

# Quantifying spatially and temporally explicit CO<sub>2</sub> fertilization effects on global terrestrial ecosystem carbon dynamics

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**Abstract.** Current terrestrial ecosystem models are usually driven with global average annual atmospheric carbon dioxide (CO<sub>2</sub>) concentration data at the global scale. However, high-precision CO<sub>2</sub> measurement from eddy flux towers showed that seasonal, spatial surface atmospheric CO<sub>2</sub> concentration differences were as large as 35 ppmv and the site-level tests indicated that the CO<sub>2</sub> variation exhibited different effects on plant photosynthesis. Here we used a process-based ecosystem model driven with two spatially and temporally explicit CO<sub>2</sub> data sets to analyze the atmospheric CO<sub>2</sub> fertilization effects on the global carbon dynamics of terrestrial ecosystems from 2003 to 2010. Our results demonstrated that CO<sub>2</sub> seasonal variation had a negative effect on plant carbon assimilation, while CO<sub>2</sub> spatial variation exhibited a positive impact. When both CO<sub>2</sub> seasonal and spatial effects were considered, global gross primary production and net ecosystem production were 1.7 Pg C·yr<sup>-1</sup> and 0.08 Pg C·yr<sup>-1</sup> higher than the simulation using uniformly distributed CO<sub>2</sub> data set and the difference was significant in tropical and temperate evergreen broadleaf forest regions. This study suggests that the CO<sub>2</sub> observation network should be expanded so that the realistic CO<sub>2</sub> variation can be incorporated into the land surface models to adequately account for CO<sub>2</sub> fertilization effects on global terrestrial ecosystem carbon dynamics.

**Key words:** atmospheric CO<sub>2</sub>; carbon dynamics; gross primary production; net ecosystem production; process-based ecosystem model.

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## INTRODUCTION

Increasing atmospheric carbon dioxide (CO<sub>2</sub>) mainly due to the global consumption of fossil fuels has direct and indirect effects on the global terrestrial ecosystem carbon budget (Canadell et al. 2007). Numerous ecosystem-level experiments were conducted to understand how the terrestrial ecosystem carbon cycle responds to rising atmospheric CO<sub>2</sub> (e.g., Norby et al. 2002, Long et al. 2004, Ainsworth and Long 2005, Norby and Zak 2011). Land surface models have also been used to investigate the CO<sub>2</sub> fertilization

effects on carbon dynamics (McGuire et al. 1993, Esser and Lautenschlager 1994, Pan et al. 1998, Gerber et al. 2004). However, these models were often driven with annual and uniformly distributed atmospheric CO<sub>2</sub> data (ESRL data set, <http://www.esrl.noaa.gov/gmd/ccgg/trends/>) at the global scale (Raich et al. 1991, White et al. 2000, Sitch et al. 2003, Krinner et al. 2005, Oleson et al. 2010, Lawrence et al. 2011).

Although atmospheric CO<sub>2</sub> is generally well mixed globally as it is chemically inert (Eby et al. 2009), it actually exhibits a large seasonal and spatial variability at the global scale (Miles

et al. 2012, Zeng et al. 2014). The seasonal and spatial characteristics have previously been reported at site levels (Yi et al. 2000, 2004, Davis et al. 2003, Bakwin et al. 2004, Haszpra et al. 2008, Miles et al. 2012). For example, Yi et al. (2000) reported that the monthly averaged diurnal pattern of CO<sub>2</sub> mixing ratio at a forest site in northern Wisconsin could be as large as 70 ppmv in summer season (Yi et al. 2000). The summer measurement of atmospheric boundary layer CO<sub>2</sub> mole fraction from a nine-tower regional network conducted during the North American Carbon Program's Mid-Continent Intensive (MCI) during 2007–2009 showed that the seasonal CO<sub>2</sub> drawdown (25–38 ppm) was five times larger than the tropospheric background as represented by Mauna Loa observations. The spatial gradient (1.5 ppmv/100 km) across the MCI region was four times as large as the interhemispheric gradient (Miles et al. 2012). Similarly, the remote sensing data agree with data obtained from ground-based observations (Yang et al. 2002, Yokota et al. 2009). For example, Atmospheric Infrared Sounder (AIRS) and Greenhouse Gases Observing (GOSAT) satellite retrievals showed that the distribution of carbon dioxide differed significantly between the Northern Hemisphere (NH) and the Southern Hemisphere (SH) (Chahine et al. 2008, Yokota et al. 2009) and the column-averaged dry air mole fractions of CO<sub>2</sub> in NH were generally higher. The spatially varied atmospheric CO<sub>2</sub> exhibited the semiannual oscillation (Ruzmaikin et al. 2012) with the stronger seasonal variation in northern high latitudes as indicated by the GLOBALVIEW CO<sub>2</sub> and GEOS-Chem model simulations (Feng et al. 2011).

As CO<sub>2</sub> transformed into plant carbohydrates through leaf stomata is the initial step in carbon cycling, the accurate representation of CO<sub>2</sub> spatiotemporal variation is crucial for ecosystem modeling. Here we first derived the surface daily CO<sub>2</sub> measurement at four sites from Fluxnet to show the spatial and temporal variations in surface CO<sub>2</sub>. Then the integrated Terrestrial Ecosystem Model (iTEM; Chen 2013, Liu et al. 2014) driven with two spatially and temporally explicit CO<sub>2</sub> data sets was used to analyze the atmospheric CO<sub>2</sub> fertilization effects on the global carbon dynamics of terrestrial ecosystems from 2003 to 2010.

## METHOD

### Overview

To reveal the spatial and temporal variations in atmospheric surface CO<sub>2</sub> concentrations, we first extracted the high-precision CO<sub>2</sub> measurement at four eddy flux tower sites from Fluxnet (<http://fluxnet.ornl.gov/>). Second, we carried out a simple test on the sensitivity of photosynthesis to the atmospheric CO<sub>2</sub> variation, using the coupled photosynthesis model with a stomatal function. Third, we conducted site-level tests to compare the simulated daily gross primary production (GPP) using the in situ CO<sub>2</sub> measurement with that using the uniformly distributed atmospheric CO<sub>2</sub> data. Finally, two spatially and temporally explicit CO<sub>2</sub> data sets were used to drive iTEM from 2003 to 2010 at the global scale. The two spatially and temporally explicit CO<sub>2</sub> data sets were obtained from the National Oceanic & Atmospheric Administration (NOAA) Carbon Tracker and Monitoring of Atmospheric Composition and Climate (MACC) project, respectively. In addition, we used mean annual CO<sub>2</sub> value computed from NOAA CO<sub>2</sub> and MACC CO<sub>2</sub> to quantify the effect of seasonal CO<sub>2</sub> variation on carbon dynamics. Totally, we had four simulations: (1) iTEM + NOAA CO<sub>2</sub> (S1-NOAA), (2) iTEM + mean annual NOAA CO<sub>2</sub> (S1-mNOAA), (3) iTEM + MACC CO<sub>2</sub> (S1-MACC), and (4) iTEM + mean annual MACC CO<sub>2</sub> (S1-mMACC). Therefore, the spatiotemporal CO<sub>2</sub> effect can be examined from the differences among the four simulations and the simulations (S1) based on the annual and uniformly distributed CO<sub>2</sub> data sets.

### Integrated terrestrial ecosystem model

The integrated terrestrial ecosystem model (iTEM; Chen and Zhuang 2014, Liu et al. 2014) was designed for assessing spatially and temporally explicit CO<sub>2</sub> effects on the global carbon dynamics of terrestrial ecosystems. In iTEM, photosynthesis in C<sub>3</sub> and C<sub>4</sub> plants was simulated using Farquhar photosynthesis algorithm and Collatz et al. (1991) model, respectively. The leaf stomatal conductance, using the Ball-Berry model (Ball et al. 1987) scheme, was coupled to leaf photosynthesis in a similar manner to Collatz et al. (1992). The canopy was modeled in a one-layer, two-big-leaf approach

(Dai et al. 2004), which diagnosed energy budget, leaf temperature, evapotranspiration, and photosynthesis separately for sunlit and shaded leaves. The boundary layer turbulent processes were modeled based on the Monin–Obukhov Similarity Theory. The hydrological processes included the interception, through fall of precipitation, snow accumulation, sublimation and melt, surface runoff, surface evapotranspiration, water infiltration, and redistribution in soil and subsurface drainage. These algorithms allowed the model to simulate the response of land surface processes to changing environmental conditions. The iTEM has been calibrated and validated using various sources of observation data. Technical details of the iTEM were documented in Chen (2013).

We also used the biochemistry of C3 and C4 photosynthesis (A) coupled with a stomatal model to test the sensitivity of C3/C4 plant carbon assimilation to the atmospheric CO<sub>2</sub> variation. The photosynthesis algorithm adopted from Collatz et al. (1991, 1992) was used to calculate carbon uptake with relevant parameters ( $V_{\max25}$ , maximum rate of carboxylation of Rubisco at 25°C) and considering environmental factors (boundary layer conductance, photosynthetic absorbed radiation, air temperature, relative humidity, and CO<sub>2</sub>). Leaf photosynthesis was linked to stomatal conductance via the internal CO<sub>2</sub> concentration, which was calculated using Ball-Berry model scheme. The typical environmental conditions (e.g., ambient temperature) at growing season and corresponding photosynthetic and stomatal model parameters were (Appendix S1: Table S1) used to derive the A–C<sub>a</sub> curve to quantify the sensitivity of photosynthesis to CO<sub>2</sub> variation.

### Data

The high-precision CO<sub>2</sub> measurement from 2003 to 2004 at four typical flux tower sites including Howland forest main (US-Ho1) (evergreen forest, Hollinger et al. 1999), Missouri Ozark (US-Moz) (deciduous forest, Gu et al. 2006), LBA Tapajos KM67 Mature Forest (BR-Sa1) (tropical forest, Grant et al. 2009), and one cropland flux tower site, Mead Irrigated (US-Ne1) (Verma et al. 2005), was used. The flux tower sites characterized by grassland, savannas, and tundra were not selected, because forest is generally more sensitive to CO<sub>2</sub>

variations (Ainsworth and Long 2005) and cropland has much larger photosynthetic capacity compared with other natural grassland ecosystems (Madani et al. 2014). We used the daytime averaged CO<sub>2</sub> mole fraction to account for the effects on photosynthesis for the summer season (June to September). To investigate the seasonal variability, we used a 31-d running mean to get a smooth CO<sub>2</sub> mole fraction daily daytime average data. In addition, the site-level tests were conducted using iTEM to compare the simulated daily GPP using in situ CO<sub>2</sub> observation with that using the uniformly distributed atmospheric CO<sub>2</sub> data. The micrometeorology data (e.g., radiation, wind, temperature) from the four flux sites above were used to drive the iTEM.

In global simulations, iTEM used spatially explicit data of climate, land cover, and soil. The details about the data sets of the vegetation (Appendix S1: Fig. S1) and soil texture can be found in Melillo et al. (1993) and Zhuang et al. (2003). The global simulations were applied at a spatial resolution of a 1° by 1° (longitude × latitude) for the global land area except the Antarctic. Forcing data including the radiation (direct, diffuse), the initial conditions, soil properties, the plant distribution, and vegetation-specific parameters as well as the 3-h meteorological data were from Chen and Zhuang (2014).

The explicitly spatial and seasonal CO<sub>2</sub> data from NOAA gridded CO<sub>2</sub> product (<ftp://aftp.cmdl.noaa.gov/products/carbontracker/co2/>) are based on global CO<sub>2</sub> observation network data obtained by employing a novel ensemble assimilation method to accurately model atmospheric CO<sub>2</sub> mole fractions (Peters et al. 2007). In the MACC project ([https://www.gmes-atmosphere.eu/news/co2\\_forecasts/](https://www.gmes-atmosphere.eu/news/co2_forecasts/)), atmospheric CO<sub>2</sub> concentration data are estimated by assimilating satellite observations into the ECMWF Integrated Forecasting System (IFS) Numerical Weather Prediction model. The global atmospheric CO<sub>2</sub> concentration is forecasted with a 5-d lead time at 3-h time step. Both spatially and temporally explicit CO<sub>2</sub> data sets were resampled to the spatial resolution of TEM. The annual and uniformly distributed CO<sub>2</sub> data sets for the period 2003–2010 were from ESRL data (<http://www.esrl.noaa.gov/gmd/ccgg/trends/>). Fig. 1 showed the spatial distributions of mean daytime CO<sub>2</sub> (9:00

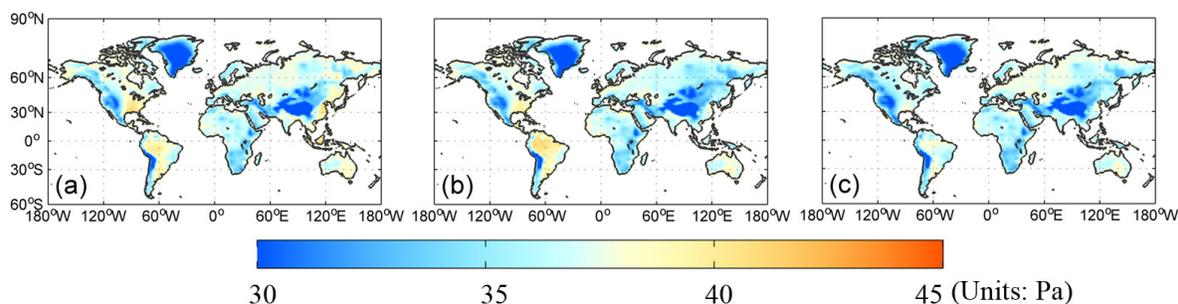


Fig. 1. The mean daytime CO<sub>2</sub> (9:00 to 15:00) partial pressure (Units: Pa) at summer (June to Sep) season during 2003–2010. (a–c) stand for the NOAA, MACC, and annual CO<sub>2</sub> partial pressure, respectively. Units: Pa.

to 15:00) partial pressure in these three products in summer (June to September) season during 2003–2010. Both NOAA CO<sub>2</sub> and MACC CO<sub>2</sub> (Fig. 1a, b) data sets indicated the CO<sub>2</sub> a large spatial variability with the value ranging from 30 to 42 Pa. Amazon and parts of China, and North America were characterized by higher CO<sub>2</sub> partial pressure (2–5 Pa) than the annual CO<sub>2</sub> data set, but Russia exhibited slightly lower partial pressure in summer season.

## RESULTS

### CO<sub>2</sub> variation among sites and sensitivity test

All of the four sites exhibited a seasonal CO<sub>2</sub> variation, ranging from 0.8 to 3 Pa (Fig. 2). US-Ne1 had the largest seasonal amplitude (3 Pa), followed by US-Ho1 and US-Moz. In addition, the in situ CO<sub>2</sub> observation only showed slightly higher concentrations than the background CO<sub>2</sub> value at BR-Sa1. Spatially, the difference also reached as large as 2.5 Pa among these sites. For example, US-Ne1 had low CO<sub>2</sub> concentrations around 34 Pa at summer time in 2003, while in US-Ho1, the observed CO<sub>2</sub> was as high as 36.5 Pa. These high-precision CO<sub>2</sub> measurements showed that there were significant spatiotemporal surface CO<sub>2</sub> variations across sites. We derived the A–C<sub>a</sub> curve for C3 and C4 plants (Fig. 3) using the coupled photosynthesis with stomatal model and the parameters in Appendix S1: Table S1. The slopes of A–C<sub>a</sub> curve at 35 Pa CO<sub>2</sub> were around 0.3 μmol CO<sub>2</sub>·m<sup>-2</sup>·s<sup>-1</sup>·Pa<sup>-1</sup> and 0.4 μmol CO<sub>2</sub>·m<sup>-2</sup>·s<sup>-1</sup>·Pa<sup>-1</sup> for C3 and C4 plants, respectively. Therefore, the 2–3 Pa CO<sub>2</sub> differences could result in the difference of A about 0.6–0.9 μmol CO<sub>2</sub>·m<sup>-2</sup>·s<sup>-1</sup>

in C3 plant and 0.8–1.2 μmol CO<sub>2</sub>·m<sup>-2</sup>·s<sup>-1</sup> in C4 plant, respectively.

### Site-level test using in situ CO<sub>2</sub> observation

The CO<sub>2</sub> diurnal cycle exhibited negative effects on photosynthesis at US-Ho1, US-Moz, and US-Ne1 sites, but little positive effects on BR-Sa1 (Fig. 4). Although the fluctuating CO<sub>2</sub> showed higher partial pressure in spring, autumn, and winter seasons in temperate regions, the low temperature inhibited the plant carbon assimilations. For US-Moz and US-Ne1, the summer daytime CO<sub>2</sub> was about 2.5 Pa lower compared with the uniformly distributed atmospheric CO<sub>2</sub> data, with expected lower photosynthesis rates. Considering the realistic CO<sub>2</sub> temporal variation at US-Moz and US-Ne1, the annual GPP was 1334 g C·yr<sup>-1</sup>, 1245 g C·yr<sup>-1</sup>, respectively, which were about 3.8% lower than that in simulations using the uniformly distributed atmospheric CO<sub>2</sub> data.

### Spatial and temporal CO<sub>2</sub> effects at the global scale

Using spatially and temporally explicit CO<sub>2</sub> data (S1-NOAA/S1-MACC), iTEM had lower annual GPP/NEP (–0.42 ± 0.06 Pg C·yr<sup>-1</sup> for GPP and –0.10 ± 0.01 Pg C·yr<sup>-1</sup> for NEP) estimation than that using the mean annual CO<sub>2</sub> value (S1-mNOAA/S1-mMACC), suggesting that CO<sub>2</sub> seasonal variation had negative effects on plant carbon assimilation (Fig. 5, Appendix S1: Fig. S2, Table 1). However, the global GPP/NEP, especially in temperate and tropical forest region, exhibited higher estimation (2.12 ± 0.11 Pg C·yr<sup>-1</sup> for GPP and 0.18 ± 0.04 Pg C·yr<sup>-1</sup> for NEP) when we only

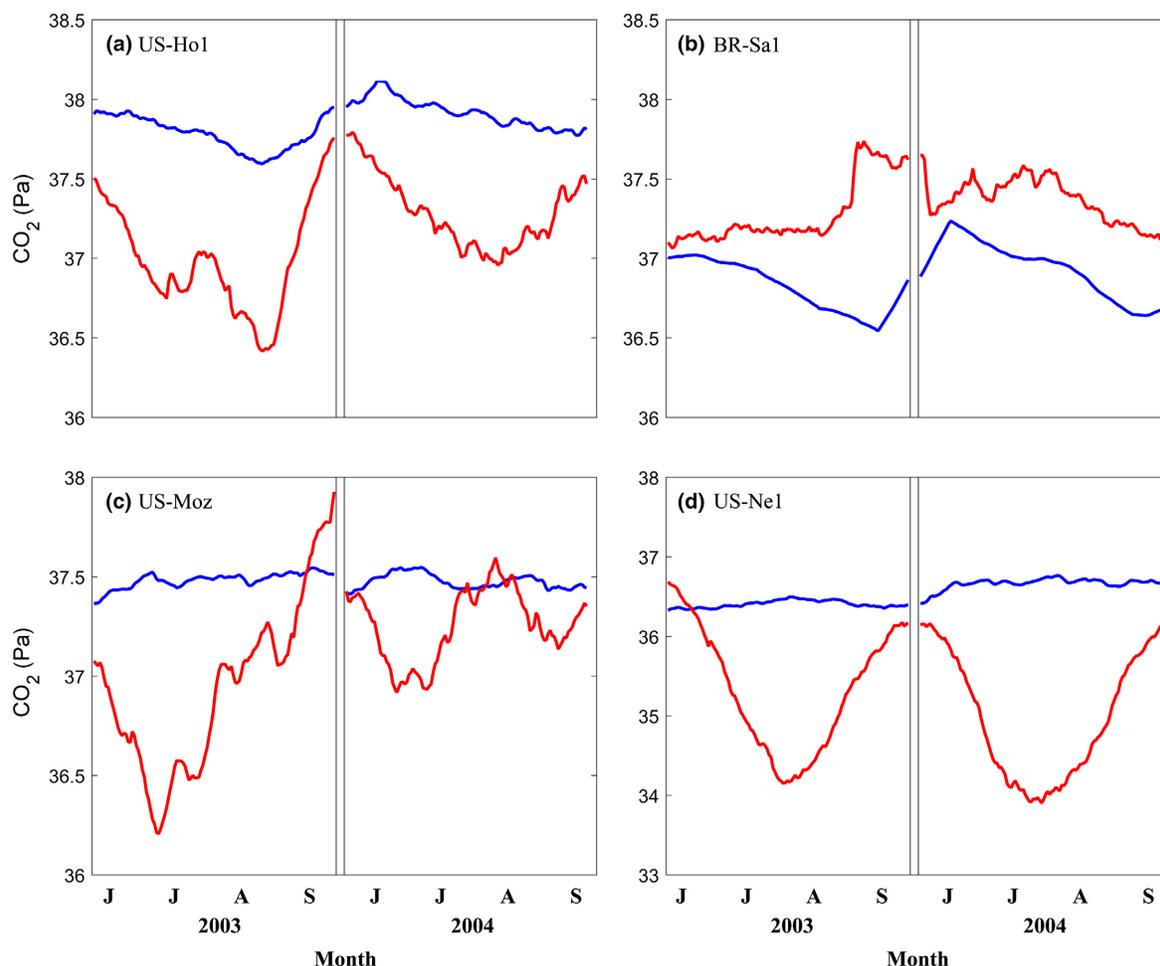


Fig. 2. Smoothed daily mean  $\text{CO}_2$  partial pressure (red line) at four flux sites at growing seasons (June to September): (a) Howland forest main (US-Ho1), (b) LBA Tapajos KM67 Mature Forest (BR-Sa1), (c) Missouri Ozark and (US-Moz), and (d) Mead Irrigated (US-Ne1). The blue line stands for the monthly tropospheric “background”  $\text{CO}_2$  concentration: see <http://www.esrl.noaa.gov/gmd/cgg/trends>.

considered the spatial  $\text{CO}_2$  effect (Fig. 5, Appendix S1: Fig. S2, comparison between S1-mNOAA/S1-mMACC and S1). This indicated that surface mean annual  $\text{CO}_2$  concentration was larger than the uniformly distributed  $\text{CO}_2$  data sets. However, when both spatial and seasonal  $\text{CO}_2$  effects were considered, GPP/NEP was slightly higher in tropical forest and temperate evergreen broadleaf forest, but lower in boreal forest compared with the simulation using the uniformly distributed  $\text{CO}_2$  data sets (Fig. 5, Appendix S1: Fig. S2, comparison between S1-NOAA/S1-MACC and S1). All of three simulations suggested that

forest showed relatively significant responses to the  $\text{CO}_2$  variation (Fig. 5, Appendix S1: Fig. S2, Table S2). In addition, the comparison among the three simulations also showed strong seasonal variations (Fig. 6, Appendix S1: Fig. S3, we did not show the NEP comparison here). The effect of  $\text{CO}_2$  seasonal variation on GPP was relatively obvious in summer season, with negative effect on the plant carbon sequestration. This was similar with the effect of  $\text{CO}_2$  spatial variation, but with positive effects. It was noted that tropical forest responded to the  $\text{CO}_2$  variation (seasonal or spatial) in all months.

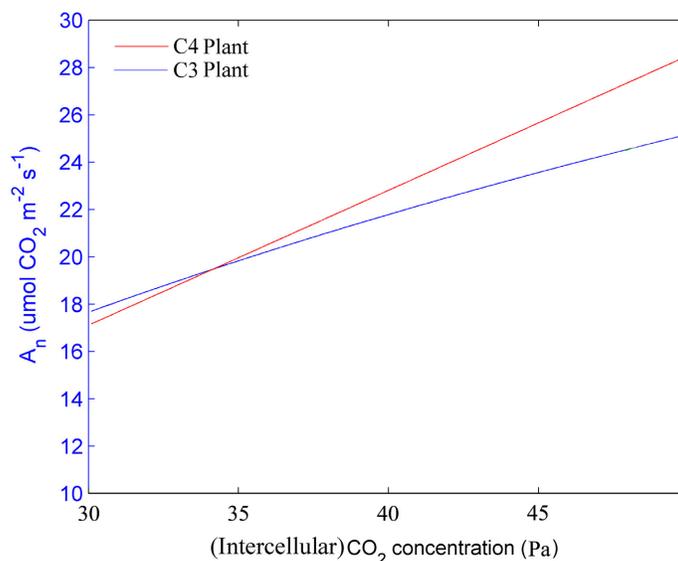


Fig. 3. The derived  $A_n$ - $\text{CO}_2$  curve in C3 and C4 plants using the biochemistry of C3 and C4 photosynthesis coupled with a stomatal model and assumption (environmental condition and parameters) in Appendix S1: Table S1.

## DISCUSSION

### *CO<sub>2</sub> spatial and temporal effects*

Few previous site and regional studies considered the  $\text{CO}_2$  temporal variations, most of which were conducted with a constant  $\text{CO}_2$  value within a year. The study by Schurgers et al. (2015) used the vertical micrometeorological profile variations (light, relative humidity, and  $\text{CO}_2$ ) within the canopy to address the importance of heterogeneous environmental conditions. Their results showed that only the light profile played an important role in photosynthesis and transpiration although large gradient  $\text{CO}_2$  existed during early morning and stable night. Cardon et al. (1995) investigated the effects of fluctuating  $\text{CO}_2$  concentrations with median level (340 ppmv) and average photosynthesis remained fairly constant under the oscillating  $\text{CO}_2$ . Although these studies indicated that the oscillating/diurnal cycle of  $\text{CO}_2$  with median level (300–450 ppmv) may exhibit small effects on carbon uptake, both were conducted at short-term (few days) and the high frequent  $\text{CO}_2$  fluctuation may not represent the natural  $\text{CO}_2$  temporal variation. In our site-level test, the US-Moz and US-Ne1, characterized as lower  $\text{CO}_2$  partial pressure in summer season, had lower GPP estimation (Fig. 4), suggesting a

negative feedback on leaf photosynthesis. This was similar with the simulations using the mean annual  $\text{CO}_2$  data set (Fig. 5, comparison between S1-NOAA and S1-mNOAA). Therefore, our results suggested that  $\text{CO}_2$  seasonal variation had a negative impact on plant photosynthesis. Due to sparse surface  $\text{CO}_2$  observation network (Shiga et al. 2013), the spatial  $\text{CO}_2$  effects have rarely been studied in land surface models except some coupled land-atmosphere models (Nicholls et al. 2004, Lu et al. 2005, Combe et al. 2015). It should be noted that the annual background  $\text{CO}_2$  data set (uniformly distributed  $\text{CO}_2$  data set, simulation S1) was not the surface  $\text{CO}_2$  which plant actually assimilates and may not correctly capture the global  $\text{CO}_2$  spatial variations. The site-level  $\text{CO}_2$  measurement (Fig. 2) and spatially, temporally explicit  $\text{CO}_2$  data sets (Fig. 1) all indicated a large variation across the globe. Compared with the uniformly distributed  $\text{CO}_2$  data set, some regions had similar value, but for tropical regions, the spatially, temporally explicit  $\text{CO}_2$  data sets showed consistent higher concentrations than annual, uniformly distributed  $\text{CO}_2$  (we only showed the summer daytime  $\text{CO}_2$  in Fig. 1), thus resulted in higher annual GPP/NEP. This was consistent with the site-level test at the tropical site (BR-Sa1) (Figs. 2 and 4).

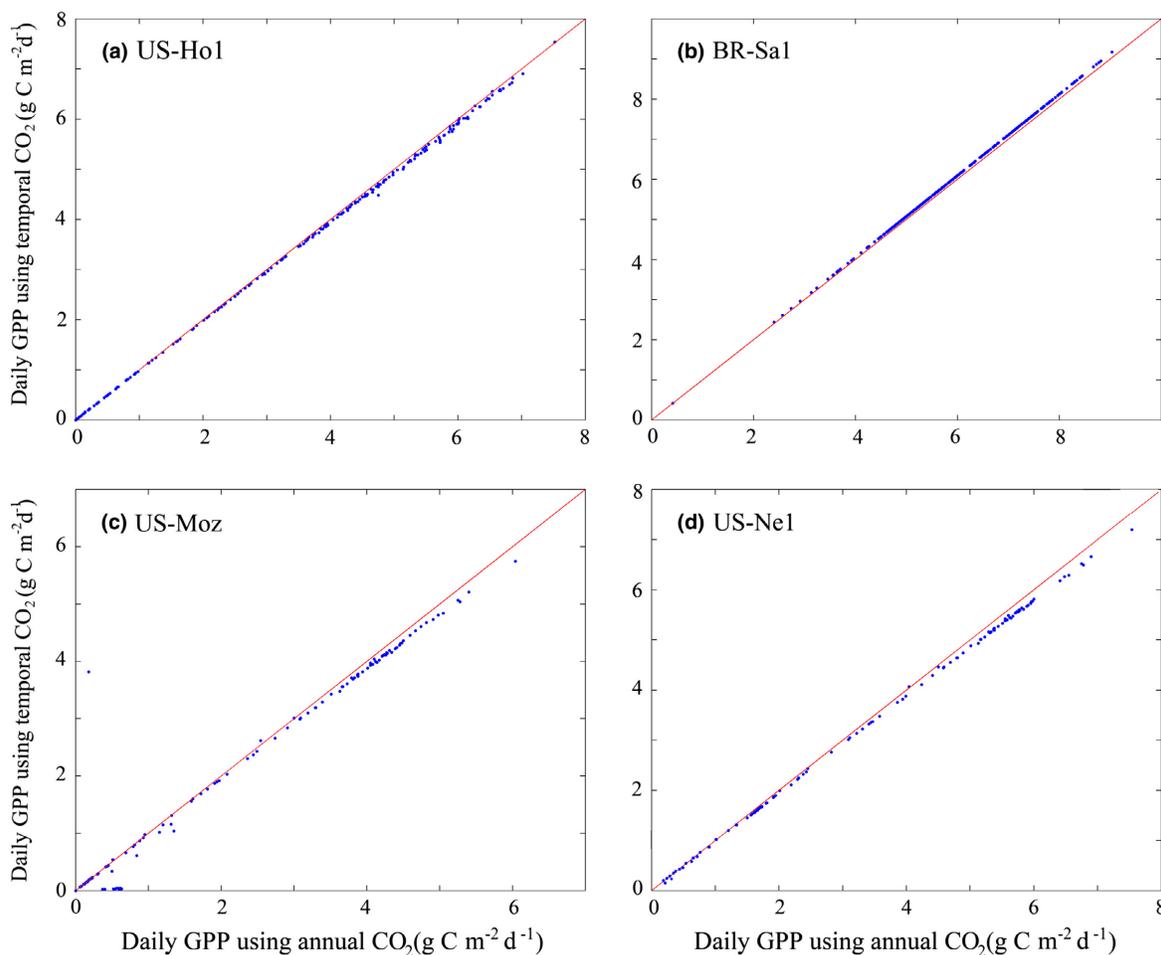


Fig. 4. Comparison between the simulated daily GPP using the in situ  $\text{CO}_2$  observation with that using the annual  $\text{CO}_2$  data sets at sites (a) Howland forest main (US-Ho1); (b) LBA Tapajos KM67 Mature Forest (BR-Sa1); (c) Missouri Ozark (US-Moz); and (d) Mead Irrigated (US-Ne1).

#### *Accurate spatial and temporal $\text{CO}_2$ representations*

We have to admit that the NOAA- $\text{CO}_2$  and MACC- $\text{CO}_2$  contained uncertainties and induced large biases to our global simulations. Both of the two spatially, temporally explicit  $\text{CO}_2$  data exhibited higher values in the tropical regions. For example, the NOAA Carbon Tracker showed 1.5 Pa higher  $\text{CO}_2$  partial pressure when compared with the uniformly distributed atmospheric  $\text{CO}_2$  data (Appendix S1: Fig. S4), while the in situ  $\text{CO}_2$  observation only exhibits 0.5 Pa differences at the BR-Sa1 site (Fig. 2b). In addition, the seasonal variation in NOAA Carbon Tracker was also different from the in situ  $\text{CO}_2$  observation in temperate regions: the in situ observed  $\text{CO}_2$  partial pressure was generally

lower in summer season (Fig. 2a, c, d), but the NOAA Carbon Tracker had similar  $\text{CO}_2$  partial pressure with the uniformly distributed atmospheric  $\text{CO}_2$  (Appendix S1: Fig. S4a, c, d). The discrepancy between the in situ  $\text{CO}_2$  observation and NOAA Carbon Tracker could be due to the following reasons. First, NOAA Carbon Tracker is a global inverse model, whose accuracy is highly dependent on the prior  $\text{CO}_2$  fluxes. Second, the global inversion lacks an explicit crop model and explicit subdaily prediction of carbon exchanges. Finally, the transport model (TM5) used in NOAA Carbon Tracker is based on a relatively coarse spatial resolution, which limits the ability to simulate the  $\text{CO}_2$  transport due to inaccurate weather data in

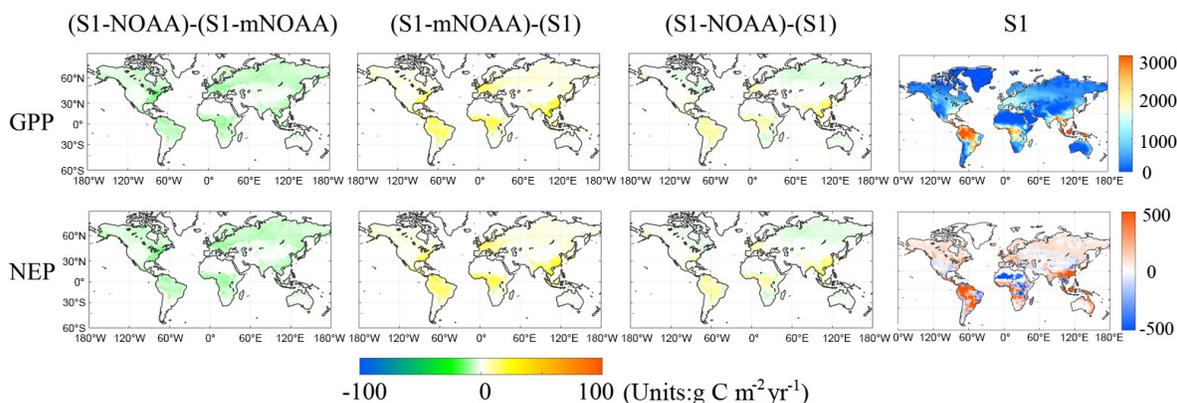


Fig. 5. Temporal averaged GPP and NEP differences from 2003 to 2010. The first column is the difference between S1-NOAA and S1-mNOAA, the second column is the difference between S1-mNOAA and S1, and the third column is the difference between S1-NOAA and S1. S1 stands for the iTem simulation using the uniformly distributed atmospheric CO<sub>2</sub>, S1-mNOAA means the simulation using mean annual CO<sub>2</sub> computed from NOAA-CO<sub>2</sub> data, and S1-NOAA means the simulations using CO<sub>2</sub> from NOAA-CO<sub>2</sub> data. Units: g C m<sup>-2</sup> yr<sup>-1</sup>.

complex terrain (Geels et al. 2007). Our simulations showed that spatially/temporally varied atmospheric CO<sub>2</sub> exerted relatively significant effects on the global carbon dynamics, especially in forest regions. However, the spatially and temporally explicit CO<sub>2</sub> product used here might be biased due to sparse monitoring network (Peters et al. 2007) and measurement errors (Masarie et al. 2011). Thus, high frequency, stable CO<sub>2</sub> measurement (Andrews et al. 2014) and more CO<sub>2</sub> observation sites capturing seasonal/spatial variation representative of large regions (Bakwin et al. 2004, Lauvaux et al. 2012) are needed to constrain estimates of regional/global net atmosphere/biosphere exchange of CO<sub>2</sub>.

#### Implications for future studies

Up to now, most of the regional and global estimations of terrestrial carbon uptake come from various ecosystem land surface models (Bonan 2008). The model constrained with eddy

flux tower observation would strengthen the understanding of ecosystem mechanisms. The data-assimilation method provides an alternative way to quantifying regional carbon exchanges between the terrestrial biosphere and the atmosphere at continental and global scales (Xiao et al. 2012). Generally, in the land surface models, using CO<sub>2</sub> data as input to compute GPP, the carbon fluxes are routinely simulated based on annual, uniformly distributed CO<sub>2</sub> data set (or to be more specific, the background CO<sub>2</sub> concentration; our study was the simulation S1) across a region or globe (Turner et al. 2003, Chen et al. 2011), without considering the site-level CO<sub>2</sub> realistic properties (Liu et al. 2016). As we demonstrated above, the high-precision CO<sub>2</sub> measurement from eddy flux towers showed that seasonal and spatial surface atmospheric CO<sub>2</sub> concentration differences were as large as 35 ppmv. Using the sensitivity analysis, the seasonal and spatial gradient can

Table 1. Annual global GPP and NEP estimation.

Measurement	S1	S1-mNOAA	S1-NOAA	S1-mMACC	S1-MACC
Annual GPP (Pg C yr <sup>-1</sup> ) flux	128.82 ± 4.12	128.43 ± 4.17	130.56 ± 4.09	128.37 ± 4.07	130.48 ± 4.09
Cumulative NEP (Pg C) flux	47.41	46.62	48.89	46.63	48.85

Notes: S1 stands for the iTem simulation using the uniformly distributed atmospheric CO<sub>2</sub>, S1-mNOAA means the simulation using mean annual CO<sub>2</sub> computed from NOAA-CO<sub>2</sub> data, and S1-NOAA means the simulations using CO<sub>2</sub> from NOAA-CO<sub>2</sub> data. S1-mMACC means the simulation using mean annual CO<sub>2</sub> computed from NOAA-CO<sub>2</sub> data, and S1-MACC means the simulations using CO<sub>2</sub> from NOAA-CO<sub>2</sub> data. Annual GPP values are presented as mean ± SE.

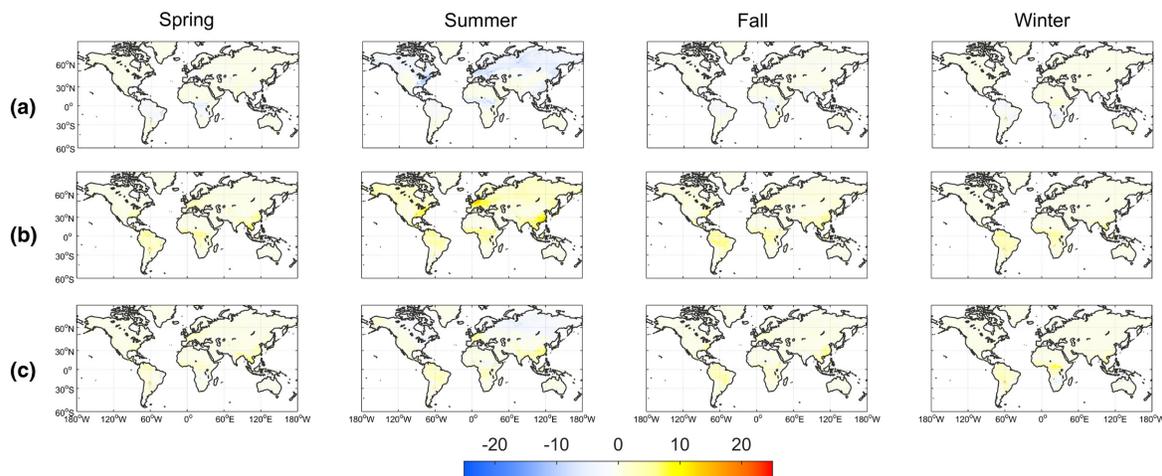


Fig. 6. Seasonal averaged GPP differences among S1-NOAA, S1-mNOAA, and S1 (S1, S1-mNOAA, and S1-NOAA stand for the iTEM simulations using the uniformly distributed atmospheric CO<sub>2</sub> (a), mean annual CO<sub>2</sub> computed from NOAA-CO<sub>2</sub> (b), and NOAA-CO<sub>2</sub> data (c), respectively. Units: g C·m<sup>-2</sup>·season<sup>-1</sup>).

induce around 0.6–1.2  $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  differences in photosynthesis (Fig. 3). We should note that the photosynthesis in C3 plant was prone to be saturated at high CO<sub>2</sub> concentrations and this difference could be small in future climate scenarios. However, the seasonal CO<sub>2</sub> amplitude is expected to increase as indicated by the fifth phase of the Coupled Model Intercomparison Project (CMIP5) (Zhao and Zeng 2014), which could still result in significant differences in photosynthesis.

As for the model scheme, we should also pay attention to the oscillation of elevated CO<sub>2</sub> effects on plant carbon assimilation. Some studies were conducted on the fluctuation of elevated CO<sub>2</sub> effects on photosynthesis when compared with the constant CO<sub>2</sub> experiments (similar to the annual CO<sub>2</sub> in this study). Hendrey et al. (1997) exposed the wheat to elevated CO<sub>2</sub> (650 ppmv) oscillating symmetrically 225 ppmv and the results showed that carbon uptake was decreased if the duration of oscillation was more than 1 min. This downregulation of photosynthesis was confirmed by other similar studies (Chaves et al. 2001, Holtum and Winter 2003, Bunce 2012). The artificially controlled CO<sub>2</sub> oscillation may not be representative of natural CO<sub>2</sub> diurnal/seasonal variations, and the response to rapid changes in ambient CO<sub>2</sub> by the experiments above indicates that plant may acclimate to the elevated

CO<sub>2</sub> diurnal cycle. In addition, the biogeochemical processes, such as the C and N interaction, allocation, turnover scheme (Friedlingstein et al. 2014, Zaehle et al. 2014, Walker et al. 2015), and the heat- or drought-induced mortality mechanism (Williams 2014, Williams et al. 2014, Yi et al. 2015), are needed to be better represented in land surface models to accurately capture the plant response to a warmer and CO<sub>2</sub> richer future.

## CONCLUSION

Atmospheric CO<sub>2</sub> is an important factor related to plant carbon assimilation and water balance. Current ecosystem models have not explored the atmospheric CO<sub>2</sub> effects in a spatially and temporally explicit manner. Our analysis indicated that there were significant differences in seasonal and spatial CO<sub>2</sub> concentrations at various eddy flux tower sites (up to 35 ppmv), which could result in 3–8% differences in photosynthesis rate. Our results demonstrated that CO<sub>2</sub> seasonal variations had a negative effect on plant carbon assimilation, while CO<sub>2</sub> spatial variation exhibited positive impacts. When both CO<sub>2</sub> seasonal and spatial effects were considered, global GPP and net ecosystem production (NEP) were 1.7 Pg C·yr<sup>-1</sup> and 0.08 Pg C·yr<sup>-1</sup> higher than the simulation using uniformly distributed CO<sub>2</sub> data set and

the difference was significant in tropical and temperate evergreen broadleaf forest regions. This study suggests that using spatially and temporally explicit atmospheric CO<sub>2</sub> data are important to accurately quantifying the regional and global carbon dynamics of terrestrial ecosystems and the observation network should be expanded to have a representative CO<sub>2</sub> surface variation.

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