



# Seasonal and Inter-Annual Variations of Carbon Dioxide Fluxes and Their Determinants in an Alpine Meadow

Song Wang<sup>1,2</sup>, Weinan Chen<sup>1,2</sup>, Zheng Fu<sup>3</sup>, Zhaolei Li<sup>4</sup>, Jinsong Wang<sup>1</sup>, Jiaqiang Liao<sup>1,2</sup> and Shuli Niu<sup>1,2\*</sup>

<sup>1</sup> Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Research, Chinese Academy of Sciences, Beijing, China, <sup>2</sup> College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China, <sup>3</sup> Laboratoire des Sciences du Climat et de l'Environnement (LSCE), CEA-CNRS-UVSQ, UMR8212, Gif-sur-Yvette, France, <sup>4</sup> College of Resources and Environment, and Academy of Agricultural Sciences, Southwest University, Chongqing, China

## OPEN ACCESS

### Edited by:

Xiaoming Kang,  
Chinese Academy of Forestry, China

### Reviewed by:

Liang Yan,  
Chinese Academy of Forestry, China  
Haijun Peng,  
Institute of Geochemistry (CAS), China

### \*Correspondence:

Shuli Niu  
sniu@igsrr.ac.cn

### Specialty section:

This article was submitted to  
Functional Plant Ecology,  
a section of the journal  
Frontiers in Plant Science

Received: 11 March 2022

Accepted: 20 May 2022

Published: 23 June 2022

### Citation:

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

The alpine meadow is one of the most important ecosystems on the Qinghai-Tibet Plateau (QTP) due to its huge carbon storage and wide distribution. Evaluating the carbon fluxes in alpine meadow ecosystems is crucial to understand the dynamics of carbon storage in high-altitude areas. Here, we investigated the carbon fluxes at seasonal and inter-annual timescales based on 5 years of observations of eddy covariance fluxes in the Zoige alpine meadow on the eastern Tibetan Plateau. We found that the Zoige alpine meadow acted as a faint carbon source of  $94.69 \pm 86.44 \text{ g C m}^{-2} \text{ y}^{-1}$  during the observation periods with large seasonal and inter-annual variations (IAVs). At the seasonal scale, gross primary productivity (GPP) and ecosystem respiration (Re) were positively correlated with photosynthetic photon flux density (PPFD), average daily temperature (Ta), and vapor pressure (VPD) and had negative relationships with volumetric water content (VWC). Seasonal variations of net ecosystem carbon dioxide (CO<sub>2</sub>) exchange (NEE) were mostly explained by Ta, followed by PPFD, VPD, and VWC. The IAVs of GPP and Re were mainly attributable to the IAV of the maximum GPP rate (GPP<sub>max</sub>) and maximum Re rate (Re<sub>max</sub>), respectively, both of which increased with the percentage of *Cyperaceae* and decreased with the percentage of *Polygonaceae* changes across years. The IAV of NEE was well explained by the anomalies of the maximum CO<sub>2</sub> release rate (MCR). These results indicated that the annual net CO<sub>2</sub> exchange in the alpine meadow ecosystem was controlled mainly by the maximum C release rates. Therefore, a better understanding of physiological response to various environmental factors at peak C uptake and release seasons will largely improve the predictions of GPP, Re, and NEE in the context of global change.

**Keywords:** carbon fluxes, seasonal variation, inter-annual variation, eddy covariance, alpine meadow

## INTRODUCTION

There are great uncertainties in estimating the carbon dioxide (CO<sub>2</sub>) budget of terrestrial ecosystems due to the inadequacies in the observational data and the incomplete conceptual framework (Hawkins and Sutton, 2009; Ito, 2019). Hence, understanding the dynamics of ecosystem carbon fluxes on different time scales and their control mechanisms is of great

significance for accurately simulating and predicting terrestrial ecosystem carbon balances (Jia et al., 2016; Green et al., 2019).

At the seasonal scale, water availability and thermal conditions were considered to affect the dynamics of ecosystem carbon fluxes (Zhang et al., 2018; Li et al., 2019b). For example, in arid and semiarid ecosystems, the amount and distribution of precipitation have been shown to dominate seasonal ecosystem carbon fluxes (Jia et al., 2016; Hao et al., 2018). In contrast, many studies in cold regions found that thermal conditions were the main drivers of the carbon fluxes at the seasonal scale (Fu et al., 2009; Saito et al., 2009). At the annual scale, the temperature fluctuations and water availability have been reported as the most important climate factors in controlling the inter-annual variation (IAV) of the gross primary productivity (GPP), ecosystem respiration (Re), and net ecosystem CO<sub>2</sub> exchange (NEE) at the global scale (Jung et al., 2017; Marcolla et al., 2017; Fernandez-Martinez et al., 2019). Compared to environmental factors, the impact of the biotic mechanisms underlying the IAV of ecosystem CO<sub>2</sub> fluxes has been less explored. Recently, it has been proposed that the maximum daily net ecosystem productivity (NEP) during the CO<sub>2</sub> uptake period (CUP; NEP<sub>max</sub>) dominated the IAV of NEE at the global scale (Fu et al., 2019), while the summer peak of GPP (GPP<sub>max</sub>) contributed more to the IAV of GPP than the photosynthetic phenology across North America (Xia et al., 2015). This indicates that community properties related to the maximum C uptake rate are crucial in determining annual C uptakes. However, the controlling factor of CO<sub>2</sub> fluxes may be divergent among different climate and vegetation types. For instance, temperature determines CO<sub>2</sub> fluxes in tropical ecosystems (Wang et al., 2014), but precipitation regulates the annual CO<sub>2</sub> flux of semiarid ecosystems (Poulter et al., 2014), and the soil moisture and species composition have been found to interactively determine CO<sub>2</sub> fluxes in dry meadows (Luan et al., 2016). Thus, the mechanism underlying the seasonal and IAV of ecosystem CO<sub>2</sub> fluxes in those less studied regions still needs further investigation.

The alpine meadow ecosystem is one of the most important ecosystems on the Qinghai-Tibet Plateau (QTP), covering an area of  $\approx 70 \times 10^4$  km<sup>2</sup> and accounting for  $\approx 35\%$  of QTP (Ni, 2002; Niu et al., 2017a). It stores about 17.6 Gt carbon, accounting for about 48% of QTP carbon storage (Wang and Zhou, 1999; Lv, 2006). A large amount of carbon was stored in the alpine meadow ecosystem due to the low temperature, high humidity, low soil humus decomposition rate, and high accumulation rate of organic matter (Saito et al., 2009). However, the alpine area is increasingly impacted by climate change with rising temperature and precipitation (Li et al., 2010, 2019a). Meanwhile, the alpine meadow ecosystem is highly susceptible to environmental changes (Liu and Chen, 2000; Wang et al., 2000; Cheng and Wu, 2007; Xu and Liu, 2007). The temperature in the alpine meadow ecosystem increases (0.3–0.4°C per decade) two times faster than the global average (Chen et al., 2013), and the temperature increases more significantly with the increase in altitude (Liu and Chen, 2000). Therefore, studying the carbon fluxes and their response to climate change in the alpine meadow ecosystem is imperative. A few studies about carbon fluxes over

alpine meadow ecosystems have been conducted on the QTP. For example, Hao et al. (2011) and Wang et al. (2016) reported that these alpine meadow ecosystems were a weak net CO<sub>2</sub> sink, but the carbon source or sink dynamic has great variations due to the changes in environmental factors. Under the background of increasing air temperature and precipitation (Li et al., 2010, 2019a; Chen et al., 2013), there will be more uncertainty in predicting carbon fluxes in alpine meadow ecosystems in the future. Hence, it is vital to explore the temporal variations of carbon fluxes and their drivers in alpine meadow ecosystems.

Eddy covariance technology provides a reliable approach to measuring the CO<sub>2</sub> fluxes. This approach can measure NEE with precision, contributes to identify the characteristics of source/sink activities of various global ecosystems, and has been widely used to interpret whole-system variability (Braswell et al., 2005; Chen et al., 2019b; Peng et al., 2021). This study focuses on the carbon fluxes dynamic at seasonal and inter-annual timescales based on 5 years (2015–2018, 2020) of eddy covariance flux observation in Zoige alpine meadow on the eastern QTP. The specific objectives of this study are to (1) quantify CO<sub>2</sub> dynamics at seasonal and inter-annual timescales for the Zoige alpine meadow; (2) understand the abiotic and biotic controlling factors for the variations in ecosystem CO<sub>2</sub> fluxes; and (3) explore the key processes associated with plant community species in controlling the inter-annual variability of CO<sub>2</sub> flux. These controlling mechanisms are essential to help us better understand the response of alpine meadows to future climate change.

## MATERIALS AND METHODS

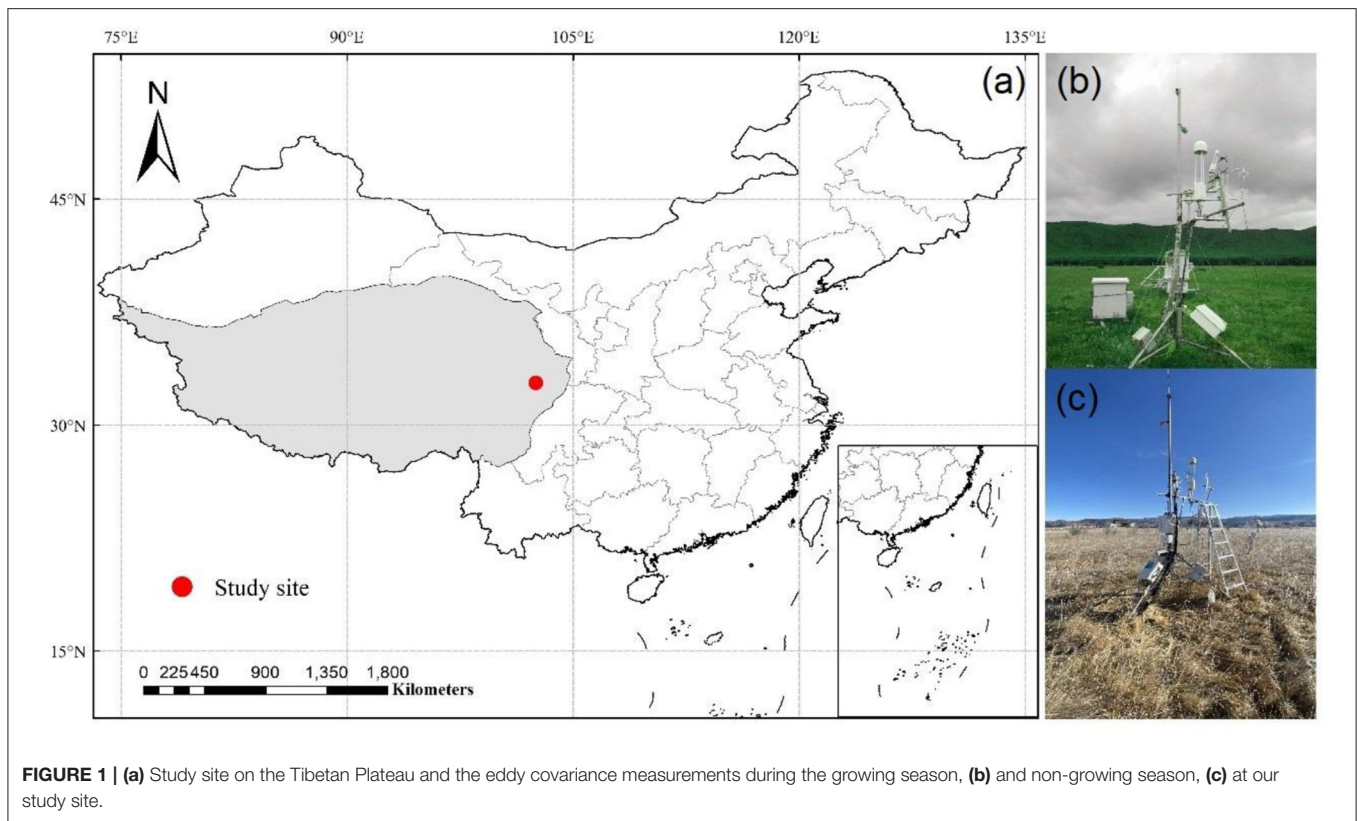
### Site Description

The study site is at an alpine meadow in the National Zoige Alpine Wetland Ecological Station (32.8°N and 102.6°E; 3,500 m a.s.l), located on the eastern Qinghai-Tibetan Plateau (Figure 1). The alpine meadow is characterized by a typical continental plateau monsoon climate with relatively low temperatures and strong solar radiation. Based on the long-term meteorology observation data (1961–2013) from Hongyuan meteorological station (<http://101.201.172.75:8888>), the annual mean temperature of this site is  $\approx 1.5^\circ\text{C}$ . The coldest month occurs in January with a mean temperature of  $-9.7^\circ\text{C}$ , while the warmest month occurs in July with a mean temperature of  $11.1^\circ\text{C}$ . The mean annual precipitation of this site is  $\approx 761.0$  mm, and over 80% of which occurs in the growing season (May to October).

The vegetation at the study site consists of a species mixture of *Deschampsia cespitosa* (Linn.) Beauv., *Koeleria cristata* (Linn.) Pers., *Gentiana sino-ornata* Balf. f., *Potentilla anserina* L., and *Anemone rivularis* Buch.-Ham (Quan et al., 2018). The dominant soil type in this ecosystem is Mat Cry-gelic Cambisol.

### Eddy Covariance and Meteorological Measurement

Net ecosystem CO<sub>2</sub> exchange was observed from 2015 to 2020 by an open-path eddy covariance measurement system installed above an alpine meadow at 2 m. The sensor was



broken at the beginning of 2019, so there was a long data gap in 2019 and the data in 2019 were discarded. The open-path eddy covariance system has a three-dimensional sonic anemometer (CSAT3; Campbell Scientific Inc. (CSI), Logan, USA) and an open-path CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (LI-7500A; Li-COR Inc, Lincoln, NE, USA). Flux data are logged with a data logger at 10 Hz (CR5000, Campbell Scientific, UT, USA). HMP45C temperature probe (Vaisala, Finland) was used to measure air temperature. Soil volumetric water content (VWC) at a depth of 5 and 10 cm was measured using a CS655 probe (CSI, Logan, USA). Precipitation was measured by a tipping bucket rain gauge (TE525, CSI, Logan, USA). Photosynthetic photon flux density (PPFD) was measured using a photosynthetic active radiation sensor (LI190, LI-Cor, USA). This eddy covariance tower is one of the ChinaFlux (China Flux Observation and Research Network) and FLUXNET long-term observation site.

### Aboveground Biomass Measurement

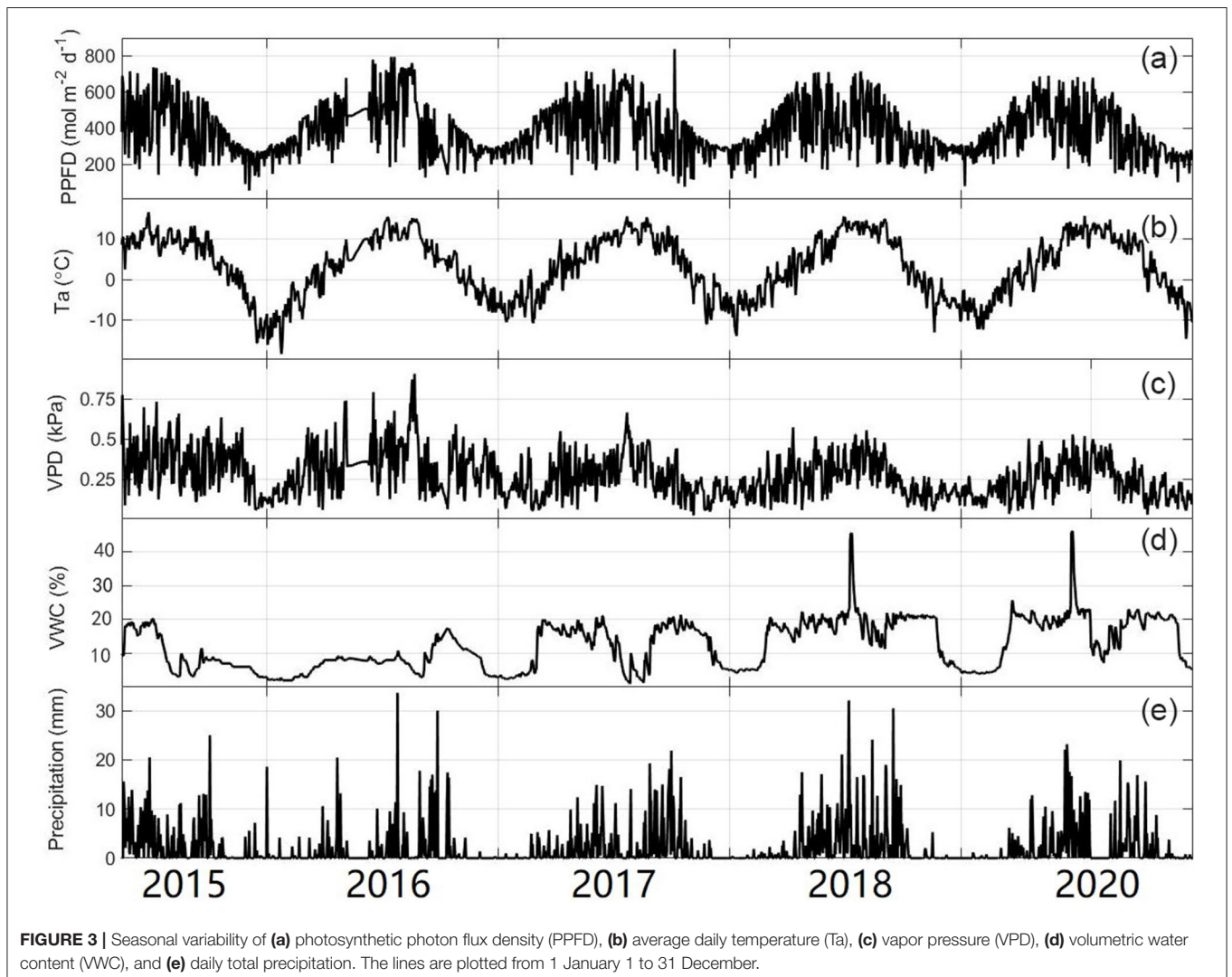
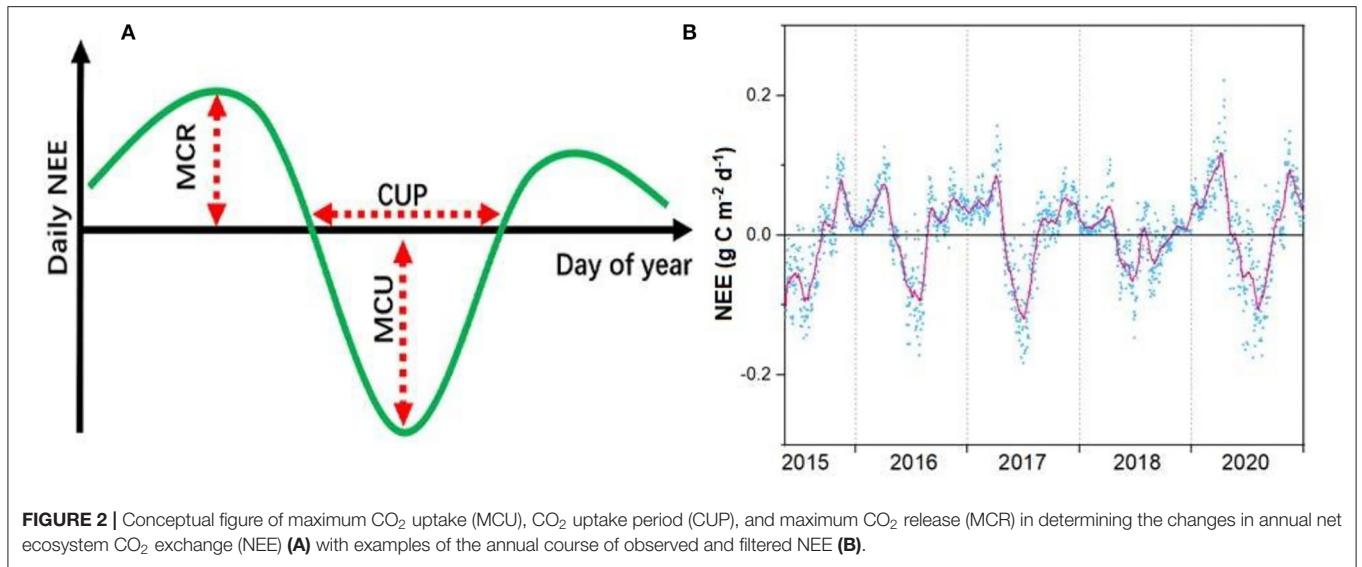
At the peak of annual biomass (usually in August), we randomly placed a quadrat frame (0.50) on each plot × 0.50 m), all the aboveground parts of the plants in the frame together, then separated them into different living species, and dried in the oven at 65°C for 48 h until they reached a constant weight and weighed. In the five replicates of each treatment, the average biomass of all living species in each quadrat was used to calculate aboveground biomass (Ma et al., 2020).

### Data Processing

EddyPro 6.2.0 software was used to preprocess and control the quality of the eddy covariance raw data. Data measured during instrument malfunction and severe conditions were filtered out. Specifically, for data quality control, half-hour CO<sub>2</sub> flux data were filtered when: (1) data values were beyond the range of  $-20$  to  $20 \mu\text{mol}/\text{m}^2/\text{s}$ ; (2) precipitation occurred; and (3) the friction velocity ( $u^*$ ) was below 0.1 m/s at nighttime. This  $u^*$  threshold was determined following Reichstein et al. (2005). The positive values represent CO<sub>2</sub> emission from the underlying surface to the atmosphere, while the negative values represent CO<sub>2</sub> consumption from the atmosphere to soil (plants). Here, we divided CO<sub>2</sub> flux data into two periods: (1) the growing season was between the day with daily mean  $T_{\text{air}} > 5$  and the day with daily mean  $T_{\text{air}} < 5^\circ\text{C}$  for 7 consecutive days, (2) the non-growing season was the days of the year except the growing season (Lund et al., 2010; Song et al., 2015; Peng et al., 2021). GPP and Re data were partitioned from CO<sub>2</sub> flux data (i.e., NEE) using rectangular hyperbolic regression (Falge et al., 2001). More information about missing NEE data gap-filling and partitioning was previously described by Chen et al. (2019b).

### Statistical Analysis

We used the daily NEE to calculate the maximum CO<sub>2</sub> uptake rate (MCU), net CUP, and maximum CO<sub>2</sub> release rate (MCR) to quantify the phenological and physiological indicators that determine the annual NEE (Fu et al., 2019) and applied the



Savitzky–Golay filter to minimize the role of random variability in flux observations (**Figure 2**) (Savitzky and Golay, 1964). We defined the CUP as the number of days with net C uptake ( $NEE < 0 \text{ g C m}^{-2} \text{ day}^{-1}$ ) (Fu et al., 2019). Following this definition, there may be multiple periods across the course of a calendar year that may have net C uptake; these were added for the calculation of CUP on an annual basis. The MCU was defined as the maximum daily net C uptake of the filtered time series. The MCR was defined as the maximum value of the daily net C release of the filtered time series (Fu et al., 2019). To explore the underlying mechanism controlling annual CO<sub>2</sub> exchanges, we split the annual NEE into growing season NEE ( $NEE_g$ ) and non-growing season NEE ( $NEE_{ng}$ ). We used the same method as those in Gu et al. (2009) to quantify the canopy photosynthetic phenology and fitted a 9-parameter

Weibull function to the data to obtain the  $GPP_{max}$  and  $Re_{max}$  value of each year.

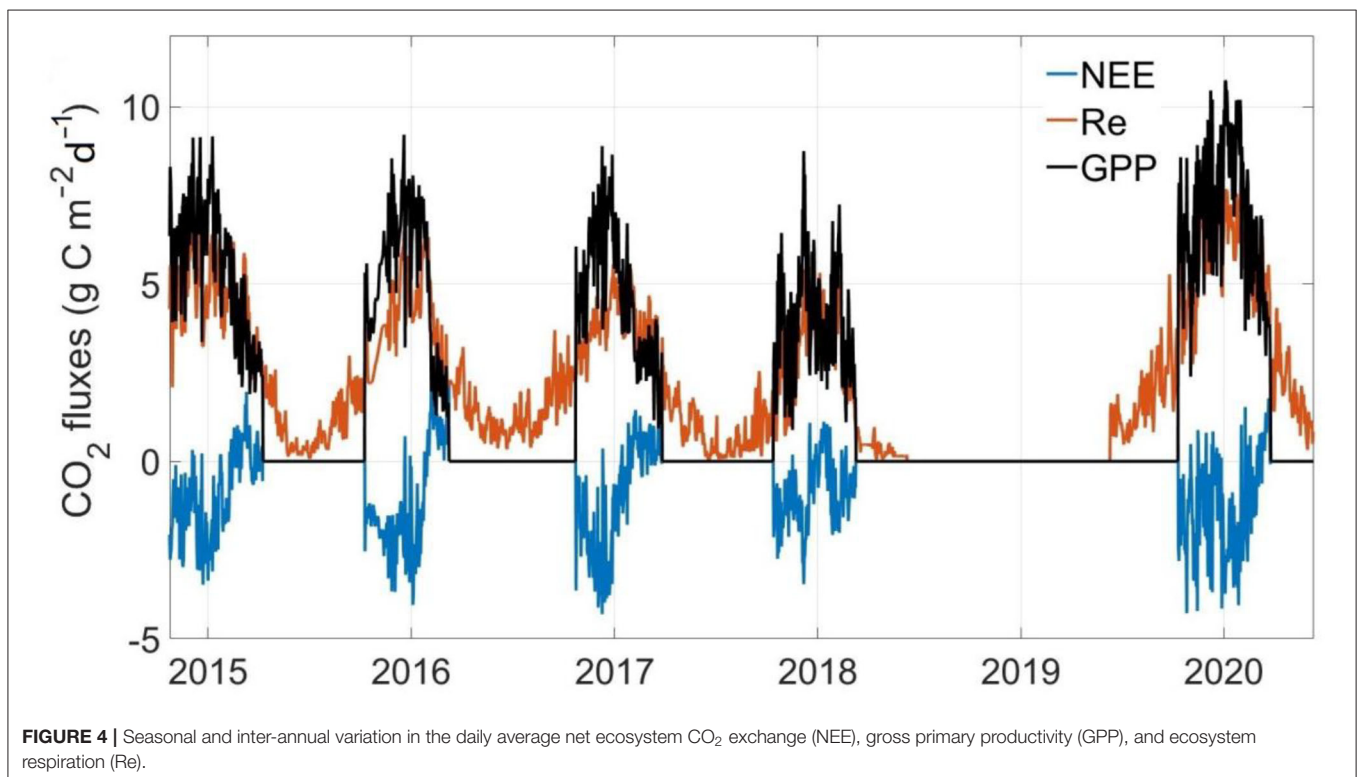
## RESULTS

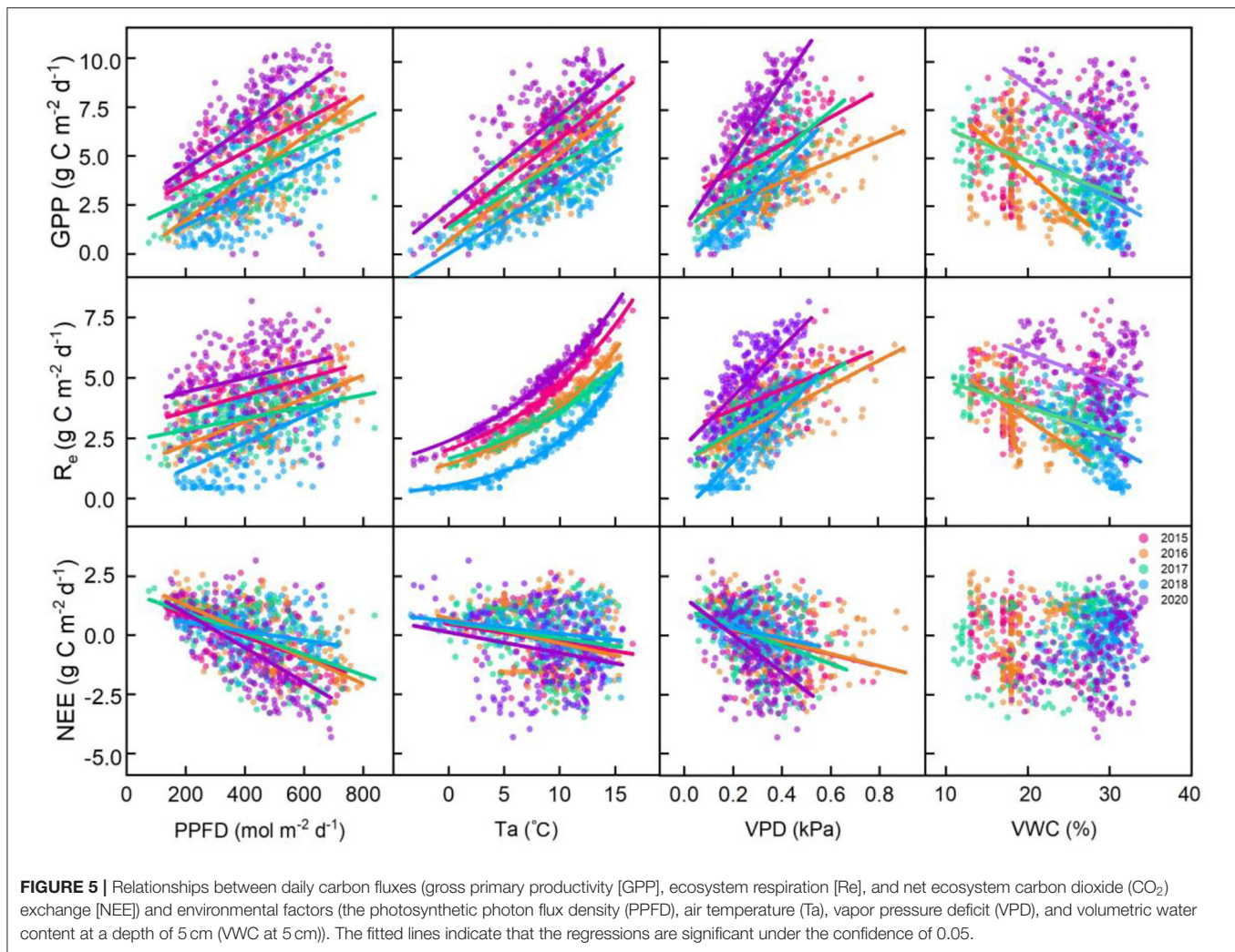
### Environmental Factors

The daily mean Ta showed large seasonal variation, ranging from  $-18.4$  to  $15.67^\circ\text{C}$  (**Figure 3**). The average annual temperature in this site from 2016 to 2020 was  $0.44^\circ\text{C}$ , of which 2020 was the coldest ( $0.15^\circ\text{C}$ ) year and 2017 was the warmest ( $0.66^\circ\text{C}$ ) year (**Figure 3** and **Table 1**). Similar to temperature, PPFD showed a single peak in late June to early July each year. The maximum daily value could exceed  $800 \mu\text{mol photons m}^{-2} \text{ d}^{-1}$  (**Figure 3**). There were significant seasonal differences in daily precipitation, and the annual total precipitation amounts

**TABLE 1** | Climatic factors and carbon fluxes for 2016–2018 and 2020.

	Year					Average	SD
	2016	2017	2018	2020			
PPFD ( $\text{mol m}^{-2} \text{ d}^{-1}$ )	366.89	363.86	357.78	333.87	355.60	14.97	
Ta ( $^\circ\text{C}$ )	0.51	0.66	0.45	0.15	0.44	0.21	
VPD (kPa)	0.32	0.22	0.22	0.20	0.24	0.05	
WVC (100%)	0.07	0.12	0.14	0.15	0.12	0.04	
Rain (mm)	710.40	860.80	995.60	1,032.50	899.82	146.26	
ER ( $\text{g C m}^{-2} \text{ year}^{-1}$ )	869.36	889.89	556.42	1,306.91	905.64	307.37	
GPP ( $\text{g C m}^{-2} \text{ year}^{-1}$ )	777.40	740.41	582.77	1,143.24	810.96	237.06	
NEE ( $\text{g C m}^{-2} \text{ year}^{-1}$ )	91.96	149.48	-26.35	163.67	94.69	86.44	





were 710.40, 860.80, 995.60, and 1,032.50 mm for 2016, 2017, 2018, and 2020, respectively (Table 1). The variation in the soil water content (SWC) and the mean vapor pressure deficit (VPD) was closely related to the precipitation at the study site. In addition, there were two sharp peaks in the VWC dynamic in 2018 and 2020 because our study site suffered flooding at that time.

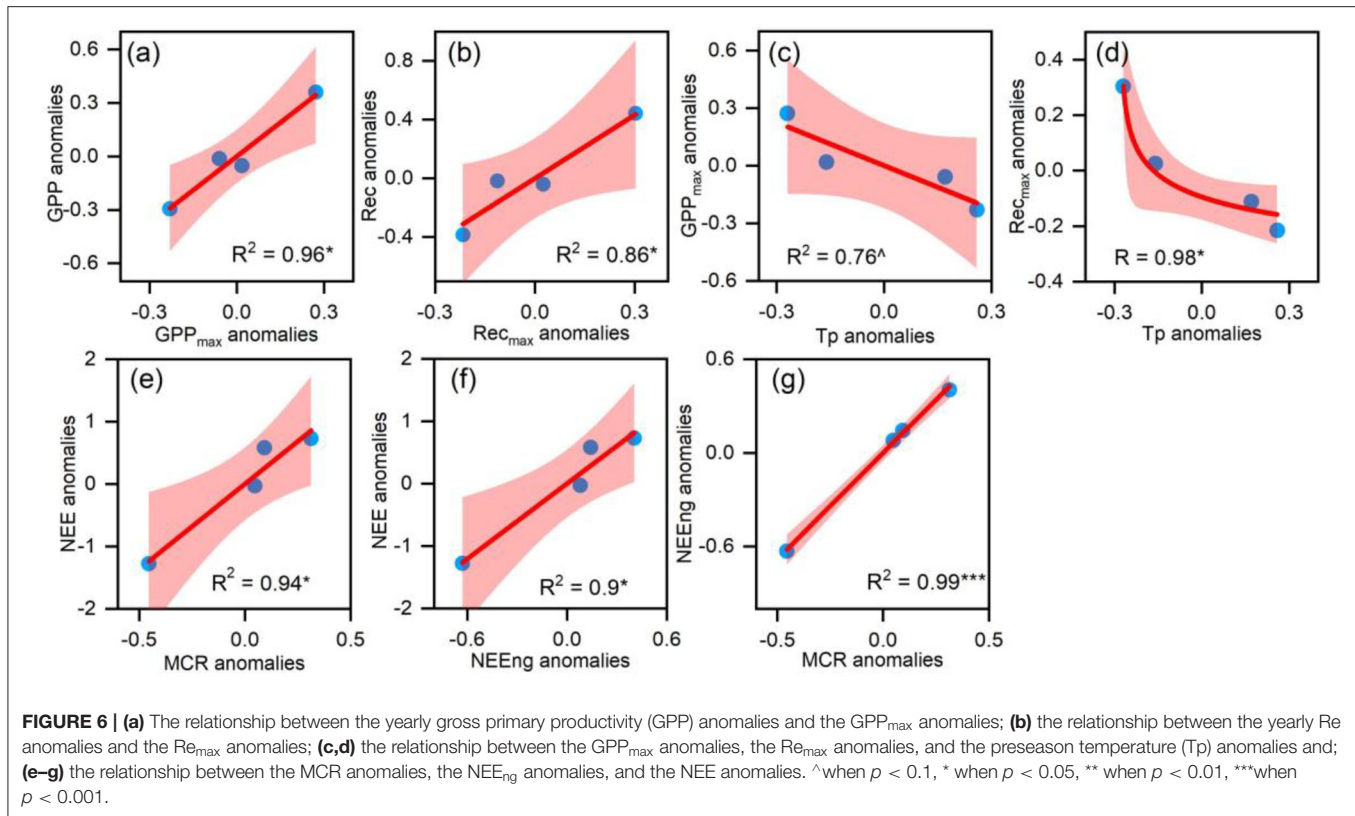
### Seasonal Variations of GPP, Re, and NEE and Their Controlling Factors

In all observational years, GPP and Re both showed similar curvilinear shapes, with zero GPP and very low Re in the non-growing season (Figure 4). The maximum daily GPP values were 4.74–8.60 g C m<sup>-2</sup> day<sup>-1</sup> among 4 research years. The daily Re was low in winter (<0.5 g C m<sup>-2</sup> day<sup>-1</sup>) with the maximum values of 4.63–6.77 g C m<sup>-2</sup> day<sup>-1</sup> in 4 research years. The maximum daily NEE value in the growing season was about -2.39 g C m<sup>-2</sup> day<sup>-1</sup>, and the maximum daily NEE value in the non-growing season was about 2.08 g C m<sup>-2</sup> day<sup>-1</sup>.

At the seasonal scale, GPP and Re were positively correlated with PPFD, Ta, and VPD and negatively correlated with VWC at 5 cm. Re and Ta showed a significant exponential relationship ( $p < 0.001$ ; Figure 5). NEE was negatively correlated with PPFD, Ta, and VPD and positively correlated with VWC ( $p < 0.01$ ; Figure 5). We analyzed the relative contributions of six environmental variables to fluxes using the random forest (RF) scheme. The RF of this alpine meadow ecosystem explained 80.01 and 78.93% of the daily GPP and Re variations during the vegetative periods, respectively (Supplementary Table S1). Meanwhile, the RF explained 53.11% of the variations in the daily NEE (Supplementary Table S1).

### IVVs of GPP, Re, and NEE and Their Controlling Factors

In general, the yearly cumulative GPP was  $810.96 \pm 237.06$  g C m<sup>-2</sup>, and the total accumulative Re was  $905.64 \pm 307.37$  g C m<sup>-2</sup> over 4 study years (Figure 4 and Table 1). The alpine meadow ecosystem was a faint carbon source during the observation



period. The mean NEE of these 4 years was  $94.69 \pm 86.44 \text{ C m}^{-2} \text{ year}^{-1}$  although the NEE in 2018 was negative. The positive NEE values indicated a net emission of CO<sub>2</sub> in the alpine meadow ecosystem during these 4 years.

There were no significant correlations between environmental factors and CO<sub>2</sub> fluxes on the annual scale. The yearly GPP anomalies and Re anomalies were significantly related to GPP<sub>max</sub> anomalies (Figure 6a) and Re<sub>max</sub> anomalies, respectively (Figure 6b). Moreover, the anomalies of GPP<sub>max</sub> and Re<sub>max</sub> were negatively correlated with the preseason temperature (Tp, the average temperature from February to April) (Figures 6c,d). NEE anomalies were positively correlated with the IAV of MCR (Figure 6e) but had no significant corrections with MCU or CUP. Meanwhile, annual NEE anomalies were positively correlated with the IAV of accumulated NEE in the non-growing season (Figure 6f), which were significantly related to MCR anomalies (Figure 6g).

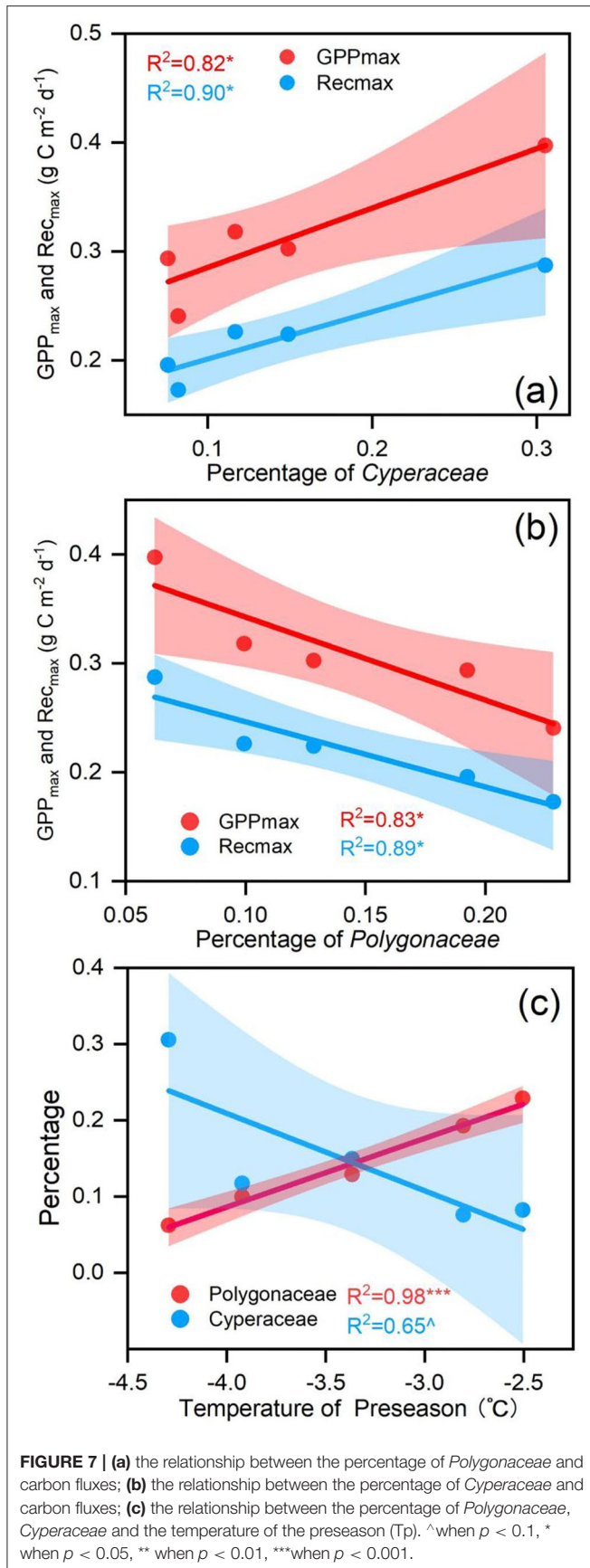
Biological factors were also considered in this study. Plant community varied considerably during the observation period (Supplementary Figure S1). The percentage of *Cyperaceae* had a positive relationship with the GPP<sub>max</sub> and Re<sub>max</sub> (Figure 7a). The percentage of *Polygonaceae* had a negative relationship with the GPP<sub>max</sub> and Re<sub>max</sub> (Figure 7b). In addition, the higher Tp had a negative effect on the percentage of *Cyperaceae* (Figure 7c) but had a positive effect on the percentage of *Polygonaceae* (Figure 7c) on the annual scale.

## DISCUSSION

### CO<sub>2</sub> Budget at Zoige Alpine Meadow

The carbon budget at Zoige alpine meadow in this study was not consistent with most alpine meadow ecosystems in the Qinghai-Tibet region, which usually acted as a carbon sink (Kato et al., 2006; Zhao et al., 2006; Sun et al., 2019; Wang et al., 2020). Different from the previous opinion that the favorable photosynthetic conditions and a low decomposition rate of organic matter result in carbon accumulation in alpine meadow ecosystems (Kato et al., 2006; Fu et al., 2009), the net carbon balance performed as a weak source among these 4 years in this study. Because the GPP and Re values were comparable in the growing season, the carbon accumulation during the growing season was less than the respiration in the non-growing season.

In this study, both the GPP ( $810.96 \text{ g C m}^{-2} \text{ year}^{-1}$ ) and Re ( $905.64 \text{ g C m}^{-2} \text{ year}^{-1}$ ) values were very high in comparison with other alpine meadow ecosystems (Tables 1, 2). The relatively high precipitation and temperature led to higher productivity and greater respiration consumption. However, the high productivity did not lead to net carbon uptake accumulation during the observation period because the Re in the cold ecosystem was large and more sensitive to the environmental change than GPP (Illeris et al., 2004; Zhu et al., 2016). For instance, favorable weather increased the Re and GPP, leading to a net carbon emission of  $163.67 \text{ g C m}^{-2}$  in 2020. However,



unfavorable weather decreased the Re and GPP, leading to a net carbon sink of 26.35 g C m<sup>-2</sup> in 2018.

## Environmental Controls on Seasonal Variation of Ecosystem CO<sub>2</sub> Fluxes

Previous studies have shown that carbon fluxes had a clear seasonal dynamic in temperate and cold ecosystems (Zhao et al., 2010; Niu et al., 2017a; Wang et al., 2020). Alpine meadow ecosystem had a low-temperature condition, and the temperature and thermal conditions were often the limiting factors for vegetation growth, which was typically considered the main factor regulating carbon fluxes (Saito et al., 2009; Li et al., 2019b). The RF analysis suggested that Ta primarily influenced the seasonal changes in GPP, Re, and NEE in this alpine meadow ecosystem, and SWC played subordinate roles in affecting seasonal GPP, Re, and NEE changes (**Supplementary Table S1**).

This result was consistent with previous studies, which found that temperature was the most critical factor for controlling NEE, GPP, and Re for an alpine meadow ecosystem (Kato et al., 2006; Fu et al., 2009; Saito et al., 2009). The reason was that although cold and humid environments provided an adequate soil water supply for plants growth during the growing season, the low temperature often became a limiting factor for plant growth, as temperature affected both the physiology and phenology of plants, which in turn determined the carbon uptake and release. In addition to Ta, SWC played a subordinate role in affecting seasonal GPP, Re, and NEE changes. Previous studies had shown that soil moisture had an important effect on controlling carbon fluxes for a water-limited ecosystem (Wang et al., 2008; Ganjurjav et al., 2016; Zhang et al., 2018) but had little effect on water-rich areas (i.e., wetland) (Zhao et al., 2010; Du et al., 2021). The soil water supply in the Zoige alpine meadow ecosystem was intermediate between grassland and wetland, leading to the subordinate role in seasonal carbon flux variations.

## Controlling Factors on IAV in GPP and Re

Our study demonstrated that the IAV of GPP<sub>max</sub> and Re<sub>max</sub> mostly determined the IAV of GPP and Re in Zoige alpine meadow, respectively, instead of plant phenology or climates. This result was consistent with previous studies that found the IAV of GPP was best explained by that in GPP<sub>max</sub> in North America, Europe, and the Tibetan Plateau (Xia et al., 2015; Zhou et al., 2016; Chen et al., 2019a), and the IAV of Re was mainly attributed to Re<sub>max</sub> at Maoershan forest (Liu et al., 2021a). The control of GPP<sub>max</sub> on annual GPP variability and the Re<sub>max</sub> on annual Re variability indicated that environmental changes influenced the IAVs of GPP and Re by affecting vegetation physiology rather than phenology. Hence, given GPP<sub>max</sub> and Re<sub>max</sub>'s importance for the alpine region's carbon cycle, it was vital to explore the physiological mechanism underlying GPP<sub>max</sub> and Re<sub>max</sub> change in the alpine ecosystem.

The maximum GPP rate was determined by the leaf area index and the leaf photosynthetic capacity of the ecosystem (Hu et al., 2018), and the Re<sub>max</sub> was also tightly associated with plant biomass and vegetable characteristics (e.g., temperature sensitivity) (Kato et al., 2004a,b; Flanagan and Johnson, 2005; Yashiro et al., 2010). These physiological factors were greatly



**TABLE 2** | Ecosystem carbon fluxes in other alpine meadows published in previous studies.

Type	Site	Period	Ta °C	GPP g C m <sup>-2</sup> y <sup>-1</sup>	Re g C m <sup>-2</sup> y <sup>-1</sup>	NEE g C m <sup>-2</sup> y <sup>-1</sup>	Reference
Alpine meadow	Haibei	2003–2004	−1.48	—	—	−282	Zhao et al. (2005)
Alpine shrub meadow				—	—	−53	
Alpine meadows				—	—	478	
Alpine shrub-meadow	Haibei	2004–2005	−1.7	527.7	459.2	−68.5	Fu et al. (2009)
Alpine meadow- steppe	Dangxung		1.3	205.8	253.8	48	
Alpine steppe	Bange	2015	0.02	—	—	21.8	Wang et al. (2018)
Alpine meadow	Lijiang		6.16	—	—	−230	
Alpine meadow	Arou	2013–2016	0.6	818.3	619.6	−198.7	Sun et al. (2019)
Alpine meadow	Dashalong		−3.4	467.5	208.6	−258.9	
Alpine meadow	Yakou	2015–2016	−4.2	228.6	123.3	−105.3	
Alpine wetland	Luanhaizi	2007–2016	−1.1	500.3	620.7	120.4	Zhu et al. (2020)
Alpine meadow	Haibei	2002–2004	−1	634.5	513.6	−120.9	Kato et al. (2006)
Alpine wetland meadow	Haibei	2004–2006	−1.1	629.9	737.1	107.2	Zhao et al. (2010)
Alpine shrubland meadow	Haibei	2003–2004		551.7	484.6	−67.1	Zhao et al. (2006)
Alpine meadow	Hongyuan	2015–2020	0.44	810.96	905.64	94.69	This study

affected by the change in plant community structure (Johnson et al., 2008; Cheng et al., 2015; Xu et al., 2015; Estruch et al., 2018). It had been widely reported that the species composition in the alpine meadow was shifting due to destruction by rodents (Zhou et al., 2005), climate change (Li et al., 2011), or other uncertain causes (Harris, 2010). These interferences could affect ecosystem processes through changing plant species composition (Poulter et al., 2014) and thus ecosystem functions (i.e., GPP and Re) (Sala et al., 2012; Kulmatiski and Beard, 2013).

Our observed changes in species' community support the above explanation. During the study period, the species communities changed significantly from a *Poaceae*-dominated meadow in 2015 to a *Cyperaceae*-dominated meadow in 2020 (Supplementary Figure S1). In our study site, *Cyperaceae*, *Polygonaceae*, *Euphorbiaceae*, *Poaceae*, and *Asteraceae* accounted for more than 80% of aboveground biomass (Supplementary Figure S1). A previous study had shown that *Cyperaceae* and *Poaceae* had the highest photosynthetic rate and water use efficiency among all of the function groups, and the photosynthetic rate of *Polygonaceae* was the lowest (Liu et al., 2015). Meanwhile, a study based on isotope labeling also found that *Cyperaceae* plants have a stronger ability to assimilate CO<sub>2</sub> and transfer more C to roots and soil, because *Cyperaceae* plants had a high primary carbon assimilation tissue area when compared with *Poaceae* (Mou et al., 2018).

Hence, the percentage of *Cyperaceae* and *Polygonaceae* explained the annual GPP<sub>max</sub> and Re<sub>max</sub> variations in Zoige alpine meadow ecosystem. A greater proportion of *Cyperaceae* and a smaller proportion of *Polygonaceae* contributed to a larger annual GPP<sub>max</sub>. Meanwhile, we found that the temperature before the growing season had a negative effect on the percentage of *Cyperaceae* ( $p < 0.1$ ; Figure 7c) but had a positive effect on the percentage of *Polygonaceae* ( $p < 0.01$ ; Figure 7c) on the annual scale. Consequently, a warmer pre-season could reduce annual GPP<sub>max</sub> by increasing the percentage of *Polygonaceae* and decreasing the percentage of *Cyperaceae*.

## Controlling Factors on IAV in NEE

Any single environmental factor could not explain the IAV of NEE in this study. Instead, it was explained well by biological processes, such as NEE<sub>ng</sub> and MCR. The environmental driving factors may ultimately impact the IAV of NEE by changing the phenological and physiological indicators (Fu et al., 2017; Niu et al., 2017b).

Moreover, we found that the IAV of NEE at Zoige alpine meadow was primarily explained by the physiological (MCR) rather than phenological indicators (CUP). Surprisingly, the MCU did not affect the IAV of NEE, which indicated that the IAV of NEE was driven mainly by the net CO<sub>2</sub> release process during the non-growing season rather than the net CO<sub>2</sub> uptake during the growing season in this area, although NEE in growing and non-growing seasons was determined predominately by MCU and MCR, respectively. Meanwhile, the CUP tended to have no significant influence on either NEE<sub>g</sub> or NEE<sub>ng</sub>. A global study also indicated that the CUP contribution to IAV of NEE was lower than the physiological indicator in Zoige alpine meadow area (Fu et al., 2019). Moreover, a study conducted on Siberian tundra also showed that the IAV of NEE had no significant relationship with CUP because of the offset effect between GPP and Re (Parmentier et al., 2011).

However, the driving factor of the IAV of NEE in this study differed from some other studies that indicated the IAV of NEE was determined predominately by MCU (Zscheischler et al., 2016; Gonsamo et al., 2018; Fu et al., 2019). Because most of the study sites in these research studies were carbon sinks, carbon uptake in the growing season was larger than the carbon release in the non-growing season, resulting in the dominant role of MCU in contributing to the IAV of NEE. In our study site, the mean NEE over the 4 years was  $94.69 \pm 86.44$  C m<sup>-2</sup> year<sup>-1</sup>. The carbon uptake in the growing season was smaller than the carbon release in the non-growing season, leading to the dominant role of MCR in contributing to the IAV of NEE in this study.

We were aware of the possible uncertainty of IAV in GPP and Re due to the short observation periods in this study. The controlling mechanisms for the IAV of GPP and Re could be different in short-term and long-term series because the effects from the influencing factors were changing over time (e.g., legacy effects and accumulation effects) (Bloom et al., 2020; Liu et al., 2021b), and the ecosystems were also acclimating to the changing environments (Luo et al., 2001; Guo et al., 2020). Hence, we suggest that more research should be conducted to explore the processes that control the long-term IAV of GPP, Re, and NEE in the future.

## CONCLUSION

The Zoige alpine meadow acted as a faint carbon source during the observation period. GPP, Re, and NEE all showed strongly seasonal and IVVs. The seasonal variations of GPP, Re, and NEE were mostly determined by Ta, followed by PPF<sub>D</sub>, VPD, and VWC, while GPP<sub>max</sub> and Re<sub>max</sub> drove the IAV of GPP and Re. Meanwhile, the higher Tp could decrease the GPP<sub>max</sub> and Re<sub>max</sub> by changing the plant species composition in the growing season and decrease GPP and Re in Zoige alpine meadow. The IAV of NEE at the Zoige alpine meadow was largely explained by the MCR, indicating the important role of carbon release in the non-growing season in determining the net C sink in the alpine region. Given the physiological indicators (i.e., GPP<sub>max</sub>, Re<sub>max</sub>, and MCR) can best explain the CO<sub>2</sub> exchange variability, future studies need to emphasize the regulatory mechanisms for the dynamics of ecosystem physiological characteristics in the alpine ecosystem.

## REFERENCES

- Bloom, A. A., Bowman, K. W., Liu, J., Konings, A. G., Worden, J. R., Parazoo, N. C., et al. (2020). Lagged effects regulate the inter-annual variability of the tropical carbon balance. *Biogeosciences*. 17, 6393–6422. doi: 10.5194/bg-17-6393-2020
- Braswell, B. H., Sacks, W. J., Linder, E., and Schimel, D. S. (2005). Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biol.* 11, 335–355. doi: 10.1111/j.1365-2486.2005.00897.x
- Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., et al. (2013). The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. *Global Change Biol.* 19, 2940–2955. doi: 10.1111/gcb.12277
- Chen, S. L., Huang, Y. F., Gao, S., and Wang, G. Q. (2019a). Impact of physiological and phenological change on carbon uptake on the Tibetan Plateau revealed through GPP estimation based on spaceborne solar-induced fluorescence. *Sci. Total Environ.* 663, 45–59. doi: 10.1016/j.scitotenv.2019.01.324
- Chen, W. N., Zhang, F. Y., Wang, B. X., Wang, J. S., Tian, D. S., Han, G. X., et al. (2019b). Diel and Seasonal Dynamics of Ecosystem-Scale Methane Flux and Their Determinants in an Alpine Meadow. *J. Geophys. Res-Biogeophys.* 124, 1731–1745. doi: 10.1029/2019JG005011
- Cheng, G. D., and Wu, T. H. (2007). Responses of permafrost to climate change and their environmental significance, Qinghai-Tibet Plateau. *J. Geophys. Res-Earth.* 112 doi: 10.1029/2006JF000631
- Cheng, S. J., Bohrer, G., Steiner, A. L., Hollinger, D. Y., Suyker, A., Phillips, R. P., et al. (2015). Variations in the influence of diffuse light on gross primary productivity in temperate ecosystems. *Agric. For. Meteorol.* 201, 98–110. doi: 10.1016/j.agrformet.2014.11.002

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

SW, WC, and SN designed this study. SW performed the laboratory analysis and wrote the paper. All authors have revised, discussed, and approved the final manuscript.

## FUNDING

This study was supported by the National Natural Science Foundation of China (31988102) and the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (2019QZKK0302).

## ACKNOWLEDGMENTS

The authors are grateful to Qiong Wu and Yingjie Yan for helping us get field data, and thank Yiheng Wang for polishing our manuscript.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2022.894398/full#supplementary-material>

- Du, Q., Liu, H., Liu, Y., Xu, L., and Sun, J. (2021). Water and carbon dioxide fluxes over a “floating blanket” wetland in southwest of China with eddy covariance method. *Agric. For. Meteorol.* 311 doi: 10.1016/j.agrformet.2021.108689
- Estruch, C., Lozano, Y. M., Armas, C., and Pugnair, F. I. (2018). Plant community changes after land abandonment control CO<sub>2</sub> balance in a dry environment. *Plant. Soil.* 425, 253–264. doi: 10.1007/s11104-018-3581-1
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., et al. (2001). Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. For. Meteorol.* 107, 43–69. doi: 10.1016/S0168-1923(00)00225-2
- Fernandez-Martinez, M., Sardans, J., Chevallier, F., Ciais, P., Obersteiner, M., Vicca, S., et al. (2019). Global trends in carbon sinks and their relationships with CO<sub>2</sub> and temperature. *Nat. Clim. Change.* 9, 73.–+. doi: 10.1038/s41558-018-0367-7
- Flanagan, L. B., and Johnson, B. G. (2005). Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agric. For. Meteorol.* 130, 237–253. doi: 10.1016/j.agrformet.2005.04.002
- Fu, Y., Zheng, Z., Hu, Y. u. G., Sun, Z., and Shi, X. P., and Zhao X (2009). Environmental influences on carbon dioxide fluxes over three grassland ecosystems in China. *Biogeosciences*. 6, 2879–2893. doi: 10.5194/bg-6-2879-2009
- Fu, Z., Dong, J., Zhou, Y., Stoy, P. C., and Niu, S. (2017). Long term trend and interannual variability of land carbon uptake: the attribution and processes. *Environ. Res. Lett.* 12. doi: 10.1088/1748-9326/aa5685
- Fu, Z., Stoy, P. C., Poulter, B., Gerken, T., Zhang, Z., Wakbulcho, G., et al. (2019). Maximum carbon uptake rate dominates the interannual variability

- of global net ecosystem exchange. *Global Change Biol.* 25, 3381–3394. doi: 10.1111/gcb.14731
- Ganjurjav, H., Gao, Q. Z., Schwartz, M. W., Zhu, W. Q., Liang, Y., and Lin, L. i. Y. (2016). Complex responses of spring vegetation growth to climate in a moisture-limited alpine meadow. *Sci. Rep.* 6, 10. doi: 10.1038/srep23356
- Gonsamo, A., Chen, J. M., and Ooi, Y. W. (2018). Peak season plant activity shift towards spring is reflected by increasing carbon uptake by extratropical ecosystems. *Global Change Biol.* 24, 2117–2128. doi: 10.1111/gcb.14001
- Green, J. K., Seneviratne, S. I., Berg, A. M., Findell, K. L., Hagemann, S., Lawrence, D. M., et al. (2019). Large influence of soil moisture on long-term terrestrial carbon uptake. *Nature*. 565, 476–+. doi: 10.1038/s41586-018-0848-x
- Gu, L., Post, W. M., Baldocchi, D. D., Black, T. A., Suyker, A. E., Verma, S. B., et al. (2009). “Characterizing the seasonal dynamics of plant community photosynthesis across a range of vegetation types,” in *Phenology of Ecosystem Processes* (<https://digitalcommons.unl.edu/cgi/viewcontent.cgi?referer=https://www.google.com/&httpsredir=1&article=1176&context=natrespapers> Berlin, Germany: Springer), 35–58.
- Guo, X., Gao, Q., Yuan, M., Wang, G., Zhou, X., Feng, J., et al. (2020). Gene-informed decomposition model predicts lower soil carbon loss due to persistent microbial adaptation to warming. *Nat. Commun.* 11, 4897. doi: 10.1038/s41467-020-18706-z
- Hao, Y., Zhang, H., Biederman, J. A., Cui, L. i. L., and Xue, X. K., and Wang Y (2018). Seasonal timing regulates extreme drought impacts on CO<sub>2</sub> and H<sub>2</sub>O exchanges over semiarid steppes in Inner Mongolia, China. *Agr. Ecosyst. Environ.* 266, 153–166. doi: 10.1016/j.agee.2018.06.010
- Hao, Y. B., Cui, X. Y., Wang, Y. F., Mei, X. R., Kang, X. M., Wu, N., et al. (2011). Predominance of Precipitation and Temperature Controls on Ecosystem CO<sub>2</sub> Exchange in Zoige Alpine Wetlands of Southwest China. *Wetlands*. 31, 413–422. doi: 10.1007/s13157-011-0151-1
- Harris, R. B. (2010). Rangeland degradation on the Qinghai-Tibetan plateau: a review of the evidence of its magnitude and causes. *J. Arid. Environ.* 74, 1–12. doi: 10.1016/j.jaridenv.2009.06.014
- Hawkins, E., and Sutton, R. (2009). The potential to narrow uncertainty in regional climate predictions. *B Am Meteorol Soc.* 90, 1095–+. doi: 10.1175/2009BAMS2607.1
- Hu, Z., Shi, H., Cheng, K., Wang, Y. P., Piao, S., and Yu, L. i. Y. (2018). Joint structural and physiological control on the interannual variation in productivity in a temperate grassland: A data-model comparison. *Global Change Biol.* 24, 2965–2979. doi: 10.1111/gcb.14274
- Illeris, L., Christensen, T. R., and Mastepanov, M. (2004). Moisture effects on temperature sensitivity of CO<sub>2</sub> exchange in a subarctic heath ecosystem. *Biogeochemistry*. 70, 315–330. doi: 10.1007/s10533-003-0855-2
- Ito, A. (2019). Disequilibrium of terrestrial ecosystem CO<sub>2</sub> budget caused by disturbance-induced emissions and non-CO<sub>2</sub> carbon export flows: a global model assessment. *Earth. System. Dyn.* 10, 685–709. doi: 10.5194/esd-10-685-2019
- Jia, X., Zha, T., Gong, J., Wang, B., Zhang, Y., Wu, B., et al. (2016). Carbon and water exchange over a temperate semi-arid shrubland during three years of contrasting precipitation and soil moisture patterns. *Agric. For. Meteorol.* 228, 120–129. doi: 10.1016/j.agrformet.2016.07.007
- Johnson, D., Phoenix, G. K., and Grime, J. P. (2008). Plant community composition, not diversity, regulates soil respiration in grasslands. *Biol. Lett.* 4, 345–348. doi: 10.1098/rsbl.2008.0121
- Jung, M., Reichstein, M., Schwalm, C. R., Huntingford, C., Sitch, S., Ahlstrom, A., et al. (2017). Compensatory water effects link yearly global land CO<sub>2</sub> sink changes to temperature. *Nature*. 541, 516–520. doi: 10.1038/nature20780
- Kato, T., Tang, Y. H., Gu, S., Cui, X. Y., Hirota, M., Du, M. Y., et al. (2004a). Carbon dioxide exchange between the atmosphere and an alpine meadow ecosystem on the Qinghai-Tibetan Plateau, China. *Agric. For. Meteorol.* 124, 121–134. doi: 10.1016/j.agrformet.2003.12.008
- Kato, T., Tang, Y. H., Gu, S., Hirota, M., Cui, X. Y., Du, M. Y., et al. (2004b). Seasonal patterns of gross primary production and ecosystem respiration in an alpine meadow ecosystem on the Qinghai-Tibetan Plateau. *J. Geophys. Res-Atmos.* 109 doi: 10.1029/2003JD003951
- Kato, T., Tang, Y. H., Gu, S., Hirota, M., Du, M. Y., and Zhao, L. i. Y. N. (2006). Temperature and biomass influences on interannual changes in CO<sub>2</sub> exchange in an alpine meadow on the Qinghai-Tibetan Plateau. *Global Change Biol.* 12, 1285–1298. doi: 10.1111/j.1365-2486.2006.01153.x
- Kulmatski, A., and Beard, K. H. (2013). Woody plant encroachment facilitated by increased precipitation intensity. *Nat. Clim. Change.* 3, 833–837. doi: 10.1038/nclimate1904
- Li, D. S., Wen, Z., Cheng, Q. G., Xing, A. G., and Zhang, M. L. (2019a). Thermal dynamics of the permafrost active layer under increased precipitation at the Qinghai-Tibet Plateau. *J. Mt. Sci.* 16, 309–322. doi: 10.1007/s11629-018-5153-5
- Li, G. Y., Liu, Y. Z., Frelich, L. E., and Sun, S. C. (2011). Experimental warming induces degradation of a Tibetan alpine meadow through trophic interactions. *J. Appl. Ecol.* 48, 659–667. doi: 10.1111/j.1365-2664.2011.01965.x
- Li, H., Zhu, L. i. H., Zhang, J., He, F., Yang, H., and Li, Y. Y., and Zhou H (2019b). Growth stage-dependant variability in water vapor and CO<sub>2</sub> exchanges over a humid alpine shrubland on the northeastern Qinghai-Tibetan Plateau. *Agric. For. Meteorol.* 268, 55–62. doi: 10.1016/j.agrformet.2019.01.013
- Li, L., Yang, S., Wang, Z. Y., Zhu, X. D., Tang, H. Y. (2010). Evidence of Warming and Wetting Climate over the Qinghai-Tibet Plateau. *Arct. Antarct. Alp. Res.* 42, 449–457. doi: 10.1657/1938-4246-42.4.449
- Liu, F., Wang, X., Wang, C., and Zhang, Q. (2021a). Environmental and biotic controls on the interannual variations in CO<sub>2</sub> fluxes of a continental monsoon temperate forest. *Agric. For. Meteorol.* 296. doi: 10.1016/j.agrformet.2020.108232
- Liu, G., Yan, G., Chang, M., Huang, B., Sun, X., Han, S., et al. (2021b). Long-term nitrogen addition further increased carbon sequestration in a boreal forest. *Eur. J. For. Res.* 140, 1113–1126. doi: 10.1007/s10342-021-01386-9
- Liu, M.-x., Liu, Y.-y., Chen, S.-w., An, Q. (2015). Plant Photosynthetic Characteristics along Slope Gradients in an Alpine Meadow Region on the Eastern Edge of Qinghai-Tibetan Plateau. *Soil Crop.* 4:104–12.
- Liu, X. D., and Chen, B. D. (2000). Climatic warming in the Tibetan Plateau during recent decades. *Int. J. Climatol.* 20, 1729–1742. doi: 10.1002/1097-0088(20001130)20:14<1729::AID-JOC556>3.0.CO;2-Y
- Luan, J., Song, H., Xiang, C., Zhu, D., and Suolang, D. (2016). Soil moisture, species composition interact to regulate CO<sub>2</sub> and CH<sub>4</sub> fluxes in dry meadows on the Tibetan Plateau. *Ecol. Eng.* 91, 101–112. doi: 10.1016/j.ecoleng.2016.02.012
- Lund, M., Lafleur, P. M., Roulet, N. T., Lindroth, A., Christensen, T. R., Aurela, M., et al. (2010). Variability in exchange of CO<sub>2</sub> across 12 northern peatland and tundra sites. *Global Change Biol.* 16, 2436–2448. doi: 10.1111/j.1365-2486.2009.02104.x
- Luo, Y., Wan, S., Hui, D., and Wallace, L. L. J. N. (2001). Acclimatization of soil respiration to warming in a tall grass prairie. 413, 622–625. doi: 10.1038/35098065
- Lv, C. Q (2006). *Storage Pattern and Influencing Factors of Soil Organic Carbon in Qinghai Xizang Plateau*. Nanjing, <http://en.wikipedia.org/wiki/Jiangsu>: Jiangsu: Nanjing University.
- Ma, F., Song, B., Quan, Q., Zhang, F., Wang, J., Zhou, Q., et al. (2020). Light Competition and Biodiversity Loss Cause Saturation Response of Aboveground Net Primary Productivity to Nitrogen Enrichment. *J. Geophys. Res-Bioge.* 125. doi: 10.1029/2019JG005556
- Marcolla, B., Roedenbeck, C., and Cescatti, A. (2017). Patterns and controls of inter-annual variability in the terrestrial carbon budget. *Biogeosciences*. 14, 3815–3829. doi: 10.5194/bg-14-3815-2017
- Mou, X. M., Zhao, L. i. X. G., Yu, N., and Kuzuyakov, Y. W. Y (2018). Tibetan sedges sequester more carbon belowground than grasses: a C-13 labeling study. *Plant. Soil.* 426, 287–298. doi: 10.1007/s11104-018-3634-5
- Ni, J. (2002). Carbon storage in grasslands of China. *J. Arid. Environ.* 50, 205–218. doi: 10.1006/jare.2001.0902
- Niu, B., He, Y. T., Zhang, X. Z., Du, M. Y., Shi, P. L., Sun, W., et al. (2017a). CO<sub>2</sub> Exchange in an Alpine Swamp Meadow on the Central Tibetan Plateau. *Wetlands*. 37, 525–543. doi: 10.1007/s13157-017-0888-2
- Niu, S., Fu, Z., Luo, Y., Stoy, P. C., Keenan, T. F., Poulter, B., et al. (2017b). Interannual variability of ecosystem carbon exchange: From observation to prediction. *Global. Ecol. Biogeogr.* 26, 1225–1237. doi: 10.1111/geb.12633
- Parmentier, F., Van Der Molen, M., Van Huissteden, J., Karsanaev, S., Kononov, A., Suzdalov, D., et al. (2011). Longer growing seasons do not increase net carbon uptake in the northeastern Siberian tundra. *J. Geophys. Res. Biogeosci.* 116. doi: 10.1029/2011JG001653

- Peng, H., Chi, J., Yao, H., Guo, Q., Hong, B., Ding, H., et al. (2021). Methane emissions offset net carbon dioxide uptake from an alpine peatland on the Eastern Qinghai-Tibetan Plateau. *J. Geophys. Res-Atmos.* 126. doi: 10.1029/2021JD034671
- Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., and van der Werf, B. i. J. (2014). Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature.* 509, 600–+. doi: 10.1038/nature13376
- Quan, Q., Zhang, F. Y., Tian, D. S., Zhou, Q. P., Wang, L. X., and Niu, S. L. (2018). Transpiration Dominates Ecosystem Water-Use Efficiency in Response to Warming in an Alpine Meadow. *J. Geophys. Res-Bioge.* 123, 453–462. doi: 10.1002/2017JG004362
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., et al. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global. Change. Biol.* 11, 1424–1439. doi: 10.1111/j.1365-2486.2005.001002.x
- Saito, M., Kato, T., and Tang, Y. (2009). Temperature controls ecosystem CO<sub>2</sub> exchange of an alpine meadow on the northeastern Tibetan Plateau. *Global. Change. Biol.* 15, 221–228. doi: 10.1111/j.1365-2486.2008.01713.x
- Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbagy, E., and Peters, D. (2012). Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philos. Trans. R. Soc. B-Biol. Sci.* 367, 3135–3144. doi: 10.1098/rstb.2011.0347
- Savitzky, A., and Golay, M. J. E. (1964). Smoothing + differentiation of data by simplified least squares procedures. *Anal. Chem.* 36, 1627. doi: 10.1021/ac60214a047
- Song, W. M., Wang, H., Wang, G. S., Chen, L. T., Jin, Z. N., Zhuang, Q. L., et al. (2015). Methane emissions from an alpine wetland on the Tibetan Plateau: Neglected but vital contribution of the nongrowing season. *J. Geophys. Res-Bioge.* 120, 1475–1490. doi: 10.1002/2015JG003043
- Sun, S., Che, T., Wang, L. i. H., Ma, T., and Liu, C. B., and Song Z (2019). 9Water and carbon dioxide exchange of an alpine meadow ecosystem in the northeastern Tibetan Plateau is energy-limited. *Agric. For. Meteorol.* 275, 283–295. doi: 10.1016/j.agrformet.2019.06.003
- Wang, L., Liu, H., Shao, Y., Liu, Y., and Sun, J. (2018). Water and CO<sub>2</sub> fluxes over semiarid alpine steppe and humid alpine meadow ecosystems on the Tibetan Plateau. *Theor. Appl. Climatol.* 131, 547–556. doi: 10.1007/s00704-016-1997-1
- Wang, L., Liu, H. Z., Sun, J. H., and Feng, J. W. (2016). Water and carbon dioxide fluxes over an alpine meadow in southwest China and the impact of a spring drought event. *Int. J. Biometeorol.* 60, 195–205. doi: 10.1007/s00484-015-1016-8
- Wang, S. L., Jin, H. J., and Zhao, L. i. S. X. (2000). Permafrost degradation on the Qinghai-Tibet Plateau and its environmental impacts. *Permafrost. Periglac.* 11, 43–53. doi: 10.1002/(SICI)1099-1530(200001/03)11:1<43: AID-PPP332>3.0.CO;2-H
- Wang, S. Q., and Zhou, C. H. (1999). Estimating soil carbon reservoir of terrestrial ecosystem in China. *Geogr. Res.* 18, 349–356.
- Wang, X., Piao, S., Ciais, P., Friedlingstein, P., Myneni, R. B., Cox, P., et al. (2014). A two-fold increase of carbon cycle sensitivity to tropical temperature variations. *Nature.* 506, 212–+. doi: 10.1038/nature12915
- Wang, Y., Ma, Y., and Yuan, L. i. H. (2020). Carbon and water fluxes and their coupling in an alpine meadow ecosystem on the northeastern Tibetan Plateau. *Theor. Appl. Climatol.* 142, 1–18. doi: 10.1007/s00704-020-03303-3
- Wang, Y., Zhou, G., and Wang, Y. (2008). Environmental effects on net ecosystem CO<sub>2</sub> exchange at half-hour and month scales over *Stipa krylovii* steppe in northern China. *Agric. For. Meteorol.* 148, 714–722. doi: 10.1016/j.agrformet.2008.01.013
- Xia, J., Niu, S., Ciais, P., Janssens, I. A., Chen, J., Ammann, C., et al. (2015). Joint control of terrestrial gross primary productivity by plant phenology and physiology. *Proc. Natl. Acad. Sci. U. S. A.* 112, 2788–2793. doi: 10.1073/pnas.1413090112
- Xu, W. X., and Liu, X. D. (2007). Response of vegetation in the Qinghai-Tibet Plateau to global warming. *Chin. Geogr. Sci.* 17, 151–159. doi: 10.1007/s11769-007-0151-5
- Xu, X., Shi, Z., Zhou, L. i. D., Sherry, X., and Luo, R. A. Y. (2015). Plant community structure regulates responses of prairie soil respiration to decadal experimental warming. *Global. Change. Biol.* 21, 3846–3853. doi: 10.1111/gcb.12940
- Yashiro, Y., Shizu, Y., Hirota, M., Shimono, A., and Ohtsuka, T. (2010). The role of shrub (*Potentilla fruticosa*) on ecosystem CO<sub>2</sub> fluxes in an alpine shrub meadow. *J. Plant. Ecol-U.* 3, 89–97. doi: 10.1093/jpe/rtq011
- Zhang, T., Zhang, Y., Xu, M., Zhu, J., Chen, N., Jiang, Y., et al. (2018). Water availability is more important than temperature in driving the carbon fluxes of an alpine meadow on the Tibetan Plateau. *Agric. For. Meteorol.* 256, 22–31. doi: 10.1016/j.agrformet.2018.02.027
- Zhao, L., Xu, L. i. J., Zhou, S., Li, H., Gu, Y., and Zhao, S. X. (2010). Seasonal variations in carbon dioxide exchange in an alpine wetland meadow on the Qinghai-Tibetan Plateau. *Biogeosciences.* 7, 1207–1221. doi: 10.5194/bg-7-1207-2010
- Zhao, L., Xu, L. i. Y., Zhou, S., Gu, H., Yu, S., and Zhao, G. X. (2006). Diurnal, seasonal and annual variation in net ecosystem CO<sub>2</sub> exchange of an alpine shrubland on Qinghai-Tibetan plateau. *Global. Change. Biol.* 12, 1940–1953. doi: 10.1111/j.1365-2486.2006.01197.x
- Zhao, L., Zhao, L. i. Y. N., Xu, X. Q., Tang, S. X., and Yu, Y. H. GR, and Wang QX (2005). Comparative study of the net exchange of CO<sub>2</sub> in 3 types of vegetation ecosystems on the Qinghai-Tibetan Plateau. *Chin. Sci. Bull.* 50, 1767–1774. doi: 10.1360/04wd0316
- Zhou, H., Zhao, X., Tang, Y., Gu, S., and Zhou, L. (2005). Alpine grassland degradation and its control in the source region of the Yangtze and Yellow Rivers, China. *Grassland. Sci.* 51, 191–203. doi: 10.1111/j.1744-697X.2005.00028.x
- Zhou, S., Zhang, Y., Caylor, K. K., Luo, Y. Q., Xiao, X. M., Ciais, P., et al. (2016). Explaining inter-annual variability of gross primary productivity from plant phenology and physiology. *Agric. For. Meteorol.* 226, 246–256. doi: 10.1016/j.agrformet.2016.06.010
- Zhu, J., Chen, N., Zhang, Y., and Liu, Y. (2016). Effects of experimental warming on net ecosystem CO<sub>2</sub> exchange in Northern Xizang alpine meadow. *Chin. J. Plant. Ecol.* 40, 1219–1229. doi: 10.17521/cjpe.2016.0186
- Zhu, J., Zhang, F., He, L. i. H., Li, H., and Yang, Y. Y., and Luo F (2020). Seasonal and Interannual Variations of CO<sub>2</sub> Fluxes Over 10 Years in an Alpine Wetland on the Qinghai-Tibetan Plateau. *J. Geophys. Res-Bioge.* 125. doi: 10.1029/2020JG006011
- Zscheischler, J., Faticchi, S., Wolf, S., Blanken, P. D., Bohrer, G., Clark, K., et al. (2016). Short-term favorable weather conditions are an important control of interannual variability in carbon and water fluxes. *J. Geophys. Res-Bioge.* 121, 2186–2198. doi: 10.1002/2016JG003503

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Publisher's Note:** All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2022 Wang, Chen, Fu, Li, Wang, Liao and Niu. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.