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Lagged climatic effects on carbon fluxes over three grassland ecosystems in China

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Abstract

Aims

The plasticity of ecosystem responses could buffer and postpone the effects of climates on ecosystem carbon fluxes, but this lagged effect is often ignored. In this study, we used carbon flux data collected from three typical grassland ecosystems in China, including a temperate semiarid steppe in Inner Mongolia (Neimeng site, NM), an alpine shrub-meadow in Qinghai (Haibei site, HB) and an alpine meadow steppe in Tibet (Dangxiong site, DX), to examine the time lagged effects of environmental factors on CO_2 exchange.

Methods

Eddy covariance data were collected from three typical Chinese grasslands. In linking carbon fluxes with climatic factors, we used their averages or cumulative values within each 12-month period and we called them 'yearly' statistics in this study. To investigate the lagged effects of the climatic factors on the carbon fluxes, the climatic 'yearly' statistics were kept still and the 'yearly' statistics of the carbon fluxes were shifted backward 1 month at a time.

Important Findings

Soil moisture and precipitation was the main factor driving the annual variations of carbon fluxes at the alpine HB and DX, respectively, while the NM site was under a synthetic impact of each climatic factor. The time lagged effect analysis showed that temperature had several months, even half a year lag effects on CO_2 exchange at the three studied sites, while moisture's effects were mostly exhibited as an immediate manner, except at NM. In general, the lagged climatic effects were relatively weak for the alpine ecosystem. Our results implied that it might be months or even 1 year before the variations of ecosystem carbon fluxes are adjusted to the current climate, so such lag effects could be resistant to more frequent climate extremes and should be a critical component to be considered in evaluating ecosystem stability. An improved knowledge on the lag effects could advance our understanding on the driving mechanisms of climate change effects on ecosystem carbon fluxes.

Keywords: climate change, carbon flux, direct effect, grasslands, lagged effect

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INTRODUCTION

Previous studies on carbon flux mostly focused on forests (Carrara *et al.* 2004; Hollinger *et al.* 2004; Xu *et al.* 2014; Zhang *et al.* 2011) due to their great potential to sequester carbon (Pacala *et al.* 2001). Recently, grassland ecosystems are attracting growing attentions (Fan *et al.* 2011; Fu *et al.* 2009; Gilmanov *et al.* 2007; Novick *et al.* 2004; Zhang *et al.* 2013), due to the high uncertainty related to their contributions to carbon balance and their high sensitivity to climatic perturbations (Novick *et al.* 2004). Especially at high altitude and latitude regions, grassland ecosystems were found to be highly sensitive and vulnerable to climate change (Guisan and Theurillat 2000) and their permafrost soil could release large amounts of carbon under climatic warming (Wang *et al.* 2002).

The factors driving grassland carbon fluxes differ with grassland types under distinct climatic conditions (Fu *et al.* 2009). Some studies reported that precipitation was mainly responsible for CO_2 flux in shortgrass steppe (Parton *et al.* 2012) while warming could also stimulate carbon sequestration in tallgrass prairie (Wan *et al.* 2005). For alpine ecosystems, some studies considered that temperature was more critical than other climatic factors (Fu *et al.* 2006; Kato *et al.* 2006), but others found that carbon fixation increased with the amount of precipitation (Yang *et al.* 2009). Weaker solar radiation increased the carbon absorption for the alpine grassland ecosystem (Fan *et al.* 2011).

Climate change could cause changes in ecosystem structure and functions, which could buffer the effects of climatic variability on carbon fluxes. Empirical evidence suggested that the variability of carbon flux was directly influenced by climatic variability among years, also by its lag effects (Odum 1969). However, most studies have only paid attention to the direct impacts of environmental factors (Fu *et al.* 2009; Xu *et al.* 2004; Zhang *et al.* 2010), while the commonly existed lag effect on long time scales (Katul *et al.* 2001; Stoy *et al.* 2009) was conventionally ignored (Braswell *et al.* 1997; Marcolla *et al.* 2011; Teklemariam *et al.* 2010).

Along with the development of research on regional carbon budget and global change, ecologists are paying mounting attention to the lag effects (Teklemariam *et al.* 2010), because they reflect the internal changes of ecosystems (Granier *et al.* 2007) and the responses of ecosystem structure and composition to climatic forcing (Marcolla *et al.* 2011). In addition, for long-term predictions of carbon budget in the context of global change, the lag effects must be taken into serious accounts so as to restrain estimation uncertainties (Wu *et al.* 2012). In this context, understanding the time lagged effects of climatic factors on ecosystem carbon fluxes is fundamental to predicting how the biosphere affects, and will be affected by climate change, and to define their roles in controlling carbon flux variability.

Many studies revealed that the lag effects of climatic drivers on carbon fluxes may be more important than their direct effects (Barford *et al.* 2001; Braswell *et al.* 1997). For example, high spring temperature was found to increase photosynthesis in the following autumn (Richardson *et al.* 2009). Spring temperature can also bring about important effects on annual ecosystem productivity (Piao *et al.* 2009; Zhang *et al.* 2011,). So a non-equilibrium framework for studying the impacts of temperature change on current or future forest carbon balance is necessary (Piao *et al.* 2009). A negative correlation between radiation and carbon fluxes was identified with a 1-year lag in an alpine meadow (Marcolla *et al.* 2011). Precipitations can also generate lag effects on ecosystem CO_2 exchange by altering LAI, changing canopy chemistry (Flanagan *et al.* 2002) and soil microbial community (Sowerby *et al.* 2005). Teklemariam *et al.* (2010) reported stronger correlations between carbon fluxes and climatic factors of the previous year than those of the current year. So it is necessary to jointly consider the direct and lagged effects of climatic factors on carbon fluxes (Braswell *et al.* 1997; Dunn *et al.* 2007).

Nowadays, a growing number of parametric models are being developed to study the carbon flux (Chen *et al.* 2011; Wu *et al.* 2008) because of their simple model structures and easily obtained parameters. However, the barely captured lag effects in parametric models resulted in increased simulation deviation (Goetz *et al.* 2000). Identifying the lag effects of environmental factors would improve our understanding on the driving mechanisms of climate change on terrestrial ecosystem carbon flux and advancing our prediction of global carbon cycle.

The extensively distributed temperate ($\sim 8.4 \times 10^5$ km^2) (Li *et al.* 1998) and alpine grasslands ($\sim 2.5 \times 10^6$ km^2) (Zhao *et al.* 2006) in China are important components of terrestrial carbon budget. It is important to know how climate change will affect the carbon fluxes in these grasslands ecosystems and how the ecosystems will feedback to the climate change. Previous studies have identified the presences of the direct and lagged effects of climatic factors on the carbon and water fluxes in several forest and grassland systems (Marcolla *et al.* 2011; Teklemariam *et al.* 2010; Xu *et al.* 2014). However, how the direct and lagged effects act on different types of grasslands in China still need to be explored. The objective of this study is to test the hypothesis whether there exist lagged climatic effects on carbon flux of Chinese grasslands and evaluate how the direct and lagged effects differentiately performed among the three typical grassland ecosystems in China. The research findings would shed light on the plasticity of Chinese grassland ecosystems in responding to climate extremes.

DATA AND METHODS

Site description

Carbon fluxes were measured over three grassland ecosystems located in the Qinghai-Tibet Plateau and north China, including: an alpine meadow-steppe ecosystem with short sparse vegetation (~10 cm) and sandy soil, located in the hinterland of Qinghai-Tibet Plateau; an alpine shrub-meadow ecosystem with moderate soil moisture, located on the northeast edge of Qinghai-Tibet Plateau; and a temperate steppe ecosystem under semi-arid climate, located in Inner Mongolia (Table 1) (Hu *et al.* 2008). Detailed descriptions are available for HB (Li *et al.* 2003), DX (Shi *et al.* 2006) and NM (Hao *et al.* 2006). The three monitoring sites are all members of the ChinaFLUX (Yu *et al.* 2006).

Observation and instrumentation

The eddy covariance (EC) flux observation systems are equipped with uniform measurement systems and sensors to monitor CO_2 and H_2O fluxes and micrometeorological conditions. The CO_2 and H_2O fluxes were measured by the open-path EC method with a CO_2/H_2O analyzer (Model LI-7500,

Table 1: site information of the three types of grasslands

Site	DX	HB	NM
Observation period	2004–11	2003–08	2004–08
Location	30°51′N, 91°05′E	37°40′N, 101°20′E	43°33′N, 116°40′E
Elevation (m)	4333	3293	1252
Mean precipitation (mm)	480	580	350
Mean temperature (°C)	1.3	−2	−0.4
Soil type	Meadow soil	Mol-Cryic Cambisols	Chestnut soil
Vegetation type	Alpine meadow-steppe	Alpine shrub-meadow	Temperate steppe
Canopy height (cm)	10	55	45
Dominant species	*Kobresia pygmaea* (C. B. Clarke) C. B. Clarke, *Stipa capillacea* Keng, *Carex montis-everestii* Kükenth.	*Potentilla fruticosa* L., *Kobresia capillifolia* (Decne.) C. B. Clarke, *Festuca rubra* L.	*Leymus chinesis* (Trin.) Tzvel., *Stipa grandis* P. Smirn., *Agropyron cristatum* (L.) Gaertn.
Maximum LAI(m^2 m^{-2})	1.0	2.8	1.5
Ground cover (%)	40	75	~100

Li-cor, Inc., NE). The wind velocity was monitored by a 3-D sonic anemometer (Model CSAT3, Campbell Scientific, Inc., Logan, UT). All the raw data were collected with a frequency of 10 Hz and then resampled to a 30-min-average using a CR5000 datalogger (Model CR5000, Campbell).

The air temperature (Ta) and relative humidity sensors (Model HMP45C, Campbell) were mounted in ventilated shields at heights of 1.2 and 2.2 m above ground. Soil temperatures were measured at five depths (5, 10, 20, 40 and 80 cm) with thermocouples (105-T and 107-L, Campbell), and soil water contents were recorded with three TDR probes (Model CS615-L, Campbell) at depths of 5, 20 and 50 cm. In this study air temperatures observed at 2.2 m height and soil temperature and soil water content measured at 5 cm deep were used. Radiation measurements were conducted using a four-component net radiometer (Model CNR-1, Kipp&Zonen, The Netherlands), a pyranometer (Model CM11, Kipp&Zonen) and a quantum sensor of photosynthetically active radiation (Model LI190SB, Licor, Inc.). Rainfall was monitored with a rain gauge (Model 52203, RM Young, Inc.). Meteorological variables were recorded at 1 Hz, then resampled to 30 min averages by three CR10X dataloggers (Model CR10XTD, Campbell) and a CR23X datalogger (Model CR23XTD, Campbell) with a 25-channel solid-state multiplexer (Model AM25T, Campbell).

Flux calculation

The carbon dioxide exchange (mg CO_2 m^{-2} s^{-1}) between biosphere and atmosphere was calculated as,

$$F_c = -\left(\overline{\omega'\rho_c'(z_r)} + \int_0^{z_r} \frac{\partial \overline{\rho_c}}{\partial t}\,dz\right)$$

where the first term on right-hand side is the eddy flux for carbon dioxide and the second is the storage below the height of observation (z_r). All advective terms in the mass conservation equation were ignored.

The carbon dioxide flux data were processed using a procedure of data processing for ChinaFLUX (Yu *et al.* 2006) implemented in Matlab 7.11 (The MathWorks, Inc., Natick, MA). Firstly, we applied a three-dimensional rotation aligning the coordinate system with mean wind direction to remove the effects of instrument tilt irregularity on the airflow (Falge *et al.* 2001; Wilczak *et al.* 2001). Then the Webb, Pearman and Leuning density correction (the WPL correction—a correction for the effects of the fluctuations of air density) was used to adjust the effects of air density change on CO_2 and H_2O fluxes (Webb *et al.* 1980). The storage of CO_2 fluxes below the EC height was also calculated (Hollinger *et al.* 1994).

The spurious data caused by rainfall, water condensation or system failure were removed from the dataset. To avoid possible underestimation of the fluxes caused by low turbulence fluxes under stable conditions during night, the night observations (solar elevation angle < 0) were excluded when the friction velocity (u*) was below the predetermined thresholds (Reichstein *et al.* 2005). The threshold values of u* for DX, HB and NM were 0.15, 0.15 and 0.2 m s^{-1}, respectively.

There are several methods for filling missing and spurious data (Fu *et al.* 2006). In this study, the data gaps were filled using the look-up table method (Reichstein *et al.* 2005). Missing meteorological data were filled using the mean diurnal variation (MDV) method (Falge *et al.* 2001). Further details about data processing were presented in the previous related studies (Li *et al.* 2003; Shi *et al.* 2006; Hao *et al.* 2006; Yu *et al.* 2006).

Calculating the correlations between climate drivers and ecosystem carbon fluxes

To identify the linkage between climatic factors and carbon fluxes, we selected six main climatic factors (net radiation (Rn), air temperature (Ta), soil temperature (Ts), precipitation (PPT), vapor pressure deficit (VPD) and soil water content (SWC)) and then analyzed their correlations with ecosystem carbon fluxes at an annual scale. For ecosystem carbon flux, we used net ecosystem productivity (NEP), whose positive value represents net CO_2 uptake while the negative value represents net CO_2 loss, gross primary productivity (GPP) and ecosystem respiration (Re). We placed emphasis on the time lag effects between climatic factors and ecosystem carbon fluxes.

To match ecosystem carbon flux, annual average Ta, Ts, SWC, VPD and cumulative Rn, PPT and carbon fluxes were calculated. The 'yearly' statistics were obtained using a 'moving time window' method, i.e. moving time window of 12 months, shifting 1 month a time (Luyssaert *et al.* 2007; Marcolla *et al.* 2011; Xu *et al.* 2014). Totally, there were 85 values generated from the eight year data at DX, 61 values from the 6-year data at HB and 49 values from the 5-year data at NM. To investigate the lag effects of the carbon fluxes' responses to the climatic factors, we shifted the carbon fluxes series backward 1 month a time (up to 12 months) and kept the climatic series still, in calculating the correlations between climate drivers and the carbon fluxes. The Student's *t*-tests were applied to verify the statistical significance of the correlation coefficients.

RESULTS

Comparisons of environmental conditions and CO_2 flux dynamics

The three grassland ecosystems showed similar seasonal and interannual temperature and radiation dynamics, but distinct for moisture (Fig. 1), as exhibited by the much smaller variations of the interannual temperature and radiation than that of moisture (Fig. 2). The annual ranges of Ta and Ts at NM were wider than those at DX and HB. The growing season Ta and Ts at NM were higher than those at HB and DX. The HB site had the highest Rn, while the DX site had comparable Rn with NM.

The SWC at HB was significantly higher than those at DX and NM ($P_{\text{HB vs. DX}} < 0.01$, $P_{\text{HB vs. NM}} < 0.01$). It had two peaks appearing in spring and the late growing season, respectively (Fig. 2), which were corresponding to the timing of snowmelt in spring and accumulated precipitation during the growing season, respectively. The single peak of SWC at DX and NM followed precipitation during the growing season and snowmelt, respectively (Fig. 2). The dynamics of SWC and PPT were approximately consistent over the three sites (Fig. 1). But the annual mean showed the increased SWC caused by precipitation had a certain time lag to PPT (Fig. 2). The PPT was concentrated in June, July and August at DX. Among the three grassland ecosystems, the NM site received the lowest PPT, coming with the highest VPD during growing seasons (Figs 1 and 2).

Among the three studied sites (Fig. 3), the interannual variations of carbon fluxes (NEP, GPP and Re) were lowest at HB. The interannual variations of GPP and Re were greatest at NM. But the interannual variation of NEP at NM was comparable to that at HB. The NEP, GPP and Re at HB during growing seasons were significantly higher than those at DX and NM ($P_{\text{HB vs. DX}} < 0.01$, $P_{\text{HB vs. NM}} < 0.01$), which are in accord with the SWC pattern over the three grasslands. As compared to DX, NM site had higher GPP and Re. Moreover, Re increased more rapidly than GPP at NM. The growing season NEP was lower at NM than that at DX (Fig. 2 and 3).

Overall, carbon fluxes and climatic factors roughly followed a sinusoidal temporal trajectory during the measuring period (Fig. 1). However, the waveforms of carbon fluxes lagged behind that of climatic factors, especially in 2007 at DX and in 2004 and 2008 at NM as circled in the box (Fig. 1). Figure 1 clearly showed that the variations of climatic factors pulled the changes of carbon fluxes.

Climatic drivers of ecosystem carbon fluxes

In order to quantify the time lagged effects of climatic factors on ecosystem carbon fluxes, a 'moving time window' method was used in this study. The lag correlation curves fit by this method were smooth rather than irregular (Fig. 4), which indicated the suitability of the statistical method for this study. The statistical results were shown in online supplementary Table S1, which is available on-line.

The driving effects of climate on ecosystem carbon fluxes changed with ecosystem type. Each climatic factor exhibited different magnitudes of lag effects (Fig. 4). Ts and Ta had a continuous and long-lasting impact on carbon fluxes. In general, temperature exhibited negative correlations with GPP and positive correlations with Re at DX and HB, and the negative correlation with GPP was significant ($R = -0.41$, $P < 0.01$) with a 6-month lag at HB. These were followed by negative correlations between NEP and temperature with about a 3-month lag ($R_{\text{Ta}} = -0.70$, $R_{\text{Ts}} = -0.64$, $P < 0.01$) at the DX site and a 5-month lag ($R_{\text{Ta}} = -0.67$, $R_{\text{Ts}} = -0.69$, $P < 0.01$) at the HB site, respectively. In temperate steppe at NM, temperature promoted GPP and Re, and the correlations between them reached a peak after approximately half a year ($P < 0.01$). NEP showed a positive correlation with temperature and peaked one month earlier ($R_{\text{Ta}} = 0.80$, $R_{\text{Ts}} = 0.84$, $P < 0.01$) than GPP and Re.

The radiation showed positive correlations with carbon fluxes (NEP, GPP and Re) and exhibited no lag effects at the DX site ($R_{\text{NEP}} = 0.38$, $R_{\text{GPP}} = 0.55$, $R_{\text{Re}} = 0.39$, $P < 0.01$). Strong radiation had a negative effect on GPP and Re and this effect had a more than half a year lag at HB ($R_{\text{GPP}} = -0.67$, $R_{\text{Re}} = -0.44$, $P < 0.01$), while Rn had no significant impact on NEP. At the relatively drier NM site, Rn showed immediate positive correlations with GPP and Re ($R_{\text{GPP}} = 0.54$, $R_{\text{Re}} = 0.56$, $P < 0.01$) and the highest negative correlations with both NEP and its two components with a nearly 1-year lag ($R_{\text{NEP}} = -0.80$, $R_{\text{GPP}} = -0.87$, $R_{\text{Re}} = -0.82$, $P < 0.01$).

Compared with other climatic factors, SWC had the highest and longest lasting correlations with carbon fluxes (NEP, GPP and Re) at HB, where, Re had a higher positive correlation with SWC than GPP ($R_{\text{GPP}} = 0.66$, $R_{\text{Re}} = 0.92$, $P < 0.01$), followed by a negative correlationship between NEP and SWC ($R = -0.68$, $P < 0.01$). The PPT had a continuous impact on NEP and GPP at DX, and their correlations reached the highest level with a 1-month lag ($R_{\text{NEP}} = 0.77$, $R_{\text{GPP}} = 0.75$, $P < 0.01$), while the

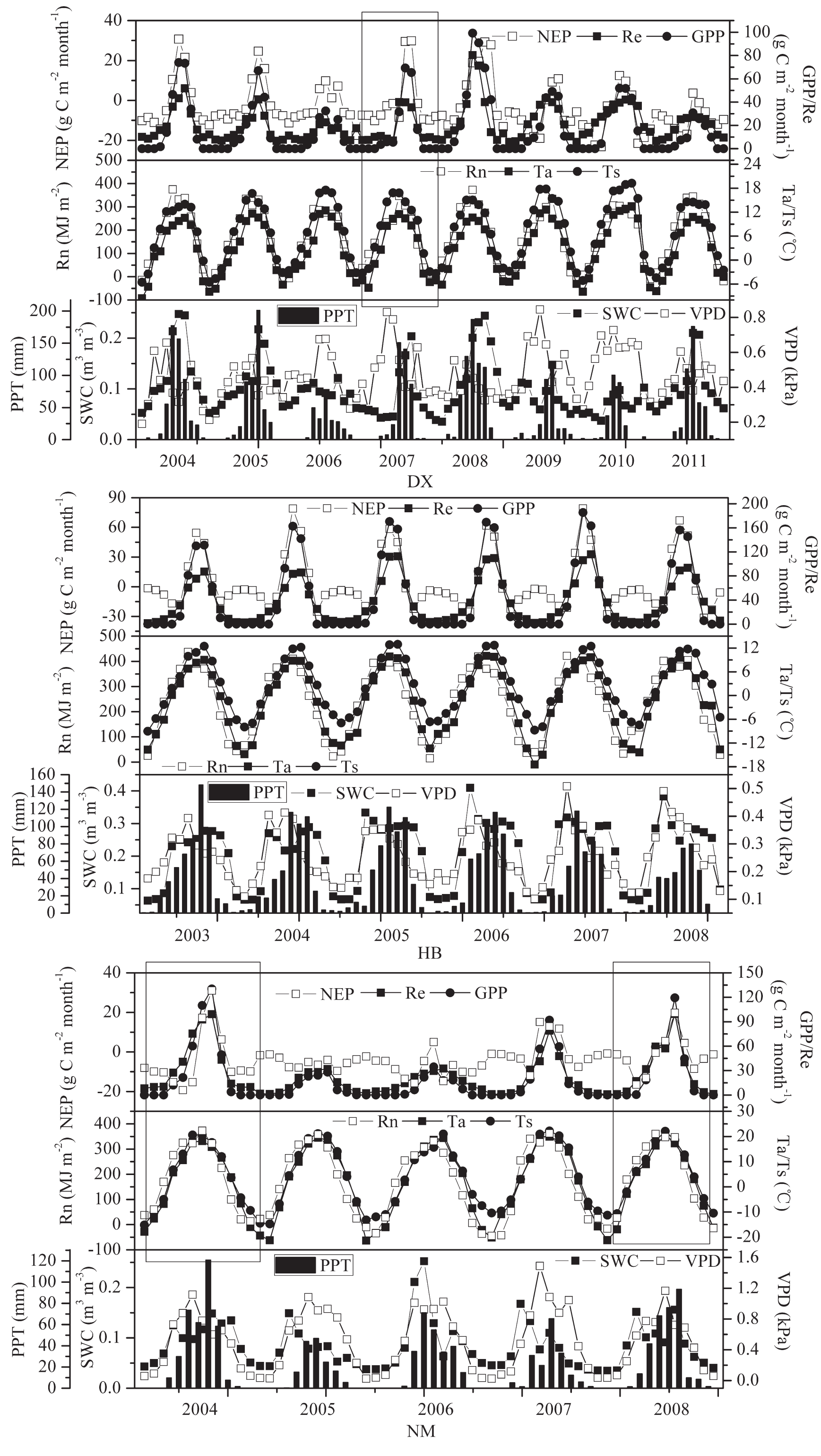

Figure 1: monthly values of carbon fluxes and climatic factors in each year over the three sites.

correlation between PPT and Re was relatively weak ($R = 0.34$, $P < 0.01$). Both GPP and Re were significantly affected by PPT at NM ($R_{GPP} = 0.69$, $R_{Re} = 0.82$, $P < 0.01$), but the correlogram between PPT and NEP showed a flat trend. The effects of VPD on carbon fluxes were approximately opposite to the effects of PPT at DX and NM. The effects of PPT and VPD on carbon fluxes at HB were weak, as revealed by their non-significant relationships (online supplementary Table S1).

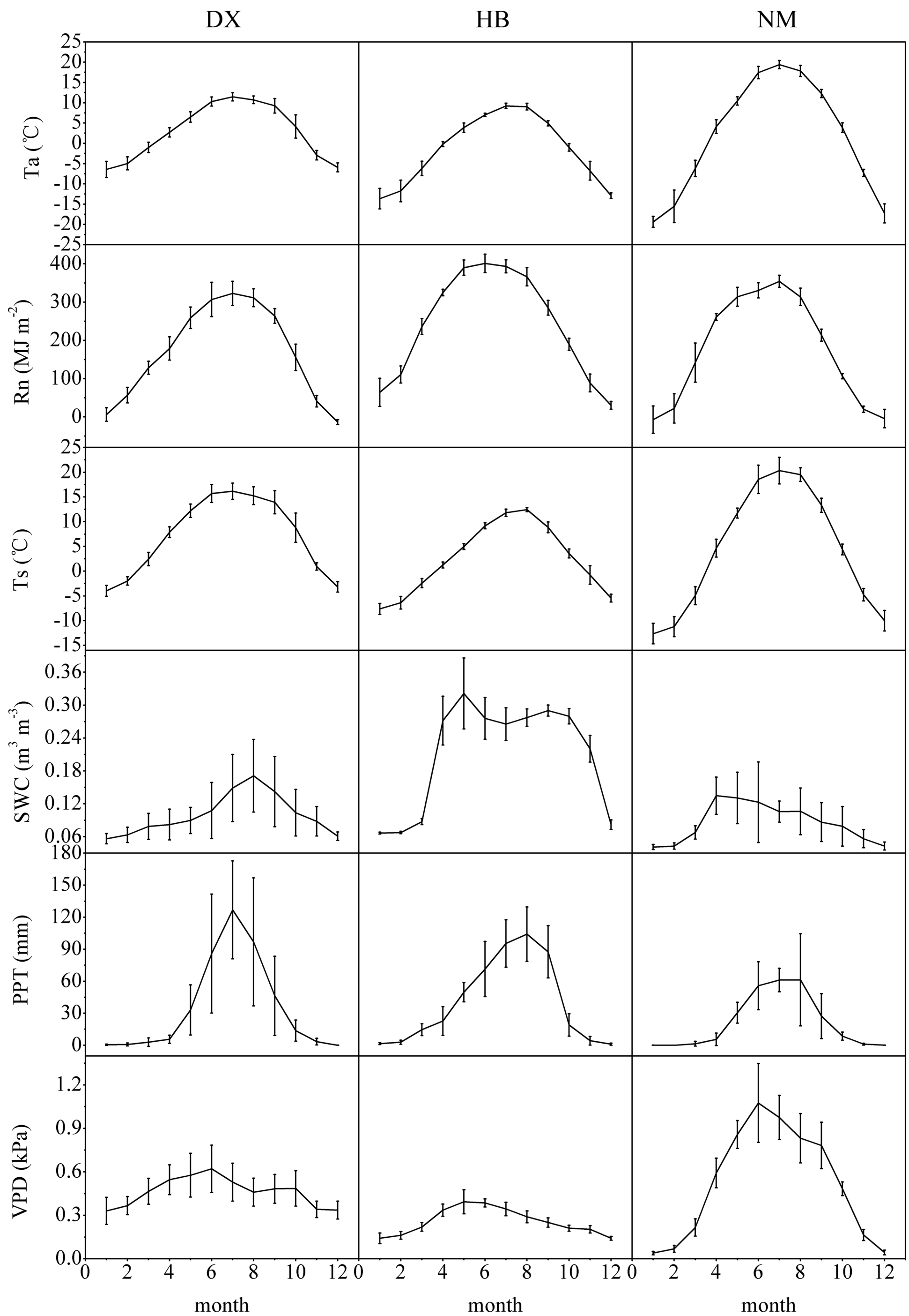

Figure 2: comparisons of monthly environmental factors among the alpine steppe-meadow (DX), the alpine shrub-meadow (HB) and the temperate steppe (NM); The error bars represent the interannual variability of environmental factors in each month.

DISCUSSIONS

Environmental controls on carbon fluxes in grasslands

The ecosystem carbon budget will reach a dynamic equilibrium within a long enough time horizon (Sitch *et al.* 2003). Our studied period is relatively short, which is possible to fall in the trough or crest. Under this situation, the annual scale relationships between climatic factors and carbon fluxes as derived from several-year measurements cannot fully represent the long term phenomena. In this study, we tried to overcome the constraint of short term data availability by regenerating the 'yearly' statistics, which turned out to be effective for those data shortage situations.

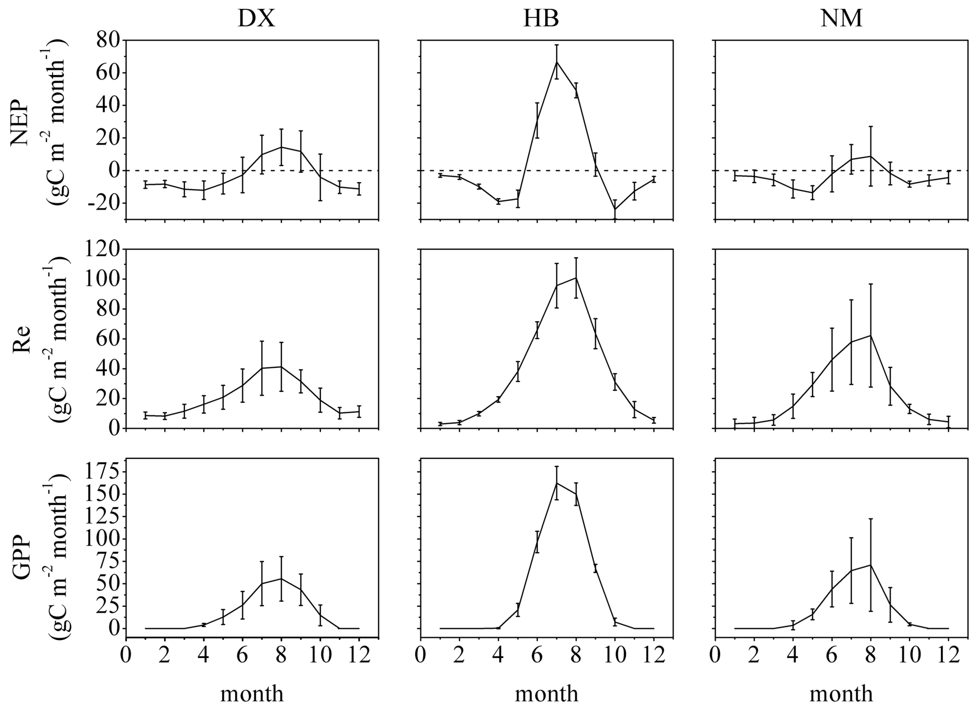

Figure 3: seasonal variations of carbon fluxes over the three grassland ecosystems. The error bars represent the interannual variability of carbon fluxes in each month.

Many previous studies considered that the alpine ecosystem was temperature limited (Fu *et al.* 2006; Kato *et al.* 2006), while some deemed that precipitation was more important than temperature (Yang *et al.* 2009). Our study showed that moisture was more critical for CO_2 exchange in the two alpine ecosystems. The PPT dominated the carbon sequestration at DX, mainly caused by a more obvious effect of PPT on GPP than on Re (Fig. 4). The SWC was the primary factor affecting the carbon fluxes at HB, while high SWC could lower carbon uptake due to the rapidly increased Re with elevated SWC. Nevertheless, PPT did not show significant correlations with carbon fluxes at HB because precipitation timing exerted greater influences than precipitation amount in this alpine shrub-meadow ecosystem (Zhao *et al.* 2006).

The variability of carbon fluxes at the NM site was resulted from an integrated effect of environment factors. Similar to findings in most of the previous studies (Parton *et al.* 2012; Suyker *et al.* 2003), we found that PPT exerted a greater influence on GPP and Re in this temperate semiarid grassland. However, the correlations between PPT and NEP at NM were not significant due to the similar magnitude responses of GPP and Re to PPT in this temperate steppe. The Ts had the strongest immediate effect on NEP, and Rn not only had immediate but also a significant long term effect on both NEP and its two components. In addition, SWC had weak correlations with GPP and Re due to the low water retention capacity of chestnut soil and a lack of groundwater supply at the NM site. Rather, PPT is a major source of SWC (Cui *et al.* 1990).

It is generally accepted that increasing temperature favors carbon sequestration for Chinese grasslands (Fu *et al.* 2009; Wan *et al.* 2005), as observed in our study for the temperate steppe at NM due to the higher temperature sensitivity of GPP compared to Re (Fig. 4, Marcolla *et al.* 2011). However, the higher temperature induced carbon uptake reduction in the alpine ecosystems of DX and HB. Possibly, the alpine plants living on the Tibet Plateau have been acclimated to the long-term low temperature conditions (Cui *et al.* 2003) and have developed photosynthetic organisms optimal for low temperatures (Fu *et al.* 2006). So the carbon sequestration capacity is depressed at relatively high temperature. In addition, the frigid soil which is rich in organic matter due to the slow decomposition of litter under low-temperature conditions could release large amounts of carbon along with increased temperature (Wang *et al.* 2002).

The lagged climatic effects on carbon flux variations

The ecosystem behaviors are driven by climatic variability (Suyker *et al.* 2003; Wen *et al.* 2006; Xu and Baldocchi 2004; Zhang *et al.* 2011). But, across a long time scale, sole climatic variability is not adequate to fully explain carbon flux variability (Barford *et al.* 2001; Stoy *et al.* 2009; Xu *et al.* 2014) because of its ignorance of the lag effects of climatic factors. The EC measurements as well as most of other related observations and experiments are conducted over relatively short periods, inadequate for capturing the lag effect of environmental factors (Misson *et al.* 2010). In this study, we used a statistical

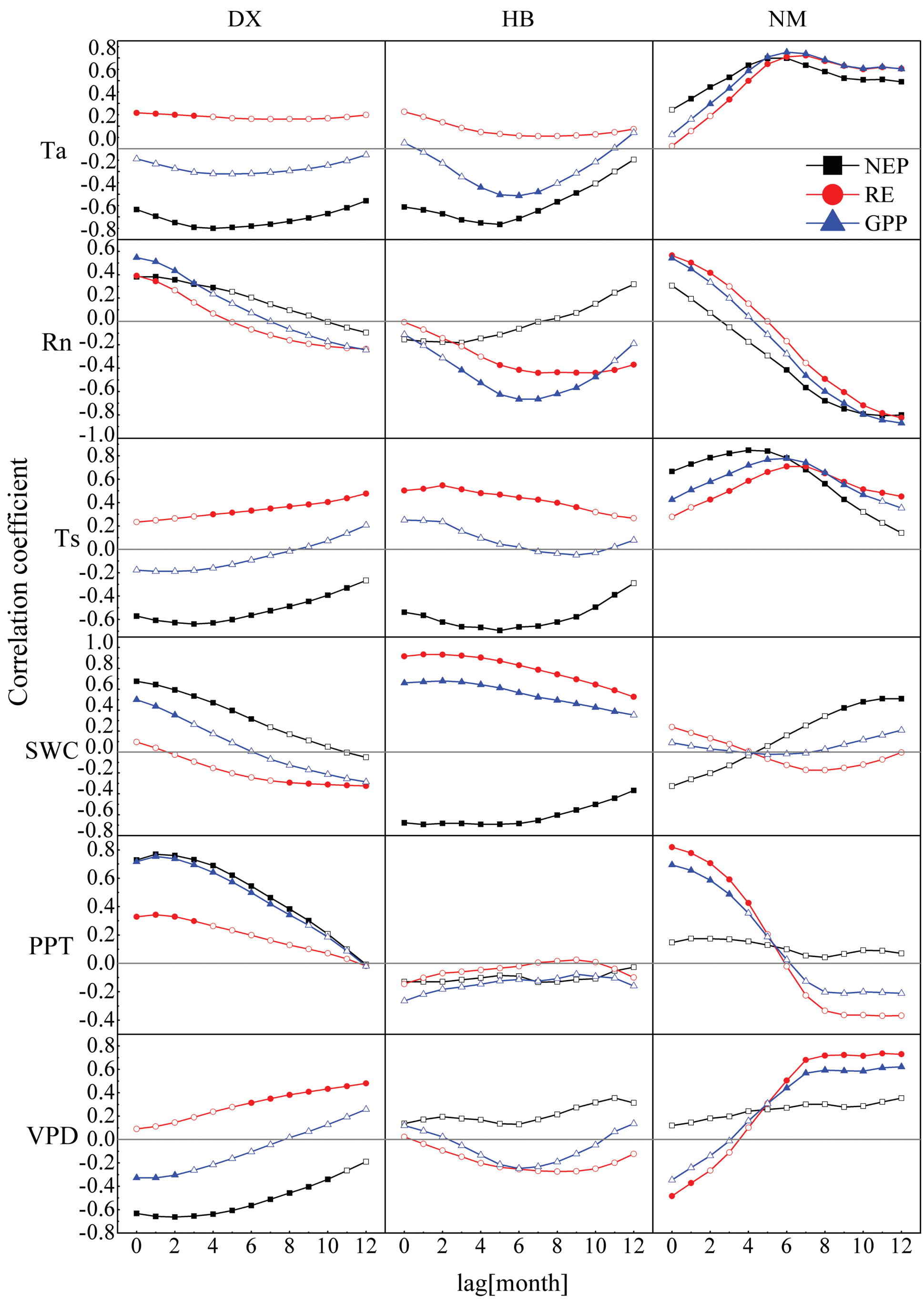

Figure 4: correlation coefficients between annual carbon fluxes and corresponding climatic factors (Ta, Rn, Ts, SWC, PPT and VPD) in DX, HB and NM. Solid patterns represent highly significant correlations ($P < 0.01$).

method to reveal and quantify the time lagged effects of climatic factors on ecosystem carbon fluxes and showed that each climatic factor has different magnitude of lag effect on carbon fluxes over the three grassland ecosystems.

The lag effects associated with temperature (Ta and Ts) were obvious at the three sites, which indicated that grassland ecosystems require longer period to respond to changes in temperature (Marcolla *et al.* 2011). This may be related to temperature's impact on phenology (Galvagno *et al.* 2013; Richardson *et al.* 2010), especially during green-up period in spring (Zhang *et al.* 2011). The changed spring phenology could accelerate nitrogen (N) cycling and leads to cascade effects on N uptake, foliar N concentrations and photosynthetic capacity (Richardson *et al.* 2009), thereby affecting ecosystem carbon cycling in the whole year (Piao *et al.* 2009). While the main part of carbon fluxes stem from vegetation growth in the peak growing season, which is several months after spring. This may explain why temperatures showed parabolic lag effects. The lag effect of temperature was weakest at DX, followed by HB. The NM site had the strongest lag effect related to temperature, meaning its greater resistance against extreme temperatures (Granier *et al.* 2007). This also reflected the higher stability of temperate steppe ecosystems than that of alpine ecosystems.

The lag effects of moisture (SWC and PPT) on carbon fluxes in alpine ecosystems were not obvious, except the 1-month PPT lag effect at DX. At NM, PPT generated both immediate effects and a certain degree of negative impacts on carbon fluxes in the following year. The reason might lie in that stronger plant growth under suitable precipitation led to increased biomass accumulation in the current year, which in turn caused enhanced microbial competition for nutrients (Van Der Heijden *et al.* 2008) and reduced plant growth in the next year (Braswell *et al.* 1997). In addition, SWC showed a significant 1-year lag effect on NEP ($R = 0.51$, $P < 0.01$) in this semiarid grassland, which indicated that the SWC in a given year may have significant effect on NEP in the subsequent year. The lag effect of SWC may be attributed to the altered water use strategies of plants under soil water stress (Granier *et al.* 2007; Hao *et al.* 2008) or long turnover time of deep soil moisture (Braswell *et al.* 1997). The 1-year lag effect of SWC on NEP was not obvious for GPP and Re. Partitioning NEP into other types of components might give a better explanation. For example, NEP can be partitioned as the difference between net primary productivity (NPP) and heterotrophic respiration. Similar findings have been reported for forest ecosystems, where reduced NPP was caused by reduced carbohydrate, lipids and protein reserves during the previous drought year (Bréda *et al.* 2006).

Without considering its interactions with other factors, Rn's driving effect on carbon flux was mostly exhibited as an immediate manner (Xu *et al.* 2014) as observed at DX. In fact, the lag effects of Rn on carbon fluxes could also become operative through its action on moisture conditions (Hollinger *et al.* 2004) due to the negative effect of Rn on SWC, as observed at HB and NM sites. The SWC was the main driver on carbon fluxes at HB, which counteracted the direct effect of Rn and resulted in negative correlation with a half-a-year lag. At the semiarid NM site, stronger Rn could lead to more water loss, which turns environment unfavorable for grass to turn green in the following year, consequently causing lower carbon fluxes of the next year (Teklemariam *et al.* 2010). Rn could stimulate GPP and Re immediately but lead to no obvious improvement for NEP, while stronger Rn could result in a rapid reduction of NEP with 1-year lag, meaning that lower carbon sink occurred 1 year after high Rn. Therefore, stronger Rn will be disadvantageous to carbon fixation for the semiarid grassland ecosystem at NM.

The components of carbon flux parameters contributing to the lag effects

The carbon flux measured by EC technique could be considered as NEP. NEP directly measures the net ecosystem carbon absorption or emission, whose spatio-temporal dynamic is controlled by its two components—GPP and Re (Baldocchi *et al.* 2001). Similar studies have been plentifully reported (Dunn *et al.* 2007; Lafleur *et al.* 2003). Furthermore, NEP varies from short to longer temporal scales and this variability is also driven by the responses of its two terms to abiotic and biotic factors (Stoy *et al.* 2009).

The time lagged effect analysis in this study showed that the dependence of NEP on climatic factors was jointly decided by the dependences of GPP and Re on climatic factors across a long time scale. Both GPP and Re showed similar correlograms with all climatic factors in this study. This lends further support to the viewpoint of their mechanistic interdependences (Lasslop *et al.* 2010). Generally, NEP is positively correlated with each climatic factor when the correlation coefficients between GPP and the climate factor are higher than those between Re and the same climate factor, and NEP is negatively correlated with each climatic factor when the correlation coefficients between GPP and the climate factor are lower than those between Re and the same climate factor (Marcolla *et al.* 2011). However, there are some exceptions. For example, the correlation curves between carbon fluxes and PPT (and VPD) at NM fell apart from this rule, probably due to its dry weather conditions. In addition, both Ta and Ts all had positive correlations with Re over the three sites. While the sign of the correlation between NEP and the temperatures cohered with those between GPP and the temperatures. For example, at DX and HB sites, the correlation between GPP and temperature was negative. So the correlation between NEP and temperature was also negative, vice versa at NM (Fig. 4). Also, the lag effect of Ta on GPP directly led to the lag effect on NEP at HB. Therefore, the variations, even hysteresis of NEP, might depend on that of GPP (Yu *et al.* 2013).

The correlation between PPT and NEP was not significant at NM. The reason could be the fast reorganization of plant community among years with different PPT in temperate grassland. For example, Xia *et al.* (2009) found plant community structure could shift fast to keep the same nitrogen and warming responses of NEP between two hydrologically contrasting years. However, we found PPT had a high correlation with GPP and Re, while NEP was not sensitive to PPT probably due to the consistent responses of GPP and Re to PPT as we discussed in Environmental controls on carbon fluxes in grasslands. Under future climate change scenarios such as climate change or interactions between changed meteorological factors, the balanced responses of GPP and Re to PPT may be broken, then the dominant effect of PPT on NEP would surface. So we can take PPT as the potential main control factor in this region.

The characteristics of the lagged effects

Climatic factors could result in step changes in ecosystem processes, which will have a continuous and long-term impact on carbon fluxes (Goldstein *et al.*, 2000). In the meantime, the impact of climatic forcing is weakened by lagged changes in ecosystem structure and functional responses to climate. That is to say, the plasticity of ecosystem responses acts as a buffer to postpone the effects of climatic factors on ecosystem carbon fluxes (Braswell *et al.* 1997; Teklemariam *et al.* 2010).

The lagged responses of ecosystem processes to climate occurred at different temporal scales (Richardson *et al.* 2007; Stoy *et al.* 2009). For example, the effects of light and temperature on the kinetics of photosynthesis are nearly instantaneous (Sage *et al.* 2007); the physiological acclimation is considered a relatively slow process occurring on a temporal scale of a day or week (Luo *et al.* 2001, Richardson *et al.* 2007); the biogeochemical processes such as changes in N cycling rates may operate over months or years' scale, or even longer (Richardson *et al.* 2009, Schimel *et al.* 1990). Therefore, it is possible that the relationships between carbon fluxes and key meteorological variables are not consistent among years (Teklemariam *et al.* 2010). Some climatic factors' effects on ecosystem process may exhibit a 1-year lag (Braswell *et al.* 1997; Teklemariam *et al.* 2010). So understanding the lag effects of climate variability is critically important for adequately evaluating the impacts of climate change on ecosystem carbon balance.

As observed in this study, the temporal responses of ecosystem carbon fluxes to each environmental factor were different, and the signs of the lag effect correlations can even be opposite to those of the immediate effects due to interactions between climatic factors (Hollinger *et al.* 2004) or tradeoff effects between plant and microbial activity (Braswell *et al.* 1997). The seasonal shedding of leaves and roots affect the input of biomass to heterotrophic microorganisms. Suitable climate could promote plant growth and biomass inputs in a given year, which could cause increased microbial competition for nutrients and reduced plant growth in subsequent years (Braswell *et al.* 1997).

The lag effects are also different among ecosystem types (Hollinger *et al.* 2004; Richardson *et al.* 2009). Structural growth restricted biomass production of trees (Körner 2003), thereby influencing carbon budget. Climatic factors could exhibit a lasting impact on growth of perennial trees, even over years (Chapin Iii and Starfield 1997). In the temperate grassland ecosystem at the NM site in this study, climatic factors also showed a strong time lag effect as seen by the up to 1 year delayed effects from Rn, SWC and PPT. In the alpine ecosystem at DX and HB site, climatic factors showed relatively weaker time lag effects. It indicates that the alpine ecosystems might become more sensitive to global environmental change.

The variations of ecosystem carbon fluxes might be driven by both climatic factors and ecosystem responses (Marcolla *et al.* 2011, Wu *et al.* 2012). The ecosystem responses could be intuitively demonstrated by time lagged effects (Marcolla *et al.* 2011, Xu *et al.* 2014), stemmmed from the plasticity of ecosystem response (Odum 1969). Compared with the direct effects caused by climatic factors, time lagged effects more clearly reflect the internal changes of ecosystems and reflect one further step into the effects of climatic factors on ecosystem.

CONCLUSION

This study analyzed the direct and lagged effects of climatic factors on carbon fluxes over the three grassland systems in China. Both temperature and moisture conditions had time lagged effects on the carbon fluxes. Several months even half a year temperature lag effects were observed at the three sites. Moisture conditions tended to show mostly immediate effects except at NM. The time lagged effect was more obvious in the temperate grassland than that in the alpine ecosystem. Therefore, alpine ecosystems would be more sensitive under future climatic change. This study showed that the time lagged effect would delay the positive feedback of carbon fluxes to climate change and emphasized the importance of optimizing models that are solely driven by climatic factors. In the future studies, longer EC data series would be critical to more accurately reveal the impacts of climate variability on ecosystem behaviors.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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