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EDITED BY
Zhongqing Yan,
Chinese Academy of Forestry, China

REVIEWED BY
Qinghai Song,
Xishuangbanna Tropical Botanical Garden (CAS), China
Bing Song,
Ludong University, China
Xiaodong Zhang,
Chinese Academy of Forestry, China

*CORRESPONDENCE
Li Zhou
✉ zhouli@cma.gov.cn
Guangsheng Zhou
✉ zhougs@cma.gov.cn

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Hydrometeorological controls on net carbon dioxide exchange over a temperate desert steppe in Inner Mongolia, China

Jiaxin Song[1], Li Zhou[2,3]*, Guangsheng Zhou[2,3]*, Yu Wang[4], Sen Zhang[1] and Yujie Yan[1]

[1]School of Geo-Science and Technology, Zhengzhou University, Zhengzhou, China, [2]State Key Laboratory of Severe Weather, Chinese Academy of Meteorological Sciences, Beijing, China, [3]Joint Laboratory of Eco-Meteorology, Chinese Academy of Meteorological Sciences, Zhengzhou University, Zhengzhou, China, [4]College of Horticulture and Plant Protection, Henan University of Science and Technology, Luoyang, China

Understanding the effect of environmental factors on the net ecosystem CO_2 exchange (NEE) and the response of NEE to rainfall events is of great significance for an accurate understanding of the carbon cycle for desert steppe ecosystems. Based on the long-term (2011–2018) eddy covariance flux data of a temperate desert steppe in Inner Mongolia, China, this study used path analysis to analyze the combined impact of the environmental factors on NEE. The results showed that during the growing season, vapor pressure deficit (VPD) and soil water content (SWC) was the most prominent environmental factor for the daytime NEE and nighttime NEE, respectively. NEE responds differently to individual environmental factors among multi-year climatic conditions. The size of rainfall event has significant impacts on NEE, it can effectively promote the CO_2 uptake of the desert steppe ecosystem when rainfall event size is greater than 5mm, and the NEE response increased with the rainfall event size. Moreover, NEE peaked approximately 1–3 days after a 5–10mm rainfall event, while the rainfall event size >10mm, it would take 3–5 days for NEE to reach a peak value; and yet, small rainfall events (< 5mm) slightly increased CO_2 emissions. During the growing season, carbon uptake increased with monthly rainfall, except in May. Our results are important for understanding the carbon cycle and its control mechanisms in the temperate desert steppe of Inner Mongolia.

KEYWORDS

desert steppe, net ecosystem CO_2 exchange, rainfall events, eddy covariance, environmental controls

1. Introduction

Over half of the carbon emitted by human activities is absorbed through nature's carbon cycle, which has become one of the core problems of global change research (Gong et al., 2018; Zhou et al., 2020). Arid and semi-arid regions account for approximately 30% of the global carbon sequestration (Adams et al., 1990; Chen et al., 2021), and the ecosystems in these regions are highly sensitive to climate change because of low precipitation, strong sunlight, and high evaporation rates (Gu et al., 2018). Previous studies have revealed that climate change causes changes in meteorological and other environmental factors that affect both ecosystem photosynthesis and respiration and, as a result, the ecosystem carbon balance (Li et al., 2015; Nyantakyi-Frimpong and Bezner-Kerr, 2015). Grassland is the dominant ecosystem type in arid and semi-arid areas, covering approximately one-third of the global natural vegetation (Parton et al., 1995). Among terrestrial ecosystems, grasslands have a large carbon storage capacity, second only to forest ecosystems, and are critical to the global carbon balance (Yang and Zhou, 2013; Li et al., 2021).

Carbon flux is regulated by both environmental and biological factors, and the study of its driving factors has been a major research topic regarding the global carbon cycle, particularly under the premise of climate change (Fang et al., 2018). Water availability is the primary driver of plant growth (Zhang et al., 2020), and previous studies have shown that carbon flux over grassland ecosystems is closely related to the vapor pressure deficit (VPD) and soil moisture (Chen et al., 2018). In semi-arid grassland ecosystems, high carbon uptake usually occurs under humid conditions, whereas high carbon release is associated with warm and dry conditions (Ahlström et al., 2015). Meanwhile, it was proposed that the effects of environmental factors on NEE might differ among different climatic years, and the variation of NEE may even have different dominant factors for different climatic years (Aguilos et al., 2018; Wang et al., 2019). However, to date, few such studies have been conducted on the desert steppe.

Desert steppe is water-limited, and the carbon cycle in grassland ecosystems is sensitive to changes in rainfall (Zhang et al., 2020). Precipitation occurs in the form of discrete, intermittent, and unpredictable pulse events (Rey et al., 2017), the size of a single rainfall event can have a large impact on grassland carbon flux (Huxman et al., 2004). A previous study showed that small-pulse rainfall events (e.g., 2.1 mm) slightly increased CO_2 emissions by stimulating microbial respiration, whereas large-pulse rainfall events (e.g., 19.7 mm) promoted CO_2 uptake by affecting plant photosynthesis (Schwinning et al., 2004; Fa et al., 2015). A study of a *Stipa* grassland in Inner Mongolia, China showed that the CO_2 uptake increased when the rainfall event size >10 mm (Peng et al., 2013), but another study of a *Leymus chinensis* grassland in Inner Mongolia showed that the CO_2 uptake increased when the rainfall event size >5 mm (Hao et al., 2017). This suggests that the size of effective rainfall event may vary among different climate and vegetation types.

Herein, this study aims to investigate the impact of environmental factors on the net ecosystem CO_2 exchange (NEE) and the response of NEE to rainfall events, based on eddy covariance flux data from 2011 to 2018 of a temperate desert steppe in Inner Mongolia, China. The long-term measurement campaign provided a broad range of conditions to thoroughly investigate the environmental regulations of NEE in the desert steppe ecosystem. The specific objectives are (1) to analyze the combined impact of the environmental factors on NEE, and compare the controlling factors of NEE between years with different climatic conditions; and (2) to determine the NEE response to rainfall events of different magnitudes.

2. Materials and methods

2.1. Site description

The research site is located in Damao Banner of Baotou city in Inner Mongolia (41°38.6′ N, 110°19.9′ E, 1409 m a.s.l.). Desert steppe vegetation covers the area including subregions with a temperate, continental, and semiarid climate. The Information and Research Institute of Meteorology, Hydrology, and Environment of Inner Mongolia reports that from 1990 to 2019, the site's mean annual air temperature was 5.22°C and its mean annual precipitation was 247.4 mm. Most of the rainfall occurs during the growing season (May–September). The vegetation is dominated by a degraded *Stipa klemenzii* community. The soil was brown and calcified, with a calcified layer at 20–50 cm. The total K, total P, and organic carbon contents are 23.29 $g\,kg^{-1}$, 0.31 $g\,kg^{-1}$, and 12.67 $g\,kg^{-1}$, respectively, and the average bulk density was 1.23 $g\,cm^{-3}$, with a pH of 7.4.

2.2. Fluxes and meteorological measurements

From 2011 to 2018, the turbulence fluxes were monitored at a height of 4 m using an open-path eddy covariance system. An infrared gas analyzer (Li-7500, LICOR, Inc., Lincoln, NE, United States) and a 3D sonic anemometer (CSAT-3, Campbell Scientific, Inc., Logan, UT, United States) were employed to calculate the variations in the densities of gaseous CO_2 and H_2O at 10 Hz and three wind speed components, respectively. The original data were recorded and stored automatically at 10 Hz and 0.5 h online flux data were provided by a datalogger (CR5000, Campbell Scientific Inc., Logan, UT, United States).

During the research project (2011–2018), a shielded sensor (model HMP45C, Vaisala, Helsinki, Finland) was used to measure the air temperature (Ta) and relative humidity (RH) at levels of 1.5 and 3.5 m. From Ta and RH, the VPD was computed. Precipitation was measured at a height of 1.2 m using a tipping-bucket rain gauge (model 52203, RM Young Inc., Traverse City, MI, United States). Using a quantum sensor, photosynthetically active radiation (PAR) was recorded (4 m; LI190SB, LI-COR, Lincoln, United States). The soil temperature sensor comprised a thermistor (107 L, Campbell Scientific Inc., Logan, UT, United States) (5, 10, 15, 20, 40, and 80 cm) that was used to measure soil temperature (Ts). The soil temperature recorded at a depth of 10 cm was used in this study, defined as Ts. The volumetric water content of the soil at depths of 10 cm (SWC10), 20 cm (SWC20), 30 cm (SWC30), and 40 cm (SWC40) were monitored using time-domain reflectometry probes (Easy AG; Campbell Scientific Inc., Logan, UT, United States). Data loggers (CR23X, Campbell Scientific Inc., Logan, UT, United States) were used to collect all data, and 30 min mean values were automatically recorded and stored.

2.3. Flux calculations and data processing

Eddy covariance data were processed by EddyPro7.0.6 (LI-COR), including double rotation, Webb–Pearman–Leuning correction, potential temporal lags correction, frequency response correction etc. (Webb et al., 1980; Moncrieff et al., 1997; Reichstein et al., 2005). In this study, positive NEE values denoted a source of atmospheric CO_2 at the location, whereas negative values denoted a carbon sink. During the observation period, the power supply may have been interrupted by abnormal weather or instruments. Half-hourly fluxes were filtered for: (1) incomplete measurements taken every half-hourly, (2) outliers,

(3) low turbulence situations, and (4) rain events (Papale et al., 2006). A cutoff friction velocity (u*) was employed, and nocturnal fluxes below the threshold were eliminated (Zhu et al., 2006). Subsequently, the gaps in the flux data were filled using a marginal distribution sampling (MDS) technique (Reichstein et al., 2005). The flux data for 2013 were not obtained because of instrument failure.

2.4. Characterization of rainfall events

Rainfall events can be described as discontinuous, highly varied, and usually comprise unpredictable pulses of rainfall (Li et al., 2013). The division of rainfall events is based on the absence of rainfall within 24 h after a certain rainfall time. Rainfall events were classified into six levels, according to their size (Table 1). Rainfall events of <10 mm were regarded as a small rainfall event, 10–25 mm as moderate rainfall event, and rainfall >25 mm as a heavy rainfall event.

Response of NEE to rainfall event ($NEE_{response}$) was determined as the difference between mean daily NEE post-event (NEE_{after}) and mean daily NEE pre-event (NEE_{before}) (Wang et al., 2017),

$$NEE_{response} = NEE_{after} - NEE_{before}$$

where, NEE is the daily NEE average (g C m^{-2} day^{-1}).

The relative response effect of NEE to rainfall event ($NEE_{response,\ r}$) was calculated as the following equation:

$$NEE_{response,r} = \left(NEE_{after} - NEE_{before}\right) / NEE_{before}$$

2.5. Path analysis

Earlier studies suggested that the combined effects of the various environmental factors should receive more attention because the independent effect of any one factor alone is insufficient to explain the variations in NEE (Wang et al., 2016). To examine the combined impact of the environmental factors on NEE, and the relative importance of these factors, the path analysis method was used in this study. Path analysis is an extension of multiple regression and can be used to understand the causal structure of data (Kozak and Kang, 2006). The path analysis method reveals the relationships between dependent and independent variables using the direct and indirect path coefficients as well as the determinative coefficient (Yuan et al., 2001; Jiang et al., 2014). Based on the determinative coefficient, the sequence of the synthetic action of every independent variable to the response variable can be decided, and which variable is the principal decision variable can be identified (Yuan et al., 2001). Path analysis were applied using IBM SPSS Statistics 26.0.

TABLE 1 The classification of rain events based on the size of rainfall.

Rainfall level	Rainfall
Level 1	< 1 mm
Level 2	1 ~ 3 mm
Level 3	3 ~ 5 mm
Level 4	5 ~ 10 mm
Level 5	10 ~ 25 mm
Level 6	> 25 mm

3. Results

3.1. Environmental conditions

Seasonal fluctuations in air temperature (Ta), soil temperature (Ts), precipitation (Prec), photosynthetically active radiation (PAR), vapor pressure deficit (VPD), and volumetric soil water content (SWC) are shown in Figure 1. During the measurement campaign (2011–2018), Ta and Ts showed similar seasonal dynamics with a single-peak curve (Figures 1A,D). The highest monthly mean Ta was 22.39°C, which typically occurs in July, and the lowest monthly mean Ta was −13.92°C, which was observed in January. The monthly mean Ts ranged from −10.5 to −24.27°C, with January and July recording the lowest and highest values, respectively. During the study period (2011–2018), the annual precipitation ranged from 229.8 mm (in 2015) to 513.2 mm (in 2018), with the growth season (May–September) accounting for roughly 92.3% of the total. Seasonal variations in SWC matched well with the seasonal distribution of precipitation (Figures 1B,E), and the daily SWC ranged from 10% to 57%. PAR and VPD exhibited relatively large day-to-day fluctuations and their seasonal variations generally showed unimodal curves (Figures 1C,F). The peak PAR values usually occurred in May, and the average PAR in May was 44.62 mol m^{-2} day^{-1}. The VPD typically peaks between May and July. The highest VPD (3.17 kPa) was observed in mid-July 2017.

In this study, the differences between the growing season temperature and precipitation and the respective multi-year averages were used to define the annual climate types (Figure 2). Mean Ta for the growing season ranged from 17.42°C (2012) to 19.61°C (2017). Growing-season precipitation was highest in 2018 (474.9 mm, 112.1% higher than the multi-year (1990–2019) average of 223.9 mm) and lowest in 2015 (174.6 mm, 22.0% lower than the multi-year average). Accordingly, 2016 was selected to represent a normal year (normal climatic conditions), 2017 was classified as a warm year, and 2018 was classified as a warm and moist year (Figure 2).

3.2. Environmental controls on NEE

Path analysis method was used to examine the combined impact of the environmental factors on NEE (Figure 3), and the determinative coefficient generated by path analysis was used to determine the relative importance of environmental factors in NEE fluctuations (Table 2). As seen in Table 2, moisture-related environmental factors (e.g., VPD and SWC) had greater effects on NEE in the desert steppe ecosystems than heat-related environmental factors (e.g., Ta and Ts).

During the growing season, VPD was the most prominent environmental factor affecting the daytime NEE, followed by SWC, Ta, and PAR. Daytime NEE increased (i.e., carbon uptake reduced) with an increase in VPD and declined (i.e., carbon uptake increased) with an increase in Ta, SWC, and PAR. From the absolute values of path coefficient, there was little difference between the direct and

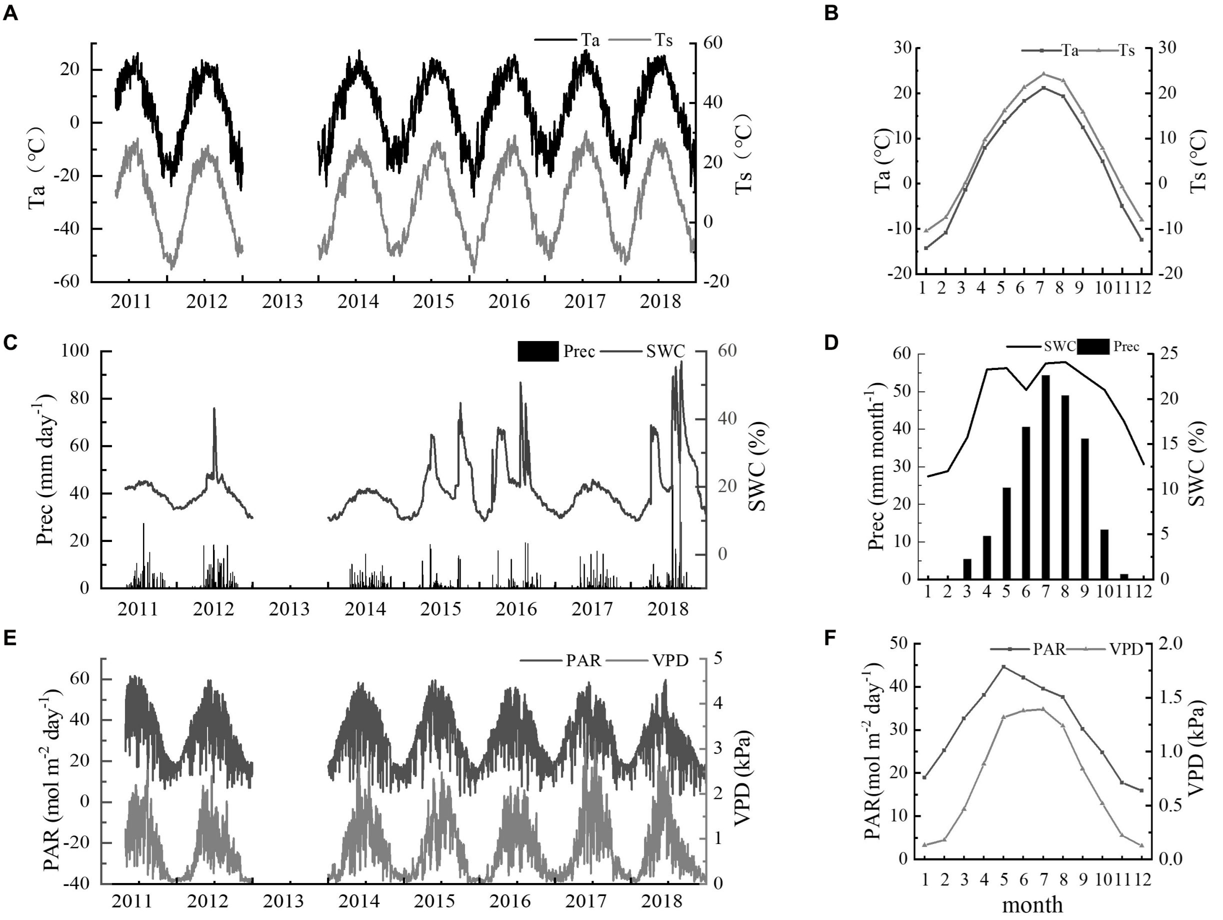

FIGURE 1
(A) Seasonal variations of daily mean air temperature (Ta) and soil temperature (Ts); **(B)** daily sum of precipitation (Prec) and daily average of volumetric soil water content (SWC) at 10cm depth; **(C)** photosynthetically active radiation (PAR) and daily mean vapor pressure deficit (VPD). Seasonal variations in monthly mean values of **(D)** Ta and Ts; **(E)** Prec and SWC; and **(F)** PAR and VPD.

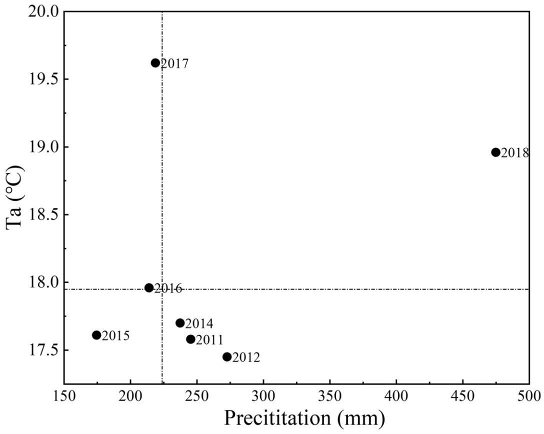

FIGURE 2
Average air temperature and cumulative precipitation during each growing season from 2011 to 2018. The growing season precipitation average over the long term (1990–2019) is shown by the horizontal dashed line (223.9mm); the long-term average air temperature for the growing season is illustrated by the vertical dashed line (17.95°C).

indirect effects of VPD and Ta, whereas SWC and PAR mainly had direct effects on daytime NEE. For night-time NEE, SWC had the strongest effect, followed by VPD, Ts, and Ta. Among these, SWC, VPD, and Ta mainly had direct effects on nighttime NEE.

During the non-growing season, VPD was the most important factor controlling NEE, followed by Ts, SWC, and Ta. In contrast to the growing season, the influence of environmental factors on NEE during the non-growing season was mainly attributed to direct effects.

Moreover, the effects of environmental factors on NEE may vary under different climatic conditions (Aguilos et al., 2018; Wang et al., 2019). In this study, we considered three types of climatic conditions: normal, warm, warm and moist, which were classified according to the average air temperature and cumulative precipitation during the growing season (see Section 3.1 and Figure 2). Path diagrams illustrating the effects of environmental factors on daytime net ecosystem CO_2 exchange for different climatic conditions (Figure 4). The results showed that in a normal year or warm year, moisture (SWC or VPD) was the primary factor controlling daytime NEE during the growing season, followed by Ta and PAR; in comparison, PAR proved to be the most important controlling factor for NEE in a warm and moist year (Table 3).

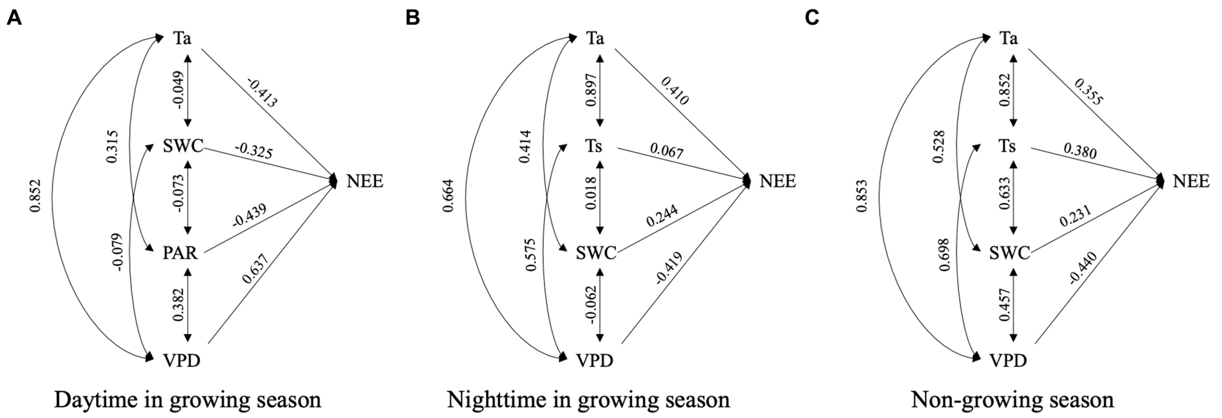

FIGURE 3
Path diagrams illustrating the effects of environmental factors on **(A)** daytime net ecosystem CO_2 exchange (NEE) during the growing season, **(B)** nighttime NEE during the growing season, and **(C)** NEE during the non-growing season.

TABLE 2 Direct and indirect path coefficients of environmental factors on the variation of NEE.

Period	Factors	Related coefficient	Direct path coefficient	Sum of indirect path coefficient	Determinative coefficient
Daytime in growing season	Ta	−0.065**	−0.413	0.348	0.117
	SWC	−0.372**	−0.325	−0.047	0.136
	PAR	−0.287**	−0.439	0.151	0.060
	VPD	0.122**	0.673	−0.551	0.288
Nighttime in growing season	Ta	0.190**	0.410	−0.221	0.013
	Ts	0.178**	0.067	0.111	0.019
	SWC	0.296**	0.244	0.052	0.085
	VPD	−0.147**	−0.419	0.272	0.053
Non-growing season	Ta	0.284**	0.355	−0.071	0.046
	Ts	0.217**	0.380	−0.163	0.097
	SWC	0.285**	0.231	0.054	0.078
	VPD	−0.369**	−0.440	0.070	0.131

The growing season generally lasts from May to September. October to April is referred to as the non-growing season. Ta, air temperature; Ts, soil temperature; SWC, soil water content; PAR, photosynthetically active radiation; VPD, vapor pressure deficit. ** indicates an extremely significant correlation between the factor and NEE ($p < 0.01$).

3.3. Effects of rainfall events on NEE

The NEE at this site was primarily water-limited according to the results of the aforementioned environmental controls. The effects of rainfall events on NEE are further explored in this section. From 2011 to 2018 (excluding 2013), 258 rainfall events were recorded in the study area, of which 196 (75% of all rainfall events) occurred during the growing season. A total of 196 events from this seven-growing-season study were used for statistical analysis (Figure 5). Most rainfall events were small in the size, with the majority (61%) being <5 mm. However, despite the low proportion of large rainfall events (> 5 mm), the total rainfall from them was greater than that of small rainfall events (80% vs. 20%).

By comparing the daily average NEE in a sliding window of 3 days after rainfall with the daily average NEE including the 3 days before rainfall, the impact of the rainfall event on NEE was evaluated (Figure 6). The results showed that the CO_2 uptake increased (negative $NEE_{response}$ in Figure 6) when the rainfall event was >5 mm, and the response increased with the size of the rainfall event. The relative response effect of NEE to rainfall event ($NEE_{response,\ r}$) represented a different trend; that is, the CO_2 uptake increased 10-, 8-, and 5-fold, respectively, compared to the uptake level before a rainfall event of 5–10 mm, 10–25 mm, and > 25 mm. Moreover, CO_2 uptake peaked approximately 1–3 days after a 5–10 mm rainfall event. However, it took 3–5 days to reach the highest carbon uptake after a rainfall event of >10 mm; On the other hand, small rainfall events (< 5 mm) slightly increased CO_2 emissions (positive $NEE_{response}$ in Figure 6).

As there were differences in the size of rainfall events that occurred in different months. For example, May is dominated by small rainfall events (rainfall events of <5 mm account for 74.3% of the total), while July and August are dominated by large rainfall events. The frequency of rainfall events of >5 mm in July and August was 45.0% and 40.5%, respectively, and the rainfall percentage of rainfall events of >5 mm in July and August was 87.1% and 88.0%, respectively. Therefore, a correlation analysis was conducted between monthly

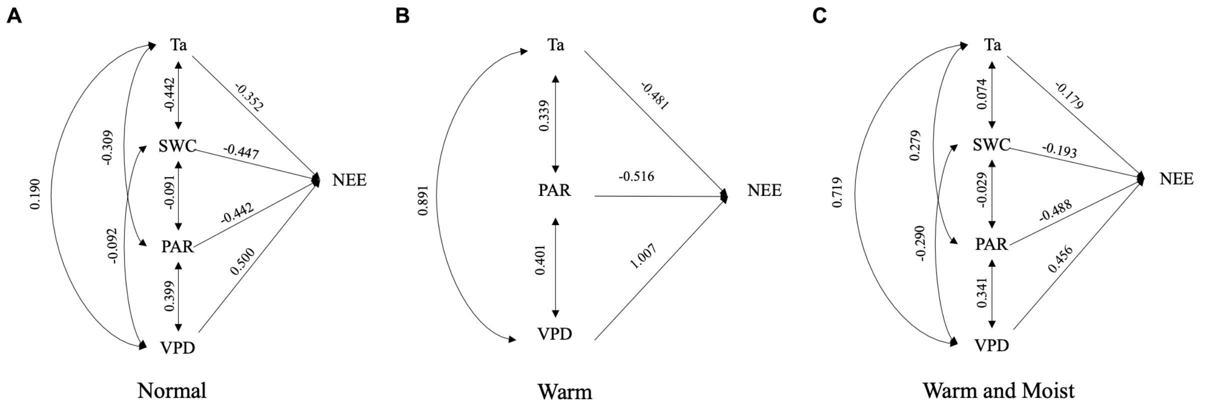

FIGURE 4
Path diagrams illustrating the effects of environmental factors on daytime net ecosystem CO_2 exchange (NEE) for **(A)** normal year, **(B)** warm year, and **(C)** warm and moist year.

TABLE 3 Direct and indirect path coefficients of environmental factors on daytime NEE changes in the growing season under different climatic conditions.

Climatic conditions	Factors	Related coefficient	Direct path coefficient	Sum of indirect path coefficient	Determinative coefficient
Normal	Ta	0.084**	−0.352	0.436	0.183
	SWC	−0.442**	−0.447	0.005	0.195
	PAR	−0.309**	−0.442	0.133	0.078
	VPD	0.190**	0.500	−0.310	0.060
Warm	Ta	0.078**	−0.481	0.559	0.306
	SWC	−0.014	–	–	–
	PAR	−0.247**	−0.516	0.269	0.011
	VPD	0.242**	1.007	−0.765	0.527
Warm and Moist	Ta	−0.098**	−0.179	0.081	0.003
	SWC	−0.363**	−0.193	−0.170	0.103
	PAR	−0.378**	−0.488	0.110	0.131
	VPD	0.162**	0.456	−0.294	0.060

The growing season was from May to September each year. Ta, air temperature; Ts, soil temperature; SWC, soil water content; PAR, photosynthetically active radiation; VPD, vapor pressure deficit. ** indicates an extremely significant correlation between the factor and NEE ($p < 0.01$).

precipitation and NEE during the growing season (Figure 7). The results showed that an increase in rainfall in May increased CO_2 emissions from the desert steppe ecosystem, whereas an increase in rainfall from June–September increased the CO_2 uptake. It supports the findings of previous related studies that seasonal distribution patterns of rainfall have important effects on the annual carbon balance (Dong, 2011). From the perspective of the entire growing season, NEE was greatly influenced by rainfall, and with an increase in rainfall, NEE decreased; that is, carbon uptake was enhanced.

4. Discussion

4.1. Constraints on NEE

It is generally agreed that in most ecosystems, radiation acts as the main regulating factor for NEE on a half-hourly scale (Baldocchi, 2014; Wang et al., 2019; Yan et al., 2023). However, certain studies have suggested that the two most important factors controlling carbon exchange in grassland ecosystems are temperature and water (Kim and Verma, 1990; Xue et al., 2014). This study showed that VPD (a function of temperature and humidity) had the largest effect on daytime NEE during the growing season, and that ecosystem carbon uptake decreased with increasing VPD, which is consistent with an earlier study in a desert steppe in Xilamuren (Li, 2020). VPD has a strong effect on stomatal conductance and can, therefore, modulate CO_2 exchange between the canopy and the atmosphere (Novick et al., 2016; Umair et al., 2020; Xie et al., 2020). Lower VPD stimulates stomatal opening, which is thought to increase CO_2 uptake (Wu et al., 2017). However, when VPD is higher than a certain threshold, plants may partially close their stomata to prevent excessive water loss; thus, ecosystem carbon uptake is constrained (Wang, 2015; Novick et al., 2016).

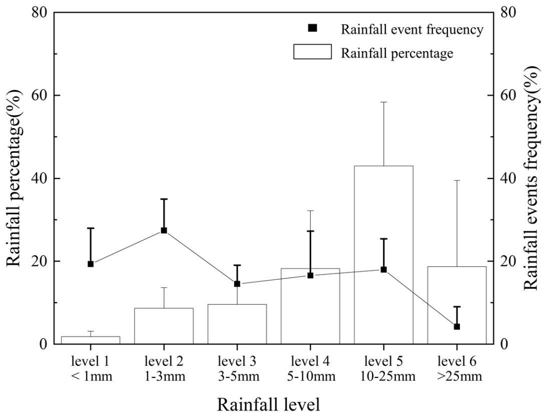

FIGURE 5
Frequency distributions of rainfall events and rainfall amounts from May to September between 2011 and 2018 (excluding 2013).

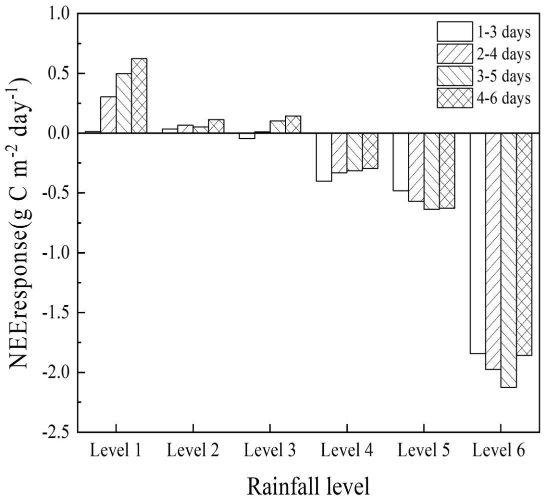

FIGURE 6
Variation of NEE before and after rainfall with different rainfall levels. The figure shows the difference between the daily average of the sliding window NEE for 3 days after a rainfall event and the daily average of the NEE for the 3 days before the rainfall event.

Our findings also revealed that SWC played a significant role in explaining nighttime variation NEE (i.e., ecosystem respiration), as reported in other previous studies (Balogh et al., 2011; Vicca et al., 2014; Meena et al., 2020). This implies that soil moisture should be considered when simulating ecosystem respiration, especially in water-limited ecosystems. Ecosystem respiration is the sum of the plant (autotrophic) and heterotrophic microbial respiration. Water availability is one of the most significant constraints on plant and microbial growth and changes in soil moisture can significantly affect ecosystem respiration (Piao et al., 2019). Reduced SWC in water-limited ecosystems such as at our study site leads to restricted plant growth and decreased microbial decomposition; thus, ecosystem respiration also shows a downward trend.

Path analysis suggested that temperature played a subordinate role in influencing half-hourly NEE changes at this site, which is consistent with previous studies in semiarid grasslands; that is, soil moisture availability is more important than soil temperature in regulating respiration in water-limited ecosystems (Vargas et al., 2010; Thomey et al., 2011; Wang et al., 2015). In this desert steppe, during the daytime of the growing season, an increase in temperature promoted ecosystem CO_2 uptake, while during the nighttime of the growing and non-growing seasons, an increase in temperature promoted ecosystem respiration and increased CO_2 emissions.

The effects of environmental factors on NEE may vary under different climatic conditions (Aguilos et al., 2018; Wang et al., 2019). Take daytime NEE during the growing season, for example, in the normal year, SWC was the primary factor controlling NEE, and the significant impact of SWC on NEE is mainly attributed to its direct impact. A previous study also showed that SWC has a strong direct impact on the eco-physiological processes of desert steppe plants (Aguilos et al., 2018); in the warm year, VPD became the most prominent environmental factor influencing NEE since variations in VPD are closely correlated with changes in temperature, which in turn influences plant stomatal conductance and modifies NEE; In the warm and moist year, water restriction for carbon uptake was lessened along with increased rainfall, and the significant impact of PAR on NEE emerged, because PAR directly promotes plant photosynthesis and increases ecosystem carbon absorption (Yue et al., 2010). The significant effects of SWC and PAR were mainly attributed to their direct effects; regarding Ta, its effects on NEE were dominated by direct effects in a warm and moist year, whereas they were primarily indirect in a normal year or a warm year, which is consistent with previous research (Jia et al., 2014; Ouyang et al., 2014; Aguilos et al., 2018).

4.2. Responses of NEE to rainfall events

Studies have shown that in grassland ecosystems with limited water resources, the ecosystem carbon flux is closely related to annual precipitation at different locations and in different years (Huxman et al., 2004; Gemechu Legesse et al., 2021). Small rainfall events predominate in arid and semi-arid ecosystems, and the results showed that small-scale rainfall events can enhance the carbon emissions of the ecosystem (Tang et al., 2018); whereas rainfall events of >5 mm can effectively increase soil water content, which enhances the carbon uptake capacity of the ecosystem and leads to a longer duration of ecosystem changes (Chen and Wang, 2009; Wang et al., 2018). This is in line with our analysis results, rainfall events of <5 mm slightly increased CO_2 emissions in the desert steppe, and rainfall events of >5 mm increased the CO_2 uptake in the desert steppe. Hence it can be inferred that a rainfall event of 5 mm is considered ecologically significant for NEE responses in desert steppe ecosystems (Li et al., 2013).

The carbon uptake peak was delayed by 1–5 days after rainfall, which was due to the faster response of ecosystem respiration to rainfall than to photosynthesis (Delgado-Balbuena et al., 2022). In addition, this pattern may be influenced by the dry period after rainfall, which offsets the soil water deficit and decreases the photosynthetic rate (Harper et al., 2005). The relationship between rainfall, infiltration depth, and the response of ecosystem carbon exchange to rainfall patterns depends on the position of soil microflora

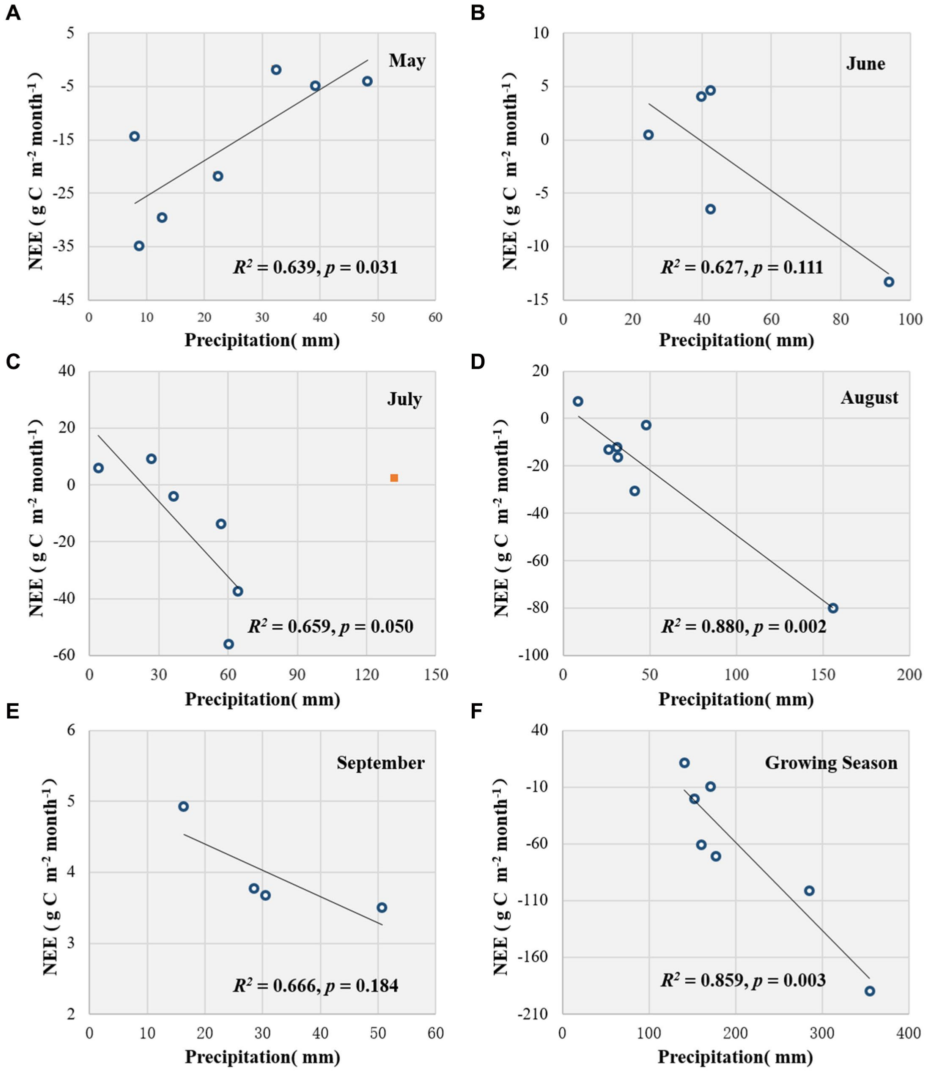

FIGURE 7
Relationship between NEE and corresponding rainfall. The relationship between NEE and rainfall in May **(A)**, June **(B)**, July **(C)**, August **(D)**, September **(E)**, and the growing season (May–September) **(F)**, respectively. The orange square in Plot C represented a singular point, and it was excluded from the regression; all the variables used in the analyses were monthly values, and if the effective observed data for a given month is less than 80%, that month's value is excluded from the analysis.

and plant roots in the soil as well as temporal changes in microbial and plant responses to wetting episodes (Huxman et al., 2004). Larger rainfall events may penetrate deep into the soil, whereas smaller rainfall events are intercepted by the canopy or directly replenished to the top soil layer, where water evaporates and cannot reach the root system (Hao et al., 2010).

This study showed that seasonal distribution patterns of rainfall have a large impact on desert steppe NEE. The CO_2 uptake increased with monthly rainfall from June to September, whereas it decreased with monthly rainfall in May. The main reason might be that small rainfall events (<5 mm) dominated in May, which are not expected to stimulate ecosystem productivity by altering the soil water content effectively, but instead increase ecosystem respiration and carbon emissions (Fay et al., 2008; Tang et al., 2018). It can be inferred that summer rainfall is more favorable for carbon sequestration than spring rainfall for desert steppe (Peng et al., 2013; Wang et al., 2018).

5. Conclusion

NEE of the studied desert steppe was primarily water-limited. Moisture-related environmental factors, VPD and SWC was the most prominent environmental factor for the daytime NEE and nighttime NEE during the growing season, respectively. But the interannual differences in climatic conditions can lead to changes in the controlling factor of NEE, e.g., PAR became the main controlling factor of NEE under climatic conditions of warm and moist.

The size of rainfall events has significant impacts on the NEE of the desert steppe. Small rainfall events (< 5 mm) slightly increased CO_2 emissions; Rainfall events of >5 mm increased the CO_2 uptake, and the NEE response increased with the rainfall event size. Moreover, NEE had a longer response time to rainfall events with a larger size, e.g., NEE peaked approximately 1–3 days after a 5–10 mm rainfall event, while the rainfall event size >10 mm, it would take 3–5 days for

NEE to reach a peak value. During the growing season, carbon uptake increased with monthly rainfall, except in May. These findings are important for predicting the carbon balance trends in desert steppe ecosystems under various climate change scenarios.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

LZ and GZ: conceptualization and funding acquisition. JS and LZ: methodology and writing—original draft preparation. JS, YY, and SZ: investigation. JS and YW: data curation. All authors contributed to the article and approved the submitted version.

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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

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