

Quantifying spatially and temporally explicit CO₂ fertilization effects on global terrestrial ecosystem carbon dynamics

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Citation: Liu, S., Q. Zhuang, M. Chen, and L. Gu. 2016. Quantifying spatially and temporally explicit CO₂ fertilization effects on global terrestrial ecosystem carbon dynamics. *Ecosphere* 7(7):e01391. 10.1002/ecs2.1391

Abstract. Current terrestrial ecosystem models are usually driven with global average annual atmospheric carbon dioxide (CO₂) concentration data at the global scale. However, high-precision CO₂ measurement from eddy flux towers showed that seasonal, spatial surface atmospheric CO₂ concentration differences were as large as 35 ppmv and the site-level tests indicated that the CO₂ variation exhibited different effects on plant photosynthesis. Here we used a process-based ecosystem model driven with two spatially and temporally explicit CO₂ data sets to analyze the atmospheric CO₂ fertilization effects on the global carbon dynamics of terrestrial ecosystems from 2003 to 2010. Our results demonstrated that CO₂ seasonal variation had a negative effect on plant carbon assimilation, while CO₂ spatial variation exhibited a positive impact. When both CO₂ seasonal and spatial effects were considered, global gross primary production and net ecosystem production were 1.7 Pg C·yr⁻¹ and 0.08 Pg C·yr⁻¹ higher than the simulation using uniformly distributed CO₂ data set and the difference was significant in tropical and temperate evergreen broadleaf forest regions. This study suggests that the CO₂ observation network should be expanded so that the realistic CO₂ variation can be incorporated into the land surface models to adequately account for CO₂ fertilization effects on global terrestrial ecosystem carbon dynamics.

Key words: atmospheric CO₂; carbon dynamics; gross primary production; net ecosystem production; process-based ecosystem model.

Received 4 November 2015; revised 17 March 2016; accepted 23 March 2016. Corresponding Editor: K. Johnson.

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INTRODUCTION

Increasing atmospheric carbon dioxide (CO₂) 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 CO₂ (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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ in NH were generally higher. The spatially varied atmospheric CO₂ exhibited the semiannual oscillation (Ruzmaikin et al. 2012) with the stronger seasonal variation in northern high latitudes as indicated by the GLOBALVIEW CO₂ and GEOS-Chem model simulations (Feng et al. 2011).

As CO₂ transformed into plant carbohydrates through leaf stomata is the initial step in carbon cycling, the accurate representation of CO₂ spatiotemporal variation is crucial for ecosystem modeling. Here we first derived the surface daily CO₂ measurement at four sites from Fluxnet to show the spatial and temporal variations in surface CO₂. Then the integrated Terrestrial Ecosystem Model (iTEM; Chen 2013, Liu et al. 2014) driven with two spatially and temporally explicit CO₂ data sets was used to analyze the atmospheric CO₂ 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 CO₂ concentrations, we first extracted the high-precision CO₂ 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 CO₂ 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 CO₂ measurement with that using the uniformly distributed atmospheric CO₂ data. Finally, two spatially and temporally explicit CO₂ data sets were used to drive iTEM from 2003 to 2010 at the global scale. The two spatially and temporally explicit CO₂ 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 CO₂ value computed from NOAA CO₂ and MACC CO₂ to quantify the effect of seasonal CO₂ variation on carbon dynamics. Totally, we had four simulations: (1) iTEM + NOAA CO₂ (S1-NOAA), (2) iTEM + mean annual NOAA CO₂ (S1-mNOAA), (3) iTEM + MACC CO₂ (S1-MACC), and (4) iTEM + mean annual MACC CO₂ (S1-mMACC). Therefore, the spatiotemporal CO₂ effect can be examined from the differences among the four simulations and the simulations (S1) based on the annual and uniformly distributed CO₂ 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 CO₂ effects on the global carbon dynamics of terrestrial ecosystems. In iTEM, photosynthesis in C₃ and C₄ 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 CO₂ 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 CO₂). Leaf photosynthesis was linked to stomatal conductance via the internal CO₂ 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_a curve to quantify the sensitivity of photosynthesis to CO₂ variation.

Data

The high-precision CO₂ 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 CO₂

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 CO₂ 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 CO₂ 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 CO₂ observation with that using the uniformly distributed atmospheric CO₂ 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 CO₂ data from NOAA gridded CO₂ product (<ftp://aftp.cmdl.noaa.gov/products/carbontracker/co2/>) are based on global CO₂ observation network data obtained by employing a novel ensemble assimilation method to accurately model atmospheric CO₂ mole fractions (Peters et al. 2007). In the MACC project (https://www.gmes-atmosphere.eu/news/co2_forecasts/), atmospheric CO₂ concentration data are estimated by assimilating satellite observations into the ECMWF Integrated Forecasting System (IFS) Numerical Weather Prediction model. The global atmospheric CO₂ concentration is forecasted with a 5-d lead time at 3-h time step. Both spatially and temporally explicit CO₂ data sets were resampled to the spatial resolution of TEM. The annual and uniformly distributed CO₂ 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 CO₂ (9:00

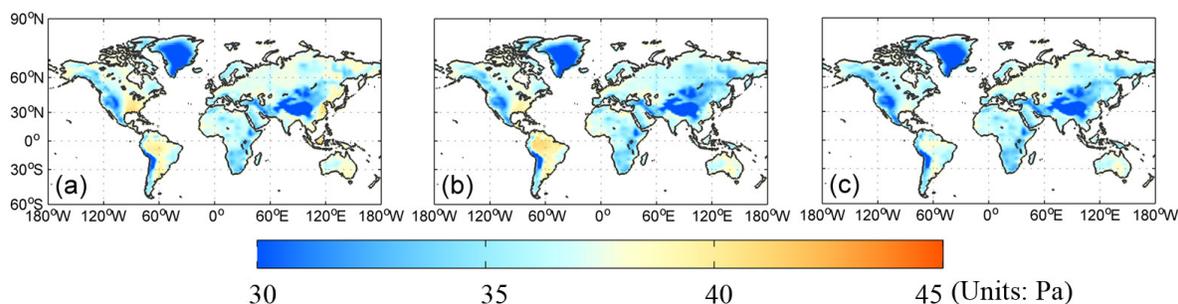


Fig. 1. The mean daytime CO₂ (9:00 to 15:00) partial pressure (Units: Pa) at summer (June to Sep) season during 2003–2010. (a–c) stand for the NOAA, MACC, and annual CO₂ partial pressure, respectively. Units: Pa.

to 15:00) partial pressure in these three products in summer (June to September) season during 2003–2010. Both NOAA CO₂ and MACC CO₂ (Fig. 1a, b) data sets indicated the CO₂ 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 CO₂ partial pressure (2–5 Pa) than the annual CO₂ data set, but Russia exhibited slightly lower partial pressure in summer season.

RESULTS

CO₂ variation among sites and sensitivity test

All of the four sites exhibited a seasonal CO₂ 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 CO₂ observation only showed slightly higher concentrations than the background CO₂ value at BR-Sa1. Spatially, the difference also reached as large as 2.5 Pa among these sites. For example, US-Ne1 had low CO₂ concentrations around 34 Pa at summer time in 2003, while in US-Ho1, the observed CO₂ was as high as 36.5 Pa. These high-precision CO₂ measurements showed that there were significant spatiotemporal surface CO₂ variations across sites. We derived the A–C_a 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_a curve at 35 Pa CO₂ were around 0.3 μmol CO₂·m⁻²·s⁻¹·Pa⁻¹ and 0.4 μmol CO₂·m⁻²·s⁻¹·Pa⁻¹ for C3 and C4 plants, respectively. Therefore, the 2–3 Pa CO₂ differences could result in the difference of A about 0.6–0.9 μmol CO₂·m⁻²·s⁻¹

in C3 plant and 0.8–1.2 μmol CO₂·m⁻²·s⁻¹ in C4 plant, respectively.

Site-level test using in situ CO₂ observation

The CO₂ 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 CO₂ 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 CO₂ was about 2.5 Pa lower compared with the uniformly distributed atmospheric CO₂ data, with expected lower photosynthesis rates. Considering the realistic CO₂ temporal variation at US-Moz and US-Ne1, the annual GPP was 1334 g C·yr⁻¹, 1245 g C·yr⁻¹, respectively, which were about 3.8% lower than that in simulations using the uniformly distributed atmospheric CO₂ data.

Spatial and temporal CO₂ effects at the global scale

Using spatially and temporally explicit CO₂ data (S1-NOAA/S1-MACC), iTEM had lower annual GPP/NEP (–0.42 ± 0.06 Pg C·yr⁻¹ for GPP and –0.10 ± 0.01 Pg C·yr⁻¹ for NEP) estimation than that using the mean annual CO₂ value (S1-mNOAA/S1-mMACC), suggesting that CO₂ 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⁻¹ for GPP and 0.18 ± 0.04 Pg C·yr⁻¹ for NEP) when we only

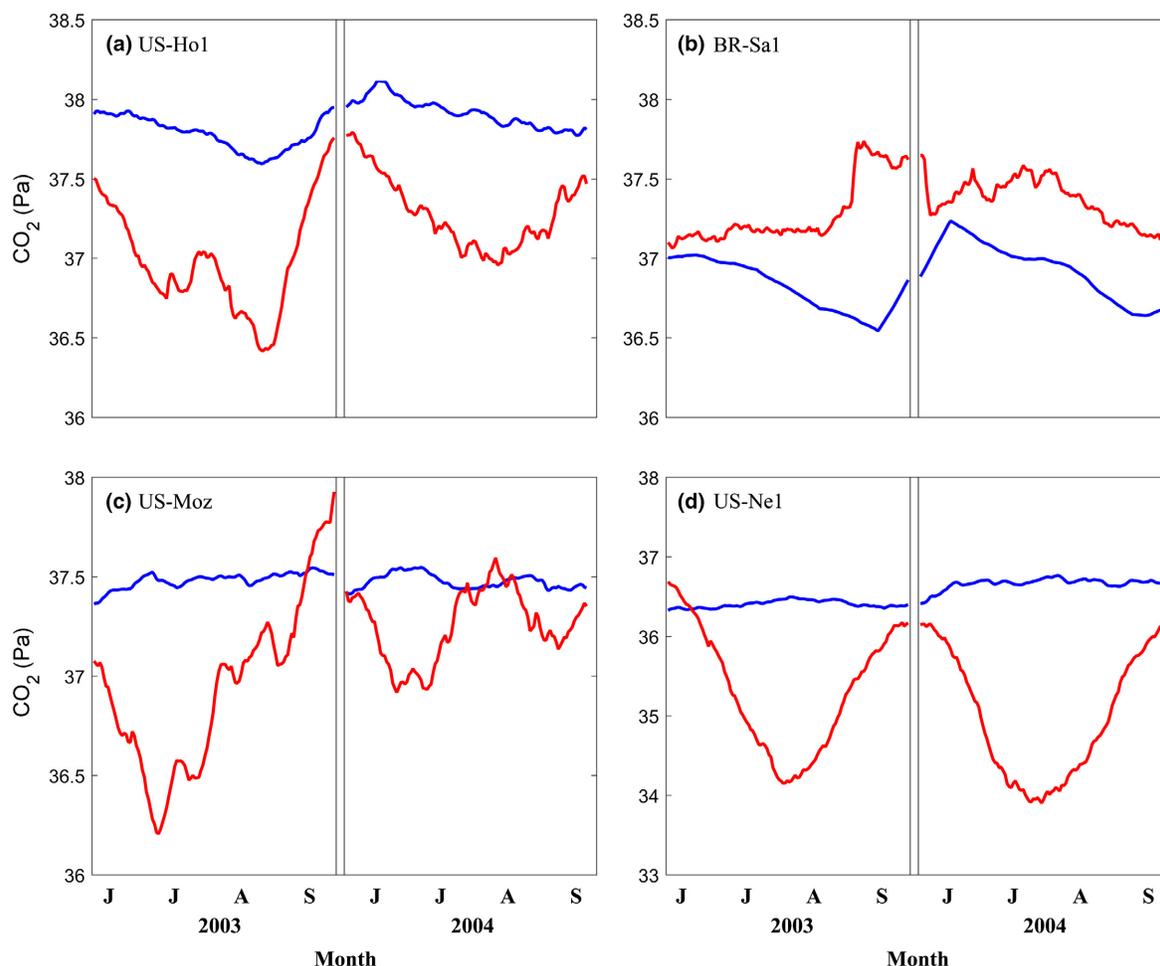


Fig. 2. Smoothed daily mean CO_2 partial pressure (red line) at four flux sites at growing seasons (June to September): (a) Howland forest main (US-Ho1), (b) LBA Tapajos KM67 Mature Forest (BR-Sa1), (c) Missouri Ozark and (US-Moz), and (d) Mead Irrigated (US-Ne1). The blue line stands for the monthly tropospheric “background” CO_2 concentration: see <http://www.esrl.noaa.gov/gmd/cgg/trends>.

considered the spatial CO_2 effect (Fig. 5, Appendix S1: Fig. S2, comparison between S1-mNOAA/S1-mMACC and S1). This indicated that surface mean annual CO_2 concentration was larger than the uniformly distributed CO_2 data sets. However, when both spatial and seasonal 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 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 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 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 CO_2 spatial variation, but with positive effects. It was noted that tropical forest responded to the CO_2 variation (seasonal or spatial) in all months.

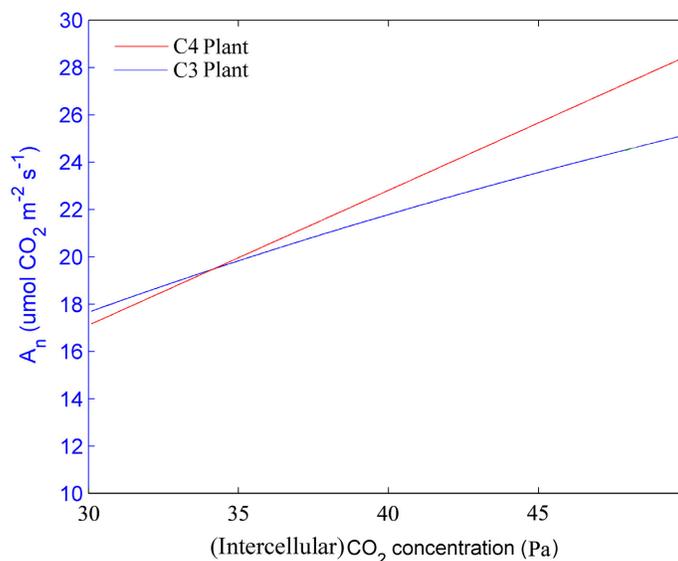


Fig. 3. The derived A_n - CO_2 curve in C3 and C4 plants using the biochemistry of C3 and C4 photosynthesis coupled with a stomatal model and assumption (environmental condition and parameters) in Appendix S1: Table S1.

DISCUSSION

CO₂ spatial and temporal effects

Few previous site and regional studies considered the CO_2 temporal variations, most of which were conducted with a constant CO_2 value within a year. The study by Schurgers et al. (2015) used the vertical micrometeorological profile variations (light, relative humidity, and 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 CO_2 existed during early morning and stable night. Cardon et al. (1995) investigated the effects of fluctuating CO_2 concentrations with median level (340 ppmv) and average photosynthesis remained fairly constant under the oscillating CO_2 . Although these studies indicated that the oscillating/diurnal cycle of 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 CO_2 fluctuation may not represent the natural CO_2 temporal variation. In our site-level test, the US-Moz and US-Ne1, characterized as lower 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 CO_2 data set (Fig. 5, comparison between S1-NOAA and S1-mNOAA). Therefore, our results suggested that CO_2 seasonal variation had a negative impact on plant photosynthesis. Due to sparse surface CO_2 observation network (Shiga et al. 2013), the spatial 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 CO_2 data set (uniformly distributed CO_2 data set, simulation S1) was not the surface CO_2 which plant actually assimilates and may not correctly capture the global CO_2 spatial variations. The site-level CO_2 measurement (Fig. 2) and spatially, temporally explicit CO_2 data sets (Fig. 1) all indicated a large variation across the globe. Compared with the uniformly distributed CO_2 data set, some regions had similar value, but for tropical regions, the spatially, temporally explicit CO_2 data sets showed consistent higher concentrations than annual, uniformly distributed CO_2 (we only showed the summer daytime 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).

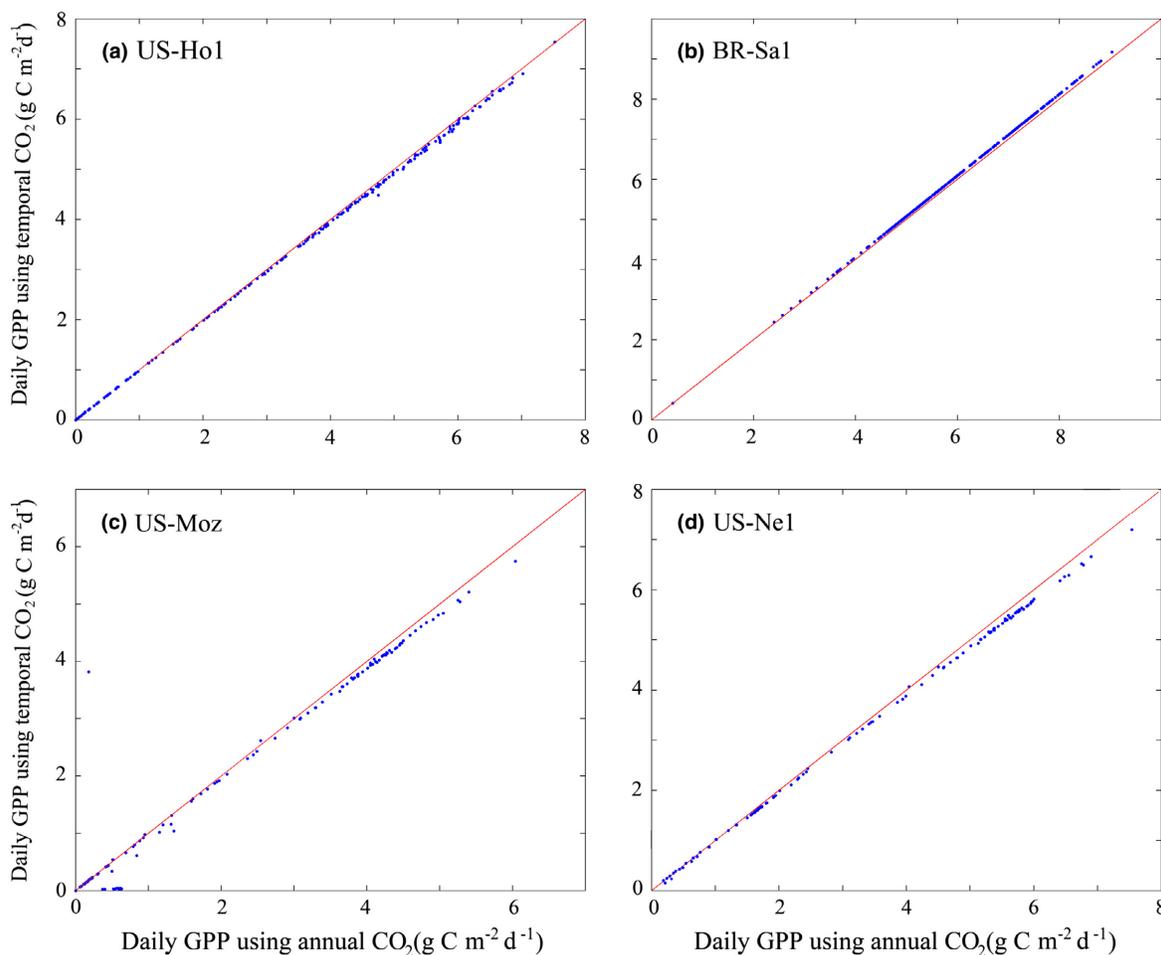


Fig. 4. Comparison between the simulated daily GPP using the in situ CO_2 observation with that using the annual CO_2 data sets at sites (a) Howland forest main (US-Ho1); (b) LBA Tapajos KM67 Mature Forest (BR-Sa1); (c) Missouri Ozark (US-Moz); and (d) Mead Irrigated (US-Ne1).

Accurate spatial and temporal CO_2 representations

We have to admit that the NOAA- CO_2 and MACC- CO_2 contained uncertainties and induced large biases to our global simulations. Both of the two spatially, temporally explicit CO_2 data exhibited higher values in the tropical regions. For example, the NOAA Carbon Tracker showed 1.5 Pa higher CO_2 partial pressure when compared with the uniformly distributed atmospheric CO_2 data (Appendix S1: Fig. S4), while the in situ 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 CO_2 observation in temperate regions: the in situ observed CO_2 partial pressure was generally

lower in summer season (Fig. 2a, c, d), but the NOAA Carbon Tracker had similar CO_2 partial pressure with the uniformly distributed atmospheric CO_2 (Appendix S1: Fig. S4a, c, d). The discrepancy between the in situ 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 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 CO_2 transport due to inaccurate weather data in

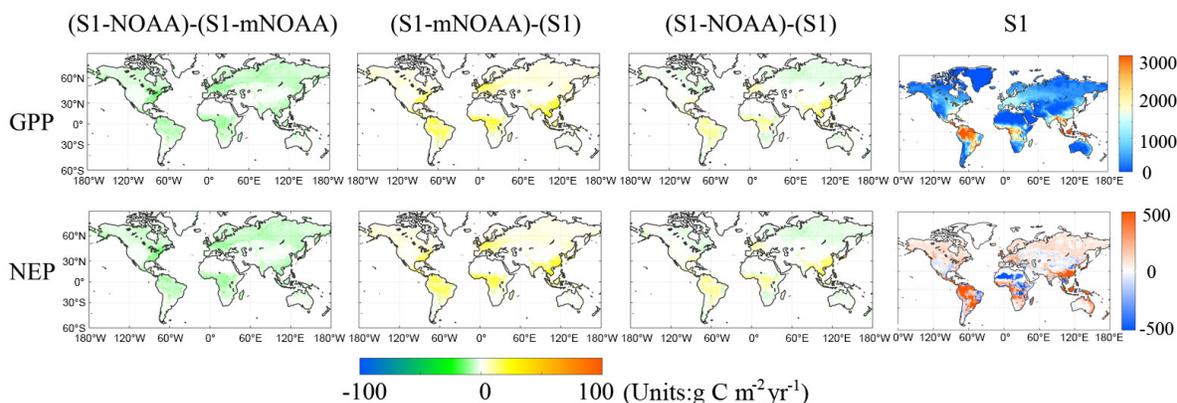


Fig. 5. Temporal averaged GPP and NEP differences from 2003 to 2010. The first column is the difference between S1-NOAA and S1-mNOAA, the second column is the difference between S1-mNOAA and S1, and the third column is the difference between S1-NOAA and S1. S1 stands for the iTem simulation using the uniformly distributed atmospheric CO₂, S1-mNOAA means the simulation using mean annual CO₂ computed from NOAA-CO₂ data, and S1-NOAA means the simulations using CO₂ from NOAA-CO₂ data. Units: g C m⁻² yr⁻¹.

complex terrain (Geels et al. 2007). Our simulations showed that spatially/temporally varied atmospheric CO₂ exerted relatively significant effects on the global carbon dynamics, especially in forest regions. However, the spatially and temporally explicit CO₂ 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 CO₂ measurement (Andrews et al. 2014) and more CO₂ 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 CO₂.

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 CO₂ data as input to compute GPP, the carbon fluxes are routinely simulated based on annual, uniformly distributed CO₂ data set (or to be more specific, the background CO₂ 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 CO₂ realistic properties (Liu et al. 2016). As we demonstrated above, the high-precision CO₂ measurement from eddy flux towers showed that seasonal and spatial surface atmospheric CO₂ 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 ⁻¹) 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 CO₂, S1-mNOAA means the simulation using mean annual CO₂ computed from NOAA-CO₂ data, and S1-NOAA means the simulations using CO₂ from NOAA-CO₂ data. S1-mMACC means the simulation using mean annual CO₂ computed from NOAA-CO₂ data, and S1-MACC means the simulations using CO₂ from NOAA-CO₂ data. Annual GPP values are presented as mean ± SE.

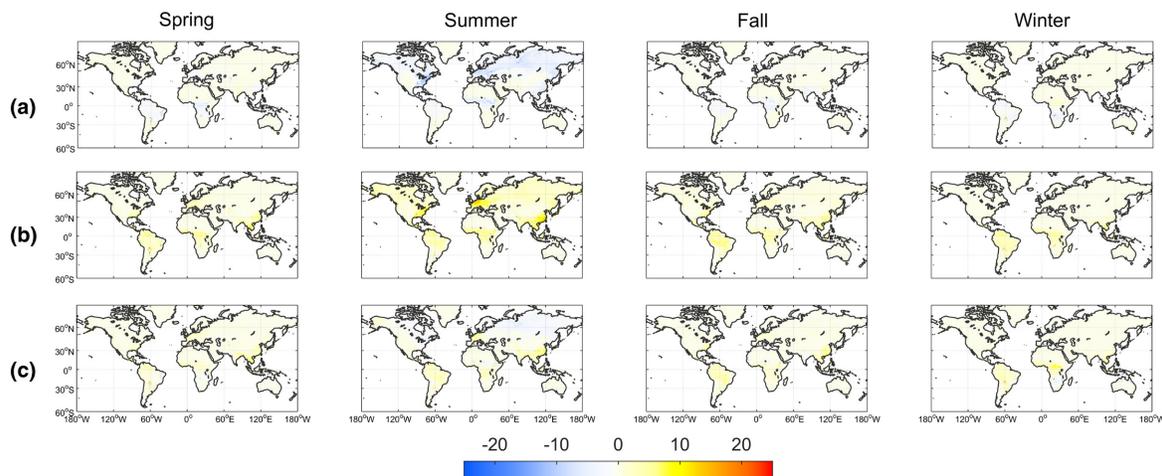


Fig. 6. Seasonal averaged GPP differences among S1-NOAA, S1-mNOAA, and S1 (S1, S1-mNOAA, and S1-NOAA stand for the iTEM simulations using the uniformly distributed atmospheric CO₂ (a), mean annual CO₂ computed from NOAA-CO₂ (b), and NOAA-CO₂ data (c), respectively. Units: g C·m⁻²·season⁻¹).

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 CO₂ concentrations and this difference could be small in future climate scenarios. However, the seasonal CO₂ 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 CO₂ effects on plant carbon assimilation. Some studies were conducted on the fluctuation of elevated CO₂ effects on photosynthesis when compared with the constant CO₂ experiments (similar to the annual CO₂ in this study). Hendrey et al. (1997) exposed the wheat to elevated CO₂ (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 CO₂ oscillation may not be representative of natural CO₂ diurnal/seasonal variations, and the response to rapid changes in ambient CO₂ by the experiments above indicates that plant may acclimate to the elevated

CO₂ 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 CO₂ richer future.

CONCLUSION

Atmospheric CO₂ is an important factor related to plant carbon assimilation and water balance. Current ecosystem models have not explored the atmospheric CO₂ effects in a spatially and temporally explicit manner. Our analysis indicated that there were significant differences in seasonal and spatial CO₂ 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 CO₂ seasonal variations had a negative effect on plant carbon assimilation, while CO₂ spatial variation exhibited positive impacts. When both CO₂ seasonal and spatial effects were considered, global GPP and net ecosystem production (NEP) were 1.7 Pg C·yr⁻¹ and 0.08 Pg C·yr⁻¹ higher than the simulation using uniformly distributed CO₂ 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 CO₂ 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 CO₂ surface variation.

ACKNOWLEDGMENTS

The model forcing data are provided by the Land Surface Hydrology Research Group at Princeton University. This research is funded through projects to Q.Z. by NASA Land Use and Land Cover Change program (NASA-NNX09A126G), Department of Energy (DE-FG02-08ER64599), National Science Foundation (NSF-102891 and NSF-0919331), NSF Carbon and Water in the Earth Program (NSF-0630319), and NSF CDI Type II project (IIS-1028291).

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