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Ecosystem response more than climate variability drives the inter-annual variability of carbon fluxes in three Chinese grasslands

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ABSTRACT

The inter-annual variability (IAV) of net ecosystem productivity (NEP) may be caused by both climatic factors and ecosystem responses. In this study, we used eddy covariance (EC) measurements over three typical grasslands in China to investigate the dynamics of NEP and its two components – gross primary productivity (GPP) and ecosystem respiration (Re) and their driving forces. We found that climatic factors and ecosystem response simultaneously influence the IAV of ecosystem carbon fluxes, with a dominant effect arising from an ecosystem response. On a daily scale, carbon fluxes were driven primarily by climatic factors, but effects from an ecosystem response strengthened when the period of analysis was extended. On an annual scale, ecosystem responses weakened the effects of climatic variability on ecosystem carbon fluxes for the three grasslands. This negative feedback demonstrated that ecosystem acclimatization to climate variability can constrain the IAV of carbon fluxes induced by such variability.

1. Introduction

Carbon flux of grassland ecosystems normally exhibits higher sensitivities to climatic perturbations than do forest ecosystems (Novick et al., 2004; Flanagan et al., 2002; Gilmanov et al., 2007; Polley et al., 2010). This leads to greater uncertainty in estimating grassland carbon budgets. More thorough knowledge about how environmental and biological factors drive carbon flux variability and related mechanisms is critical to account for their present status and predict their future status. In addition, the longer the time scale, the more complex the driving mechanisms become. To date, our knowledge on the aforementioned aspects is still severely limited (Hui et al., 2003).

A number of factors interact to influence the variability of carbon fluxes and make separating their respective effects difficult (Hui et al., 2003). Moreover, such effects are dynamic across multiple spatial and temporal scales (Stoy et al., 2009). These factors include temperature, precipitation, radiation and other climatic factors (Griffis et al., 2000); interrelated physiological and ecological processes (Botta et al., 2000; Griffis et al., 2000); and a dynamic balance between photosynthesis and respiration (Potter et al., 2001; Schimel et al., 2001). According to their sources, the drivers of carbon flux can generally be divided into two categories (Marcolla et al., 2011; Wu et al., 2012): abiotic (climate) and biotic (ecosystem responses).

Previous studies have focused mainly on direct impacts of climatic factors, while neglecting effects of ecosystem responses (Xu and Baldocchi, 2004; Zhang et al., 2011; Wu et al., 2012). However, effects of ecosystem responses are in fact persistent phenomena. Fire affects ecosystem structure and generates spatial heterogeneity across a landscape (Goetz et al., 2007). Nitrogen deposition causes changes in plant species composition and ecosystem productivity (Berendse et al., 2001; Stevens et al., 2004). Defoliation can transfer stress signals to interspecific neighbors through ectomycorrhizal networks to facilitate ecosystem recovery and succession after disturbance (Song et al., 2015). All these disturbances and management practices are expected to weaken the

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relationship between carbon fluxes and climatic variables, resulting in a larger contribution of ecosystem responses (Shao et al., 2013; Shao et al., 2015; Zhang et al., 2015b). In certain situations, ecosystem responses might exert an even greater influence on carbon fluxes than those generated by climate (Hollinger et al., 2004; Richardson et al., 2007; Desai et al., 2010; Marcolla et al., 2011). Especially for studies conducted on temporal scales longer than one year, effects of ecosystem responses require more adequate attention (Katul et al., 2001). For example, high spring temperatures were found to enhance photosynthesis in the following autumn (Richardson et al., 2009). Favorable climate may promote plant growth in a given year, but in subsequent years plant growth might decrease due to tradeoff effects between plant and microbial activities (Braswell et al., 1997).

Parametric models are commonly used in studying carbon flux patterns (Griffis and Rouse, 2001; Katul et al., 2001; Richardson et al., 2007; Stoy et al., 2009) and their relationships to climatic variability. However, these models are invariably constrained in being biased toward effects of environmental drivers (Gunderson et al., 2010), while neglecting effects of ecosystem responses. Water stress can amplify the effects of ecosystem responses (Granier et al., 2007; Hao et al., 2008). As a result, the accuracy of VPM models that fail to include ecosystem responses decreases under conditions of severe drought (Wu et al., 2008). In addition, ecosystem responses may act as a buffer and result in lagged effects of climatic factors on ecosystem carbon fluxes (Braswell et al., 1997; Teklemariam et al., 2010). Such lagged effects induced by temperature on CO_2 can last for several months, even half a year (Zhang et al., 2015a), yet these effects are often neglected by parametric models. Therefore, ecosystem response effects must be taken into account to improve the accuracy of parametric models.

To date, few studies have been reported in quantifying ecosystem responses (Hui et al., 2003; Richardson et al., 2007; Polley et al., 2010; Marcolla et al., 2011; Wu et al., 2012) or on the relative contribution of climatic factors and ecosystem responses to carbon fluxes (Xu et al., 2014), especially for grassland systems. To address the aforementioned issues, we chose three typical grassland ecosystems in China and used their nearly-continuous eddy-covariance flux data to: (1) characterize the IAV of carbon fluxes; and (2) separate the sources of IAV into climate effects and ecosystem responses.

2. Data and methodology

2.1. Site description

Measurements were conducted across three grassland ecosystems located on the Qinghai-Tibet Plateau and Inner Mongolia Plateau, which represent two typical grasslands in China. The three grassland ecosystems include an alpine *Kobresia pygmaea* meadow-steppe ecosystem with an alpine monsoon climate at Dangxiong site (DX) located in the hinterland of the Qinghai-Tibet Plateau; an alpine *Potentilla fruticosa* shrub-meadow ecosystem with a continental monsoon climate at Haibei site (HB) located on the northeast edge of the Qinghai-Tibet Plateau; and a temperate *Leymus chinensis* steppe ecosystem with a continental semi-arid climate at Neimeng site (NM) located in the Xilin River Basin in Inner Mongolia (Table 1). Detailed descriptions of these study sites may be found in Li et al. (2003) for HB, Shi et al. (2006) for DX, and Fu et al. (2006b) and Hao et al. (2006) for NM.

2.2. Measurements and data processing

Eddy covariance carbon fluxes at the three sites were measured at a height of 2.5 m with standard systems, including an open-path EC infrared CO_2/H_2O analyzer (Model LI-7500, Li-cor Inc., Nebraska, USA) and a three-dimensional sonic anemometer (Model CSAT-3, Campbell Scientific Inc., Logan, Utah, USA). All raw data were sampled with a frequency of 10 Hz and then recorded at 30-min intervals by a CR5000 datalogger (Model CR5000, Campbell Scientific). Micrometeorological conditions, including air temperature (Ta), net radiation (Rn), precipitation (PPT) and soil volumetric water content at a depth of 5 cm (SWC) were measured at 1 Hz, then averaged for half-hour intervals.

We utilized Matlab7.11 software (MathWorks Inc., Natick, MA, USA) to process flux data. A three-dimension rotation was used to align the coordinate system with mean wind direction (Falge et al., 2001; Wilczak et al., 2001). Then we applied the WPL correction – the Webb, Pearman and Leuning density correction for effects of air density fluctuations—to adjust air density changes caused by heat and water vapor fluctuations (Webb et al., 1980). Anomalous or spurious values caused by sensor malfunction and interference from rain, dew, hoarfrost, and birds, etc. were excluded from our analysis. The eddy covariance technique is likely to underestimate nighttime CO_2 fluxes due to low-atmospheric turbulence under stable conditions (Reichstein et al., 2005). We excluded night observations (solar elevation angle <0) when the friction velocity (u^*) was under the thresholds as determined by plotting nighttime CO_2 fluxes to friction velocity at each site (Reichstein et al., 2005). The thresholds were identified as 0.15 m s^{-1} for DX and HB and 0.2 m s^{-1} for NM, respectively. We did not consider self-heating as it only occurred in winter for the open-path eddy covariance system. Winter temperature is extremely low in our study area and carbon fluxes in winter only account for a small proportion of the annual fluxes, thus contributing little to the inter-annual variation of annual carbon fluxes (Burba et al., 2008; Reverter et al., 2011; Zhu et al., 2012). Linear and nonlinear fittings and mean diurnal variations were adopted to fill missing and spurious data (Fu et al., 2006a). Finally, we aggregated 30-min-average flux data to daily, monthly and annual sums.

2.3. Partitioning the sources of the inter-annual variability of carbon flux

The IAV of ecosystem carbon fluxes can be ascribed to two main sources—climate and ecosystem responses. We used a look up table (LUTs) method to separate the respective effects of climate and ecosystem responses (Marcolla et al., 2011; Xu et al., 2014). In the process, the key was to build LUTs for each individual year and data averaged over multiple years. The two types of LUTs can be used to extract the individual effects of climate or ecosystem responses from their strongly coupled interactions.

Among the set of climate factors potentially regulating carbon fluxes, hydrothermal conditions play a primary role (Piao et al., 2008; Barron-Gafford et al., 2012; Parton et al., 2012). Thus for climate data, we included only temperature and soil water content. To create the LUTs, we merged 30-min-average temperature, soil water content and carbon flux data (NEP, GPP, Re) to a daily sum for each year. We integrated these daily sums into one table, the daily data table (DD, Table S1).

(1) Generating the LUTs for Variable Climate and Variable Ecosystem Response (VC_VER). We classified the flux data into each range of temperature (Ta, per 0.2 °C) and soil water content (SWC, per 0.03 m^3 m^{-3}) for each year using DD. Within each climatic data range, each carbon flux component (NEP, GPP, Re) might have several daily values, and we took their separate averages. This enabled the generation of a second table of data comprised of a series of climate data ranges and their corresponding carbon fluxes, this table being referred to as the annual LUT (ANN_LUT, Table S2). We used the daily climate