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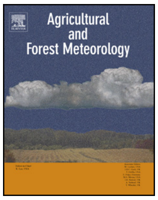

# Covariation between gross primary production and ecosystem respiration across space and the underlying mechanisms: A global synthesis

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ABSTRACT

Gross primary production (GPP) and ecosystem respiration (RE) are two important processes in the terrestrial carbon cycle. Understanding the relationships between GPP and RE across space, as well as the underlying mechanisms, is helpful for understanding the terrestrial carbon cycle and predicting the global carbon budget. In this study, we investigated the correlation between the spatial variations in GPP and RE by compiling carbon flux data from 264 sites across the Asian, European, North American, South American, African, and Oceanian regions. The results indicated that GPP and RE covaried across space regionally and globally ($P < 0.001$). The spatial variations in GPP explained 66–98% of the variations in RE in the six regions (approximately explained 60–76% when considered the effects of self-correlation caused by current flux partitioning algorithm), and it explained 90% of RE variations at the global scale (about 70% when considered the effects of self-correlation). RE/GPP values were not significantly different among the six regions or between the two hemispheres. RE/GPP values consistently averaged at $0.87 \pm 0.04$ along the spatial variations in climate and vegetation index. This covariation between GPP and RE across space is largely attributed to the parallel responses of GPP and RE to the common climatic and vegetation factors, but the underlying mechanism lies in productivity as the primary and direct substrate supplier for respiration which fundamentally constrains RE. These results suggest that the variation in photosynthate availability is the dominant driver for respiration across space and that this process must be fully considered in the cross-site RE comparisons.

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## 1. Introduction

Global $CO_2$ emissions are projected to continue to rise. Increasing terrestrial ecosystem carbon (C) uptake has been proposed as an effective way to mitigate future climate change (Lal, 2012). Gross primary production (GPP) and ecosystem respiration (RE) are two essential components of the terrestrial carbon cycle. GPP represents the gross $CO_2$ uptake through photosynthesis by all plants at the ecosystem level (Chapin et al., 2002; Luyssaert et al., 2007). RE is the gross $CO_2$ release from the ecosystem through both autotrophic respiration ($R_a$), which provides energy for the growth and maintenance of foliage, wood, and roots (Chapin et al., 2002; Waring et al., 1998), and heterotrophic respiration ($R_h$), which derives from the process of decomposition through microbial activities (Luyssaert et al., 2007). Understanding the variations in GPP and RE and their relationships is helpful for better understanding the terrestrial carbon cycle and predicting the global carbon budget.

The eddy covariance technique provides a useful independent approach to the quantification of GPP and RE by measuring and partitioning net ecosystem exchange (NEE). Extensive research has been conducted to explore the GPP and RE seasonal dynamics (Goulden et al., 2004), interannual variability (Wilkinson et al., 2012; Yu et al., 2008), and responses to extreme droughts (Ciais et al., 2005; Reichstein et al., 2007a) and disturbances (Amiro et al., 2010; Dore et al., 2010). From these findings, researchers have gradually recognized that GPP and RE are not independent, but are two strongly associated ecological processes. RE is strongly coupled with GPP across timescales (Dunn et al., 2007; Migliavacca et al., 2011). For example, RE follows the same dynamic patterns as GPP from daily to seasonal scales (Krishnan et al., 2009; Migliavacca

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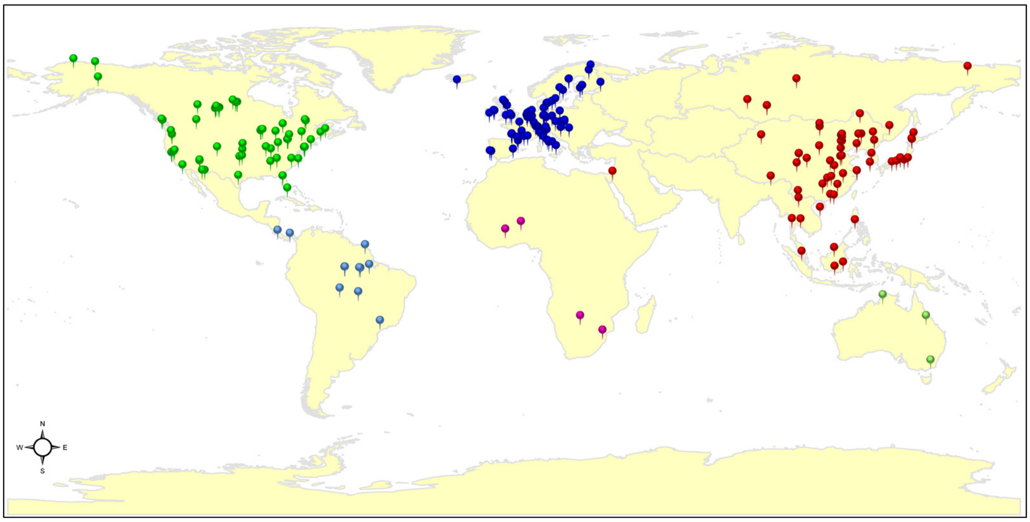

**Fig. 1.** Location and spatial distribution of the flux sites used in this study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Symbols indicate the location of the flux sites. Red, dark blue, dark green, light blue, pink, and light green symbols indicate the flux sites in the Asian ($n = 70$), European ($n = 91$), North American ($n = 83$), South American ($n = 13$), African ($n = 4$), and Oceanian regions ($n = 3$), respectively.

et al., 2011; Thomas et al., 2009). Annually, GPP and RE are both enhanced in humid years, but repressed in dry years (Hussain et al., 2011; Rodrigues et al., 2011); especially, both of them are remarkably reduced in extreme drought years (Granier et al., 2007; Reichstein et al., 2007a).

In fact, the tightly coupled relationship between GPP and RE is not only temporal, but occurs at the spatial scale as well. Janssens et al. (2001) showed that annual RE increases linearly with GPP across 18 European forest ecosystems. Law et al. (2002) gave further evidence for the linear correlation between GPP and RE across space by examining 34 FLUXNET sites. Yu et al. (2013) showed that GPP and RE exhibit tight covariation across space in China.

Although several studies have examined the relationships between the spatial variations in GPP and RE, the study sites were mainly located in the Northern Hemisphere, particularly concentrated in the North America and Europe (Janssens et al., 2001; Law et al., 2002; Reichstein et al., 2007b). We still lack knowledge about the covariation between GPP and RE in Asia and in the Southern Hemisphere. More importantly, the underlying mechanism for the GPP and RE covariation is not fully clear, and the ecological implications are much less discussed.

This study was conducted to analyze carbon flux data at the global scale to: (1) reveal the covariation between GPP and RE across global ecosystems, (2) explore the underlying mechanisms for the covariation between GPP and RE, (3) and discuss the ecological implications of the covariation.

## 2. Materials and methods

### 2.1. Data collection and screening

We collected global carbon flux data (GPP and RE) measured by the eddy covariance technique from published literature over the past two decades (1990–2010). The data were required to be filtered and corrected by researchers of each site, using coordinate rotation, WPL correction, storage flux calculation, outlier filtering, nighttime flux correction, NEE gap filling and partitioning. Additionally, data must continuously be measured at least for an entire year, and the annual GPP and RE values were both available.

In total, 913 site-year GPP and RE records from 264 sites were included in this study. These studied sites span from 35.66°S to 71.32°N in latitude, and from 156.63°W to 161.34°E in longitude across the Asian (70 sites), European (91 sites), North American (83 sites), South American (13 sites), African (4 sites), and Oceanian regions (3 sites) (Fig. 1). They covered five major climate zones: tropical, subtropical, temperate, boreal, and subarctic, and included eight biomes: evergreen broad-leaved forests (22 sites), evergreen needle-leaved forests (68 sites), deciduous broad-leaved forests (26 sites), deciduous needle-leaved forests (5 sites), mixed forests (14 sites), grasslands (67 sites), croplands (34 sites), and wetlands (28 sites). The locations, ecosystem types, and GPP and RE values are listed in Table S1 in the Supplements.

### 2.2. Climatic data

Climatic variables including the mean annual temperature (MAT), mean annual precipitation (MAP), and mean annual solar radiation (MAR) were also collected. For sites missing temperature and precipitation data, we used the global surface summary of daily data produced by the National Climatic Data Center (NCDC) (ftp://ftp.ncdc.noaa.gov/pub/data/gsod/) from their neighboring meteorological stations to fill the gaps. Ten sites were filled for temperature, two sites for precipitation, and six sites for both. MAR was less available compared to MAT and MAP, so we extracted MAR data from the Climate Research Unit (CRU05) Monthly Climate Database (http://daac.ornl.gov/ISLSCP_II/guides/cru_monthly_mean_xdeg.html) provided by the International Satellite Land Surface Climatology Project (ISLSCP). The 30-year (1961–1990) MAR from the CRU database showed good agreement ($R^2 = 0.79$) with the MAR measured at the flux tower sites during the period of interest. In the analysis, we used the 30-year averaged MAR from the CRU database for uniformity.

### 2.3. Vegetation data

The Enhanced Vegetation Index (EVI) combines the reflectance values from multiple spectral bands and can provide useful land cover information (Huete et al., 2002). The satellite-borne Moderate Resolution Imaging Spectroradiometer (MODIS) data product (MOD13Q1) provides global EVI at a spatial resolution of 250 m and a temporal resolution of 16 days from 2000 to present (Huete et al., 2002). For each flux site, we obtained its MOD13Q1 subset from the Oak Ridge National Laboratory's Distributed Active Archive Center (http://daac.ornl.gov/MODIS/). Accounting for the 1 km spatial

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