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Carbon fluxes and environmental controls across different alpine grassland types on the Tibetan Plateau

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A R T I C L E I N F O

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A B S T R A C T

The magnitude and spatial patterns of carbon fluxes in alpine grasslands determine the regional terrestrial carbon balance of the Tibetan Plateau. However, the patterns and controlling factors of carbon fluxes on the plateau remain unclear, hampering the understanding of the carbon cycle of these vulnerable ecosystems. In this study, we compared the spatial variations of carbon fluxes of ten alpine ecosystems with diverse grassland types and explored their environmental controls across these different ecosystems. Our results show that the mean annual net ecosystem exchange (NEE) of carbon dioxide (CO_2) varied from -284 to 31 g C m^{-2} across sites. The alpine meadow ecosystems in the northeast and east of the plateau were strong CO_2 sinks (~x223C 200 g C m^{-2} y^{-1}), while the western alpine grasslands were weak CO_2 sinks or even sources. During the growing season, soil temperature generally played the dominant role in regulating the daily variations of the carbon fluxes for the alpine meadow ecosystems in the cold and humid northeastern areas, while soil moisture was the main controlling factor for the alpine grassland ecosystems in the dry western areas. Annual gross primary productivity (GPP), ecosystem respiration (Re) and the carbon sink capacity linearly increased with the increasing longitude but linearly decreased with elevation. The spatial pattern of annual NEE was primarily controlled by surface soil moisture, and higher soil water content (SWC) led to greater carbon sink capacity. SWC, vapor pressure deficit (VPD) also had favorable effects on the annual GPP and Re. The spatial variations of carbon fluxes resulted primarily from the longitudinal or altitudinal variations of the dominant environmental factors. This study provides guidance for the assessment of carbon fluxes on the Tibetan Plateau.

1. Introduction

Terrestrial ecosystems can regulate the climate system and mitigate global warming by sequestering carbon dioxide (CO_2) from the atmosphere (Ahlstrom et al., 2015; Le Quéré et al., 2009; Shevliakova et al., 2013). Grassland ecosystems, important components of the terrestrial biosphere, cover approximately one-third of the global land surface and play a considerable role in the global carbon cycle (Adams et al., 1990; Liang et al., 2017). Moreover, grassland ecosystems are mainly located in arid and semi-arid regions, and therefore they are more sensitive and vulnerable to climate change and human activities than other terrestrial ecosystems (Ponce-Campos et al., 2013; Ahlstrom et al., 2015). Therefore, elucidating the spatial patterns and environmental drivers of the carbon fluxes in grassland ecosystems is essential for accurately

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assessing regional carbon balance and carbon-climate feedbacks in a changing climate (Wagle et al., 2015).

Carbon fluxes of terrestrial ecosystems can show large spatial variability due to the influences of different environmental and biological factors, such as temperature, precipitation, radiation, canopy coverage, and nutrient availability (Hirata et al., 2008; Wagle et al., 2015). The eddy covariance technique has been widely used to continuously measure net ecosystem exchange of CO_2 (NEE) that is routinely partitioned into gross primary productivity (GPP) and ecosystem respiration (Re). There are currently a large number of eddy covariance flux sites across the globe, which provides valuable carbon flux measurements for synthesis studies. More and more studies have examined the geographic patterns of carbon fluxes and their controlling mechanisms by synthesizing eddy covariance flux data for various climate types and ecosystems at the regional scale (Biederman et al., 2017; Chen et al., 2013; Kato and Tang, 2008; Wang et al., 2019; Xiao et al., 2013). These studies demonstrate that synthesizing eddy covariance and climate data from multiple sites across a region can improve our understanding of the spatial patterns of the carbon fluxes and their controlling mechanisms (Chen et al., 2019; Han et al., 2020). For example, the clear latitudinal patterns of carbon fluxes in China's terrestrial ecosystems were mainly driven by mean annual temperature and precipitation (Xiao et al., 2013). Nonetheless, the majority of these studies only considered multiple vegetation types in the study areas and could not reveal the dominant environmental factors in the spatial gradient of a single vegetation type, for example, grasslands. Moreover, due to the availability of eddy covariance flux data, the synthesis studies on carbon fluxes of multiple grassland ecosystems were mainly in Europe and the US. Previous studies indicated that the spatial variations in carbon fluxes of grassland ecosystems were closely related to the variations of precipitation, temperature, water availability and management (Gilmanov et al., 2007; Wagle et al., 2015).

The Tibetan Plateau, known as the "third pole" of the Earth (Qiu et al., 2008), encompasses more than 80% of the Earth's terrain with elevation higher than 4000 m and hosts the world's largest alpine vegetation distribution area (Hopping et al., 2018; Miehe et al., 2019; Yao et al., 2019). Alpine meadow and alpine steppe are the dominant vegetation types of the plateau. The alpine grassland ecosystems grow in extremely harsh environments characterized by low annual mean temperature and rainfall, high solar radiation and wind speed, shallow soil profiles, limited nutrient and water availability, and short growing season (Liu et al., 2018; Miehe et al., 2019). Thus, these alpine ecosystems are extraordinarily vulnerable and sensitive to climate change. Based on eddy covariance observations, previous studies have analyzed the carbon fluxes of distinct alpine grassland types and their influencing factors on the plateau, but these studies were typically based on data from a single site or two sites (Fu et al., 2009; Li et al., 2019; Qi et al., 2021; Song et al., 2020; Sun et al., 2019; Zhu et al., 2015). Moreover, the sites used in these studies are distributed in the eastern or northeastern part of the plateau and are mainly alpine meadows (Kato et al., 2006; Niu et al., 2017; Wang et al., 2016; Shang et al., 2016). Obviously, a synthesis analysis of flux data from multiple alpine grassland sites across the Tibetan Plateau can provide more insight into the spatial pattern of carbon fluxes and environmental controls in grasslands on the Tibetan Plateau than studies from a single site. Additionally, a comprehensive analysis of spatial patterns and its controlling mechanisms of carbon fluxes in alpine grassland ecosystems is the key to accurately assess and predict the regional carbon budget of the Tibetan Plateau. However, due to the limitations of carbon flux observations in extremely difficult and remote areas and data-sharing policy, the magnitude, the spatial distribution pattern of carbon fluxes along geographic gradients, and their controlling factors for diverse alpine grassland ecosystems across the Tibetan Plateau remain unclear. Therefore, it is urgent to integrate observations from multiple observation stations to explore the geographical patterns of carbon fluxes and environmental controls in alpine grasslands on the Tibetan Plateau.

In this study, we examined the carbon fluxes and environmental controls of 10 alpine grassland eddy covariance flux sites across the Tibetan Plateau. The compiled dataset is valuable and can represent the main alpine grassland ecosystems on the Tibetan Plateau. To our knowledge, this is the first study to analyze the geographical patterns of carbon fluxes and environmental controls for a wide variety of grassland ecosystems across the Tibetan Plateau with eddy covariance data based on the same processing procedures (e.g., gap-filling, partitioning). Specifically, this study aims to achieve the following goals: (1) to disentangle the driving roles of environmental factors on carbon fluxes of each grassland type during the growing season; (2) to examine the magnitude and spatial patterns in the carbon fluxes across different types of alpine grassland; (3) to investigate the controls of the environmental factors on the spatial distribution of annual carbon fluxes for different types of alpine grassland.

2. Materials and methods

2.1. Study area and observation sites

The Tibetan Plateau, with an average elevation above 4000 m sea level, is called the "third pole" of the Earth, and has an area of approximately 2.5 million km^2, ranging from about 73°E to 105°E and 25°N to 40°N (Yang et al., 2014). The climate of the Tibetan Plateau is mainly influenced by the interaction of the Asian monsoon and the mid-latitude westerlies (Yao et al., 2019). The mean annual temperature over the plateau ranges from -4.9 to 6.1 ℃ and increases from west to east. The mean annual precipitation gradually increases from less than 50 mm in the northwest to over 1000 mm in the southeast, and most of the precipitation is concentrated in summer (Kuang et al., 2016). Alpine meadow and alpine steppe are the two dominant vegetation types, accounting for about 27% and 34% of the total area of the plateau, respectively (Ding et al., 2017).

We compiled eddy covariance flux and ancillary data for ten alpine grassland ecosystems distributed across the Tibetan Plateau. Fig. 1 illustrates the locations and geographical distribution of these sites. The site characteristics are provided in Table 1. The 10 grassland ecosystems consist of almost all of the alpine grassland vegetation types of the Tibetan Plateau: three alpine meadow grassland types and two alpine steppe grassland types. Specifically, the four alpine Kobresia meadow sites (Arou, Maqu, BJ and NPAM) are located in the eastern and central part of the plateau; the alpine swamp meadow sites (DSL and Longbao) are distributed in the northeastern and central eastern part of the plateau; the alpine shrub meadow site (Haibei) is located in the Northeast; the alpine meadow steppe site (NAMORS) is in the hinterland of the plateau; the alpine desert steppe sites (Muztagh and NASDE) are located in the West. Besides, all these observation sites are natural alpine grassland ecosystems which are far away from human habitation and are largely surrounded by iron fences to prevent livestock grazing. There were large variations in climatic factors, vegetation characteristics and altitude gradients among the ten sites: alpine meadow sites generally had higher precipitation and surface soil moisture content, while alpine steppe sites had lower soil moisture content and greater atmospheric dryness and solar radiation (Fig. 2).

2.2. Data collection and processing

NEE was continuously measured at the each of the ten observation sites in this study using the open-path eddy covariance (OPEC) system. The OPEC system primarily consists of a 3D ultrasonic anemometer (CSAT3, Campbell Scientific, UT, USA), an open-path infrared gas analyzer (Li-7500, Licor Inc., Lincoln, NE, USA) and a high frequency data logger. The former measured the sonic temperature, wind speed and wind direction and speed sound, while the latter measured molar densities of CO_2 and H_2O at a sample frequency of 10 Hz, from which the CO_2 fluxes were calculated. In addition, there is an accompanying

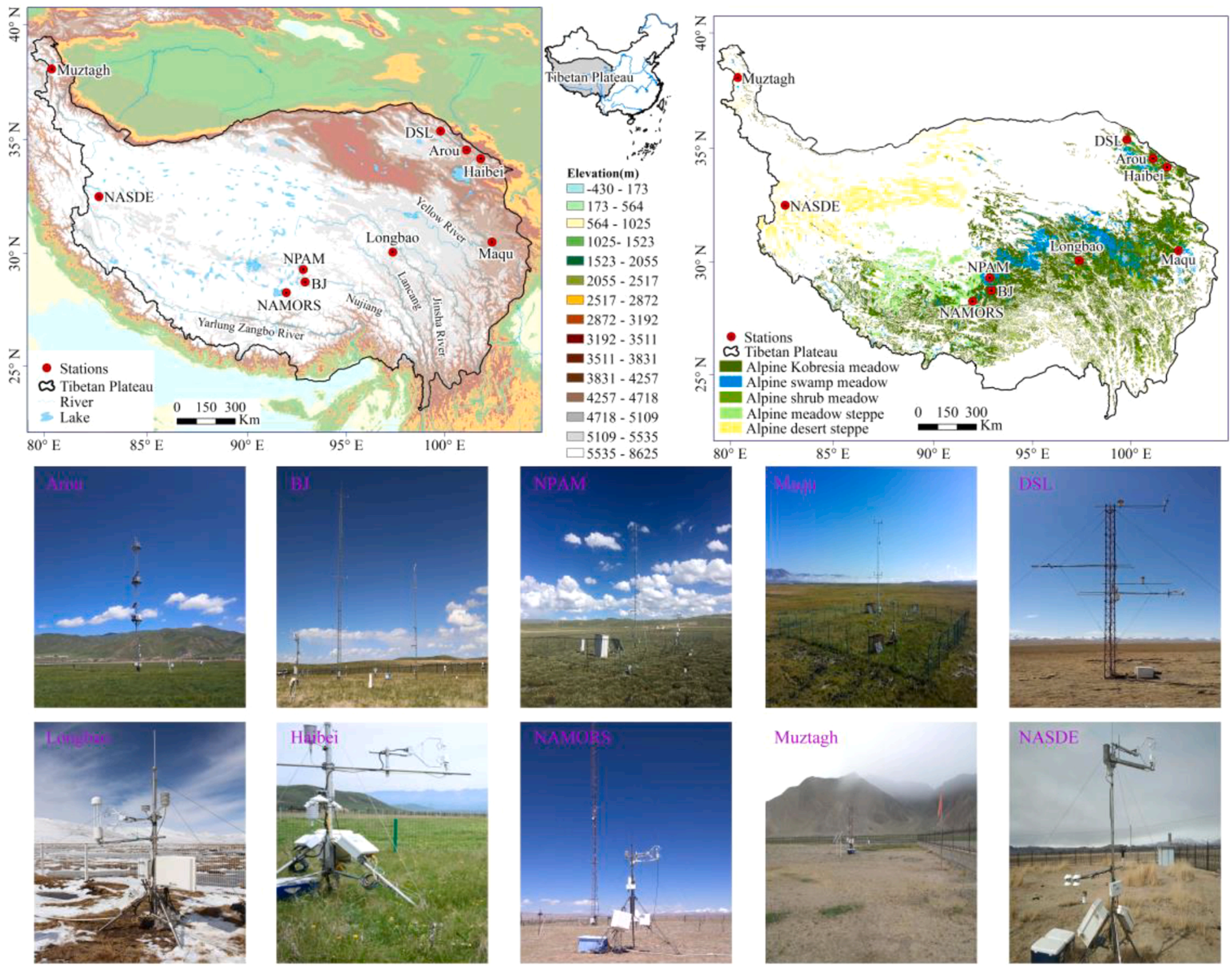

Fig. 1. The location and distribution of the eddy covariance (EC) flux sites across the Tibetan Plateau. The top left and the top right maps are the Digital elevation model (DEM) and the alpine grassland distribution map, respectively.

Table. 1
Site information in this study.

Grassland types	Site Name	Elevation (m)	Canopy height (m)	Tower height (m)	Temperature (C)	Precipitation (mm)	Time periods
Alpine Kobresia meadow	Arou	3033	0.3–0.4	3.5	-0.15	440	2013–2018
	Maqu	3533	0.2–0.3	3.15	2.42	508	2014, 2016
	BJ	4509	<0.2	3.02	0.54	436	2013–2014
	NPAM	4620	0.2	2.75	-1.78	–	2013
Alpine swamp meadow	DSL	3739	0.2–0.3	4.5	-4.19	338	2014–2018
	Longbao	4167	0.2–0.5	2	-0.52	–	2017–2018
Alpine shrub meadow	Haibei	3293	0.6–0.7	2.2	-1.20	409	2008–2010
Alpine desert steppe	Muztagh	3668	<0.2	2.3	1.06	183	2015–2016
	NASDE	4270	<0.2	2.75	1.36	109	2013,2015
Alpine meadow steppe	NAMORS	4730	<0.2	3.1	-0.36	462	2008–2009

- indicated there is an error in the precipitation data for the year of obsevation.

automatic weather station system at each site to monitor the micrometeorological variables including air temperature (T_a, °C), relative humidity (RH, %), four-component radiation (including upward and downward radiation of both short and long waves, W m^{-2}), precipitation (PPT, mm) and surface soil volumetric water content (SWC, %) and soil temperature (T_s, °C). In addition to the directly measured variables, vapor pressure deficit (VPD) was calculated using the measured T_a and RH. Moreover, the results within Sections 3.5 and 3.6 also included data from three alpine grassland sites-Damxung, Bange and Maoniuping on the plateau from other studies, and the carbon fluxes and the related climatic data of these sites were obtained from Wang et al. (2016) for Bange, Wang et al. (2017) for Maoniuping and ChinaFLUX database (http://www.chinaflux.org/general/index.aspx?nodeid=25) for Damxung.

The standardized procedures were adopted to process the raw 10 Hz data to 30-minute carbon flux and meteorological data. The procedures mainly involved spike detection, coordinate rotation, cross wind correction of the sonic temperature, frequency response correction, and density correction (Webb-Pearman-Leuning (WPL) correction) (Liu et al., 2011). In addition to these above steps, the half-hourly carbon flux data were further filtered according to additional standards following Liu et al. (2011). In order to obtain the daily, monthly and annually

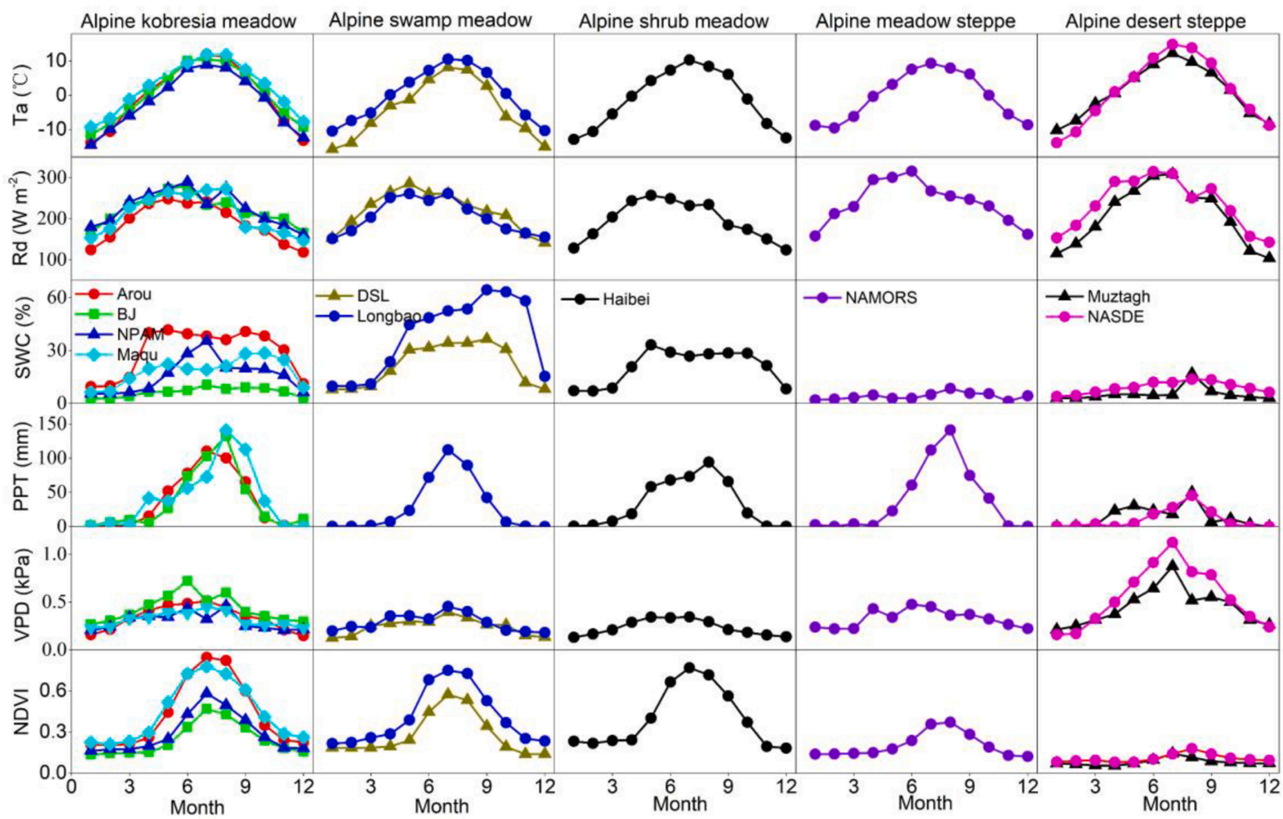

Fig. 2. Seasonal variations of monthly mean air temperature (T_a,°C), downward shortwave radiation (R_d, W m^{-2}), soil water content (SWC, %), soil temperature (T_s,°C), precipitation (PPT, mm), vapor pressure deficit (VPD, kPa) and monthly maximum normalized difference vegetation index (NDVI) of different alpine grassland ecosystems. (dots stand for mean values of each variables of different alpine grassland ecosystem, and alpine Kobresia meadow sites included Arou, Maqu, BJ and NPAM, alpine swamp meadow sites included DSL and Longbao, alpine shrub meadow site included Haibei, alpine meadow steppe site included NAMORS and alpine desert steppe sites included Muztagh and NASDE).

integrated values, we used the R-based package developed by the Max Planck Institute for Biogeochemistry (Reichstein et al., 2005; Wutzler et al., 2018) to fill the gaps of the half-hour NEE. The standard partitioning procedures were used to partition NEE into GPP and Re. Specifically, the empirical relationship between temperature and nighttime NEE (i.e., Re) was established and was then used to estimate Re for each half-hour during the daytime, while GPP was calculated as the difference between Re and NEE. The resulting 30-minute carbon fluxes data and micrometeorological data were further aggregated to daily, monthly, and annual timescales for further analyses.

Additionally, the satellite-derived normalized difference vegetation index (NDVI) is a vital proxy of vegetation growth status at ecosystem to global scales (Xiao et al., 2019). The MODIS 16 days composite NDVI product (MOD13A2) at a 1 km × 1 km spatial resolution was used in this study (LAADS DAAC, https://ladsweb.modaps.eosdis.nasa.gov/search/). The original 16-day NDVI data were further aggregated into the monthly timescale by using the maximum value composite method in order to minimize atmospheric effects and cloud contamination effects (Li et al., 2020). Then for each site we extracted the NDVI values for the pixel that the flux site is located in. Furthermore, the 8-day MODIS GPP (MOD17A2H version 6, https://search.earthdata.nasa.gov/search/) at a 500 m × 500 m spatial resolution was used to compare the discrepancies between remote sensing and in situ observation.

2.3. Statistical analysis

Partial least square regression (PLSR) analyses were applied to examine the responses of carbon fluxes (GPP, Re, NEE) to daily variations in environmental factors (T_a, T_s, VPD, SWC and R_d) during the growing season for the ten alpine grassland ecosystems across the Tibetan Plateau. The PLSR combines the advantages of principal component analysis, typical correlation analysis, and multiple regression analysis, and can effectively solve the problem of multicollinearity caused by the high correlation between independent variables in the regression modeling process (Wold et al., 1984; Wu et al., 2019). In this study, the regression coefficients of PLSR were used to measure the sensitivity of carbon fluxes to variations of different environmental factors, which reflects the direct effects of these environmental variables on the carbon fluxes. All variables were normalized prior to the PLSR analyses. The PLSR analyses were performed using the "pls" package (Mevik and Wehrens, 2007) in R (https://cran.r-project.org/web/packages/glm2/glm2.pdf).

3. Results

3.1. Diurnal variations of carbon fluxes and meteorological factors during the peak growing season

Hourly carbon fluxes data and meteorological factors were averaged to reveal the averaged diurnal variation during the peak growing season (July and August) in the study periods (Fig. 3). The carbon fluxes and major climatic factors exhibited obvious diurnal dynamics and almost all the variables followed unimodal distribution patterns. However, the magnitude and timing of the peak values were different among various alpine grassland types. After dawn, the plants started to photosynthesize and GPP increased and peaked around 12:00–13:00. The mean maximum GPP varied from 2.76 μ mol m^{-2} s^{-1} in alpine desert steppe (NASDE) to 21.13 μ mol m^{-2} s^{-1} in alpine Kobresia meadow (Arou). The timing of the GPP peaks essentially corresponded to that of the maximum solar radiation. After noon, as radiation decreased GPP also

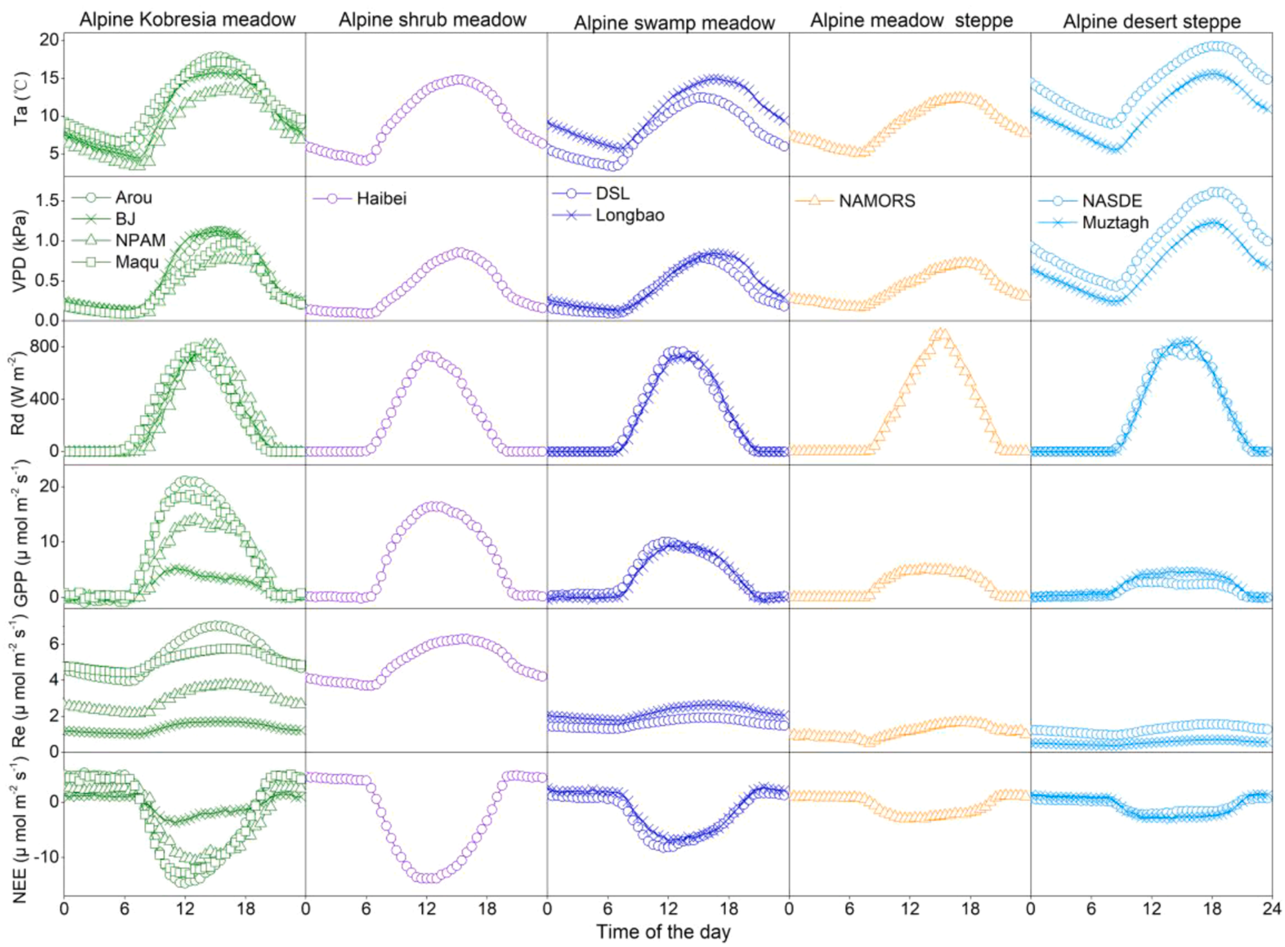

Fig. 3. Diurnal variations of average gross primary productivity (GPP), ecosystem respiration (Re), net ecosystem CO_2 exchange (NEE) during the peak growing season (July and August) in the study period of different alpine grassland ecosystems. The negative NEE values indicated a net uptake of CO_2. (dots stand for mean values of each variables of different alpine grassland ecosystem, and alpine Kobresia meadow sites included Arou, Maqu, BJ and NPAM, alpine swamp meadow sites included DSL and Longbao, alpine shrub meadow site included Haibei, alpine meadow steppe site included NAMORS and alpine desert steppe sites included Muztagh and NASDE).

followed the same decreasing pattern. However, the diurnal variations in Re were approximately consistent with those of air temperature, and maximum respiration generally occurred when the air temperature was at its maximum in the early afternoon. During the daytime, Re had smaller changes than GPP, and therefore net carbon uptake (i.e., NEE) was largely dependent on GPP; the diurnal variations of net carbon uptake and the timing of its maximum value were almost consistent with those of GPP. The alpine Kobresia meadow ecosystems (except for BJ) and alpine shrub meadow ecosystem had the highest maximum net carbon uptake (for example, Arou: -14.71 μ mol m^{-2} s^{-1}, Haibei: -13.85 μ mol m^{-2} s^{-1}), followed by alpine swamp meadow ecosystems (for example, DSL: -8.26 μ mol m^{-2} s^{-1}, Longbao: -6.89 μ mol m^{-2} s^{-1}) and the alpine steppe ecosystems had the lowest maximum net carbon uptake (for example, NAMORS: -3.01 μ mol m^{-2} s^{-1}, NASDE: -2.24 μ mol m^{-2} s^{-1}).

3.2. Seasonal variations in GPP, Re, and NEE across different alpine grassland types

Fig. 4 illustrates the seasonal variations of the daily GPP, Re and NEE across different grassland types on the Tibetan Plateau. The 10 sites varied substantially in the seasonal variations of carbon fluxes, although they generally showed single-peak distribution patterns. The highest daily carbon flux values were observed in summer, especially in July and August. During the growing season, the peaks and fluctuations in carbon fluxes were much larger at alpine meadow sites than at alpine steppe sites, except for the BJ site. For the alpine Krobresia meadow sites, the highest and lowest daily mean GPP and Re appeared at the Arou (GPP/Re: 10.98/7.68 g C m^{-2} d^{-1}) and BJ (GPP/Re: 3.27/2.18 g C m^{-2} d^{-1}) sites, respectively; the unimodal patterns of GPP and Re at Arou were steeper and narrower than at Maqu and the longer carbon assimilation time at Maqu resulted in larger cumulative NEE than at Arou in absolute magnitude; compared to the other three sites, BJ had small fluctuations in GPP and Re, leading to little variations in NEE (-1.25 g C m^{-2} d^{-1} ~x223C 0.96 g C m^{-2} d^{-1}). The alpine swamp meadow sites had smaller daily maximum GPP but much lower daily maximum Re than other alpine meadow sites (for example, Longbao GPP/Re: 4.99/3.03 g C m^{-2} d^{-1}), and therefore the daily NEE of the alpine swamp meadow sites was close to or even slightly higher than that of other alpine meadow sites in absolute magnitude. Among the alpine steppe sites, NASDE had the smallest peaks, fluctuations and interannual variability in GPP (1.60 g C m^{-2} d^{-1}) and Re (0.71 g C m^{-2} d^{-1}), and Muztagh had the greatest net carbon uptake (-2.10 g C m^{-2} d^{-1}). Additionally, the maximum values and the fluctuation of carbon flux components of these 10 ecosystems basically had longitudinal zonal distribution patterns, which showed a tendency to decline with decreasing longitude.

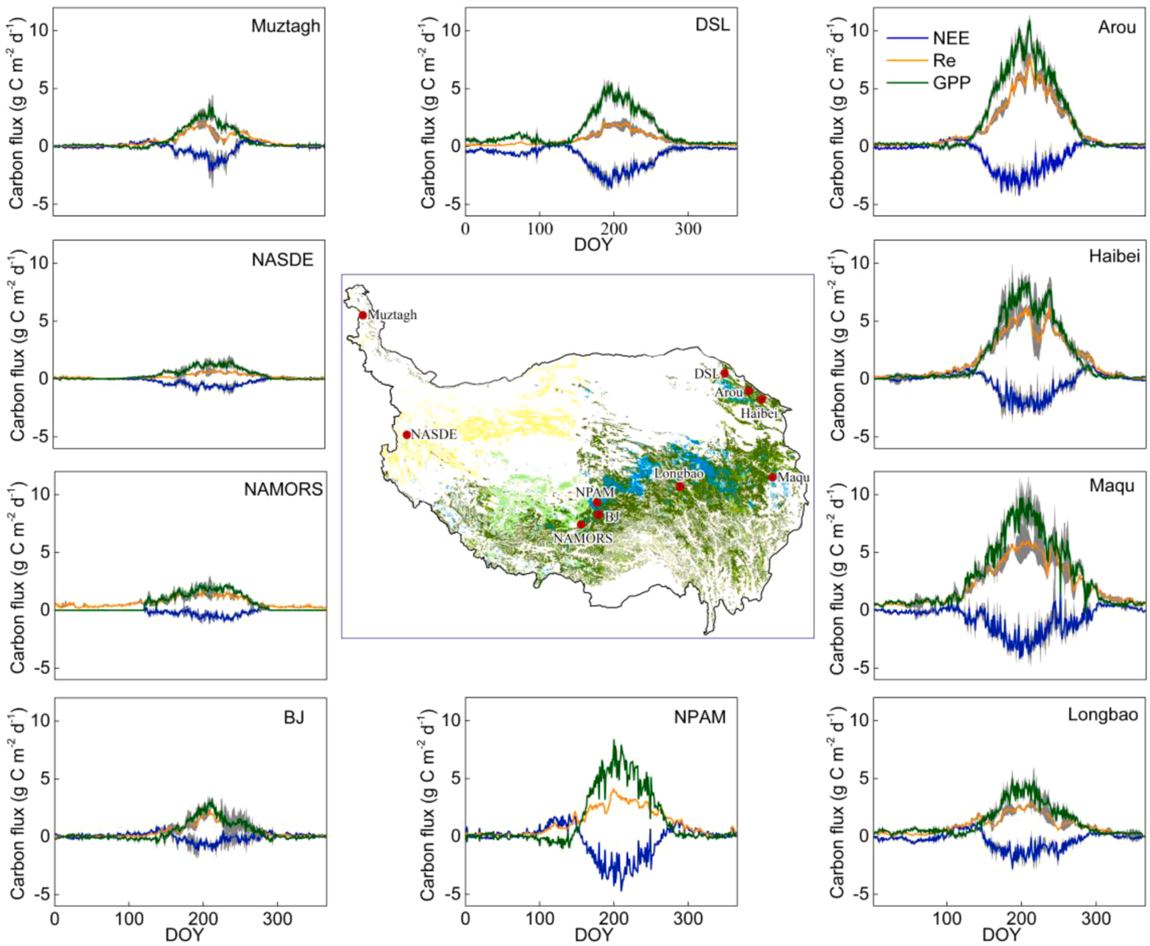

Fig. 4. Seasonal variations in gross primary productivity (GPP), ecosystem respiration (Re), net ecosystem CO_2 exchange (NEE) across different grassland ecosystems. The negative NEE values indicated a net uptake of CO_2. (The blue, orange and green line stand for daily NEE, Re and GPP, respectively, and the gray line indicates the standard error between the seasonal dynamic of different years). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Drivers of daily GPP, Re and NEE during the growing season for different alpine grassland types

The PLSR analyses revealed how the environmental factors regulated daily carbon fluxes (Fig. 5). GPP and NEE were significantly correlated with T_s and R_d at Arou, Maqu and NPAM, while T_s played the leading role in regulating Re. In contrast to the other three alpine Kobresia meadow sites, BJ showed positive responses in daily GPP and Re and negative response in daily NEE (favorable for carbon sequestration) to the variations in SWC (Fig. 5). For the alpine swamp meadow, GPP and NEE had stronger correlations with T_s and R_d than with T_a and SWC at DSL; SWC had negative effects on GPP and Re but positive effect on NEE at the Longbao site, probably due to the inhibition of photosynthesis and respiration by high SWC (>40%) during the growing season. At Haibei, T_s and R_d also exerted favorable effects on GPP and negative effects on NEE, while Re was driven by T_s. At NAMORS, SWC played a crucially positive or unfavorable role in regulating the variations of carbon fluxes. For the alpine desert steppe, temperature and soil moisture had crucial effects on GPP and NEE, while VPD inhibited both GPP and NEE at Muztagh; SWC and T_s played the largest roles in regulating the carbon fluxes at NASDE. Additionally, positive correlations between VPD on NEE were found at the most sites, suggesting that increased atmospheric dryness may be detrimental to carbon sequestration. Generally, for almost all of the observation sites, the environmental drivers that regulated NEE and GPP tended to be similar, while Re was usually controlled by surface soil temperature and soil moisture.

3.4. Magnitude of annual carbon fluxes across different sites and vegetation types

The average annual GPP, NEE and Re across the 10 alpine ecosystems were shown in Fig. 6-a. The results show that annual carbon fluxes exhibited large variability across sites and vegetation types. The average annual NEE ranged from -284.12 to 31.08 g C m^{-2} yr^{-1}; and the alpine swamp ecosystem site - DSL had the largest annual net carbon uptake, followed by the alpine Kobresia ecosystem sites - Maqu (-246.90 g C m^{-2} yr^{-1}) and Arou (-218.69 g C m^{-2} yr^{-1}), while the alpine desert steppe ecosystem site - Muztagh had the lower net carbon uptake. BJ (1.51 g C m^{-2} yr^{-1}) and NAMORS (31.08 g C m^{-2} yr^{-1}) were carbon sources, while all other sites were carbon sinks. The annual mean GPP ranged from138.32 to 1064.82 g C m^{-2} yr^{-1}. Among these sites, Maqu had the highest GPP, Arou (832.86 g C m^{-2} yr^{-1}) and Haibei (758.80 g C m^{-2} yr^{-1}) had intermediate GPP and NASDE had the lowest GPP. The annual Re of the 10 sites was between 81.40 and 817.81 g C m^{-2} yr^{-1}, and the Re of Maqu, Arou and Haibei sites was much higher than that of other sites. Although the annual GPP was much larger at Maqu than at DSL (506.12 g C m^{-2} yr^{-1}), the strong respiration at Maqu and weak respiration at DSL (222.28 g C m^{-2} yr^{-1}) led to larger net carbon uptake at DSL than at Maqu (-246.90 g C m^{-2} yr^{-1}). Besides, BJ, NAMORS, NASDE and Muztagh were weak carbon sources or sinks due to the small differences between GPP and Re.

The average of annual mean NEE for all sites of the alpine Kobresia meadow, alpine swamp meadow, alpine shrub meadow, alpine meadow

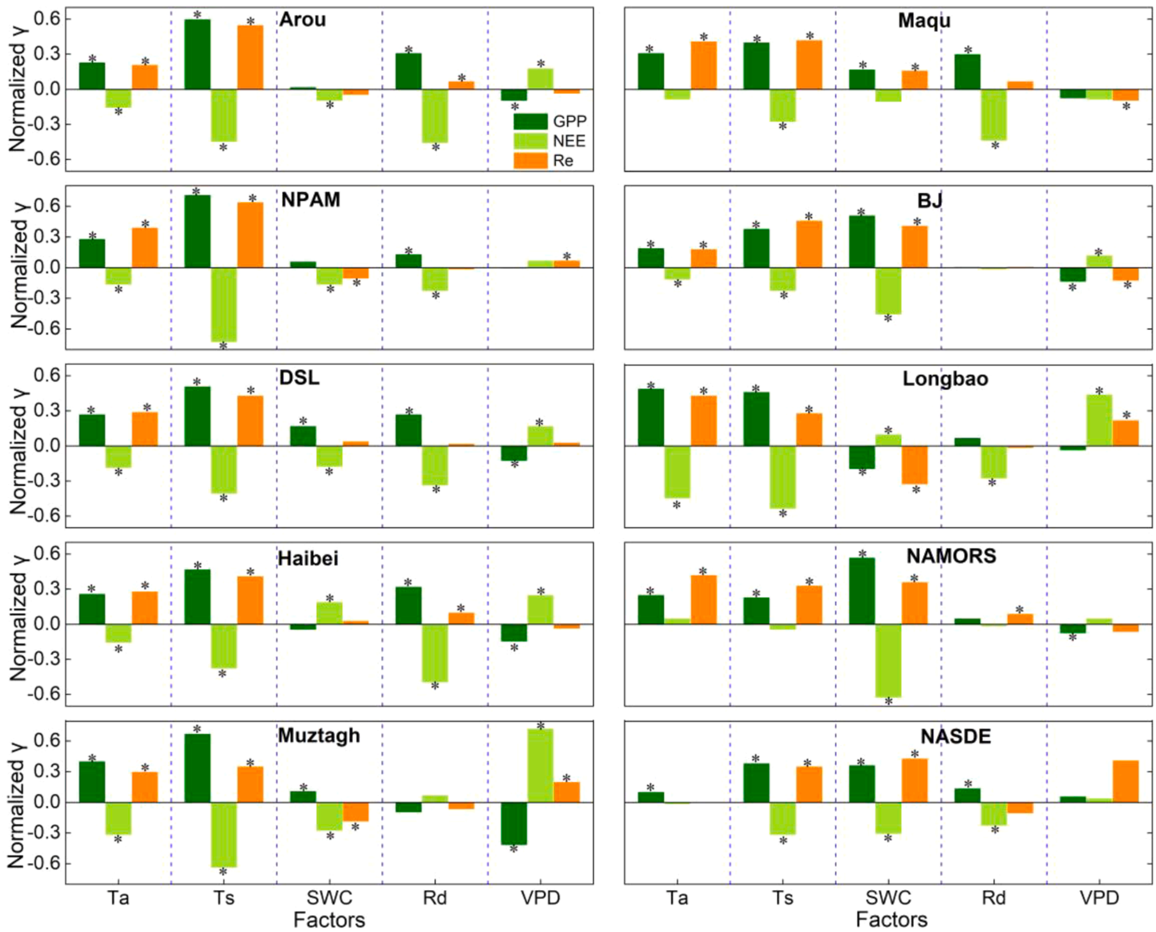

Fig. 5. Responses of gross primary productivity (GPP), ecosystem respiration (Re), net ecosystem CO_2 exchange (NEE) to environmental factors at the ten alpine grassland ecosystems during the growing season. The environmental variables included daily air temperature (T_a), soil temperature (T_s), vapor pressure deficit (VPD), soil water content (SWC) and downward shortwave radiation (R_d). Stars over the bars indicate statistically significant ($p < 0.05$).

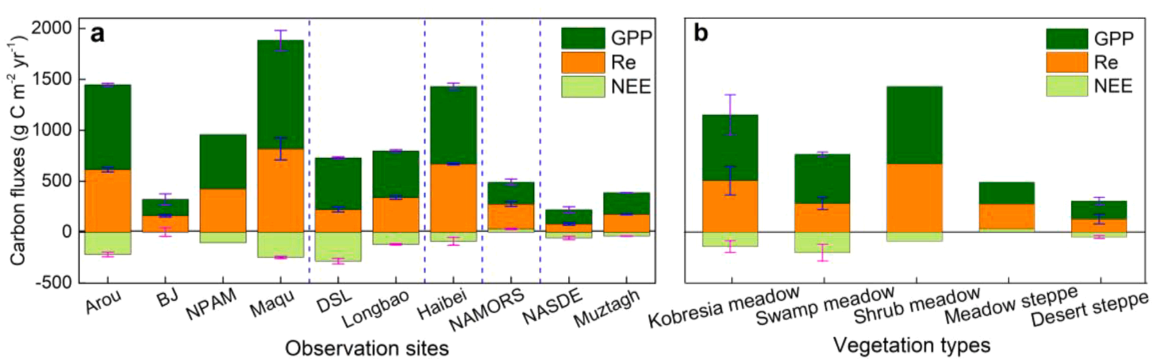

Fig. 6. Magnitude of annual averages of gross primary productivity (GPP), ecosystem respiration (Re), net ecosystem CO_2 exchange (NEE) across different sites and vegetation types. The negative NEE values indicated a net uptake of CO_2. Error bars indicate standard errors. Fig. 6-a refers to the mean of carbon fluxes for multiple years for each site, Fig. 6-b refers to the average of annual mean carbon fluxes for all sites for each vegetation type.

steppe and alpine desert steppe was -141.89 ± 56.98, -201.65 ± 82.47, -89.54, 31.08 and -47.11 ± 13.75 g C m^{-2} yr^{-1}, respectively. The alpine swamp meadow and alpine Kobresia meadow were strong carbon sinks, followed by alpine shrub meadow, while the alpine meadow steppe and alpine desert steppe were weak carbon sources. Alpine shrub meadow had a higher annual respiratory intensity (670.38 ± 13.50 g C m^{-2} yr^{-1}) than other grassland types, and therefore its NEE was only half that of alpine Kobresia meadow despite their similar GPP values. In contrast, both GPP, Re and net carbon uptake were much smaller in alpine steppes than in alpine meadows (Fig. 6-b).

3.5. *Longitudinal and elevational patterns of carbon fluxes*

Fig. 7 shows the trends of carbon fluxes along the latitude, longitude and elevation for the observation sites on the Tibetan Plateau. GPP, NEE and Re had weak relationships with latitude. The carbon fluxes all showed relatively strong longitudinal and elevational patterns and the longitudinal pattern was more pronounced (GPP = 27.10Lon-2054, R = 0.77, $p < 0.01$; NEE = -7.82Lon+631, R = -0.61, $p < 0.05$; Re=19.69Lon-1469, R = 0.74, $p < 0.01$; GPP = -0.39Alt+1955, R = -0.71, $p < 0.05$; Re = -0.26Alt+1403, R = -0.69, $p < 0.05$; NEE =

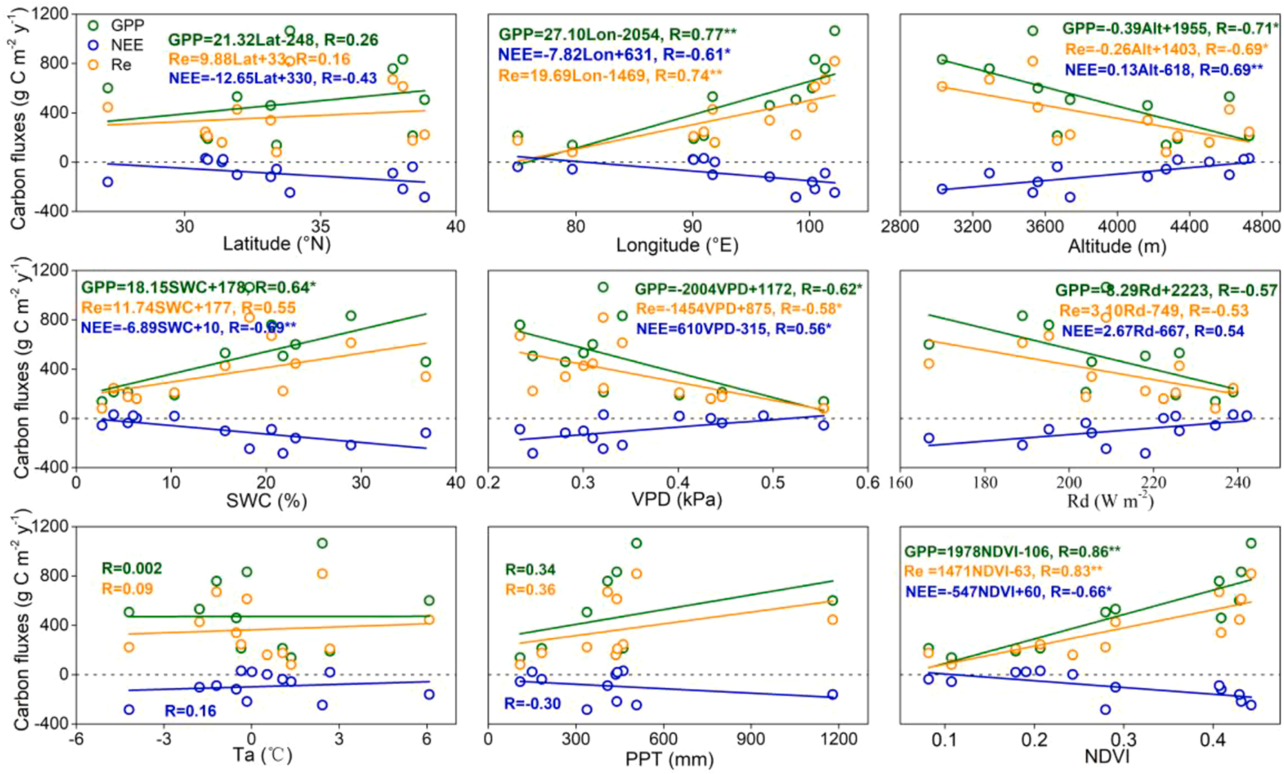

Fig. 7. Relationships between annual carbon fluxes and a series of variables including latitude, longitude, environmental factors and NDVI across different grassland ecosystems. The negative NEE values indicated a net uptake of CO_2.

0.13Alt-618, R = 0.69; p < 0.01). GPP, Re and the carbon sink capacity all linearly increased with the increasing longitude, but linearly decreased with elevation. GPP increased or decreased faster than Re along the longitudinal and elevational gradients. With 1° increase of longitude, NEE decreased by 7.82 g C m^{-2} yr^{-1}, while GPP and Re increased by 27.1 and 19.7 g C m^{-2} yr^{-1}, respectively. The NEE was positive when longitude was below 90°, indicating a carbon source in low longitude.

3.6. Relationships between carbon fluxes and climatic factors

In addition, the effects of major environmental factors on annual mean carbon flux components were also analyzed to elucidate the regulation of key factors on annual carbon fluxes (Fig. 7). The result showed that NEE exhibited a significant negative correlation with SWC (NEE = -6.89SWC+10, R = -0.69, p < 0.01). For every percent increase in SWC, NEE decreased by 6.89 g C m^{-2} yr^{-1}, suggesting that ecosystems with high SWC had greater carbon sink capacity. Moreover, VPD and R_d also had positive correlations with NEE (NEE = 610VPD-315, R = 0.56, p < 0.05; NEE = 2.67R_d-667, R = 0.54, p = 0.055), indicating that the carbon sink capacity of the ecosystems tended to decrease with increasing atmospheric dryness and enhanced radiation. GPP and Re also had positive or negative correlations with SWC, VPD and R_d, but the relationships were weaker for GPP than for NEE. In addition, the carbon flux components showed poor correlations with temperature, but had weak correlations with precipitation, suggesting that the spatial patterns of carbon fluxes were not dependent on temperature and was weakly correlated with precipitation. Fig. 7 also indicated that there were significant correlations between carbon fluxes and NDVI, especially for the GPP (GPP = 1978NDVI-106, R = 0.86, p < 0.001) and Re (Re = 1471NDVI-63, R = 0.83, p < 0.001). The increase in NDVI, GPP, Re, and caron sink capacity grew significantly in a linear way, indicating that vegetation indices can be prominent indicators for characterizing the spatial distribution of annual carbon fluxes. Meanwhile, the multi-year average of daily carbon fluxes and climate factors during the growing season were also analyzed and obtained similar results to the annual mean analysis (Fig. 8). That is, on a regional scale, SWC, VPD and R_d had positive or negative impact on carbon fluxes, and the sites with low mean daily SWC and high mean daily VPD and R_d tended to have low GPP, Re, and net carbon uptake.

4. Discussion

4.1. Environmental controls on the spatial variation of carbon fluxes during the growing season on the Tibetan Plateau

Our results revealed that the drivers of carbon fluxes in alpine grassland ecosystems of the Tibetan Plateau varied not only among vegetation types but also among the sites within the same type. Previous studies pointed out that drivers of carbon fluxes for the alpine grassland ecosystems on the Tibetan Plateau during the growing season were generally dominated by variations in soil temperature (Saito et al., 2009; Sun et al., 2019), soil water availability (Zhang et al., 2018), water table (Sun et al., 2021), and growing season degree days (Li et al., 2019). However, these studies were mostly based on single-site analyses and thus the conclusions of environment influences on alpine grassland ecosystems might be inadequate. The responses of daily GPP, NEE and Re to environmental factors during the growing season in our study suggested that for the alpine meadow sites (except for the BJ site) in the eastern and central parts of the plateau where there was no water stress, temperature and solar radiation were often the limiting factors, and soil temperature generally played the leading role. This finding was similar to the results of previous studies for alpine ecosystems around the world, such as southwestern Greenland (López-Blanco et al., 2017), north-eastern Tibetan Plateau (Sun et al., 2019) and Australian mountain grassland (Marchin et al., 2018).

Temperature, soil moisture and solar radiation are crucial environmental factors in regulating carbon fluxes in ecosystems, mainly by

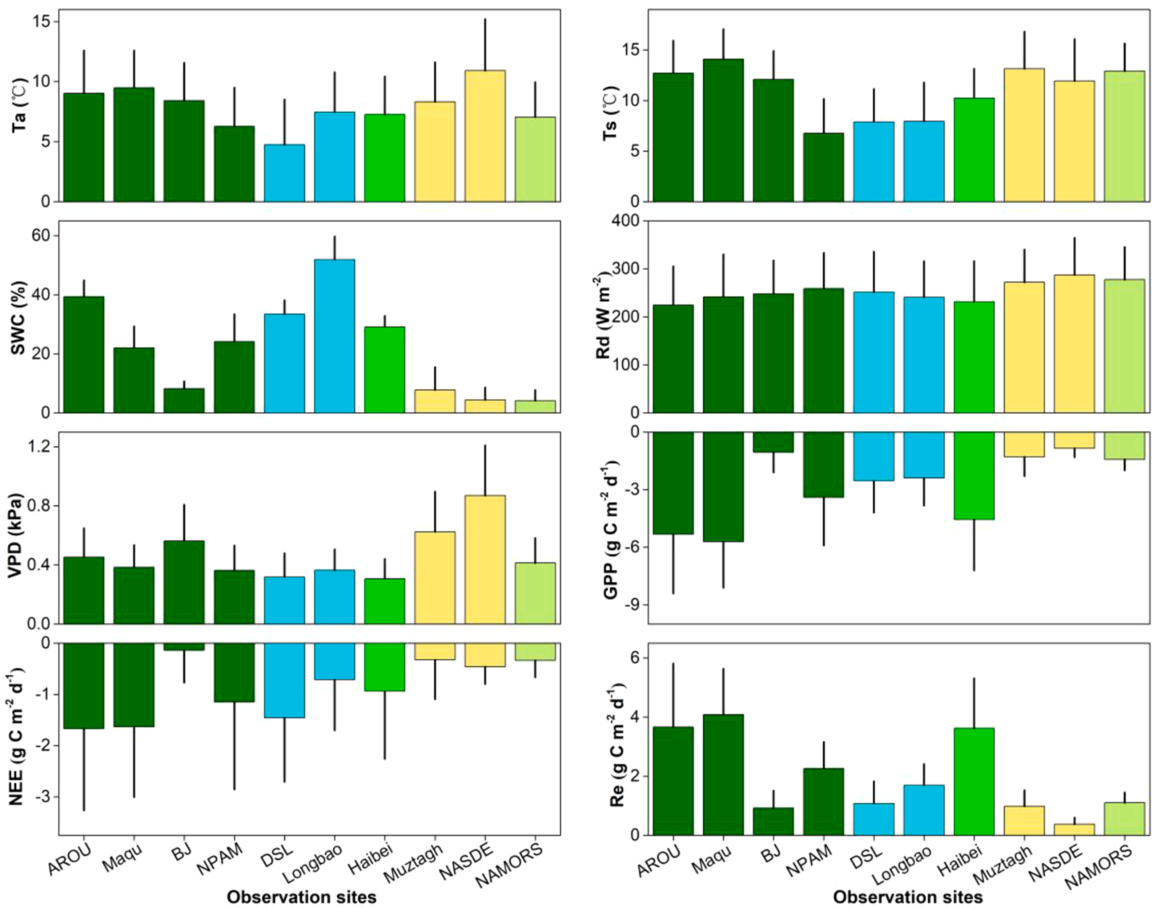

Fig. 8. The relationship between carbon fluxes and the environment factors during the growing season. The error bars stand for the standard deviations.

influencing photosynthesis and respiration in plants (Sun et al., 2019; Zhang et al., 2018). Due to the cold climate of the alpine ecosystems, temperature and radiation were often limiting factors when water availability was adequate during the growing season, indicating that these ecosystems were energy-limited (Saito et al., 2009; Sun et al., 2019). By contrast, at sites with insufficient water supply during the growing season (e.g., BJ and NAMORS), surface soil moisture was often the controlling factor. This was consistent with the study of Zhang et al. (2018) indicating that water availability was the most important environmental factor governing the carbon fluxes for a water-limited alpine meadow ecosystem in the central part of the Tibetan Plateau. For the water-limited alpine grassland ecosystems, the physiological activities of plants are sensitive to the changes of available water; water stress caused by reduced surface soil water content can depress photosynthesis by affecting stomatal conductance of plants, leading to decreases in GPP and net carbon uptake (van der Molen et al., 2011; Wang et al., 2020; Zhang et al., 2018).

Therefore, the differences in water availability may account for the discrepancies in the spatial patterns of the carbon fluxes during the growing season among different ecosystems. However, for alpine desert steppe, the influencing factors tended to be more complicated, and surface soil moisture played an important but not the leading role in regulating carbon fluxes. This is most likely because the alpine desert ecosystems are adapted to the arid environments and are less sensitive to surface soil moisture.

4.2. *Comparison with other grassland ecosystems*

The magnitude of the annual NEE can reflect its carbon source/sink strength of the ecosystem, which is critical for assessing the carbon balance of regional ecosystems (Xiao et al., 2013). In order to understand the carbon sink or source size of the alpine grassland ecosystems on the Tibetan Plateau, we compared the annual mean NEE from the 10 alpine ecosystems of this study with other grassland ecosystems around the world (Fig. 9). The result indicated that the strong carbon sink ecosystems in this study were mainly located in the northeastern and eastern part of the plateau (about 200–300 g C m^{-2} y^{-1}), while the carbon sink intensity was less than that of some grassland ecosystems in the central Europe and the U.S. Great Plains (~ x223C 300–500 g C m^{-2} yr^{-1}) (Ammann et al., 2007; Gilmanov et al., 2003, 2007; Jacobs et al., 2007; Peichl et al., 2010; Wagle et al., 2015; 2020; Sharma et al., 2019; Zeeman et al., 2010). Some grasslands of the central Europe and the U.S. Great Plains had higher carbon sink capacity because the hydrothermal conditions were beneficial and most of these grassland sites were under intensive management or were artificially planted (Wagle et al., 2020; Yu et al., 2013). Meanwhile, some grassland ecosystems in the Europe and the USA also had strikingly lower carbon uptake capacity than the alpine meadows of the northeastern Tibetan Plateau or even provided carbon sources (Jacobs et al., 2007; Gilmanov et al., 2007; Wagle et al., 2015). The grassland ecosystems in northern China included meadow steppe (Jing et al., 2014; Qu et al., 2016), temperate steppe (Hao et al., 2008) and desert steppe (Shao et al., 2013; Yang et al., 2011; Wang et al., 2018), and among these ecosystems, the SN meadow steppe site had the strongest carbon sequestration capacity (-111.83±32.95 g C m^{-2} yr^{-1}). The carbon sink capacity of this site was close to that of the NPAM and Longbao alpine meadow sites in this study but much lower than that of the alpine meadows on the northeastern Tibetan Plateau. The eastern and northeastern Tibetan Plateau alpine meadow sites had larger carbon sinks than northern China grassland ecosystems mainly because the humid and cold climate resulted in the dramatically larger

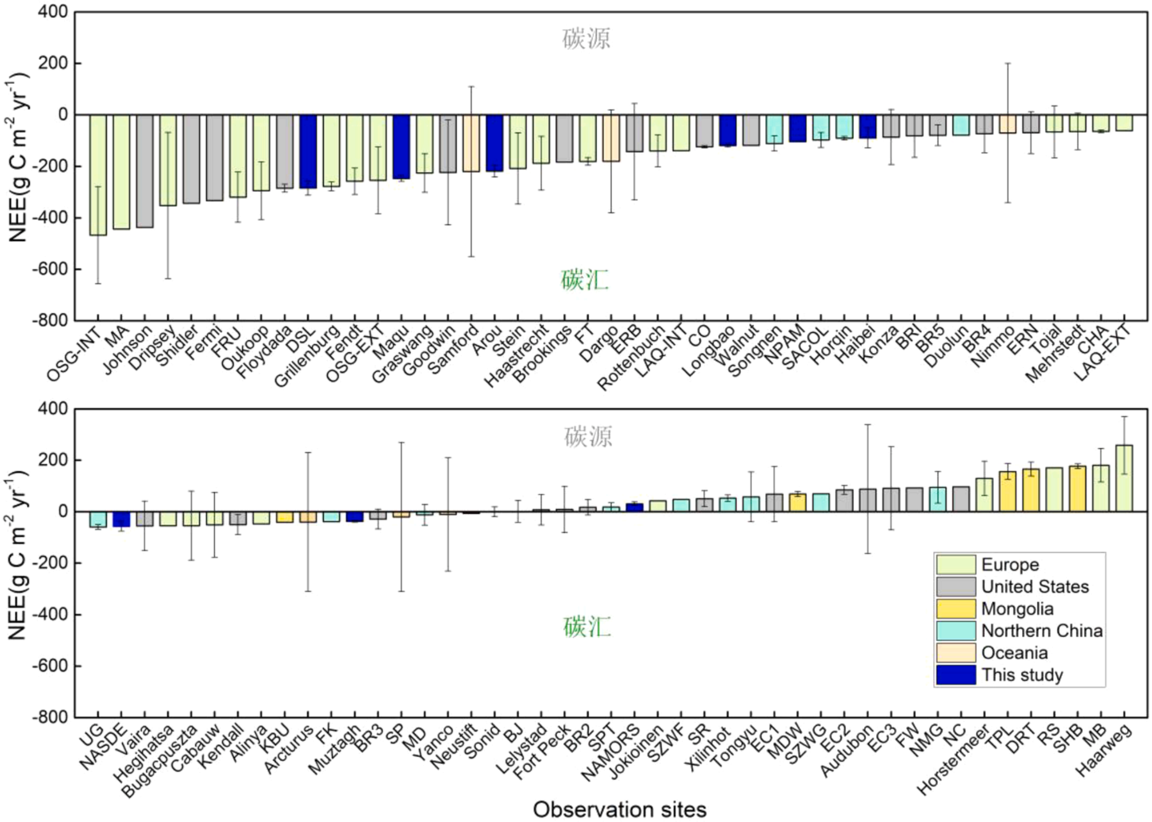

Fig. 9. Comparison of the mean (±SD) annual net ecosystem CO_2 exchange (NEE) with other grassland ecosystems around the typical regions around the world. The negative and positive NEE values indicated net uptake and release of CO_2.

photosynthetic production and relatively smaller ecosystem respiration (Sun et al., 2019; Wang et al., 2020). The grasslands of northern China, especially the temperate steppe and desert steppe, were located in semi-arid or arid regions, where insufficient water supply during the growing season limited GPP accumulation and the relatively high temperature and larger amount of surface litter fall might lead to higher respiration, ultimately resulting in a smaller net carbon uptake (Fu et al., 2009; Gao et al., 2012; Hao et al., 2018). Among our sites, only BJ and

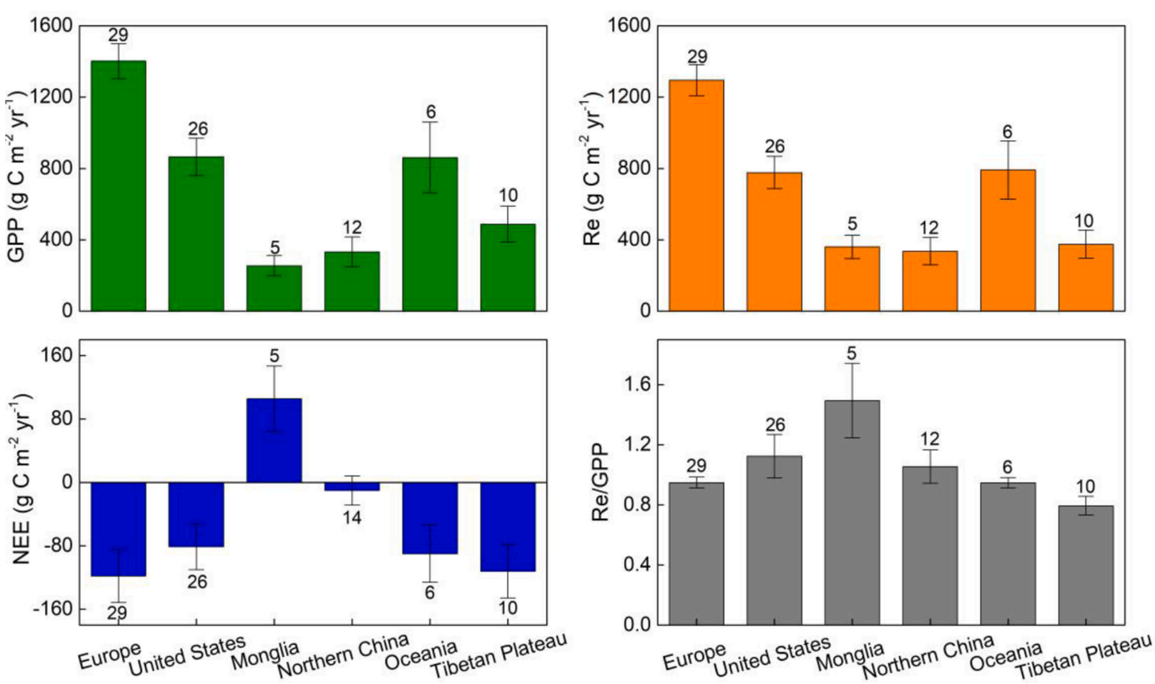

Fig. 10. Comparison of the annual gross primary productivity (GPP), ecosystem respiration (Re), net ecosystem CO_2 exchange (NEE) and Re/GPP among different regions. For each region, the carbon fluxes were averaged for all the sites within the region. The carbon flux data for each site are illustrated in Fig. 9. The numbers on the bars stand for the number of sites. The error bars stand for the standard errors.

NAMORS exhibited carbon sources, and NAMORS had the largest carbon release capacity, which was close to that of the desert steppe of northern China (Wang et al., 2008) but much smaller than that of the Mongolian steppe sites (Shao et al., 2017).

Additionally, we compared the annual carbon fluxes and carbon use efficiency (Re/GPP) averaged for all sites in this study with averages for the other regions around the world based on the sites of Fig. 9 (Fig. 10). The results indicated that the regional averaged annual GPP and Re of the Tibetan Plateau were significantly lower than those of Europe and United States but slightly higher than those of Northern China and Mongolia. Despite its smaller GPP, the Tibetan Plateau had the lowest Re and thus its NEE was even equivalent to that of Europe and the United States. The average elevation of the Tibetan Plateau is more than 4000 m, and the low temperature and semi-arid environment limited the respiration of the grassland ecosystems, leading to the substantially lower Re than other regions (Saito et al., 2009; Chen et al., 2019).

Furthermore, we also compared the carbon fluxes data in this study with the data from satellite and models. The result showed that MODIS GPP coincided with the eddy observation data (Fig. A1), but it was systematically underestimated in high vegetation productivity sites and overestimated in low vegetation productivity sites; there was no MODIS GPP data in the alpine desert steppe sites with sparse vegetation. This indicated the poor ability of MODIS GPP data in dryland areas, which was also confirmed by previous studies (Biederman et al., 2017). We also compared the annual GPP derived from the modified Vegetation Photosynthesis Model (VPM) (He et al., 2014), Biome-BGC Model (You et al., 2019) and P-model (Ren et al., 2021) with in-situ measured annual GPP, and the results suggested that except for the absence of data at the alpine desert steppe sites, the modeling results reasonably predicted spatial patterns of the annual GPP. Besides, compared with GPP, the model simulated NEE and Re had slightly larger errors compared with the measured data in this study (Ge et al., 2018; Guo et al., 2021; You et al., 2020), but they basically captured the spatial distribution patterns. Meanwhile, some studies indicated that the spatial patterns of the upscaled modeling NEE were not in agreement with the in-situ observations and that there were large errors in simulated NEE (Ichii et al., 2017). This is likely because the inadequacy of explanatory variables in the predictor sets could lead to large uncertainty in NEE (Jung et al., 2011; Xiao et al. 2011, 2014; Tramontana et al., 2016).

4.3. Environmental controls on the spatial patterns of annual carbon fluxes on the Tibetan Plateau

The regional climate of the Tibetan Plateau is characterized by complex zonal changes, not only in latitudinal and longitudinal directions but also in elevational direction (Kuang and Jiao, 2016), and these spatial gradients in climate to some extent shaped the spatial patterns of carbon fluxes. Our results showed that surface soil moisture was the dominant driver for the spatial variations of NEE. SWC, VPD, and R_d explained 48%, 31% and 29% of the variations in NEE, respectively, but explained lower variance in GPP and Re. Moreover, the previous model-based study also confirmed that the distribution pattern of soil moisture and carbon fluxes were generally consistent with each other, and therefore the carbon fluxes were larger in the alpine meadow areas with higher surface soil moisture in the eastern part of the plateau and lower in the alpine grassland areas with low surface soil moisture in the western plateau (You et al., 2020). The distribution patterns of these environmental factors largely determined the distribution patterns of carbon fluxes on the Tibetan Plateau. At regional scales, mean annual temperature and mean annual precipitation were reported to be the dominant factors controlling the spatial variability in annual carbon fluxes of grassland ecosystems by previous synthesis studies, for example, in the United States (Wagle et al., 2015), the Europe (Gilmanov et al., 2007) and the China (Yu et al., 2013). However, the dominant roles of mean annual temperature and mean annual precipitation on the spatial patterns of carbon fluxes were not found for the Tibetan Plateau in this study. In general, precipitation dominates the distribution pattern of alpine grassland vegetation on the Tibetan Plateau: alpine meadows are distributed in the East and Southeast with abundant precipitation, while alpine steppes are distributed in the West with low precipitation (Miehe et al., 2019). However, the spatial patterns of carbon fluxes were weakly correlated with precipitation. This is likely because some portion of precipitation is lost to runoff and drainage due to the influence of local soil characteristics and is unavailable to ecosystems (Zhu et al., 2015; Biederman et al., 2017). The grassland ecosystems in this study were all distributed in the alpine region with little difference in mean annual temperature among most sites, and therefore the spatial distribution of carbon fluxes was insensitive to mean annual temperature. The weak relationships between carbon fluxes and mean annual temperature were also found in other arid regions (Biederman et al., 2017; Wang et al., 2019), and the spatial pattern of carbon fluxes of the ecosystems tended to be determined by water availability rather than temperature in this water-limited region. The Tibetan Plateau also belongs to arid and semi-arid regions. Besides, VPD reflects the dryness of the atmosphere and can influence plant photosynthesis and transpiration through affecting the closure of plant stomata; atmospheric dryness and high radiation intensity limited plant photosynthesis and hence influenced the spatial distribution of carbon fluxes (Ding et al., 2018).

Additionally, our results showed that annual mean GPP, Re and NEE of the ecosystems on the Tibetan Plateau presented large spatial gradients from east to west and generally declined with decreasing longitude (Fig. 7). In contrast, the annual carbon fluxes were weakly correlated with latitude on the Tibetan Plateau, which was not consistent with previous studies for other geographical regions (Chen et al., 2015; Valentini et al., 2000). For example, annual carbon fluxes of major terrestrial ecosystems in China showed clear latitudinal patterns and increased linearly with decreasing latitude (Xiao et al., 2013; Yu et al., 2013). Besides, a clear latitudinal trend in net carbon uptake was found in the European forests, although GPP showed independence of latitude (Valentini et al., 2000). Latitude or longitude per se is not the variable which drives the spatial distribution of carbon fluxes, and the climatic factors that depend on longitude or latitude instead determine the spatial distribution of carbon fluxes (Valentini et al., 2000). This was also confirmed in our study, that is, the complex longitudinal distribution of climatic factors on the Tibetan Plateau resulted in the complex distribution of GPP, Re, and NEE, leading to the clear longitudinal variability in carbon fluxes (Fig. 11). The weak relationship between latitude and the annual carbon fluxes of the alpine grasslands on the Tibetan Plateau was probably related to the narrow latitude range of the observation sites. In addition to the longitudinal pattern, the annual carbon fluxes of these alpine grassland ecosystems also displayed an elevational pattern, suggesting that the alpine grasslands in higher altitude regions tend to have lower GPP, Re and carbon sequestration capacity. Undoubtedly, the elevational pattern of carbon fluxes is inextricably linked to the elevation-dependence of the climatic variables that dominate their variability. On the Tibetan Plateau, as elevation increases, surface soil moisture decreases, and solar radiation and atmospheric dryness increase (Yang et al., 2014; Yao et al., 2019), GPP, Re, and net carbon uptake of alpine grassland ecosystems generally decrease.

5. Conclusions

We analyzed the magnitude and spatial patterns of carbon fluxes and environmental controls for 10 alpine grassland ecosystems across the Tibetan Plateau. We found that in the mesic eastern and central parts of the plateau, temperature was often the limiting factors of carbon uptake during the growing season, while at xeric sites in the western plateau, surface soil moisture was often the controlling factor during the growing season. The alpine meadow ecosystems had strong carbon sink capacity (about 200–300 g C m^{-2} y^{-1}) in the northeastern and eastern part of the plateau. Annual carbon fluxes exhibited primarily a longitudinal pattern

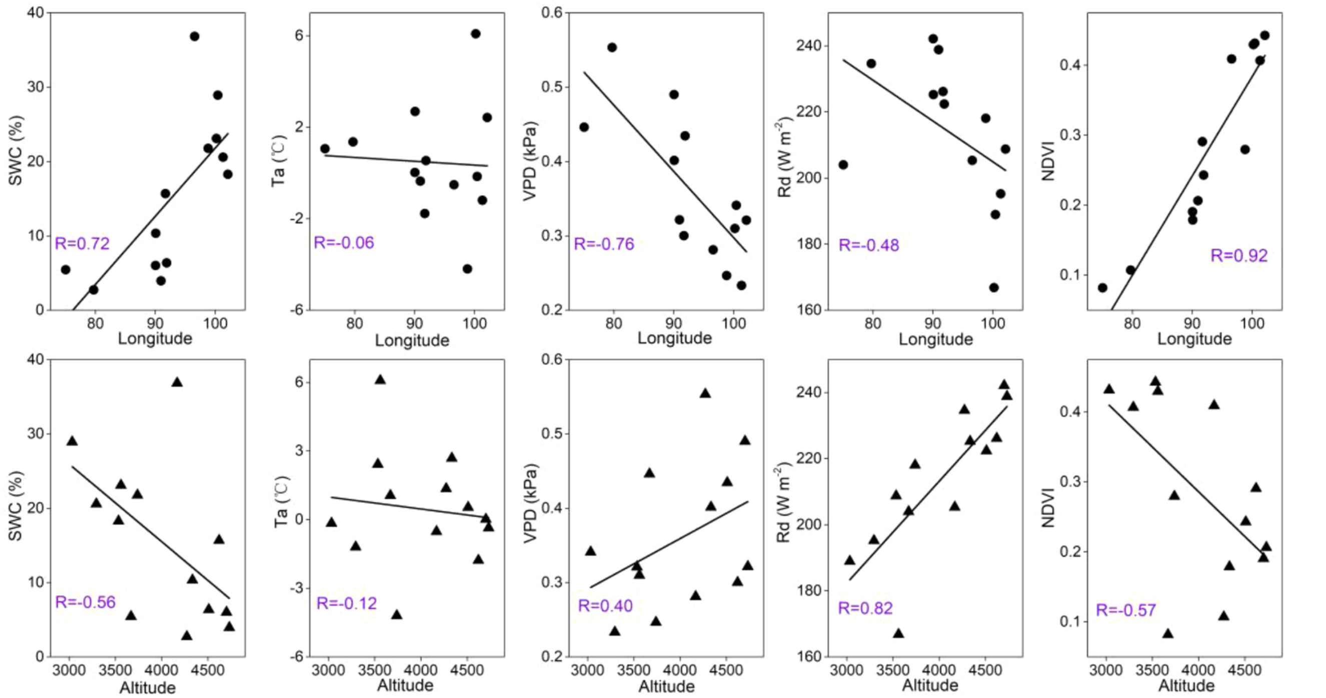

Fig. 11. The relationships between longitude, altitude and the annual mean soil water content (SWC, %), air temperature (T_a,°C), vapor pressure deficit (VPD, kPa), down short radiation (R_d, W m^{-2}), and monthly maximum normalized difference vegetation index (NDVI) for different alpine grassland ecosystems in the Tibetan Plateau.

and secondly an elevational pattern. The annual GPP, Re and the carbon sink capacity all linearly increased with the increasing longitude from west to east but linearly decreased with elevation. Additionally, on a regional scale, SWC, VPD and R_d had marked impacts on carbon fluxes, and the sites with low mean daily SWC and high mean daily VPD and R_d tended to have low carbon flux components. With the increase of alpine grassland flux observation sites and the further integration of data, future studies are anticipated to further improve our understanding of the spatial patterns of carbon fluxes in the alpine grassland ecosystems of the Tibetan Plateau in the context of climate change.

Declaration of Competing Interest

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

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References

Adams, J.M., Faure, H., Fauredenard, L., McGlade, J.M., Woodward, F.I., 1990. Increases in terrestrial carbon storage from the last glacial maximum to the present. Nature 348 (6303), 711–714.

Ahlstrom, A., Raupach, M.R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Zeng, N., 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink. Science 348 (6237), 895–899.

Ammann, C., Flechard, C.R., Leifeld, J., Neftel, A., Fuhrer, J., 2007. The carbon budget of newly established temperate grassland depends on management intensity. Agric. Ecosyst. Environ. 121 (1-2), 5–20.

Biederman, J.A., Scott, R.L., Bell, T.W., Bowling, D.R., Dore, S., Garatuza-Payan, J., Goulden, ML., 2017. CO2 exchange and evapotranspiration across dryland ecosystems of southwestern North America. Glob. Change Biol. 23 (10), 4204–4221.

Chen, Z., Yu, G., Ge, J., 2013. Temperature and precipitation control of the spatial variation of terrestrial ecosystem carbon exchange in the Asian region. Agr. Forest. Meteorol. 182-183, 266–276.

Chen, Z., Yu, G., Wang, Q., 2019. Magnitude, pattern and controls of carbon flux and carbon use efficiency in China's typical forests. Glob. Planet. Change 172, 464–473.

Ding, J., Chen, L., Ji, C., Hugelius, G., Li, Y., Liu, L., Yang, Y., 2017. Decadal soil carbon accumulation across Tibetan permafrost regions. Nat. Geosci. 10 (6), 420–424.

Ding, J., Yang, T., Zhao, Y., Liu, D., Wang, X., Yao, Y., Piao, S., 2018. Increasingly important role of atmospheric aridity on Tibetan Alpine Grasslands. Geophys. Res. Lett. 45 (6), 2852–2859.

Fu, Y., Zheng, Z., Yu, G., Hu, Z., Sun, X., Shi, P., Wang, Y., Zhao, X., 2009. Environmental influences on carbon dioxide fluxes over three grassland ecosystems in China. Biogeosciences 6 (12), 2879–2893.

Gao, Y., Li, X., Liu, L., Jia, R., Yang, H., Li, G., Wei, Y., 2012. Seasonal variation of carbon exchange from a revegetation area in a Chinese desert. Agric. For. Meteorol. 156, 134–142.

Ge, R., He, H., Ren, X., Zhang, L., Li, P., Du, M., 2018. A satellite-based model for simulating ecosystem respiration in the Tibetan and Inner Mongolian Grasslands. Remote Sens. 10 (1), 1–20.

Gilmanov, T.G., Soussana, J.F., Aires, L., Allard, V., Ammann, C., Balzarolo, M., Wohlfahrt, G., 2007. Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. Agric. Ecosyst. Environ. 121 (1-2), 93–120.

Gilmanov, T.G., Verma, S.B., Sims, P.L., Meyers, T.P., Bradford, J.A., Burba, G.G., Suyker, A.E., 2003. Gross primary production and light response parameters of four Southern Plains ecosystems estimated using long-term CO_2-flux tower measurements. Glob. Biogeochem. Cycles 17 (2).

Guo, D., Song, X., Hu, R., Zhu, X., Jiang, Y., Cui, X., 2021. Large-Scale Analysis of the Spatiotemporal Changes of Net Ecosystem Production in Hindu Kush Himalayan Region. Remote Sens. 13, 1180.

Han, L., Wang, Q.F., Chen, Z., Yu, G.R., Zhou, G.S., Chen, S.P., Guo, J.X., 2020. Spatial patterns and climate controls of seasonal variations in carbon fluxes in China's terrestrial ecosystems. Glob. Planet. Change 189.

Hao, Y., Wang, Y., Mei, X., Huang, X., Cui, X., Zhou, X., Niu, H., 2008. CO_2, H_2O and energy exchange of an Inner Mongolia steppe ecosystem during a dry and wet year. Acta Oecol. 33 (2), 133–143.

Hao, Y., Zhang, H., Biederman, J.A., Li, L., Cui, X., Xue, K., Wang, Y., 2018. Seasonal timing regulates extreme drought impacts on CO2 and H2O exchanges over semiarid steppes in Inner Mongolia, China. Agric. Ecosyst. Environ. 266, 153–166.

He, H., Liu, M., Xiao, X., Ren, X., Zhang, L., Yu, G., 2014. Large-scale estimation and uncertainty analysis of gross primary production in Tibetan alpine grasslands. J. Geophys. Res. 119 (3), 466–486.

Hirata, R., Saigusa, N., Yamamoto, S., Ohtani, Y., Ide, R., Asanuma, J., Wang, H., 2008. Spatial distribution of carbon balance in forest ecosystems across East Asia. Agric. For. Meteorol. 148 (5), 761–775.

Hopping, K.A., Knapp, A.K., Dorji, T., Klein, J.A., 2018. Warming and land use change concurrently erode ecosystem services in Tibet. Global Change Biol. 24 (11), 5534–5548.

Ichii, K., Ueyama, M., Kondo, M., Saigusa, N., Zhao, F., 2017. New data-driven estimation of terrestrial CO2 fluxes in Asia using a standardized database of eddy covariance measurements, remote sensing data, and support vector regression. J. Geophys. Res. 122 (4), 767–795.

Jacobs, C.M.J., Jacobs, A.F.G., Bosveld, F.C., Hendriks, D.M.D., Hensen, A., Kroon, P.S., Veenendaal, E.M., 2007. Variability of annual CO_2 exchange from Dutch grasslands. Biogeosciences 4, 803–816.

Jing, Y., Wang, A., Guan, D., Wu, J., Yuan, F., Jin, C., 2014. Carbon dioxide fluxes over a temperate meadow in eastern Inner Mongolia, China. Environ. Earth Sci. 72 (11), 4401–4411.

Jung, M., Reichstein, M., Margolis, H., Cescatti, A., Richardson, A., Williams, C., 2011. Global patterns of land-atmosphere fluxes of carbon dioxide,latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. J. Geophys. Res. 116, G00J07.

Kato, T., Tang, Y., 2008. Spatial variability and major controlling factors of CO_2 sink strength in Asian terrestrial ecosystems: evidence from eddy covariance data. Glob. Change Biol. 14, 2333–2348.

Kato, T., Tang, Y., Gu, S., Hirota, M., Du, M., Li, Y., Zhao, X., 2006. Temperature and biomass influences on interannual changes in CO_2 exchange in an alpine meadow on the Qinghai-Tibetan Plateau. Glob. Change Biol. 12 (7), 1285–1298.

Kuang, X., Jiao, J.J., 2016. Review on climate change on the Tibetan Plateau during the last half century. J. Geophys. Res. 121 (8), 3979–4007.

Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland, G., Bopp, L., Ciais, P., Woodward, F.I., 2009. Trends in the sources and sinks of carbon dioxide. Nat. Geosci. 2 (12), 831–836.

Li, H., Zhu, J., Zhang, F., He, H., Yang, Y., Li, Y., Zhou, H., 2019. Growth stage-dependant variability in water vapor and CO_2 exchanges over a humid alpine shrubland on the northeastern Qinghai-Tibetan Plateau. Agric. For. Meteorol. 268, 55–62.

Liang, W., Lü, Y., Zhang, W., Li, S., Jin, Z., Ciais, P., Su, H., 2017. Grassland gross carbon dioxide uptake based on an improved model tree ensemble approach considering human interventions: global estimation and covariation with climate. Glob. Change Biol. 23 (7), 2720–2742.

Li, P., Zhu, D., Wang, Y., Liu, D., 2020. Elevation Dependence of Drought Legacy Effects On Vegetation Greenness Over the Tibetan Plateau. Agricultural and Forest Meteorology, p. 295.

Liu, S.M., Xu, Z.W., Wang, W.Z., Jia, Z.Z., Zhu, M.J., Bai, J., Wang, J.M., 2011. A comparison of eddy-covariance and large aperture scintillometer measurements with respect to the energy balance closure problem. Hydrol. Earth Syst. Sci. 15 (4), 1291–1306.

Liu, S., Zamanian, K., Schleuss, P.-M., Zarebanadkouki, M., Kuzyakov, Y., 2018. Degradation of Tibetan grasslands: Consequences for carbon and nutrient cycles. Agric. Ecosyst. Environ. 252, 93–104.

López-Blanco, E., Lund, M., Williams, M., Tamstorf, M.P., Westergaard-Nielsen, A., Exbrayat, J.-F., Christensen, T.R., 2017. Exchange of CO_2 in Arctic tundra: impacts of meteorological variations and biological disturbance. Biogeosciences 14 (19), 4467–4483.

Marchin, R.M., McHugh, I., Simpson, R.R., Ingram, L.J., Balas, D.S., Evans, B.J., Adams, M.A., 2018. Productivity of an Australian mountain grassland is limited by temperature and dryness despite long growing seasons. Agric. For. Meteorol. 256-257, 116–124.

Peichl, Matthias, L, P., Gerard, K, 2010. Six-year stable annual of carbon dioxide managed humid temperate grassland. Ecosystems 14, 112–126.

Mevik, B.H., Wehrens, R., 2007. The pls package: principal component and partial least squares regression in R. J. Stat. Softw. 18, 1–23.

Miehe, G., Schleuss, P.M., Seeber, E., Babel, W., Biermann, T., Braendle, M., Wesche, K., 2019. The Kobresia pygmaea ecosystem of the Tibetan highlands - Origin, functioning and degradation of the world's largest pastoral alpine ecosystem: Kobresia pastures of Tibet. Sci. Total Environ. 648, 754–771.

Niu, B., He, Y., Zhang, X., Du, M., Shi, P., Sun, W., Zhang, L., 2017. CO_2 Exchange in an Alpine Swamp Meadow on the Central Tibetan Plateau. Wetlands 37 (3), 525–543.

Ponce Campos, G.E., Moran, M.S., Huete, A., Zhang, Y., Bresloff, C., Huxman, T.E., Starks, P.J., 2013. Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature 494 (7437), 349–352.

Qi, Y., Wei, D., Zhao, H., Wang, X., 2021. Carbon Sink of a Very High Marshland on the Tibetan Plateau. J. Geophys. Res. 126 (4) e2020JG006235.

Qiu, J., 2008. The third pole. Nature 454 (7203), 393–396.

Qu, L., Chen, J., Dong, G., Jiang, S., Li, L., Guo, J., Shao, C., 2016. Heat waves reduce ecosystem carbon sink strength in a Eurasian meadow steppe. Environ. Res. 144, 39–48.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Valentini, R., 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob. Change Biol. 11 (9), 1424–1439.

Ren, Y., Yang, K., Wang, H., Zhao, L., Zhu, La, 2021. The South Asia Monsoon Break Promotes Grass Growth on the Tibetan Plateau. J. Geophys. Res.-Biogeosci. 126 (3) e2020JG005951.

Saito, M., Kato, T., Tang, Y., 2009. Temperature controls ecosystem CO_2exchange of an alpine meadow on the northeastern Tibetan Plateau. Global Change Biol. 15 (1), 221–228.

Shang, L., Zhang, Y., Lyu, S., Wang, S., 2016. Seasonal and inter-annual variations in carbon dioxide exchange over an Alpine Grassland in the Eastern Qinghai-Tibetan Plateau. PLoS One 11 (11), e0166837.

Shao, C., Chen, J., Li, L., 2013. Grazing alters the biophysical regulation of carbon fluxes in a desert steppe. Environ. Res. Lett. 8 (2), 025012.

Shao, C., Chen, J., Chu, H., Lafortezza, R., Dong, G., Abraha, M., Qi, J., 2017. Grassland productivity and carbon sequestration in Mongolian grasslands: The underlying mechanisms and nomadic implications. Environ. Res. 159, 124–134.

Sharma, S., Rajan, N., Cui, S., Maas, S., Casey, K., Ale, S., Jessup, R., 2019. Carbon and Evapotranspiration Dynamics of a Non-Native Perennial Grass With Biofuel Potential in the Southern U.S. Great Plains, 269-270. Agricultural and Forest Meteorology, pp. 285–293.

Song, C., Wang, G., Hu, Z., Zhang, T., Huang, K., Li, Y., 2020. Net ecosystem carbon budget of a grassland ecosystem in central Qinghai-Tibet Plateau: integrating terrestrial and aquatic carbon fluxes at catchment scale. Agric. For. Meteorol. 290, 108021.

Shevliakova, E., Stouffer, R.J., Malyshev, S., Krasting, J.P., Hurtt, G.C., Pacala, S.W., 2013. Historical warming reduced due to enhanced land carbon uptake. Proc. Thal. Acad. Sci. U. S. A. 110 (42), 16730–16735.

Sun, S., Che, T., Li, H., Wang, T., Ma, C., Liu, B., Song, Z., 2019. Water and carbon dioxide exchange of an alpine meadow ecosystem in the northeastern Tibetan Plateau is energy-limited. Agric. For. Meteorol. 275, 283–295.

Sun, S., Che, T., Li, H., Gentine, P., Chen, Q., Song, Z., 2021. Shallow groundwater inhibits soil respiration and favors carbon uptake in a wet alpine meadow ecosystem. Agric. For. Meteorol. 297, 108254.

Tramontana, G., Jung, M., Schwalm, C., Ichii, K., Camps-Valls, G., Papale, D., 2016. Predicting carbon dioxide and energy fluxes across global FLUXNET sites with regression algorithms. Biogeosciences 13, 4291–4313.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, EJ., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404 (6780), 861–865.

van der Molen, M., Dolmana, A., Ciais, P., Eglinc, T., Gobron, N., Wang, G., 2011. Drought and ecosystem carbon cycling. Agric. For. Meteorol. 151 (7), 765–773.

Wagle, P., Gowda, P.H., Billesbach, D.P., Northup, B.K., Torn, M.S., Neel, J.P.S., Biraud, S.C., 2020. Dynamics of CO_2 and H_2O Fluxes in Johnson grass in the U.S. Southern Great Plains, 739. Science of the Total Environment, 140077.

Wagle, P., Xiao, X., Scott, R.L., Kolb, T.E., Cook, D.R., Brunsell, N., Bajgain, R., 2015. Biophysical controls on carbon and water vapor fluxes across a grassland climatic gradient in the United States. Agric. For. Meteorol. 214-215, 293–305.

Wang, H., Li, X., Xiao, J., 2019. Carbon fluxes across alpine, oasis, and desert ecosystems in northwestern China: The importance ofwater availability. Sci. Total. Environ. 697, 133978.

Wang, L., Liu, H., Shao, Y., Liu, Y., Sun, J., 2016. Water and CO_2 fluxes over semiarid alpine steppe and humid alpine meadow ecosystems on the Tibetan Plateau. Theor. Appl. Climatol. 131 (1-2), 547–556.

Wang, L., Liu, H., Song, J.H., Shao, Y.P., 2017. Biophysical effects on the interannual variation in carbon dioxide exchange of an alpine meadow on the Tibetan Plateau. Atmos. Chem. Phys. 17, 5119–5129.

Wang, Y., Zhou, G., Wang, Y., 2008. Environmental effects on net ecosystem CO_2 exchange at half-hour and month scales over Stipa krylovii steppe in northern China. Agric. For. Meteorol. 148 (5), 714–722.

Wang, Y.H., Chen, J.Q., Zhou, G.S., Shao, C.L., Chen, J., Wang, Y., Song, J.M., 2018. Predominance of precipitation event controls ecosystem CO2 exchange in an Inner Mongolian desert grassland, China. J. Clean. Prod. 197, 781–793.

Wang, Y., Zhu, Z., Ma, Y., Yuan, L., 2020. Carbon and water fluxes in an alpine steppe ecosystem in the Nam Co area of the Tibetan Plateau during two years with contrasting amounts of precipitation. Int. J. Biometeorol. 64 (7), 1183–1196.

Wold, S., Ruhe, A., Wold, H., Dunn, W.J.I, 1984. The collinearity problem in linear regression. The partial least squares (PLS) approach to generalized inverses. SIAM J. Sci. Stat. Comput. 5 (3), 735–743.

Wu, X.C., Li, X.Y., Chen, Y.H., Bai, Y., Tong, Y.Q., Wang, P., Shi, C.M., 2019. Atmospheric water demand dominates daily variations in water use efficiency in Alpine Meadows, Northeastern Tibetan Plateau. J. Geophys. Res.-Biogeosci. 12 (7), 2174–2185.

Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Šigut, L., Reichstein, M., 2018. Basic and extensible post-processing of eddy covariance flux data with REddyProc. Biogeosciences 15 (16), 5015–5030.

Xiao, J., Sun, G., Chen, J., Chen, H., Chen, S., Dong, G., Zhou, J., 2013. Carbon fluxes, evapotranspiration, and water use efficiency of terrestrial ecosystems in China. Agric. For. Meteorol. 182-183, 76–90.

Xiao, J., Chevallier, F., Gomez, C., Guanter, L., Hicke, J.A., Huete, A.R., Ichii, K., Ni, W., Pang, Y., Rahman, A.F., Sun, G., Yuan, W., Zhang, L., Zhang, X., 2019. Remote sensing of the terrestrial carbon cycle: A review of advances over 50 years. Remote Sens. Environ. 233, 111383.

Xiao, J.F., Zhuang, Q., Law, B.E., Baldocchi, D.D., Chen, J., Richardson, A.D., Melillo, J. M., Davis, K.J., Hollinger, D.Y., Wharton, S., Oren, R., Noormets, A., Fischer, M.L., Verma, S.B., Cook, D.R., Sun, G., McNulty, S., Wofsy, S.C., Bolstad, P.V., Burns, S.P., Curtis, P.S., Drake, B.G., Falk, M., Foster, D.R., Gu, L., Hadley, J.L., Katul, G.G., Litvak, M., Ma, S., Martin, T.A., Matamala, R., Meyers, T.P., Monson, R.K., Munger, J.W., Oechel, W.C., Paw U, K.T., Schmid, H.P., Scott, R.L., Starr, G., Suyker, A.E., Torn, M.S, 2011. Assessing net ecosystem carbon exchange of U.S. terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations. In: Agric. For. Meteorol., 151, pp. 60–69.

Xiao, J.F., Ollinger, S.V., Frolking, S., Hurtt, G.C., Hollinger, D.Y., Davis, K.J., Pan, Y., Zhang, X., Deng, F., Chen, J., Baldocchi, D.D., Law, B.E., Arain, M.A., Desai, A.R., Richardson, A.D., Sun, G., Amiro, B., Margolis, H., Gu, L, Scott, R.L., Blanken, P.D.,

Suyker, A.E., 2014. Data-driven diagnostics of terrestrial carbon dynamics over North America. Agric. For. Meteorol. 197, 142–157.
Yang, F., Zhou, G., Hunt, J.E., Zhang, F., 2011. Biophysical regulation of net ecosystem carbon dioxide exchange over a temperate desert steppe in Inner Mongolia, China. Agricul. Ecosyst. Environ. 142 (3-4), 318–328.
Yang, K., Wu, H., Qin, J., Lin, C.G., Tang, W.J., Chen, Y.Y, 2014. Recent climate changes over the Tibetan Plateau and their impacts on energy and water cycle: A review. Global Planet. Change 112, 79–91.
Yao, T., Xue, Y., Chen, D., Chen, F., Thompson, L., Cui, P., Li, Q., 2019. Recent third pole's rapid warming accompanies cryospheric melt and water cycle intensification and interactions between monsoon and environment: multidisciplinary approach with observations, modeling, and analysis. Bull. Am. Meteorol. Soc. 100 (3), 423–444.
You, Y., Wang, S., Ma, Y., Wang, X., Liu, W., 2019. Improved modeling of gross primary productivity of Alpine grasslands on the Tibetan Plateau using the biome-BGC model. Remote Sens. 11 (11), 1287.
You, Y., Wang, S., Pan, N., Ma, Y., Liu, W., 2020. Growth stage-dependent responses of carbon fixation process of alpine grasslands to climate change over the Tibetan Plateau, China. Agric. For. Meteorol. 291, 108085.
Yu, G.R., Zhu, X.J., Fu, Y.L., He, H.L., Wang, Q.F., Wen, X.F., Tong, C.L., 2013. Spatial patterns and climate drivers of carbon fluxes in terrestrial ecosystems of China. Glob. Change Biol. 19 (3), 798–810.
Zeeman, M.J., Hiller, R., Gilgen, A.K., Michna, P., Plüss, P., Buchmann, N., Eugster, W., 2010. Management and climate impacts on net CO_2 fluxes and carbon budgets of three grasslands along an elevational gradient in Switzerland. Agric. For. Meteorol. 150 (4), 519–530.
Zhang, T., Zhang, Y., Xu, M., Zhu, J., Chen, N., Jiang, Y., Yu, G., 2018. Water availability is more important than temperature in driving the carbon fluxes of an Alpine Meadow on the Tibetan Plateau. In: Agric. For. Meteorol., 256-257, pp. 22–31.
Zhu, Z., Ma, Y., Li, M., Hu, Z., Xu, C., Zhang, L., Ichiro, T., 2015. Carbon dioxide exchange between an alpine steppe ecosystem and the atmosphere on the Nam Co area of the Tibetan Plateau. Agric. For. Meteorol. 203, 169–179.