) bands were included in the correlation plots to indicate the

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

uncertainty of the estimates. Significance testing was performed for the correlations, with different approaches depending on the sample size. For small samples, a t-distribution test was applied.

3 Result

3.1 Variations of biometeorological factors

Meteorological observations from the Maqu County Meteorological Station recorded that the annual Ta and PRE from 1967 to 2020 were 1.84 ± 0.78 ℃ and 611.9 ± 89.2 mm, respectively (Figure 2). A significant warming trend was observed during this period, with the annual mean temperature rising at a rate of approximately 0.06 ℃ per year. From 1967 to 1997, temperature generally fluctuated between 0.4 ℃ and 2.1 ℃, whereas between 2012 and 2017, it consistently exceeded 2.5 ℃ and, in certain years, approached 3.5 ℃, indicating a considerable increase. In contrast, annual PRE displayed substantial inter-annual variability, exhibiting a long-term pattern of initial decline followed by partial recovery. The lowest annual PRE was recorded in 1996 (448.4 mm), while the highest occurred in 2020 (821.2 mm). During the period 2012-2017, PRE levels fluctuated markedly, with an average of 627.1 ± 83.9 mm, slightly above the long-term mean. In summary, the climate of the Maqu region from 2012 to 2017 was characterized by warmer temperature and increased PRE than before, reflecting a distinct warming trend.

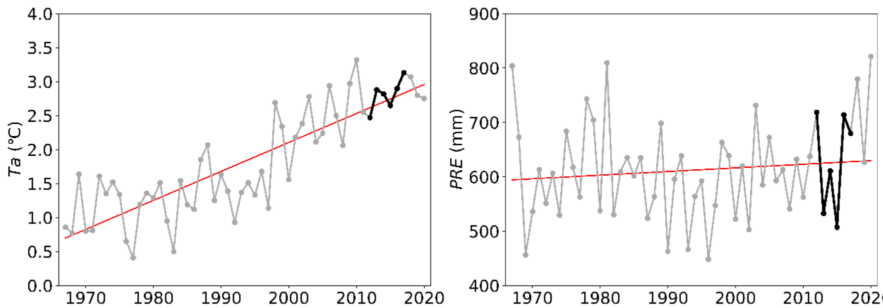


Figure 2: Annual average temperature and annual cumulative precipitation at Maqu Station from 1967 to 2020.

From 2012 to 2017, the dynamics of monthly mean (or accumulated) environmental factors in the Maqu alpine meadow ecosystem are shown in Figure 3. Ta peaked in July and August and reached its minimum in January. Over the six years, the mean monthly Ta ranged from -10.5 ℃ to 13.5 ℃. (Figure 3 (a)). The annual variation pattern of monthly mean Ts at multiple depths was similar to that of Ta (Figure 3 (b)).

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

Differences in monthly mean Ts across depths were relatively small, with the highest annual mean observed at 40 cm (5.3 ℃), followed by 10 cm and 5 cm (5.13 ℃ and 5.11 ℃, respectively), while the lowest occurred at 20 cm (4.7 ℃). Among all depths, the 5 cm Ts exhibited the greatest variability, ranging from -6.3 ℃ to 17.1 ℃. PRE was largely concentrated in summer, with the highest monthly mean occurring in July (135.0 mm) (Figure 3 (c)). For the 5–40 cm soil layers, SWC increased during the spring thaw following the winter freezing period and remained at approximately 0.3 $m^3\ m^{-3}$ (Figure 3 (d)). The monthly mean VPD ranged from 0.08 to 0.39 kPa, with the maximum occurring in July (0.32 kPa) and the minimum in January (0.15 kPa). (Figure 3 (e)). PAR reached its annual maximum during spring and summer but exhibited a declining trend during the growing season, particularly in August, which may be associated with variations in atmospheric water vapor and cloud cover during the rainy season (Tao et al., 2023). At Maqu, PAR ranged from 220.3 to 548.2μmol photons $m^{-2}s^{-1}$ across the year, with an annual mean of 357.1 μmol photons $m^{-2}s^{-1}$, indicating generally favorable light conditions (Figure 3 (f)). During the growing season, the monthly LAI was 2.0, with the highest values observed in July and August, averaging 3.7 and 2.7 $m^2\ m^{-2}$, respectively. (Figure 3 (g)).

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

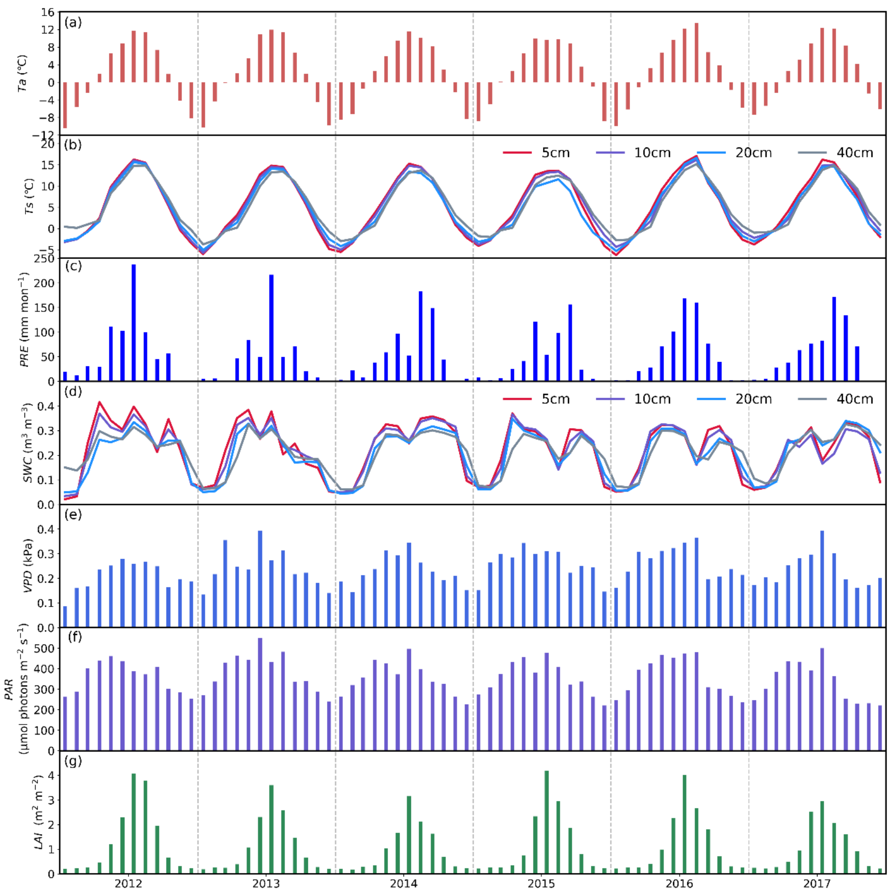


Figure 3: Seasonal variation characteristics of environmental factors. (a) Air temperature; (b) Soil temperature; (c) Precipitation; (d) Soil water content; (e) Vapor pressure deficit; (f) Photosynthetically active radiation; (g) Leaf area index.

3.2 Characteristics of carbon flux variation

The daily variations of carbon fluxes in the alpine meadow ecosystem varied significantly across seasons (Figure 4). The amplitude of daily variation was greatest in summer. NEE reached its minimum around 12:00 in summer (approximately –0.25 gC m^{-2} 30min^{-1}), indicating the strongest carbon uptake at midday. GPP peaked at about 13:00, exceeding 0.33 gC m^{-2} 30min^{-1}, reflecting the highest photosynthetic activity. The peak of GPP occurred later than that of NEE, likely due to differences in the optimum temperatures for photosynthesis and respiration. Re was generally higher in summer, as elevated temperatures

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

enhanced respiratory processes; however, the increase in GPP was greater, resulting in an overall enhancement of carbon uptake.

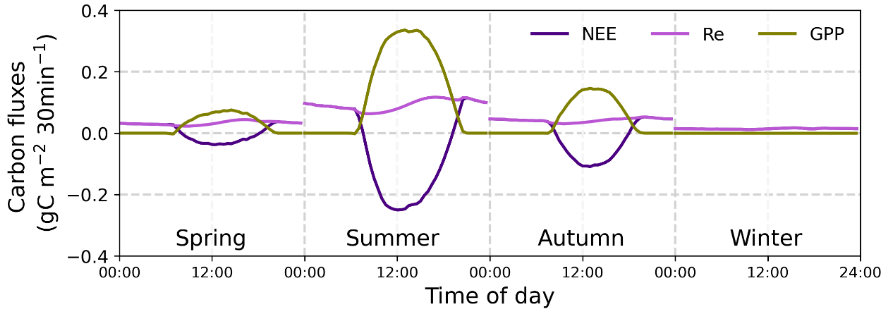
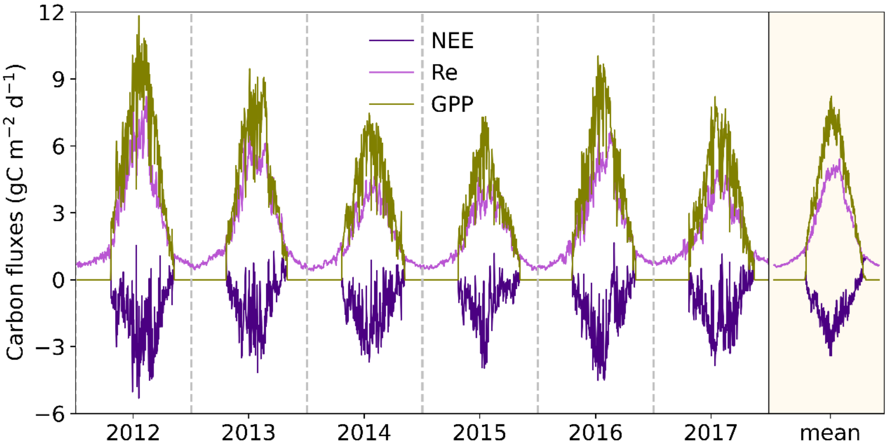


Figure 4: Daily variation characteristics of carbon fluxes in different seasons.

On a multi-year average, NEE exhibited a seasonal peak during the growing season, with a bimodal variations observed in 2012, 2016, and 2017, indicating pronounced seasonal variability. At the daily scale, the ecosystem did not consistently function as a carbon sink; on certain days, NEE values were positive, suggesting net carbon release, likely influenced by meteorological factors such as cloud cover fluctuations or precipitation events. GPP showed clear seasonal dynamics, with a unimodal variations each year. Re displayed smaller daily fluctuations but pronounced seasonal variability, with annual peaks occurring close to those of GPP, although slightly lagging, due to the temperature regulation of respiration rates. Across the six years, the minimum NEE was recorded on 19 July 2012 (-5.31 gC m^{-2} d^{-1}), while the maximum Re occurred on 12 August 2012 (8.21 gC m^{-2} d^{-1}), and the maximum GPP appeared on 19 July 2012 (11.83 gC m^{-2} d^{-1}).

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025



240 **Figure 5: Seasonal variation characteristics of carbon flux from 2012 to 2017.**

Summer represented the peak period of carbon uptake, with the cumulative NEE from May to October. The largest monthly carbon uptake generally occurred in July 2012, August accounted for the greatest proportion of annual carbon accumulation, reaching –63.54 gC m^{-2} mon^{-1}, exceeding the long-term mean for August (–51.36 gC m^{-2} mon^{-1}). Re peaked in July and August, showing a strong and regular annual trend. GPP also reached its maximum in July or August, with monthly mean cumulative values up to 210 gC m^{-2} mon^{-1}, reflecting intense photosynthetic activity. During the non-growing season, low temperature almost completely inhibited photosynthesis, with GPP approaching zero and Re declining to its minimum, averaging approximately 26.6 gC m^{-2} mon^{-1}, making the ecosystem a weak carbon source.

Multi-year monthly averages showed that the extreme NEE occurred in July (-75.96 gC m^{-2} mon^{-1}), the maximum Re also in July (147.96 gC m^{-2} mon^{-1}), and the peak GPP in July (223.87 gC m^{-2} mon^{-1}).

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

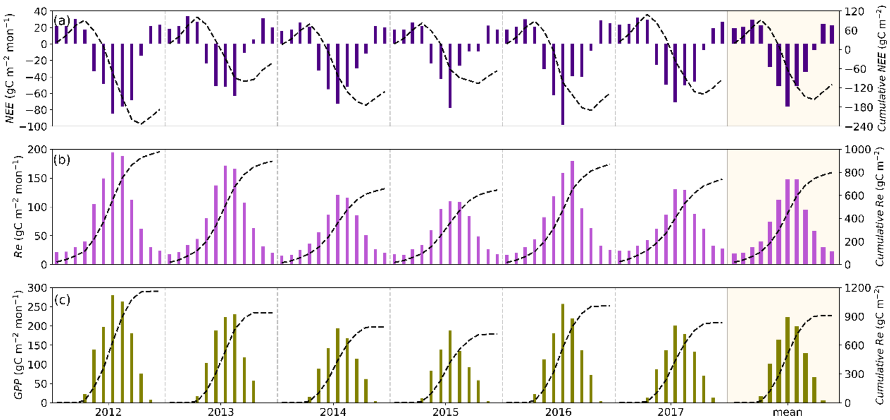


Figure 6: Seasonal variation and annual accumulation characteristics of carbon flux from 2012 to 2017.

The inter-annual variations of carbon fluxes in the Maqu alpine meadow from 2012 to 2017 are shown in Figure 6. Over the six years, NEE fluctuated, with a six-year mean of -109.69 gC m^{-2} y^{-1}, indicating that the ecosystem acted as a carbon sink. The annual cumulative NEE in 2012 was -187.48 gC m^{-2} y^{-1}, markedly higher than in other years. Re decreased initially and then increased over the six years, with a six-year mean of 798.62 gC m^{-2} y^{-1}. The highest Re occurred in 2012 (979.39 gC m^{-2} y^{-1}), while the lowest was in 2015 (646.13 gC m^{-2} y^{-1}). During the growing season, the six-year average Re was 656.30 gC m^{-2} y^{-1}, accounting for 82% of the annual total, indicating that the majority of Re occurred during the growing season.

Annual GPP showed a declining trend from 2012 to 2015, followed by an increase trend over the rest of two years. Over the six years, annual GPP ranged from 789.71 to 1166.87 gC m^{-2} y^{-1}, with a mean of 908.31 gC m^{-2} y^{-1}. The ratio of annual Re to GPP varied between 83.3% and 95.5%, with the highest ratio observed in 2013, indicating that most of the carbon fixed by the ecosystem was lost through ecosystem respiration.

During the growing season, the mean NEE was -252.01 gC m^{-2} y^{-1}, while net carbon release during the non-growing season averaged 142.32 gC m^{-2} y^{-1}, resulting in a growing-to-non-growing season carbon flux ratio of approximately 5:3. The six-year mean NEE was -109.69 gC m^{-2} y^{-1}.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

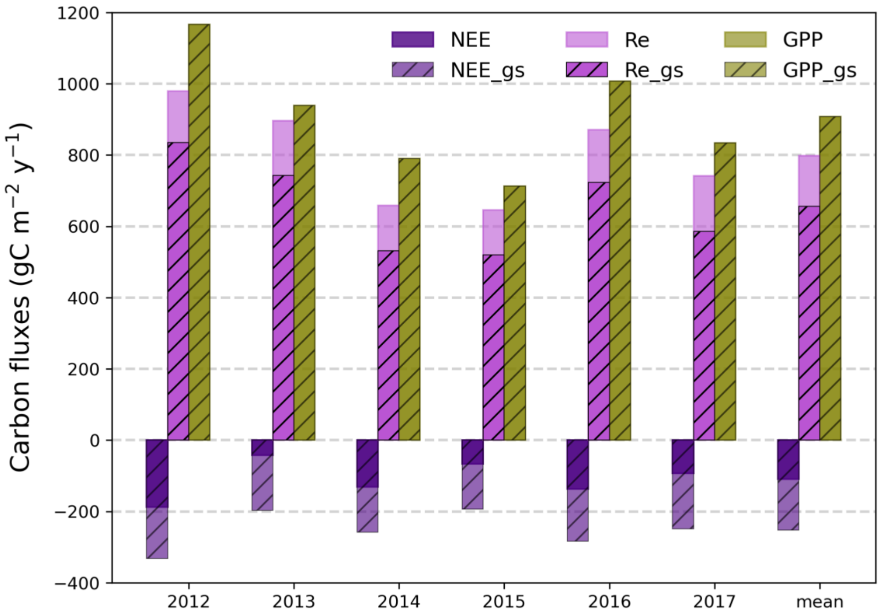


Figure 7: Inter-annual variation characteristics of carbon flux from 2012 to 2017.

3.3 Characteristics of ET variation

Seasonal averages of daily ET showed the highest values in summer, with spring and autumn exhibiting similar variations, while winter only displayed weak evaporation around noon. The ET peak occurred around 14:00, reaching 0.15 kg m^{-2} $30min^{-1}$ in summer, 0.07 kg m^{-2} $30min^{-1}$ in both spring and autumn, and approximately 0.02 kg m^{-2} $30min^{-1}$ in winter. During nighttime (21:00–07:30), ET was minimal and approaching zero in winter.

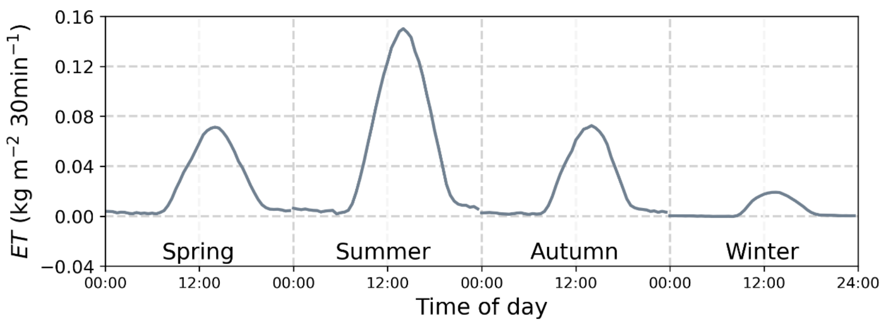


Figure 8: Daily variability of ET in different seasons.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

The seasonal variations of ET in the Maqu alpine meadow from 2012 to 2017 showed pronounced inter-annual differences (Figure 9), with high ET in summer and low ET in winter. Summer ET typically peaked in early August, with daily ET reaching up to 4.2 kg m^{-2} d^{-1}. During this period, vegetation photosynthesis was at its maximum, contributing to the annual peak in ET, while sufficient PRE provided ample water for evapotranspiration. In winter, daily mean ET generally ranged from 0 to 0.5 kg m^{-2} d^{-1}. Low temperature and vegetation dormancy limited transpiration, and evaporation was further reduced by cold conditions and snow cover. Inter-annual differences in ET peaks and cumulative ET were observed. For instance, summer ET was slightly higher in 2013 and 2015 than the multi-year average, likely due to greater PRE and sufficient soil water availability, whereas summer ET peaks in 2014 and 2016 were relatively lower, potentially associated with drought or abnormal temperatures. Winter ET showed relatively small variations, remaining consistently low.

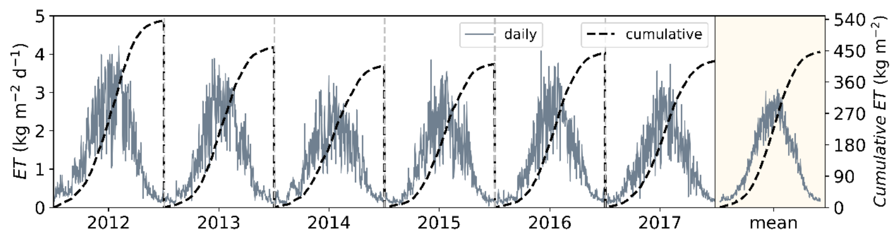


Figure 9: Seasonal variation and annual accumulation characteristics of ET daily from 2012 to 2017.

At the monthly and seasonal scales, the growing season from April to October contributed the majority of annual ET, with June to August being the three months with the highest ET. July typically exhibited the maximum monthly ET of the year, averaging approximately 80.59 kg m^{-2} mon^{-1}. Over the six years, the highest monthly ET occurred in July 2012, exceeding the long-term average, with a monthly cumulative value of 88.03 kg m^{-2} mon^{-1}.

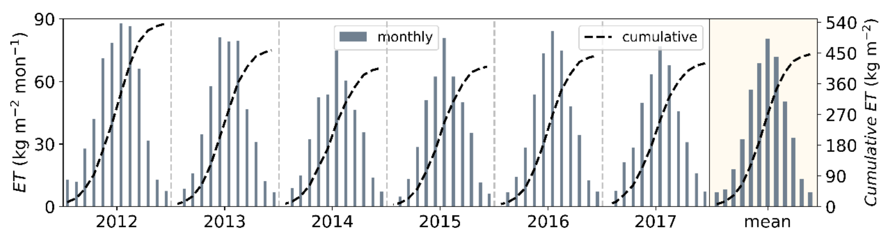


Figure 10: Seasonal variation and annual accumulation characteristics of ET monthly from 2012 to 2017.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

The inter-annual variations of ET showed a decreasing trend firstly, followed by a slight increasing trend. The mean annual ET was 446.5 kg $m^{-2}y^{-1}$, with relatively higher values in 2012 and 2013, reaching 536.9 and 459.5 kg $m^{-2}y^{-1}$, respectively. The six-year average ET during the growing season was 376.1 kg $m^{-2}y^{-1}$, accounting for 84% of the annual total. Annual ET represented 69.6% of annual PRE, indicating that approximately 70% of PRE may be lost through evapotranspiration.

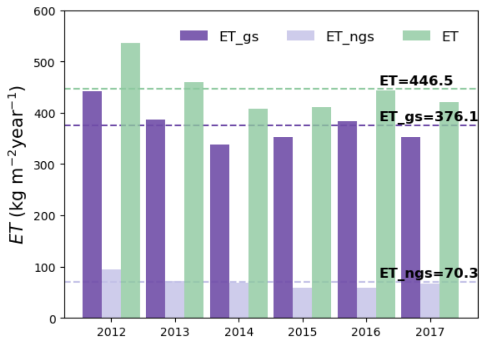


Figure 11: Inter-annual variation characteristics of ET from 2012 to 2017.

3.4 Characteristics of WUE variation

The seasonal averages of daily WUE (Figure 12) exhibited an asymmetric "U"-shaped variation, being highest in summer, intermediate in autumn, and lowest in spring, with peak morning values around 08:00 driven by elevated CO_2 concentrations that enhanced photosynthesis (5.82 gC $kg^{-1}H_2O$ in summer, 3.71 in autumn, and 2.65 in spring). WUE declined to its daily minimum as GPP decreased while ET peaked at noon, before partially recovering when both GPP and ET decreased but ET declined more rapidly. Overall, WUE was higher in the morning than in the afternoon (Wang et al., 2020), as high afternoon temperatures and low humidity enhanced ET, particularly soil water evaporation, leading to increased total ecosystem water loss and lower WUE.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

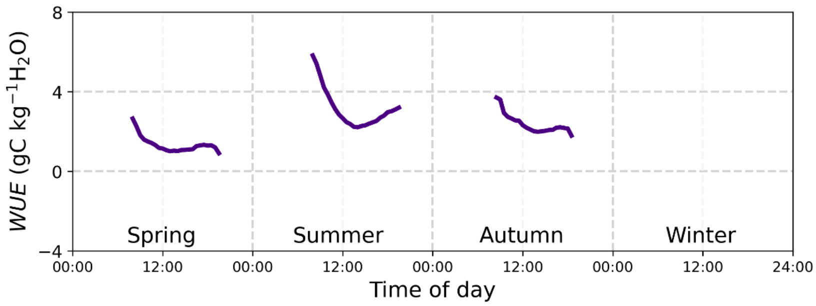


Figure 12: Daily variability of WUE in different seasons.

WUE exhibited pronounced seasonal variability. During the growing season, daily WUE values were mostly concentrated between 1 and 5 gC kg^{-1}H$_2$O. The annual variations of daily WUE showed a first increase followed by a decline, reaching its peak in July. WUE exceeded 3 gC kg^{-1}H$_2$O for approximately 41 days each year,, primarily from June to September, when high temperature, favorable light conditions, and elevated atmospheric CO_2 concentrations enhanced plant WUE.

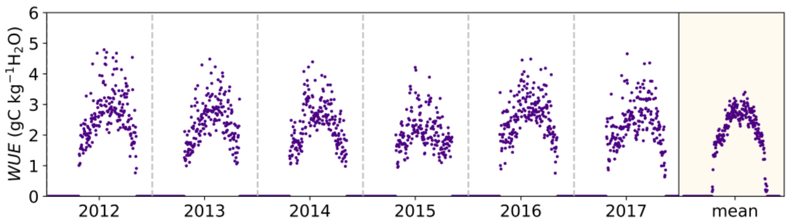


Figure 13: Seasonal variation characteristics of daily WUE from 2012 to 2017.

The month of maximum WUE varied among years. In 2012, 2015, and 2016, WUE peaked in July, whereas in 2013 and 2014, the peak occurred in August. In 2017, the highest WUE was observed in September. The overall maximum monthly WUE during the study period occurred in July 2012, reaching 3.17 gC kg^{-1}H$_2$O. Multi-year average results indicated that WUE peaked in July at 2.77 gC kg^{-1}H$_2$O, followed by August at 2.74 gC kg^{-1}H$_2$O. Inter-annual variations in meteorological conditions, vegetation growth, and soil water availability were likely the main factors driving differences in the timing of WUE peaks across years.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

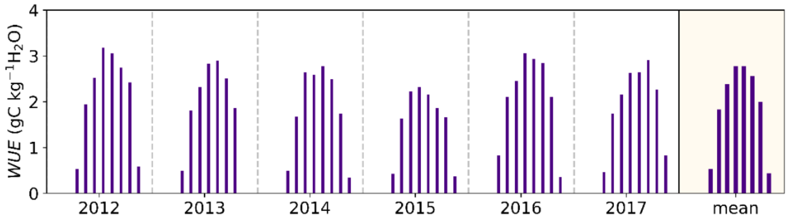


Figure 14: Seasonal variation characteristics of monthly WUE from 2012 to 2017.

The inter-annual variation of WUE during 2012–2017 exhibited a variations of first decline followed by a slight increase, with a mean value of 2.02 gC kg^{-1}H_2O. This level was notably higher than that observed at the Haibei site (0.40 gC kg^{-1}H_2O), as well as the regional average across the TP (1.17 gC kg^{-1}H_2O). It also exceeded the mean values reported in the Chinese grassland ecosystems (1.10 gC kg^{-1}H_2O) and alpine meadows specifically (0.90 gC kg^{-1}H_2O), suggesting that WUE is relatively higher in Maqu both within the Plateau and across Chinese grassland ecosystems. During the research periods, WUE was comparatively higher in 2012, 2013, and 2016, with values of 2.17, 2.04, and 2.27 gC kg^{-1}H_2O, respectively.

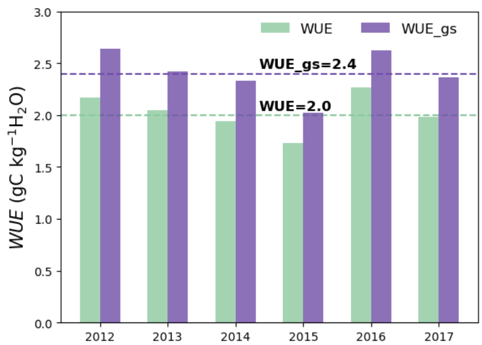


Figure 15: Inter-annual variation characteristics of WUE from 2012 to 2017.

3.5 Relationships between carbon and water fluxes, WUE, and environmental drivers at different time-scale

To further examine the effects of environmental factors on carbon and water fluxes as well as WUE, ridge regression was employed to quantify the relative contributions of different variables at both daily and monthly to seasonal scales. At the daily scale, Ts and LAI emerged as the dominant factors regulating carbon fluxes during the growing season. Specifically, LAI was identified as the primary determinant of

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

NEE, followed by PAR, whereas Ts was the leading control on both Re and GPP, with LAI playing a secondary role (Figure 16 (a–c)). Given that LAI itself was strongly correlated with Ts ($R^2 = 0.85$), Ts can be considered the overarching driver of carbon fluxes during the growing season. Moreover, the results suggest that when temperature increases or soil moisture declines, the enhancement of Re exceeds that of GPP. During the non-growing season, Ts remained the dominant factor influencing both NEE and Re.

Both in the growing and non-growing seasons, ET at the daily scale was primarily controlled by PAR (Figure 16 (d)), indicating the dominant role of solar radiation in regulating evapotranspiration. During the growing season, Ts and PAR jointly influenced WUE (Figure 16 €), with PAR exerting a negative effect. Since PAR positively affected both GPP and ET, higher radiation enhanced photosynthesis and transpiration simultaneously, but reduced WUE.

Throughout the year (including both growing and non-growing seasons), LAI was identified as the most influential factor for carbon fluxes, followed by Ts. Given that Ts was also strongly correlated with LAI ($R^2 = 0.88$), Ts can be regarded as the overarching driver of carbon flux dynamics. Ts further emerged as the most critical determinant of WUE, whereas both PAR and Ts exerted substantial impacts on ET, reflecting the respective roles of radiation in controlling transpiration and temperature in driving surface evaporation. Therefore, at the daily scale, Ts is considered the primary factor governing carbon and water fluxes as well as WUE.

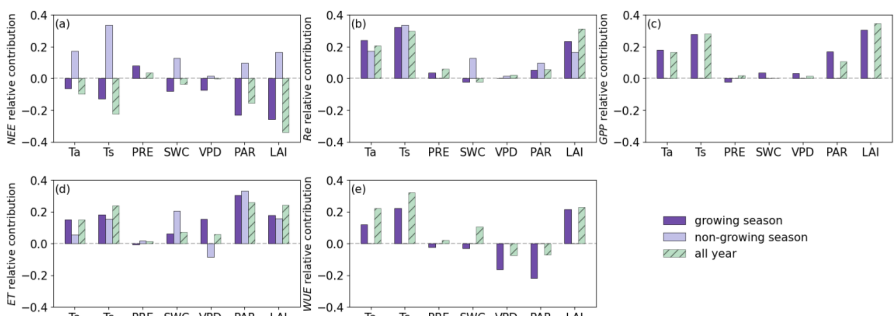


Figure 16: Relative contributions of environmental factors to daily scalce carbon, water flux, and WUE.

Based on ridge regression, LAI was identified as the strongest contributor to NEE at the monthly scale during the growing season, while both Ts and LAI exerted substantial influences on Re and GPP. ET was

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

jointly regulated by PAR and LAI, whereas Ts dominated the control of WUE. During the non-growing season and at the transitional periods at the beginning (late April) and end (early November) of the growing season, Ts emerged as the dominant factor controlling NEE and Re, while GPP was primarily influenced by LAI, followed by SWC. In contrast, ET was largely determined by PRE and SWC, and WUE was regulated by LAI and SWC. These results indicate that compared with the growing season the relative contributions of water-related factors particularly precipitation and surface soil moisture increased during the non-growing season and became the primary drivers of ET. Throughout the year, LAI was the most important determinant of carbon fluxes and ET, followed by Ts, while WUE was primarily controlled by Ts and secondarily by LAI. Overall, carbon and water fluxes at the monthly scale were strongly regulated by temperature.

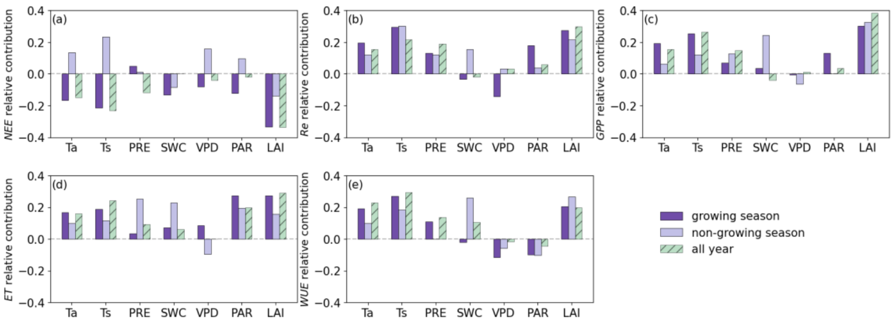


Figure 17: Relative contributions of environmental factors to monthly scale carbon, water flux, and WUE.

At the inter-annual timescale, the linear regression analysis of carbon and water fluxes, WUE, and environmental factors is shown in Figure 18, with the shaded area representing the 95% confidence interval. During the 2012 to 2017, annual NEE exhibited strong correlations with annual PRE and SWC (R^2 = 0.85 and 0.56, respectively), indicating that water-related variables exert a significant influence on NEE at the inter-annual timescale. Ecosystem Re was more strongly correlated with PAR and LAI at the inter-annual timescale, whereas it was more closely associated with temperature at daily and monthly scales. Annual GPP showed stronger correlations with PRE and LAI, suggesting that both water availability and vegetation exert greater controlled over GPP at the inter-annual timescale. ET displayed significant inter-annual timescale correlations with LAI and Ta. WUE was more strongly correlated with PRE at the inter-annual timescale, highlighting the dominant role of PRE in regulating WUE.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

Temperature variations directly determine the rate and duration of photosynthesis. During the daytime, higher temperature enhances photosynthetic activity, whereas at night, lower temperature intensifies plant respiration. Consequently, at shorter time-scale (e.g., daily or monthly), plant physiological processes and carbon sequestration in terrestrial ecosystems are more sensitive to shorter time-scales temperature fluctuations. At longer inter-annual timescales, however, ecosystem carbon fluxes represent a slower cumulative process that depends more on vegetation growth status, LAI, and related factors. In our study region, although inter-annual temperature fluctuations exist, their variation magnitude is relatively small compared with the large inter-annual variability of PRE (Figure 2). Therefore, water availability exerts a longer-term influence throughout the growing season, ultimately driving the inter-annual variability of carbon fluxes.

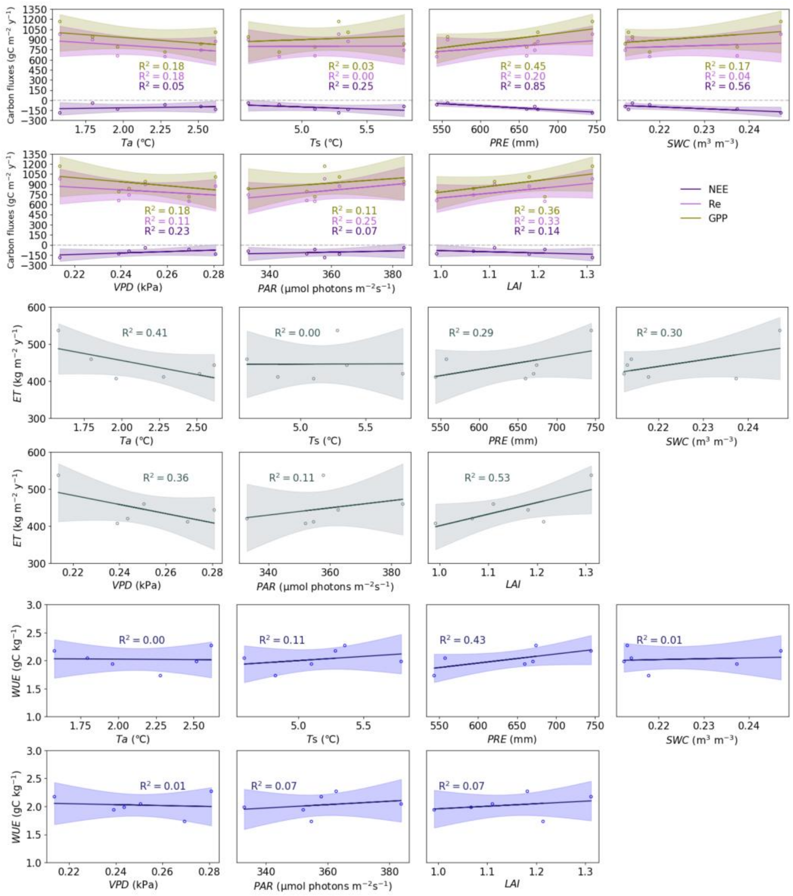


Figure 18: Correlation analysis between WUE and environmental factors (The shaded area is the 95% confidence interval).

4 Discussion

4.1 Carbon and water flux

At the daily scale, carbon fluxes in alpine meadows of humid regions generally exhibit a carbon sink during the daytime and a carbon source at night, with a unimodal variations over the course of the day. This phenomenon has been confirmed by multiple grassland studies on the TP (Gu et al., 2003; Zhao et al., 2010; Wang et al., 2017). Around noon, under conditions of elevated temperature, radiation, and VPD, plants experience transient photoinhibition, stomatal closure, or intensified soil-vegetation water stress, leading to a decline in GPP. As a result, NEE peaks at midday and shows a "midday depression" (Mengoli et al., 2022; Tang et al., 2024). In humid meadows, relatively high soil moisture often buffers this midday depression; however, when temperature rises or soil moisture decreases, the increase in Re exceeds the enhancement of GPP (Figure 16), thereby weakening the carbon sink strength (Wei et al., 2022)。

At the monthly to seasonal time scale, alpine meadow ecosystems function as carbon sinks from May to October. In the northeastern TP, NEE is negative in June, reaches its maximum uptake in July, and shifts to a carbon source in September-October. In the Maqu meadow, the peak of Re occurs later than that of GPP. A similar phenomenon was also observed in the Zoige alpine wetland grassland (Zhao et al., 2010). This lag arises because soluble carbon produced by photosynthesis must be transported downward through the plant body and subsequently utilized by roots and rhizosphere microorganisms. The transport and metabolic processes of these substrates typically span from several hours to several days, causing Re to lag behind photosynthetic peaks at both daily and seasonal scales (Kuzyakov and Gavrichkova, 2010). Temperature can modulate the translocation of photosynthetic products (Plain et al., 2009), thereby influencing both the timing of the peak and the magnitude of the lag.

At the inter-annual timescale, alpine meadow carbon fluxes exhibit substantial year-to-year variability, but overall act as carbon sinks, with marked regional differences across different underlying surfaces of the TP. Alpine marsh ecosystems show the highest annual net carbon uptake, such as at the Dashalong site (NEE = -284.1gC m^{-2} y^{-1}). This is followed by alpine meadow ecosystems (Heihe River Basin, northeastern TP), where the mean annual GPP, Re, and NEE are 504.8, 317.2, and -187.6 gC m^{-2} y^{-1} (Sun et al., 2019). Alpine meadows, such as those in Maqu (this study, NEE = -109.7 gC m^{-2} y^{-1}) and Arou, rank next. By contrast, alpine desert steppe ecosystems have the lowest carbon uptake, and the NamCo site even acts as a carbon source (NEE is 31.1 gC m^{-2} y^{-1})(Wang et al., 2021).

Even for the same land underlying surface type, carbon source-sink capacity varies due to the combined effects of topography, climate, and other factors. For example, in the Heihe River Basin, all three observation sites are alpine meadow ecosystems, yet their carbon sink capacities differ (Sun et al., 2019). For the same vegetation type, carbon sequestration capacity is closely related to the ratio of Re to GPP. At the Arou, Dashalong, and Yakou sites, the Re/GPP ratios are 75.7%, 44.6%, and 53.9%, respectively. Although Arou has the highest annual GPP among the three sites, its annual NEE is lower than that of Dashalong. In the Maqu alpine meadow ecosystem, the multi-year mean GPP is 908.31 gC m^{-2} y^{-1} and Re is 798.62 gC m^{-2} y^{-1}, with the Re/GPP ratio ranging from 83.3% to 95.5% over six years. This indicates that more than 80% of photosynthetically fixed carbon is consumed by respiration. Despite higher GPP in Maqu than in Arou, the annual net carbon uptake in Maqu is lower.

4.2 Different drivers of carbon and water fluxes at different time-scale

Results from the ridge regression analysis indicate that Ts and LAI are the primary environmental factors controlling the daily and monthly to seasonal variations of carbon fluxes (NEE, Re, and GPP) in the Maqu station. In particular, during the growing season, the promotive effects of Ts on GPP and Re are most pronounced. Because higher Ts accelerates root activity and nutrient uptake, it enhances photosynthesis and carbon allocation to shoots, and therefore increases the aboveground biomass of grassland ecosystems (Chen et al., 2016; Duo, 2023). Higher LAI typically corresponds to greater leaf area and chlorophyll content (Lichtenthaler et al., 1981), which enhances photosynthetic capacity and consequently increases both CO_2 uptake and release. Therefore, this study suggests that Ts is the primary factor driving carbon flux variations at daily and monthly timescales. Wei et al. (2022) indicated that daily variations in humid meadows are more constrained by energy availability than by water deficit

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

(Wei et al., 2022). Previous studies have also confirmed the promotive effects of temperature on GPP and Re during the growing season (Wang et al., 2020, 2021).

At the inter-annual timescale, ecosystem carbon fluxes, particularly NEE, show a significant correlation with PRE. This is because moderate increases in PRE over longer timescales enhance SWC, which directly promotes photosynthesis , while Re often responds with a lag-making the short-term increase in GPP more pronounced and thereby enhancing net carbon sink capacity. In addition, higher SWC maintains root and microbial activity, preventing a sharp increase in Re due to drought and thus stabilizing ecosystem carbon uptake. Previous studies have also confirmed the significant influence of water availability on annual (Wang et al., 2021; Li et al., 2021). Shang et al. (2016) reported that annual PRE is the main driver of inter-annual NEE in eastern TP alpine meadows (Shang et al., 2016). Likewise, Chen et al. (2019) showed that PRE exerts a stronger influence than temperature on carbon flux variability in cold, humid alpine grasslands (Chen et al., 2019). Consistent with these findings, our results indicate that at the inter-annual timescale, PRE enhances water availability, promotes GPP, and delays Re responses, thereby increasing net ecosystem carbon uptake.

Previous studies on the relationship between carbon fluxes and environmental factors have mostly focused on a single timescale (Sun et al., 2019; Tao et al., 2023; Wang et al., 2020c), lacking systematic investigations of the drivers of carbon flux variations across multiple timescales. This study demonstrates that the dominant drivers differ at daily, seasonal, and inter-annual timescales, and the relative importance of climatic factors for a variable changes with timescale. At short timescales, carbon fluxes are mainly regulated by immediate climatic conditions, with Ts exerting a strong influence on photosynthesis, whereas at seasonal to inter-annual timescales, the correlation with temperature weakens and responses are increasingly shaped by cumulative factors such as heat accumulation and total PRE (Chen and Wei, 2025; Liu et al., 2022; Wu et al., 2017). Moreover, climatic influences often involve both lagged and cumulative effects (Cheng et al., 2024). Therefore, multi-scale analysis is essential for understanding the climatic drivers of carbon flux dynamics.

This study also examined the environmental drivers of ET across different timescales, and the results show that ET is regulated primarily by PAR at both daily and seasonal scales in alpine meadows. Previous research has demonstrated that daily variations in ET are dominated by net radiation in the northeastern

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

TP (Zhang et al., 2018; Sun et al., 2019), the effectiveness of radiative energy, and VPD (Li et al., 2019; McFadden et al., 2003; Y. Wang et al., 2020). These findings collectively support the conclusion that radiation plays a critical role in regulating ET on relatively short daily and monthly timescales.

At the inter-annual timescale, ET exhibited the strongest correlation with LAI (R^2= 0.53), while water-related factors (SWC and PRE) also exerted certain influences. Studies on grasslands in the U.S. The Great Plains have shown that PRE enhances vegetation ET by promoting plant productivity (Chen et al., 2019). Research in the northeastern TP indicated that PRE and vegetation greening jointly drive the increase in ET (Yang et al., 2021). Similarly, findings from African savannas demonstrated that PRE is the primary driver of inter-annual ET variability in humid grasslands (Räsänen et al., 2022). Collectively, these studies confirm that vegetation and water availability play significant roles in regulating ET at the inter-annual scale.

4.3 Temperature is the primary control of WUE and be modulated by other environmental factors

At the daily timescale, Ts exerted a significant positive effect on WUE, although its influence was jointly constrained by other environmental factors. To further assess this relationship, nonlinear fittings between WUE and Ts were conducted under different levels of environmental factors (Figure 19). The results revealed that under three levels of Ta, WUE exhibited variations of “slow increase”, “rapid increase”, and “inhibited increase” with rising Ts (Figure 19 (a)). Under varying levels of VPD, WUE consistently increased significantly with Ts (Figure 19 (c)), these findings suggest that in the Maqu region, VPD is not a limiting factor for WUE, which differs from contrasts with previous studies in alpine meadows of the northeastern TP, where daily WUE dynamics were reported to be mainly regulated by VPD (Wu et al., 2019). At the low LAI, Ts exerted a strong promoting effect on WUE, whereas under high vegetation conditions, the correlation between Ts and WUE was weak (Figure 19 (e)), indicating that vegetation also influenced WUE. In summary, WUE increased rapidly with Ts under conditions of moderate temperature, sufficient atmospheric moisture, and low LAI; however, in environments characterized by high temperature, dryness, or higher LAI, the positive effect of temperature on WUE weakened and could even turn into a negative effect.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

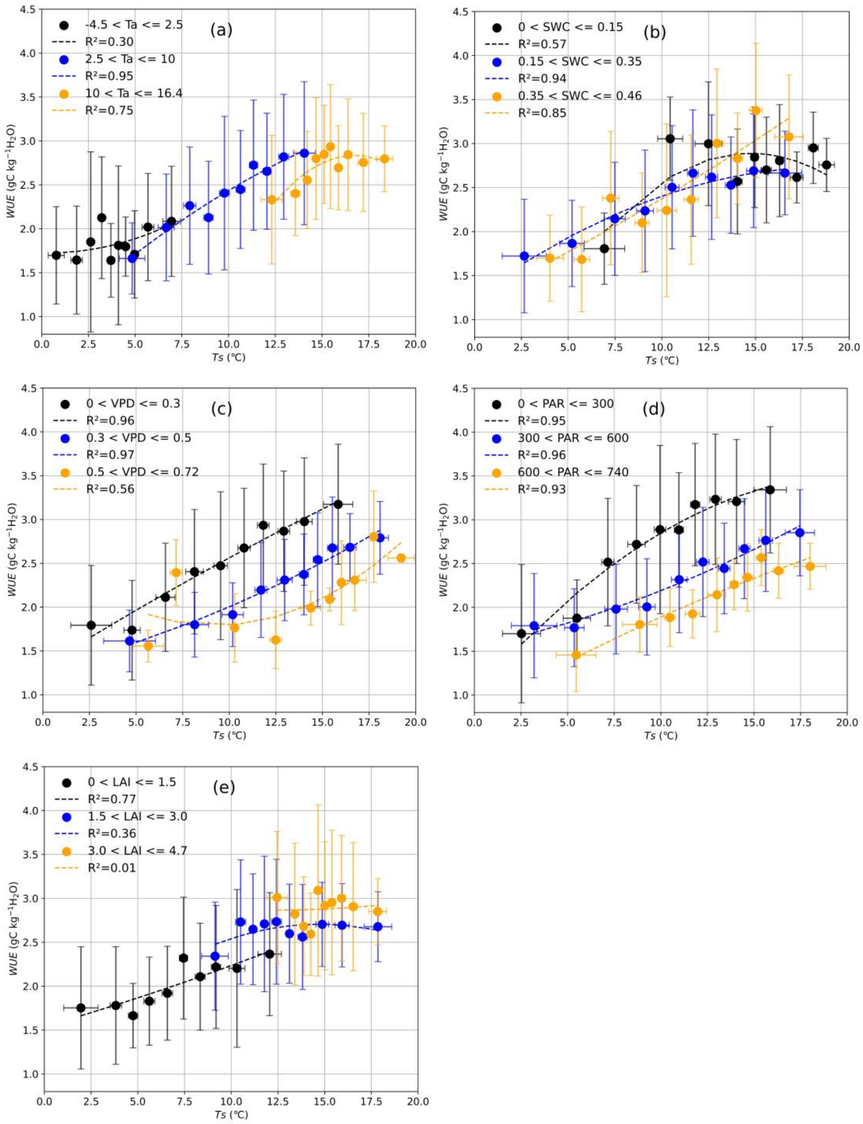


Figure 19: Relationship between WUE and Ts under different environmental conditions.

At the seasonal timescale, temperature is the key controlling factor of WUE, as it simultaneously regulates photosynthesis and transpiration. Research on humid grasslands in Europe demonstrated that variations in WUE largely result from the regulation of transpiration by temperature and VPD, as well as from stomatal adaptive adjustments (Poppe Terán et al., 2023). In Chinese meadow ecosystems, it was shown that temperature and LAI affect the proportion of transpiration in total evapotranspiration (T/ET), thereby driving seasonal WUE dynamics (Zhu et al., 2014). Model and remote sensing results from the TP further revealed that temperature (and its effect on evapotranspiration) is one of the primary drivers of spatiotemporal variations in regional WUE (Jia et al., 2023). In addition, modeling studies also indicated that temperature is a crucial driver of both spatial and temporal variability in WUE at the seasonal timescale on the TP (Lin et al., 2020). Collectively, these studies suggest that the mechanism by which temperature influences WUE at the seasonal timescale lies mainly in its integrative regulation of the coupled carbon-water flux processes.

At the inter-annual timescale, PRE is the dominant environmental factor influencing WUE (Figure 18). In the alpine grasslands, inter-annual PRE variability alters soil water content and groundwater recharge, thereby directly affecting leaf stomatal conductance, community leaf area, and growing-season GPP, which in turn determine the strength of carbon-water coupling at the inter-annual timescale (Zhang et al., 2020; Ji et al., 2022). Modeling studies have shown that increased PRE enhances growing-season carbon uptake and improves WUE (Zhang et al., 2023), whereas reduced PRE suppresses GPP and may increase the relative contribution of ET, leading to lower WUE (Song et al., 2016)。. Moreover, Hou et al. (2025) reported that in humid regions, the area where GPP dominates extreme WUE variability expands, while the area dominated by ET decreases, underscoring the critical role of GPP in shaping inter-annual WUE variation. (Hou et al., 2025). Taken together, these findings highlight the pivotal role of PRE in regulating inter-annual variations of ecosystem carbon-water coupling.

5 Conclusions

Used eddy covariance observation data, the daily, monthly to seasonal, and inter-annual variations of carbon fluxes (NEE, Re, GPP), water fluxes (ET), and WUE were analyzed. Furthermore, ridge regression was applied to identify the main drivers of carbon and water fluxes and WUE across different time-scale. Results show that carbon and water fluxes exhibit pronounced temporal variability in alpine meadow ecosystems. The Maqu alpine meadow functions as an important carbon sink on the TP, acting as a strong carbon sink during the growing season and a weak carbon source during the non-growing season. The dominant drivers of carbon fluxes vary with timescales: at daily and seasonal timescales, Ts is the primary control, whereas PRE exerts a stronger influence at the inter-annual timescale. ET is mainly regulated by radiation at daily and seasonal timescales, but by LAI at the inter-annual timescale. WUE is controlled by Ts at daily and seasonal timescales, while PRE becomes the key factor regulating carbon-water coupling at the inter-annual timescale.

Based on site-level observations, this study examined the carbon and water fluxes of alpine meadow ecosystems in the eastern TP, and investigated their coupling characteristics, and the dominant drivers across multi time scale. Future research should incorporate long-term observations from multiple sites across the Plateau to extend the analysis to the regional scale, thereby providing a theoretical basis and technical support for a more comprehensive understanding of the functional dynamics and adaptive mechanisms of alpine meadow ecosystems.

Code and Data availability. All remote sensing data are publicly available from the respective supplier. Post-processed data and code used in this paper are available from the authors upon request (gaoyerong@nieer.ac.cn).

Author contributions. **Yerong Gao:** Writing - original draft, Investigation, Conceptual ization, Methodology, Formal analysis. **Suosuo Li:** Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Writing - review & editing. **Haipeng Yu:** Funding acquisition, Supervision, Writing - review & editing. **Shaoying Wang:** Data curation, Supervision, Writing - review&editing. **Yongjie Pan:** Investigation, Supervision, Writing - review & editing. **Zongming Li:** Writing - review&editing.

Competing interests. The contact author has declared that neither they nor their co-authors have any competing interests.

Financial support. This study was supported by National Natural Science Foundation of China (grants: 42275096, 42075090) and Central Guidance Fund for Local Science and Technology Development Projects in Gansu (No.24ZYQA031).

References

Ahlstrom, A., Raupach, M. R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Reichstein, M., Canadell, J. G., Friedlingstein, P., Jain, A. K., Kato, E., Poulter, B., Sitch, S., Stocker, B. D., Viovy, N., Wang, Y. P., Wiltshire, A., Zaehle, S., and Zeng, N.: The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink, Science, 348, 895–899, https://doi.org/10.1126/science.aaa1668, 2015.

Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drösler, M., Williams, M., Ammann, C., Berninger, F., Flechard, C., Jones, S., Balzarolo, M., Kumar, S., Newesely, C., Priwitzer, T., Raschi, A., Siegwolf, R., Susiluoto, S., Tenhunen, J., Wohlfahrt, G., and Cernusca, A.: Soil respiration in european grasslands in relation to climate and assimilate supply, Ecosystems, 11, 1352–1367, https://doi.org/10.1007/s10021-008-9198-0, 2008.

Baldocchi, D. D., Xu, L. K., and Kiang, N.: How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak-grass savanna and an annual grassland, Agric. For. Meteorol., 123, 13–39, https://doi.org/10.1016/j.agrformet.2003.11.006, 2004.

Cai, W., Ullah, S., Yan, L., and Lin, Y.: Remote sensing of ecosystem water use efficiency: A review of direct and indirect estimation methods, Remote Sens., 13, 2393, https://doi.org/10.3390/rs13122393, 2021.

Campos, G. E. P., Moran, M. S., Huete, A., Zhang, Y., Bresloff, C., Huxman, T. E., Eamus, D., Bosch, D. D., Buda, A. R., Gunter, S. A., Scalley, T. H., Kitchen, S. G., McClaran, M. P., McNab, W. H., Montoya, D. S., Morgan, J. A., Peters, D. P. C., Sadler, E. J., Seyfried, M. S., and Starks, P. J.: Ecosystem resilience despite large-scale altered hydroclimatic conditions, Nature, 494, 349–352, https://doi.org/10.1038/nature11836, 2013.

Chang, Y., Ding, Y., Zhang, S., Qin, J., and Zhao, Q.: Variations and drivers of evapotranspiration in the Tibetan Plateau during 1982–2015, J. Hydrol.: Reg. Stud., 47, 101366, https://doi.org/10.1016/j.ejrh.2023.101366, 2023.

Chen, J., Luo, Y., Xia, J., Shi, Z., Jiang, L., Niu, S., Zhou, X., and Cao, J.: Differential responses of ecosystem respiration components to experimental warming in a meadow grassland on the Tibetan Plateau, Agric. For. Meteorol., 220, 21–29, https://doi.org/10.1016/j.agrformet.2016.01.010, 2016.

Chen, J. Q., U, K., Ustin, S. L., Suchanek, T. H., Bond, B. J., Brosofske, K. D., and Falk, M.: Net ecosystem exchanges of carbon, water, and energy in young and old-growth douglas-fir forests, Ecosystems, 7, 534–544, https://doi.org/10.1007/s10021-004-0143-6, 2004.

Chen, L. and Wei, W.: Time-Lag and Accumulation Effects of Climate Change on Habitat Quality in the Chinese Loess Plateau, Ecosyst Health Sustain, 11, 0360, https://doi.org/10.34133/ehs.0360, 2025.

Chen, M., Parton, W. J., Hartman, M. D., Del Grosso, S. J., Smith, W. K., Knapp, A. K., Lutz, S., Derner, J. D., Tucker, C. J., Ojima, D. S., Volesky, J. D., Stephenson, M. B., Schacht, W. H., and Gao, W.: Assessing precipitation, evapotranspiration, and NDVI as controls of U.S. great plains plant production, Ecosphere, 10, e02889, https://doi.org/10.1002/ecs2.2889, 2019a.

Chen, N., Zhang, Y., Zhu, J., Zu, J., Huang, K., Li, J., Liu, Y., Cong, N., Tang, Z., Wang, L., and Zhu, Y.: Temperature-mediated responses of carbon fluxes to precipitation variabilities in an alpine meadow ecosystem on the Tibetan Plateau, Ecol. Evol., 9, 9005–9017, https://doi.org/10.1002/ece3.5439, 2019b.

Chen, X., Yuan, L., Ma, Y., Chen, D., Su, Z., and Cao, D.: A doubled increasing trend of evapotranspiration on the Tibetan Plateau, Sci. Bull., 69, 1980–1990, https://doi.org/10.1016/j.scib.2024.03.046, 2024.

Cheng, M., Wang, Z., Wang, S., Liu, X., Jiao, W., and Zhang, Y.: Determining the impacts of climate change and human activities on vegetation change on the chinese loess plateau considering human-induced vegetation type change and time-lag effects of climate on vegetation growth, Int. J. Digital Earth, 17, 2336075, https://doi.org/10.1080/17538947.2024.2336075, 2024.

Duo Y.: Effects of Winter and Growing Season Warming on Carbon and Nitrogen Processes in Grassland Ecosystems: Based on Meta-analysis and Control Experiments, Northwest A&F University, Xian yang, 65 pp., https://doi.org/10.27409/d.cnki.gxbnu.2022.001364, 2023.

Fischer, M., Torn, M., Billesbach, D., Doyle, G., Northup, B., and Biraud, S.: Carbon, water, and heat flux responses to experimental burning and drought in a tallgrass prairie, Dep. Biol. Syst. Eng.: Fac. Publ., 2012.

Gu, S., Tang, Y., Du, M., Kato, T., Li, Y., Cui, X., and Zhao, X.: Short-term variation of CO2 flux in relation to environmental controls in an alpine meadow on the qinghai-tibetan plateau, J. Geophys. Res.: Atmos., 108, https://doi.org/10.1029/2003JD003584, 2003.

Guan, X., Huang, J., Guo, N., Bi, J., and Wang, G.: Variability of soil moisture and its relationship with surface albedo and soil thermal parameters over the Loess Plateau, Adv. Atmos. Sci., 26, 692–700, https://doi.org/10.1007/s00376-009-8198-0, 2009.

Han, C., Ma, Y., Wang, B., Zhong, L., Ma, W., Chen, X., and Su, Z.: Long-term variations in actual evapotranspiration over the Tibetan Plateau, Earth Syst. Sci. Data, 13, 3513–3524, https://doi.org/10.5194/essd-13-3513-2021, 2021.

Hou, S., Lai, W., Zhang, J., Zhang, Y., Liu, W., Zhang, F., and Zhang, S.: Analysis of the dominant factors and interannual variability sensitivity of extreme changes in water use efficiency in China from 2001 to 2020, Forests, 16, 454, https://doi.org/10.3390/f16030454, 2025.

Hu, Z., Yu, G., Fu, Y., Sun, X., Li, Y., Shi, P., Wang, Y., and Zheng, Z.: Effects of vegetation control on ecosystem water use efficiency within and among four grassland ecosystems in China, Global Change Biology, 14, 1609–1619, https://doi.org/10.1111/j.1365-2486.2008.01582.x, 2008.

Hu, Z., Yu, G., Wang, Q., and Zhao, F.: Ecosystem level water use efficiency: A review, Acta Ecologica Sinica, 29, 1498–1507, 2009.

Hu, Z., Dai, Q., Li, H., Yan, Y., Zhang, Y., Yang, X., Zhang, X., Zhou, H., and Yao, Y.: Response of ecosystem water-use efficiency to global vegetation greening, Catena, 239, 107952, https://doi.org/10.1016/j.catena.2024.107952, 2024.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

Huang, J., Zhang, W., Zuo, J., Bi, J., Shi, J., Wang, X., Chang, Z., Huang, Z., Yang, S., Zhang, B., Wang, G., Feng, G., Yuan, J., Zhang, L., Zuo, H., Wang, S., Fu, C., and Jifan, C.: An overview of the Semi-arid Climate and Environment Research Observatory over the Loess Plateau, Adv. Atmos. Sci., 25, 906–921, https://doi.org/10.1007/s00376-008-0906-7, 2008.

Ipcc: Climate change 2022 – impacts, adaptation and vulnerability: working group II contribution to the sixth assessment report of the intergovernmental panel on climate change, 1st ed., Cambridge University Press, https://doi.org/10.1017/9781009325844, 2023.

Ji, Z., Pei, T., Chen, Y., Wu, H., Hou, Q., Shi, F., Xie, B., and Zhang, J.: The driving factors of grassland water use efficiency along degradation gradients on the qinghai-tibet plateau, china, Global Ecol. Conserv., 35, e02090, https://doi.org/10.1016/j.gecco.2022.e02090, 2022.

Jia, B., Luo, X., Wang, L., and Lai, X.: Changes in water use efficiency caused by climate change, CO2 fertilization, and land use changes on the tibetan plateau, Adv. Atmos. Sci., 40, 144–154, https://doi.org/10.1007/s00376-022-2172-5, 2023.

Körner, C., Möhl, P., and Hiltbrunner, E.: Four ways to define the growing season, Ecology Letters, 26, 1277–1292, https://doi.org/10.1111/ele.14260, 2023.

Kuzyakov, Y. and Gavrichkova, O.: REVIEW: time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls, Global Change Biol., 16, 3386–3406, https://doi.org/10.1111/j.1365-2486.2010.02179.x, 2010.

Li, H., Zhu, J., Zhang, F., He, H., Yang, Y., Li, Y., Cao, G., and Zhou, H.: Growth stage-dependant variability in water vapor and CO2 exchanges over a humid alpine shrubland on the northeastern Qinghai-Tibetan Plateau, Agricultural and Forest Meteorology, 268, 55–62, https://doi.org/10.1016/j.agrformet.2019.01.013, 2019.

Li, H., Wang, C., Zhang, F., He, Y., Shi, P., Guo, X., Wang, J., Zhang, L., Li, Y., Cao, G., and Zhou, H.: Atmospheric water vapor and soil moisture jointly determine the spatiotemporal variations of CO2 fluxes and evapotranspiration across the qinghai-tibetan plateau grasslands, Sci. Total Environ., 791, 148379, https://doi.org/10.1016/j.scitotenv.2021.148379, 2021.

Li, S.-G., Eugster, W., Asanuma, J., Kotani, A., Davaa, G., Oyunbaatar, D., and Sugita, M.: Response of gross ecosystem productivity, light use efficiency, and water use efficiency of mongolian steppe to seasonal variations in soil moisture, J. Geophys. Res.: Biogeosci., 113, https://doi.org/10.1029/2006JG000349, 2008.

Liang, W., Lü, Y., Zhang, W., Li, S., Jin, Z., Ciais, P., Fu, B., Wang, S., Yan, J., Li, J., and Su, H.: Grassland gross carbon dioxide uptake based on an improved model tree ensemble approach considering human interventions: global estimation and covariation with climate, Global Change Biol., 23, 2720–2742, https://doi.org/10.1111/gcb.13592, 2017.

Lichtenthaler, H. K., Buschmann, C., Döll, M., Fietz, H.-J., Bach, T., Kozel, U., Meier, D., and Rahmsdorf, U.: Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves, Photosynth. Res., 2, 115–141, https://doi.org/10.1007/BF00028752, 1981.

Lin, S., Wang, G., Hu, Z., Huang, K., Sun, J., and Sun, X.: Spatiotemporal Variability and Driving Factors of Tibetan Plateau Water Use Efficiency, JGR Atmospheres, 125, e2020JD032642, https://doi.org/10.1029/2020jd032642, 2020.

Liu, S., Zamanian, K., Schleuss, P.-M., Zarebanadkouki, M., and Kuzyakov, Y.: Degradation of tibetan grasslands: Consequences for carbon and nutrient cycles, Agric. Ecosyst. Environ., 252, 93–104, https://doi.org/10.1016/j.agee.2017.10.011, 2018.

Liu, X., Tian, Y., Liu, S., Jiang, L., Mao, J., Jia, X., Zha, T., Zhang, K., Wu, Y., and Zhou, J.: Time-lag effect of climate conditions on vegetation productivity in a temperate forest-grassland ecotone, Forests, 13, 1024, https://doi.org/10.3390/f13071024, 2022.

Luo, Y.: The independent and interactive roles of procedural, distributive, and interactional justice in strategic alliances, Acad. Manage. J., 50, 644–664, 2007.

McFadden, J. P., Eugster, W., and Chapin III, F. S.: A regional study of the controls on water vapor and Co2 exchange in arctic tundra, Ecology, 84, 2762–2776, https://doi.org/10.1890/01-0444, 2003.

Melillo, J. M., Frey, S. D., DeAngelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F. P., Pold, G., Knorr, M. A., and Grandy, A. S.: Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world, Science, 358, 101–104, https://doi.org/10.1126/science.aan2874, 2017.

Mengoli, G., Agustí-Panareda, A., Boussetta, S., Harrison, S. P., Trotta, C., and Prentice, I. C.: Ecosystem photosynthesis in land-surface models: a first-principles approach incorporating acclimation, JAMES, 14, e2021MS002767, https://doi.org/10.1029/2021MS002767, 2022.

Miehe, G., Schleuss, P.-M., Seeber, E., Babel, W., Biermann, T., Braendle, M., Chen, F., Coners, H., Foken, T., Gerken, T., Graf, H.-F., Guggenberger, G., Hafner, S., Holzapfel, M., Ingrisch, J., Kuzyakov, Y., Lai, Z., Lehnert, L., Leuschner, C., Li, X., Liu, J., Liu, S., Ma, Y., Miehe, S., Mosbrugger, V., Noltie, H. J., Schmidt, J., Spielvogel, S., Unteregelsbacher, S., Wang, Y., Willinghöfer, S., Xu, X., Yang, Y., Zhang, S., Opgenoorth, L., and Wesche, K.: The *kobresia pygmaea* ecosystem of the tibetan highlands – origin, functioning and degradation of the world's largest pastoral alpine ecosystem, Sci. Total Environ., 648, 754–771, https://doi.org/10.1016/j.scitotenv.2018.08.164, 2019.

Monson, R. K., Prater, M. R., Hu, J., Burns, S. P., Sparks, J. P., Sparks, K. L., and Scott-Denton, L. E.: Tree species effects on ecosystem water-use efficiency in a high-elevation, subalpine forest, Oecologia, 162, 491–504, https://doi.org/10.1007/s00442-009-1465-z, 2010.

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

Niu, Y., Li, Y., Yun, H., Wang, X., Gong, X., Duan, Y., and Liu, J.: Variations in diurnal and seasonal net ecosystem carbon dioxide exchange in a semiarid sandy grassland ecosystem in China's horqin sandy land, Biogeosciences, 17, 6309–6326, https://doi.org/10.5194/bg-17-6309-2020, 2020.

Plain, C., Gerant, D., Maillard, P., Dannoura, M., Dong, Y., Zeller, B., Priault, P., Parent, F., and Epron, D.: Tracing of recently assimilated carbon in respiration at high temporal resolution in the field with a tuneable diode laser absorption spectrometer after in situ 13CO2 pulse labelling of 20-year-old beech trees, Tree Physiol., 29, 1433–1445, https://doi.org/10.1093/treephys/tpp072, 2009.

Poppe Terán, C., Naz, B. S., Graf, A., Qu, Y., Hendricks Franssen, H.-J., Baatz, R., Ciais, P., and Vereecken, H.: Rising water-use efficiency in european grasslands is driven by increased primary production, Commun. Earth Environ., 4, 95, https://doi.org/10.1038/s43247-023-00757-x, 2023.

Räsänen, M., Aurela, M., Vakkari, V., Beukes, J. P., Tuovinen, J.-P., Van Zyl, P. G., Josipovic, M., Siebert, S. J., Laurila, T., Kulmala, M., Laakso, L., Rinne, J., Oren, R., and Katul, G.: The effect of rainfall amount and timing on annual transpiration in a grazed savanna grassland, Hydrol. Earth Syst. Sci., 26, 5773–5791, https://doi.org/10.5194/hess-26-5773-2022, 2022.

Schuman, G. E., Janzen, H. H., and Herrick, J. E.: Soil carbon dynamics and potential carbon sequestration by rangelands, Environ. Pollut., 116, 391–396, https://doi.org/10.1016/S0269-7491(01)00215-9, 2002.

Seager, R., Hooks, A., Williams, A. P., Cook, B., Nakamura, J., and Henderson, N.: Climatology, variability, and trends in the U.S. vapor pressure deficit, an important fire-related meteorological quantity, J. Appl. Meteor. Climatol., https://doi.org/10.1175/JAMC-D-14-0321.1, 2015.

Shang, L., Zhang, Y., Lyu, S., and Wang, S.: Seasonal and inter-annual variations in carbon dioxide exchange over an alpine grassland in the eastern qinghai-tibetan plateau, PLOS One, 11, e0166837, https://doi.org/10.1371/journal.pone.0166837, 2016.

Shen, M., Piao, S., Jeong, S.-J., Zhou, L., Zeng, Z., Ciais, P., Chen, D., Huang, M., Jin, C.-S., Li, L. Z. X., Li, Y., Myneni, R. B., Yang, K., Zhang, G., Zhang, Y., and Yao, T.: Evaporative cooling over the Tibetan Plateau induced by vegetation growth, Proc. Natl. Acad. Sci. U. S. A., 112, 9299–9304, https://doi.org/10.1073/pnas.1504418112, 2015.

Song, B., Niu, S., and Wan, S.: Precipitation regulates plant gas exchange and its long-term response to climate change in a temperate grassland, J. Plant Ecol., 9, 531–541, https://doi.org/10.1093/jpe/rtw010, 2016.

Sun, H., Bai, Y., Lu, M., Wang, J., Tuo, Y., Yan, D., and Zhang, W.: Drivers of the water use efficiency changes in China during 1982–2015, Science of The Total Environment, 799, 149145, https://doi.org/10.1016/j.scitotenv.2021.149145, 2021.

Sun, S., Che, T., Li, H., Wang, T., Ma, C., Liu, B., Wu, Y., and Song, Z.: Water and carbon dioxide exchange of an alpine meadow ecosystem in the northeastern Tibetan Plateau is energy-limited, Agricultural and Forest Meteorology, 275, 283–295, https://doi.org/10.1016/j.agrformet.2019.06.003, 2019.

Tang, E., Zeng, Y., Wang, Y., Song, Z., Yu, D., Wu, H., Qiao, C., van der Tol, C., Du, L., and Su, Z.: Understanding the effects of revegetated shrubs on fluxes of energy, water, and gross primary productivity in a desert steppe ecosystem using the STEMMUS–SCOPE model, Biogeosciences, 21, 893–909, https://doi.org/10.5194/bg-21-893-2024, 2024.

Tao, J., Wei, D., Qi, Y., Wang, Z., Hua, L., and Wang, X.: Soil moisture rather than atmospheric dryness dominates CO2 uptake in an alpine steppe, J. Geophys. Res.: Biogeosci., 128, e2023JG007593, https://doi.org/10.1029/2023JG007593, 2023.

Walker, E. and Birch, J. B.: Influence measures in ridge regression, Technometrics, 30, 221–227, https://doi.org/10.2307/1270168, 1988.

Wang, B., Jin, H., Li, Q., Chen, D., Zhao, L., Tang, Y., Kato, T., and Gu, S.: Diurnal and seasonal variations in the net ecosystem CO2 exchange of a pasture in the three-river source region of the qinghai−tibetan plateau, PLOS One, 12, e0170963, https://doi.org/10.1371/journal.pone.0170963, 2017.

Wang, G., Lin, S., Hu, Z., Lu, Y., Sun, X., and Huang, K.: Improving actual evapotranspiration estimation integrating energy consumption for ice phase change across the Tibetan Plateau, J. Geophys. Res.: Atmos., 125, e2019JD031799, https://doi.org/10.1029/2019JD031799, 2020a.

Wang, S., Zhang, Y., Lv, S., Shang, L., and Zhang, S.: Seasonal Variation Characteristics of Radiation and Energy Budgets in Alpine Meadow Ecosystem in Maqu Grassland, Plateau Meteorology, 31, 605–614, 2012.

Wang, S., Zhang, Y., Meng, X., Shang, L., Su, Y., and Li, Z.: Fill the Gaps of Eddy Covariance Fluxes Using Machine Learning Algorithms, Plateau Meteorology, 39, 1348–1360, 2020b.

Wang, S., Chen, W., Fu, Z., Li, Z., Wang, J., Liao, J., and Niu, S.: Seasonal and Inter-Annual Variations of Carbon Dioxide Fluxes and Their Determinants in an Alpine Meadow, Front. Plant Sci., 13, 894398, https://doi.org/10.3389/fpls.2022.894398, 2022.

Wang, Y., Ma, Y., Li, H., and Yuan, L.: Carbon and water fluxes and their coupling in an alpine meadow ecosystem on the northeastern Tibetan Plateau, Theor Appl Climatol, 142, 1–18, https://doi.org/10.1007/s00704-020-03303-3, 2020c.

Wang, Y., Xiao, J., Ma, Y., Luo, Y., Hu, Z., Li, F., Li, Y., Gu, L., Li, Z., and Yuan, L.: Carbon fluxes and environmental controls across different alpine grassland types on the Tibetan Plateau, Agricultural and Forest Meteorology, 311, 108694, https://doi.org/10.1016/j.agrformet.2021.108694, 2021.

Wei, J., Li, X., Liu, L., Christensen, T. R., Jiang, Z., Ma, Y., Wu, X., Yao, H., and López-Blanco, E.: Radiation, soil water content, and temperature effects on carbon cycling in an alpine swamp meadow of

https://doi.org/10.5194/egusphere-2025-5170
Preprint. Discussion started: 27 November 2025

the northeastern qinghai–tibetan plateau, Biogeosciences, 19, 861–875, https://doi.org/10.5194/bg-19-861-2022, 2022.

Wu, X., Liu, H., Li, X., Piao, S., Ciais, P., Guo, W., Yin, Y., Poulter, B., Peng, C., Viovy, N., Vuichard, N., Wang, P., and Huang, Y.: Higher temperature variability reduces temperature sensitivity of vegetation growth in northern hemisphere, Geophys. Res. Lett., 44, 6173–6181, https://doi.org/10.1002/2017GL073285, 2017.

Wu, X., Li, X., Chen, Y., Bai, Y., Tong, Y., Wang, P., Liu, H., Wang, M., Shi, F., Zhang, C., Huang, Y., Ma, Y., Hu, X., and Shi, C.: Atmospheric Water Demand Dominates Daily Variations in Water Use Efficiency in Alpine Meadows, Northeastern Tibetan Plateau, JGR Biogeosciences, 124, 2174–2185, https://doi.org/10.1029/2018jg004873, 2019.

Yang, L., Feng, Q., Adamowski, J. F., Alizadeh, M. R., Yin, Z., Wen, X., and Zhu, M.: The role of climate change and vegetation greening on the variation of terrestrial evapotranspiration in northwest China's qilian mountains, Sci. Total Environ., 759, 143532, https://doi.org/10.1016/j.scitotenv.2020.143532, 2021.

Yu, G., Gao, Y., Wang, Q., Liu, S., and Shen, W.: Discussion on the key processes of carbon-nitrogen-water coupling cycles and biological regulation mechanisms in terrestrial ecosystem, Chinese Journal of Eco-Agriculture, 21, 1–13, 2013.

Zhang, F., Li, H., Wang, W., Li, Y., Lin, L., Guo, X., Du, Y., Li, Q., Yang, Y., Cao, G., and Li, Y.: Net radiation rather than surface moisture limits evapotranspiration over a humid alpine meadow on the northeastern Qinghai-Tibetan Plateau, Ecohydrology, 11, e1925, https://doi.org/10.1002/eco.1925, 2018.

Zhang, M., Ma, Y., Chen, P., Shi, F., and Wei, J.: Growing-season carbon budget of alpine meadow ecosystem in the qinghai lake basin: a continued carbon sink through this century according to the biome-BGC model, Carbon Balance Manage., 18, 25, https://doi.org/10.1186/s13021-023-00244-y, 2023.

Zhang, X., Du, X., and Zhu, Z.: Effects of precipitation and temperature on precipitation use efficiency of alpine grassland in northern tibet, china, Sci. Rep., 10, 20309, https://doi.org/10.1038/s41598-020-77208-6, 2020.

Zhao, F. and Yu, G.: A Review on the Coupled Carbon and Water Cycles in the Terrestrial Ecosystems, Progress In Geography, 32–38, 2008.

Zhao, L., Li, J., Xu, S., Zhou, H., Li, Y., Gu, S., and Zhao, X.: Seasonal variations in carbon dioxide exchange in an alpine wetland meadow on the qinghai-tibetan plateau, Biogeosciences, 7, 1207–1221, https://doi.org/10.5194/bg-7-1207-2010, 2010.

Zhou, G., Wang, Y., Bai, L., Xu, Z., Shi, R., Zhou, L., and Yuan, W.: Study on the interaction between terrestrial ecosystems and global change, Acta Met Eorologica Sinica, 692–707, 716, 2004.

Zhu, X., Yu, G., Wang, Q., Hu, Z., Han, S., Yan, J., Wang, Y., and Zhao, L.: Seasonal dynamics of water use efficiency of typical forest and grassland ecosystems in China, J. For. Res., 19, 70–76, https://doi.org/10.1007/s10310-013-0390-5, 2014.