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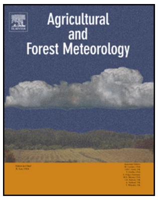

Biotic and climatic controls on interannual variability in carbon fluxes across terrestrial ecosystems

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ABSTRACT

Interannual variability (IAV, represented by standard deviation) in net ecosystem exchange of CO_2 (NEE) is mainly driven by climatic drivers and biotic variations (i.e., the changes in photosynthetic and respiratory responses to climate), the effects of which are referred to as climatic (CE) and biotic effects (BE), respectively. Evaluating the relative contributions of CE and BE to the IAV in carbon (C) fluxes and understanding their controlling mechanisms are critical in projecting ecosystem changes in the future climate. In this study, we applied statistical methods with flux data from 65 sites located in the Northern Hemisphere to address this issue. Our results showed that the relative contribution of BE (CnBE) and CE (CnCE) to the IAV in NEE was 57% ± 14% and 43% ± 14%, respectively. The discrepancy in the CnBE among sites could be largely explained by water balance index (WBI). Across water-stressed ecosystems, the CnBE decreased with increasing aridity (slope = 0.18% mm^{-1}). In addition, the CnBE tended to increase and the uncertainty reduced as timespan of available data increased from 5 to 15 years. Inter-site variation of the IAV in NEE mainly resulted from the IAV in BE (72%) compared to that in CE (37%). Interestingly, positive correlations between BE and CE occurred in grasslands and dry ecosystems ($r > 0.45$, $P < 0.05$) but not in other ecosystems. These results highlighted the importance of BE in determining the IAV in NEE and the ability of ecosystems to regulate C fluxes under climate change might decline when the ecosystems experience more severe water stress in the future.

1. Introduction

Atmospheric CO_2 concentration has been dramatically increased since the Industrial Revolution, which has caused a

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corresponding rise of 0.85 °C in global air temperature from 1880 to 2012 (IPCC, 2013). The interannual fluctuation of atmospheric CO_2 concentration is primarily attributed to the interannual variability (IAV) in net ecosystem exchange of CO_2 (NEE) between the atmosphere and global terrestrial ecosystems (Le Quéré et al., 2009). The IAV in NEE is a phenomenon observed at almost all eddy-flux sites around the world (Baldocchi, 2008). The factors driving the IAV in NEE include (1) climate, (2) physiological processes, (3) phenology, (4) ecosystem structure, (5) nutrient cycling in ecosystems, and (6) disturbance (Hui et al., 2003; Marcolla et al., 2011; Polley et al., 2008; Richardson et al., 2007). Among these, the changes in climatic variables and physiological processes can directly affect the IAV in NEE. In this study, we defined the direct effects of climatic drivers as the climatic effects (CE) and the effects of ecological and physiological changes (i.e., the changes in photosynthetic and respiratory responses to climate) on the IAV in carbon (C) fluxes caused by either climate or other factors ((3)–(6) above-mentioned) as the biotic effects (BE). As a result, the IAV in NEE can be considered as the combined consequence of CE and BE on NEE.

Quantifying the magnitude of CE and BE and their relative contributions to the IAV is essential to understand the mechanisms underlying the IAV in NEE and to forecast the potential response of ecosystem C cycling to future climate change. Previous studies have shown that the importance of BE could be larger than (Delpierre et al., 2012; Polley et al., 2008; Wu et al., 2012), equivalent to (Hui et al., 2003; Richardson et al., 2007), or less than (Delpierre et al., 2012; Polley et al., 2008; Teklemariam et al., 2010) that of CE at the interannual scale. However, whether such discrepancy was related to disturbances (Polley et al., 2008), vegetation types (Adkinson et al., 2011; Wu et al., 2012), or other factors is not well quantified. In addition, weak or strong negative correlations between CE and BE have been found (Richardson et al., 2007; Shao et al., 2014), which reflects the responses of ecosystem C cycling to climatic variations. Exploring whether such a negative correlation is common among ecosystems will be helpful in clarifying the debate on the positive feedback between C cycling and climatic change (Cox et al., 2000; Friedlingstein et al., 2006; Luo et al., 2009).

At the regional and global scales, the spatial differences of the IAV in NEE might be influenced by ecosystem characteristics (e.g., climate, nutrient, and plant community). Modeling studies suggested that those areas with El Niño-Southern Oscillation (ENSO) and in tropical regions had the relatively larger IAV in NEE (Gurney et al., 2008; Jung et al., 2011), while a synthesis of FLUXNET data showed a latitudinal trend of the IAV in NEE at deciduous broadleaf forests (DBF), in which temperature was the main controlling factor (Yuan et al., 2009). A comparative study in two similar grasslands in Hungary suggested that soil type significantly affected the IAV in NEE by modifying the relationships between precipitation and C fluxes (Pintér et al., 2008). Adkinson et al. (2011) found that nutrient conditions and plant functional types also affected the IAV in NEE between two fens in Canada. However, to our knowledge, no study has investigated the relative importance of CE and BE to the inter-site differences of the IAV in NEE.

To address these issues, it is necessary to quantify the magnitude of CE and BE and their relative importance to the IAV in NEE. Delpierre et al. (2012) defined the relative importance of biotic and climatic variables in a model as the relative contributions of BE and CE to the IAV, respectively. Unfortunately, this approach is not always appropriate because biotic drivers are usually difficult to obtain. Hui et al. (2003) and Richardson et al. (2007) attributed the CE and BE to the changes in the model outputs caused by changed values of variables and parameters, respectively. However, model-data mismatching (Hui et al., 2003; Polley et al., 2008; Teklemariam et al., 2010) and site-specific relationships between climatic variables and C fluxes (Richardson et al., 2007) caused the great difficulty in multi-site comparisons. Therefore, a more flexible method should be developed to compare multi-site results.

In this study, we applied an additive model (a non-parametric regression method) and a model averaging technique (based on Akaike weights) to simulate the relationships between climatic variables and C fluxes. The observed IAV in NEE was then partitioned into BE and CE. Consequently, we were able to examine the relative importance of BE and CE to the IAV in NEE within an ecosystem and to the differences of IAV among ecosystems, and the relationships between BE and CE. Our primary objectives were to distinguish the main factors influencing the relative importance of BE (or CE) to the IAV in NEE, and to evaluate the potential responses of ecosystem C cycling to climatic variations.

2. Materials and methods

2.1. Data sources and sites information

Our study was based on 481 site-years of data from 65 eddy covariance measurement sites, which belong to AmeriFlux (public.ornl.gov/ameriflux/index.html), CarboEurope (www.carboeurope.org), and ChianFLUX (www.chinaflux.org) from 1992 to 2010 (Fig. 1). The original data includes half-hour CO_2 flux (Fc), friction velocity (u^*), photosynthetically active radiation

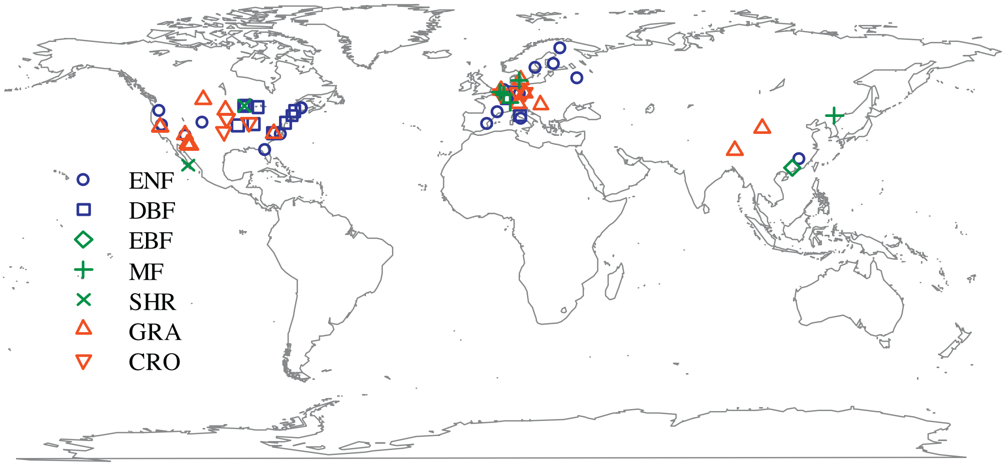

Fig. 1. Study sites distribution map. The abbreviations of ecosystem types are the same as those in Table 1. Our study contained 22 evergreen needleleaf forests (ENF), 12 deciduous broadleaf forests (DBF), 1 evergreen broadleaf forest (EBF), 5 mixed forests (MF), 16 grasslands (GRA), 7 croplands (CRO) and 2 shrublands (SHR) from North America, Europe and China.