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Spatial pattern of GPP variations in terrestrial ecosystems and its drivers: Climatic factors, CO₂ concentration and land-cover change, 1982-2015

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Abstract: Quantitative estimation of spatial pattern of gross primary production (GPP) trends and its drivers plays a crucial role in global change research. This study applied C-Fix model to estimate the net effect of each factor on GPP trends of 1982-2015, used an unsupervised classifier to group similar GPP trend behaviors, and analyzed the responses of GPP to changes in climatic, atmospheric and environmental drivers. According to the features of monthly GPP trends and the patterns of growing season, we presented nine categories as aids in interpreting large-scale behavior. Land-cover change (LCC), rising CO₂, temperature and water conditions changes have the positive overall effect on GPP over the entire world, contrary to radiation change effects. The global average contributions of LCC, CO₂, temperature, radiation and water on GPP trend are 4.57%, 65.73%, 13.07%, -7.24 and 11.74%, respectively. LCC and climatic factors changes have had a greater impact on GPP in terms of a specific location or regional rather than globally, and the interactions between factors are positive on GPP. The effects of climatic factors trends on GPP in different locations can be opposite, in general: regionally, GPP changes at middle and high latitudes are likely dominated by rises in radiation and

temperature; at lower latitudes, GPP changes are likely to be driven by shifts in water conditions; at high altitudes, GPP changes are probably caused by changes in temperature and water conditions. These results will increase the understanding of the variations of carbon flux under future CO₂, LCC and climate conditions.

Keywords: Climate change, Atmospheric CO₂ concentration, Land-cover change, Gross primary production, Terrestrial ecosystems, C-Fix.

1. Introduction

Terrestrial gross primary production (GPP) is the amount of CO₂ fixed as organic compounds by vegetation through photosynthesis at the ecosystem scale (Beer et al. 2010); GPP plays a pivotal role in the global carbon balance and almost all ecosystem processes (Gilmanov et al., 2003). The patterns of the variation and distribution of GPP in terrestrial ecosystems show large spatial variability due to interactions between the biological characteristics of plants and external environmental factors (e.g., rising CO₂ concentration, land-cover change, and climatic variables) (Beer et al., 2010; Anav et al., 2015). In recent decades, approximately 1.2 PgC yr⁻¹ has been sequestered by terrestrial ecosystems as the net result of the impact of the changing climate and rising CO₂ on ecosystem productivity (CO₂-climate driven flux) and deforestation, harvesting and secondary forest regrowth (land-cover change (LCC) flux) (Haverd et al., 2017). However, their contributions are highly uncertain. Therefore, it is important and necessary to accurately describe the changes of GPP in different regions and to quantitatively evaluate how environmental factors influence GPP. Furthermore, a deeper understanding of how GPP has responded to past climate change, LCC and rising CO₂ concentration will provide insight into how the carbon cycle will change under future CO₂ and climate conditions (Poulter et al., 2014; Huang et al., 2015; Li et al., 2016). However, directly measuring GPP at the global scale is infeasible (Ma et al. 2015), and the discrepancies associated with the spatial distribution of environmental controls on GPP variation simulated by different models are considerable (Anav et al. 2015, Beer et al. 2010).

In recent years, with the development of space technology, satellite-based light use efficiency (LUE) models have been widely used because they rely on simple algorithms to estimate the macroscale terrestrial GPP (Yuan et al., 2014b). In this study, the carbon fixation (C-Fix) model (Verstraeten et al., 2006) was selected to perform a series of factorial estimations to explore the drivers' net effect on GPP because in C-Fix, a CO₂ fertilization factor exists that differs from other LUE models, and we can directly introduce the effect of the atmospheric CO₂ concentration, which is considered one of the main causes of global warming (Bazzaz 1990; Gillett et al., 2013).

Many studies have been performed, and various models and approaches, from individual sites to global scales, have been developed and used to examine climate factors that affect GPP (Nemani et al. 2003, Beer et al. 2007, 2010, de Jong et al. 2013, Anav et al. 2015, Liang et al. 2015). Simultaneously, that CO₂ concentration effect on GPP has also been found by many scholars (Farquhar 1997; Norby et al. 2005; Luo et al. 2006; Yang et al., 2016; Sun et al., 2018), and numerous studies (van Oijen et al., 2004; Ainsworth and Long, 2005; Yang et al., 2016) have been conducted to reveal how ecosystems respond to elevated CO₂ levels, although the magnitude and the spatial distribution of the influence remain unclear. Moreover, it is an indisputable fact that large-scale land-cover changes have taken place over the past few decades (Lambin et al., 2001; Hansen et al., 2013), and large-scale estimates of terrestrial carbon fluxes are highly dependent on the land cover (Quaife et al., 2008). However, studies that combined climate change, LCC, rising CO₂ concentration and their interactions into the effects on the pattern and trend of GPP are few.

In this study, we first used the C-Fix model to estimate the global monthly GPP over the past 34 years and tested the performance by comparing it with MTE GPP and MODIS products. Second, we analyzed the individual effect of each factor and the interactions through a series of factorial estimations around the world. Third, we zoned the categories of GPP variations according to seasonal and dimensional characteristics using an unsupervised classifier. Finally, we analyzed the GPP trend and its attribution spatially. The overarching goals of this study are to (globally during the period of 1982-2015) investigate the spatial distribution and magnitude

of GPP trend; separate the contributions of climate factors, the rising CO₂ concentration, LCC and their interactions on the pattern of GPP trends spatially and quantitatively; and explain how the possible factors influence GPP in different regions.

2. Materials and methods

2.1 Materials

2.1.1 Climate data

For the global estimation of GPP, we used input datasets of sensible heat flux, latent heat flux, air temperature (T) and photosynthetically active radiation (PAR) from MERRA (Rienecker et al., 2011), which is a NASA reanalysis for the satellite era based on the main new version of the Goddard Earth Observing System Data Assimilation System Version 5 (GEOS-5) to produce an estimate of global climatic conditions at a resolution of 0.5° latitude × 0.6° longitude. More information on the MERRA dataset is available from NASA GES DISC/ Modeling/ Data Holding ([http:// disc.gsfc.nasa.gov/daac-bin/DataHoldings.pl](http://disc.gsfc.nasa.gov/daac-bin/DataHoldings.pl)). The uncertainties of various meteorological factors at the global scale have been validated and evaluated by using surface meteorological datasets (Rienecker et al., 2011; Li et al., 2013).

2.1.2 Vegetation indices data

The VI we used in this study, NDVI dataset, is Global Inventory Modelling and Mapping Studies (GIMMS)-3g (Tucker et al., 2005), which spanned 1982 to 2015 at a spatial resolution of 8×8 km² and a 15-day interval and was acquired from NOAA-AVHRR (Advanced Very High Resolution Radiometer). The dataset provides the only continuous and longest time series of approximately three decades that has been continually assessed and validated, and it has been widely used for long-term global vegetation condition monitoring and detecting (Piao et al., 2006; Wu et al., 2015; Liang et al., 2015). We conducted the biweekly data composite with pixels using the maximum value composite (MVC) method (Holben 1986) to generate a monthly temporal scale NDVI dataset to calculate fPAR (Myneni and Williams 1994) for running the C-Fix model.

2.1.3 Land cover data

The land cover map from 1982 to 1991 was acquired from the Global Land Cover Facility (GLCF): AVHRR Global Land Cover Classification (<http://glcf.umd.edu/data/landcover/>). The images from the AVHRR satellites between 1981 and 1994 were utilized and analyzed to distinguish 14 land cover classes (Hansen et al., 1998). Three spatial scales are available in this product (1, 8 km and 1°), and we selected the highest resolution of 1 km. The other is the European Space Agency (ESA) Climate Change Initiative (CCI) Land Cover (LC) dataset (<https://www.esa-landcover-cci.org/>), a 300m annual global land cover time series from 1992 to 2015. These 24 annual global land cover maps were produced by state-of-the-art reprocessing of the full archives of five different satellite missions that provided daily observations of the Earth. CCI-LC provides information for 22 classes of dominant land cover types defined using the Land Cover Classification System (LCCS), which was found to be compatible with the Plant Functional Types (PFTs) used in the climate models (CCI-LC URD Phase I). Detailed information on the CCI-LC is available on the CCI-Viewer (<http://maps.elie.ucl.ac.be/CCI/viewer/>). The land cover data need to be crossed with the grids analyzed in this study at a 0.5° spatial resolution; all 300-m and 1-km pixels falling in the 0.5° cells were used to calculate the proportion of the dominant land cover type.

2.1.4 Atmospheric CO₂ concentration data

Two datasets of the atmospheric CO₂ concentration were used to normalize the CO₂ fertilization factor in the present study; one is the global monthly continuous spatial CO₂ concentration data from 2000 to 2015, Carbon Tracker CT2016, which is an open product of NOAA's Earth System Research Laboratory that uses data from the NOAA ESRL greenhouse gas observational network and collaborating institutions (Peters et al., 2007), released on Feb 17th, 2017. In CT2016, land biosphere, wildfire, fossil fuel emissions, atmospheric transport and other factors are data-assimilated to produce the estimates of surface fluxes and atmospheric CO₂ mole fractions (<https://www.esrl.noaa.gov/gmd/ccgg/carbontracker/index.php>). The other is globally averaged surface monthly mean CO₂ data from 1982 to 1999 obtained from NOAA/ESRL (www.esrl.noaa.gov/gmd/ccgg/trends/). A global average is constructed by first fitting a smoothed curve as a function of time to each site, after which the smoothed value for each site

is plotted as a function of the latitude for 48 equal time steps per year. A global average is calculated from the latitude plot at each time step (Masarie 1995). The spatial continuous CO₂ concentration data were resampled to the 0.5°×0.5° spatial resolution by linear method.

2.1.5 Soil property data

The Climate Prediction Center (CPC) soil moisture (SM) dataset v2 (van den Dool et al., 2003) provided by the NOAA/OAR/ESRL PSD (<http://www.esrl.noaa.gov/psd/>) and the Global Gridded Surfaces of Selected Soil Characteristics (IGBP-DIS) dataset (Global Soil Data Task, 2014) (<http://www.daac.ornl.gov>) were used in this study to calculate the water limitation on LUE by considering the stomatal regulating factor from soil moisture deficits. Since globally measuring soil moisture is impossible, we used the model-calculated CPC-SM dataset, which provides global monthly data from 1948 to 2017 consists of a file containing the averaged soil moisture water height equivalents at a spatial resolution of 0.5°×0.5°. On the other hand, IGBP-DIS dataset is a global product generated at a resolution of 5×5 arc-minutes by the SoilData System (SDS), which generates soil information and maps for geographic regions at user-selected soil depths and resolutions. We used the wilting point and field capacity maps derived from this dataset and converted the data to the values at a soil depth of 1.6 m, the same as CPC-SM. The data were resampled to the 0.5°×0.5° spatial resolution by linear method.

Table 1 Overview of the datasets used in this study

Data used to estimate GPP	Datasets /products	Period	Resolution	Data source / acquisition
NDVI	GIMMS-3g	1982-2015	8 km×8 km	NOAA AVHRR
Land-cover classification	UMD Land-cover Classification	1981-1994	1 km×1 km	GLCF
	CCI-LC	1992-2015	300 m×300 m	ESA
Atmospheric CO ₂ concentration	CO ₂ records	1982-1999	global	
	CT2016	2000-2015	2° latitude × 3° longitude	NOAA ESRL
Photosynthetically active radiation				
Air temperature	MERRA	1980-2015	0.5° latitude ×	NASA GES
Sensible heat flux			0.6° longitude	DISC
Latent heat flux				
Soil moisture	CPC-SM v2	1980-2015	0.5°×0.5°	NOAA ESRL PSD
Wilting point & field capacity	IGBP-DIS	1950-1996	0.5°×0.5°	NASA ORNL DAAC

2.2 Model description

C-Fix is a parametric LUE model with a strong prognostic capability that is driven by plant-related, meteorological, climatic, and hydrological data to estimate carbon mass fluxes in terrestrial ecosystems (Veroustraete et al., 2006) from local (Veroustraete et al., 2002, 2004; Yuan et al., 2014a) and regional (Maselli et al., 2009; Chiesi et al., 2011; Yan et al., 2016) to global scales (Yuan et al., 2014b; Ma et al., 2015). Comparing with other LUE models, C-Fix has a module of carbon fertilization effects caused by increases in the atmospheric CO₂ concentration, which is considered to be the major reason for global warming. C-Fix can use inputs averaged over different time periods (most commonly 10-day to monthly periods) and is conceptually simple and generally applicable (Chiesi et al., 2011). For a given geographic coordinate (x, y), GPP is calculated as (Veroustraete et al., 2006):

$$GPP = PAR \times fPAR \times \varepsilon_{wl} \times T_s \times S_{CO_2} \quad (1)$$

where PAR is the incident photosynthetically active radiation, fPAR is the fractional absorbed PAR, ε_{wl} is the LUE with water stress, T_s is the temperature dependency factor, and S_{CO_2} is the

carbon fertilization factor due to the rising atmospheric CO₂ concentration levels. The details of calculations of the parameters can be found in the Support Materials section 1 (SM-1.1). The datasets used in this study to calculate these parameters are shown in Table 1.

2.3 Attribution method of GPP trends

Five drivers were considered for their impact on estimated GPP trends: I) rising global CO₂ concentration, II) land-cover change and changes in III) solar radiation, IV) temperature and V) water conditions. These five drivers were prescribed in the C-Fix model and the sources are introduced in Table 1. To assess the contribution of each of the five factors and possible interactions between them, we conducted a series of C-Fix factorial estimates where one driver remains fixed while the others vary during the period of 1982-2015. The estimation protocol is shown in Table 2.

Table 2 Illustration of the estimation protocol and the five factors used as input data for factorial estimates.

Factorial estimates	Water forcing	Temperature forcing	Radiation forcing	CO ₂ level increasing	Land-cover change
GPP _{Control}	1982-2015	1982-2015	1982-2015	1982-2015	1982-2015
GPP _{Water}	1980-1984	1982-2015	1982-2015	1982-2015	1982-2015
GPP _{Temperature}	1982-2015	1980-1984	1982-2015	1982-2015	1982-2015
GPP _{Radiation}	1982-2015	1982-2015	1980-1984	1982-2015	1982-2015
GPP _{CO2}	1982-2015	1982-2015	1982-2015	1982	1982-2015
GPP _{LCC}	1982-2015	1982-2015	1982-2015	1982-2015	1982

The estimation with all factors varying defines the GPP_{Control}. In each factorial estimate (Table 2), the selected factor is held to the fixed value as the gray background in Table 2, while all other factors vary as the group of GPP_{Control}. In the case of “constant water, temperature and radiation”, to eliminate the particularity of one year, we used the averaged values of five years from 1980 to 1984.

The individual contribution of each factor is defined as the difference, δX (X represents the individual factor), between GPP trends from each corresponding estimation and that of GPP_{control} (Trend_{control}), in which all factors are varied (Chang et al., 2016). Since the factors influence each other, in this study, the nonlinear interaction as a residual is defined as δ Residual:

$$\delta \text{Residual} = \text{Trend}_{\text{control}} - \sum_{i=1}^n \text{Trend}_{X_i} \quad (2)$$

where n is the number of factors and Trend_{X_i} denotes the linear trend of Factorial X_i .

2.4 Study process

First, due to the different spatial resolutions of global datasets, all grid data were resampled by mean values or dominated indicators to a $0.5^\circ \times 0.5^\circ$ spatial resolution. Second, all data were inputted into C-Fix to estimate the $\text{GPP}_{\text{Control}}$. We used two widely used GPP products to test the accuracy of the estimated GPP. If the accuracy of the estimates were acceptable, the factorial estimates would be calculated to obtain the estimates of $\text{GPP}_{\text{FactorX}}$. Based on the attribution method of the GPP trend, we can obtain the spatial distributions of the individual effect of each factor. We can better know the spatial and seasonal patterns of GPP variations through the monthly trend information, therefore, the GPP trend for each month of the year was calculated (e.g., the monthly GPP trends of all 34 Decembers were averaged to obtain a December trend). After spatially calculating, we got the map that shows the annual cycle of monthly GPP trends. We then calculated the monthly GPP mean values of 34 years from January to December for each pixel. Therefore, we can obtain information on the vegetation average growing situation in one year to represent the annual cycle of growing season. The two annual cycles revealed the month of one year when GPP increases or decreases at a given location were caused by changes in the GPP amplitude or the growing season length (Hicke et al., 2002); and we draw the description figure following Hicke et al. (2002) as Fig.2. We used this characteristic as the index of vegetation growth changes in the cluster classification to obtain the spatial distribution of the GPP change types. Finally, according to the spatial distribution of each factor monthly trends, net effects and GPP change types, we will more clearly understand the spatial patterns and the drivers of GPP variations. Fig 1 shows the logical process of this study.

Fig. 1 Study flowchart.

Fig. 2 Schematic showing monthly trends in GPP in response to an increase in the amplitude if the GPP annual cycle (dashed-dotted curve) and an increase in the length of the growing season (dashed curve) occurred from a baseline GPP annual cycle (solid curve).

3. The results

3.1 Accuracy assessment of estimated GPP

In this study, we estimated a relative long-term series global GPP at a spatial resolution of 0.5°, which is larger than the footprint size of ground-based observations. Hence, we relied on the model and other remotely sensed data for a comparison on the global scale. As a benchmark, we compared the estimates against the MTE model GPP from 1982 to 2011 (Jung et al., 2011) because it is based on direct eddy-covariance flux tower measurements of GPP and is thus

considered close to the truth where the flux tower density is high (Beer et al., 2010; Frankenberg et al., 2011). MODIS GPP products from 2000 to 2014 were also used because MODIS products have been widely known and used (Turner et al., 2006b; Zhao and Running, 2010; Frankenberg et al., 2011). As well as the results from process-based models of 1982-2010 from the Inter-Sectoral Impact Model Intercomparison Project II (ISIMIP2a) (Reyer et al., 2017; Chang et al., 2017) were selected to test the accuracy of estimated GPP. For the annual GPP, we found a strong linear spatial correlation between the estimated GPP with process-based models, MTE and remotely sensed GPP values, most notably with MTE_GL GPP (averaged $r=0.9269$, averaged slope= 1.0977), followed by MTE_MR GPP (averaged $r=0.9266$, averaged slope= 1.1008) and MODIS GPP (averaged $r=0.9205$, averaged slope= 1.3089) (SM 2.1). The performs of the comparing with the results from different process-based models were different (SM 2.3), but all show a strong correlation. Compared with the results of multiple models, the spatial correlation coefficient could reach 0.8377 with the slope of 1.0159 . We find that the estimated GPPs are highly consistent with MTE GPP and MODIS products; thus, the estimated GPP in the present study can be used in subsequent analyses.

3.2 GPP trends

3.2.1 Contributions of different factors to GPP trends

For the global terrestrial ecosystems, the overall effect of all the five factors considered is positive (Table 3). The key result is that the increases in the atmospheric CO_2 concentration make the largest contribution to the globally averaged GPP trend. The changes in water conditions and temperature caused comparable but lower GPP positive trends. The changes in solar radiation caused the whole effect of decreasing GPP. Although the change in GPP attributed to land-cover change is positive around the world, the regional maximum negative effect also occurred due to land-cover changes. That the sum of the effects of each factor on GPP trends is $0.0795 \text{ gCm}^{-2}\text{yr}^{-1}$ smaller than the overall GPP trend attributed to all factors indicates that the interactions between each factor are positive.

Table 3 Trends in GPP globally during the period 1982-2015 and the effects of the factors on the trend.

Factors	Average effect*	Max effect*	Min effect*	Standard deviation*	Globally averaged contribution %	Positive effect fraction %
Overall effect	0.6560	7.6213	-4.9341	0.7811	100.00	75.76
Temperature	0.0857	5.8234	-4.4056	0.5412	13.07	73.16
Water	0.0770	3.6817	-2.3074	0.2944	11.74	42.68
Radiation	-0.0475	1.5470	-3.2759	0.3480	-7.24	35.74
CO ₂ concentration	0.4312	2.7181	-0.0027	0.5088	65.73	57.74
LCC	0.0300	3.7428	-6.1646	0.2244	4.57	63.08
Residual	0.0795	2.1355	-2.5261	0.2115	12.13	46.23

* All values are at the level of p_value < 0.1, and the unit is gCm⁻²yr⁻¹.

3.2.2 Spatial distribution of the GPP trend and its attribution

The spatial distribution of annual GPP trend in the period of 1982-2015 is shown in Fig. 3. The contribution of different factors in different areas vary considerably (Fig. 4). The figure shows that the largest increases in GPP are found in the southern parts of the Amazon rainforest with increases of 5 gCm⁻²yr⁻¹, where the changes in temperature and water conditions play the major roles in causing the increasing GPP trends (Fig. 4). Positive GPP trends greater than 3 gCm⁻²yr⁻¹ were found in the InterTropical Convergence Zone (ITCZ) except for Congo rainforest, which has the largest decreases in GPP with values that exceed -2 gCm⁻²yr⁻¹, where the changes in water conditions and the enhanced interactions play the most important roles in explaining those GPP trends. Followed by humid temperature regions in eastern North America, western and central Europe and eastern China, with an increment of approximately 2.5 gCm⁻²yr⁻¹ is found, and solar radiation and temperature have positive effects on GPP trends. Not all regions show the positive GPP trends, we also found negative GPP trends in the Borbolima Plateau, Diamantine Plateau, Pampas grassland, Cordillera Mountains, Australian desert and the areas east of Caspian Sea. And relatively concentrated are the trends of the Congo Basin which were attributed to the effect of the changes in temperature and water conditions.

Fig. 3 The spatial distribution of linear trends in GPP during the period 1982-2015. The pixels that are not satisfied at $p_value < 0.1$ are drawn in gray.

The changes in the atmospheric CO_2 concentration make almost no negative contribution to the pattern of the GPP trend globally. Significant positive GPP trend effects of land-cover changes were found in regions such as high latitudes, mid-latitudes inland areas, high altitude areas and some barren vegetation areas. In contrast, in many areas, especially the dry forest of South America and eastern Africa and the Eurasian rainforest, the land-cover change shows a decreasing GPP effect. Regarding contributions of climatic factors (temperature, water, and radiation), regionally, climate change can have either a positive or a negative effect on GPP trends. In addition, the interactions among different factors also have regional characteristics.

Fig. 4 Spatial distribution of the trends in GPP due to (a) increases in atmospheric CO_2 concentration, (b) land-cover change, (c) solar radiation changes, (d) temperature changes, (e) changes in water conditions, and (f) their nonlinear interactions or non-attributed. The pixels ((a) to (e)) that are not satisfied at $p_value < 0.1$ are drawn in gray.

3.3 GPP trend category zoning

To further investigate the seasonal dynamics and varying patterns of GPP during the period of 1982-2015, we classified the monthly GPP and monthly GPP trends to group locations with similar behaviors. This isolated regions that had lengthening growing seasons, for example, or had increased GPP in the rapid growth stage (RGS). We used the average monthly GPP in the classification as an index of the vegetation growth stage. The monthly GPP and GPP trends were first normalized to allow these variables to be used together in the classification (Hicke et al., 2002).

Fig. 5 The spatial distribution of classes on variations in GPP during the period 1982-2015.

Nine general categories (Fig. 5) resulted from using a k-means (Hartigan, 1975) classifier according to the statistical characteristics information of GPP variations. Here, we focus our results on the large-scale patterns that occurred. Because specifying fewer groups obscured some information in the analysis, and although the classification assigns each pixel to a group and we present the class mean information (Fig. 6), we have to admit that the circumstance that a pixel may not behave in a manner close to the class mean exists. This categorization is necessarily approximate; we used the groups as an aid to explain the large-scale behavior of GPP variations: Class 1: Mainly in the African rainforest, GPP trends are negative, especially in July between two RGSs; the first RGS ends early and the second RGS has a delayed start; Class 2: Mainly in high latitudes and high altitudes, GPP trends are positive, and the main

reason for the increasing GPP is the changes in the amplitude. Class 3: Mainly in polar and barren areas, there are low or almost no GPP in these areas, and the increases or decreases are almost equal to 0; Class 4: Mainly in cool temperate zones, GPP trends are positive, and the RGS has an early lengthening trend. However, the changes in the amplitude play a more important role. In Class 5, Mainly in equatorial, winter dry climate zones, the GPP trends are positive throughout the growing season; and the increasing trend in the early period is less than that in the middle and later periods. The RGS has a trend of delayed ends; Class 6: Mainly in equatorial, fully humid climate zones, the GPP trends were positive throughout the growing season, and the end of the RGS has a slightly delayed trend. In Class 7: Mainly in warm temperate zones, the curve of the GPP trends are similar to a bimodal curve, and the trend of lengthening in growing season is obvious; Class 8: Mainly distributed in desert areas, the vegetation has two RGSs, and the increment in the first RGS is larger than that in the second RGS; Class 9: Mainly distributed in the fully humid zones of Amazon rainforest, the GPP is stable at a high level throughout the year, and the RGS extends backwards.

Fig. 6 Characteristics of the annual cycle of the growing season distribution and GPP trends associated with each class.

4. Discussions

4.1 Increases in atmospheric CO₂ concentration

In this study, the contribution of the rising CO₂ concentration on the globally averaged GPP trend is the largest proportion. However, we cannot conclude that the effect of the increasing CO₂ concentration on GPP variations is more important than the changes in other factors. The main reason is that the increases in the CO₂ concentration occurred in a globally synchronous manner, while the global averaged effects of the other factors are neutralized because the attributions can be positive or negative in different locations (Fig. 7). An elevated atmospheric CO₂ concentration enhances vegetation photosynthesis and has indirect effects on increasing

water use efficiency (Donohue et al., 2013; Fensholt et al., 2012), and in this study, we can see that the regions with a relatively larger increasing GPP trend also had better water condition trends (e.g., Asian rainforest, Amazon rainforest, eastern Africa, and large areas in the middle-high latitudes in the Northern Hemisphere). In our estimation, the rising CO₂ concentration causes an average of a 2.63% increase around the globe over 34 years which falls within the range of a sensitivity analysis on GPP affected by increasing CO₂ (Wang et al. 2014). Models that do not consider CO₂ fertilization modules might be a source of uncertainty (Anav et al. 2015) in estimating GPP, and elevated atmospheric CO₂ concentration is one of the main reasons for global climate change. Therefore, we used the C-Fix model, which has a carbon fertilization module instead of other LUE models such as the CASA (Potter et al., 1993), CFlux (Turner et al., 2006a) VPM (Xiao et al., 2004), VPRM (Mahadevan et al., 2008), EC-LUC (Yuan et al., 2007) and MODIS-GPP algorithms (Running et al., 2000). We used the MTE GPP and MODIS product to compare our estimated GPP and found that we estimated a higher GPP than the MTE GPP and MODIS product. The relationship with MODIS GPP is consistent with previous studies (Heinsch et al., 2006; Avan et al., 2015), which reported that the products are smaller than the GPP observed at many flux tower sites. The growth rate of the slopes of our estimated GPP on the MODIS product shows a significant correlation with the trend of rising CO₂ concentrations with a correlation coefficient of 0.9290. This finding can better illustrate that without considering carbon, fertilization is the main reason for the lower values in MODIS product. Regarding the comparison with MTE GPP, our estimates are larger than MTE GPP, with an average slope of 1.1985 from 1982 to 2011, with the trend of following the rising CO₂ concentration. This result is almost the same as the finding by Piao (2013), who used 10 process-based terrestrial biosphere models used for the IPCC Fifth Assessment Report compared to MTE GPP, and the models were found to produce a higher GPP than MTE with a trend of 1.1271 from 1982 to 2008. Therefore, our estimates can successfully reflect the effect of elevated CO₂ concentration on GPP during the period of 1982-2015.

Fig. 7 The range of contributions of GPP to different factors globally and on each continent (The bottom of the box is the lower quartile, and the top is the upper quartile. The whiskers extend to the maximum and minimum values).

4.2 Effects of LCC

For the globe, the greatest negative impact on the GPP trend is from LCC, which has a direct effect on PFTs (Chen et al., 2006). These negative effect areas are concentrated in South America (especially Brazil, Argentina, Bolivia and Paraguay), Eurasian rainforests (especially Indonesia), and tropical dry forests in Africa (especially Ethiopia), all of which had the highest rate of forest loss (Lepers et al., 2005; Hansen et al., 2017). In addition, the rates of forest loss were relative lower in the temperate climate zones of North America and Europe, where the LCC also had a relatively lower negative effect on GPP. In Europe and Oceania, the latitudinal span is not as great as on other continents; therefore, the range of the effects of radiation, water and temperature are relatively consistent, and the most significant spatial difference effect is from LCC (Fig. 7).

4.3 Effects of climatic factors on GPP

The changes in the temperature and water over the past 34 years are estimated to cause increases in GPP around the world as a whole, which is contrary to the results caused by changes in radiation. However, the effect of these factor trends can be positive or negative in different regions. To further investigate the possible climate drivers that cause the seasonal dynamics and varying patterns of GPP during the period of 1982-2015, we analyzed the monthly trends for each factor (SM2.4) and summarized the distribution of the regions where GPP has varied due to different possible drivers.

The productivity of vegetation in tropical dry zone is weak; climate change induces a slight

trend in GPP in those regions. The GPP trends in tropical wet zones (i.e. Indonesian- Malaysian rainforest, Latin America) are positive because their dominant factor, water conditions, have become increasingly suitable for vegetation growth, which is also suitable for the high altitudes in Africa. In cool temperate moist zones, the positive trend is the result from the early growing season lengthening caused by radiation shifts and plant growth enhancement caused by temperature and radiation changes. With respect to cool temperate dry zones, the positive effects of the temperature and radiation during the rapid growth stage are the main drivers causing increases in the amplitude of vegetation growth. For most warm temperate dry zones, the changes of the GPP are dominated by radiation; hydrothermal conditions in the regions are almost unchanged during the growing season (from May to September). Conversely, radiation and water conditions together led to an increasing GPP trend in warm temperate moist zones, where water condition changes enhance the plant growth magnitudes and radiation lengthens the growing season. Additionally, in tropical moist zones, the evapotranspiration is reduced by the decreasing temperature; simultaneously, the water conditions become more suitable for plant growth. Therefore, the GPP trends are positive. Moreover, in South America, the growing season length has been extended by increased radiation in the later period of the rapid growth stage. In boreal moist zones, radiation and hydrothermal conditions in the growing season jointly promote vegetation growth. Regarding polar moist zones, in September, the rapid growth stage has an early end due to the declining radiation, but the water conditions and temperature elevating the GPP magnitude during the growing season result in a positive effect. For Congo Basin and Brazilian Highlands where following by increasing temperatures and decreasing water the monthly GPP decreased mostly. The Congo rainforest has some continental climate characteristics, where water is the dominant factor inducing the trend in GPP. Water conditions become more unsuitable; although radiation became more abundant, it is accompanied by increasing temperatures and evapotranspiration, ultimately inducing a negative trend in GPP. Additionally, in South Central Australia, three factors contribute to the conditions: water conditions dominate the GPP changes, including the magnitudes and growing season length; radiation increased during the later growth period; and temperatures became

more suitable during the growing season.

Combined with terrain and location, we can generally and summarily conclude that radiation and temperature are relatively sufficient for vegetation in lower latitudes since solar irradiation occurs twice a year. Therefore, water conditions have become the dominant climatic factor affecting GPP trends. In addition, adequate water conditions are associated with decreasing radiation due to cloud cover and reducing temperature due to evaporation. Hence, the trends of GPP in lower latitudes are also affected by radiation and temperature synergistically, while in the middle and high latitudes, the main climatic factors affecting GPP trends are temperature and radiation, which have improved the demand for suitable conditions during the growing season and explains much of the increasing GPP trends in temperature and radiation variability in the northern regions of North America and Eurasia. Additionally, in high altitude regions, since the hydrothermal conditions are further from the ideal situation, temperature and water conditions are the main climatic factors in GPP trends in these regions.

5. Conclusions

In this study, we estimated the global monthly GPP at a $0.5^{\circ} \times 0.5^{\circ}$ spatial resolution during the period of 1982-2015, analyzed the effects of drivers on GPP trend and zoned the categories of GPP variation.

The five factors considered in this study resulted in an overall positive effect on the GPP trend but with different spatial patterns, magnitudes, and mechanisms. Globally, increases in GPP occurred in over 75% of the areas; the interactions between factors were positive, and the increases in atmospheric CO₂ concentration had the greatest contribution on global increasing GPP. However, regionally, the LCC and climatic factors appear play more important roles in GPP changes.

Larger areas in the lower latitudes showed increases in the amplitude of the GPP annual cycle which dominated by shifts in water conditions; in contrast, in the middle latitudes GPP expressed not only the amplitude changes but also a lengthened rapid growth stage during the early period which were likely to be driven by increases in temperature and radiation; in large

areas of the Southern Hemisphere, GPP increased in both the early and later period of the growing season, resulting in a lengthening growing season. However, at high altitudes, the changes in GPP were probably caused by the changes in the temperature and water conditions. The CO₂ fertilization effect was explicitly expressed in this study by comparisons with MTE and MODIS GPP. By contrast, the effect of nutrition cannot be quantified from our study since any resulting changes were implicit in the satellite-observed NDVI and were not explicitly modeled. Many studies show that nutrient availability strongly constrains vegetation growth through water availability, the CO₂ assimilation rate and other factors (Reich et al., 2014; Wieder et al., 2015). The potential effects of nutrient limitation should be considered in estimates of the terrestrial GPP in future studies.

In summary, we found a wide range of GPP trends, both spatially and seasonally. It appears that CO₂, LCC and climatic factors together played a role in global terrestrial GPP changes.

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Supporting Materials

Spatial patterns of GPP variations in terrestrial ecosystems and its drivers: climatic factors, CO₂ concentration and land-cover change, 1982-2015

Supporting Materials

This supporting material presents 1) detailed descriptions of the method, and 2) ancillary descriptions of the results.

SM 1. Detailed descriptions of the method

SM 1.1 C-Fix model

SM 2. Ancillary descriptions of the results

SM 2.1 Comparison with the MTE GPP and MODIS product

SM 2.2 Comparison with the DGVM GPP product

SM 2.3 Spatial Distribution of GPP trend in each month of a year

SM 2.4 Spatial distribution of monthly trends in GPP drivers

Reference

SM 1. Detailed descriptions of the method

The C-Fix model uses the following equations to estimate GPP (Veroustraete et al., 2006):

$$GPP = PAR \times fPAR \times \varepsilon_{wl} \times T_s \times S_{CO_2} \quad (\text{Equ-S1})$$

fPAR is the fraction of absorbed photosynthetic active radiation (PAR) (0,1). Myneni and Williams (1994) used a set of empirical constants to establish a linear equation to describe the relationship between fPAR and NDVI:

$$fPAR = 0.8624 \times NDVI + 0.0814 \quad (\text{Equ-S2})$$

ε_{wl} is the LUE by considering the impact of water limitation. Veroustraete (2006) combined the soil moisture deficit and vapor pressure deficit to calculate a linearly water limited LUE delimited between ε_{max} and ε_{min} :

$$\varepsilon_{wl} = \varepsilon_{min} + (a \times F_s + b \times F_a) \times (\varepsilon_{max} - \varepsilon_{min}) \quad (\text{Equ-S3})$$

where ε_{max} and ε_{min} are the maximum and minimum LUE, respectively, which are biome-dependent invariant. We used the values from Yuan (2014), which is based on the measurements of ecosystem carbon fluxes from 168 globally distributed sites in a range of vegetation types. a and b are the empirical coefficients in the weighting of water limitations in LUE originating from soil and air according to Veroustraete (2006) ($a=0.5$, $b=0.5$). F_s and F_a are stomatal regulating factors from soil and air, which are simulated by soil moisture (SM) and evaporative fraction (EF), respectively:

$$F_s = 1 - a_1 \times \exp[a_2 \times (FC - SM) \times (FC - WP)^{-1}] \quad (\text{Equ-S4a})$$

$$F_a = b_1 \times \exp(b_2 \times EF) \quad (\text{Equ-S4b})$$

$$EF = \lambda E \times (\lambda E + H)^{-1} \quad (\text{Equ-S4c})$$

where a_1 (0.5), a_2 (0.5), b_1 (0.1) and b_2 (2.88) are empirical coefficients in the stomatal regulating factor relation (Veroustraete et al., 2006). SM is the volumetric moisture content, FC and WP are the volumetric moisture content at the field capacity and wilting point. λE is the latent heat flux, and H is the sensible heat flux.

The temperature dependency factor was defined by Wang (1996) as:

$$T_s = \frac{\exp[C_l - \Delta H_{a,p} \times (R_g \times T)^{-1}]}{1 - \exp[(\Delta S \times T - \Delta H_{d,p}) \times (R_g \times T)^{-1}]} \quad (\text{Equ-S5})$$

where R_g , $H_{d,p}$, $H_{a,p}$, S and C_l in the temperature dependency factor equation are 8.31 J K⁻¹ mol⁻¹, 211 kJ mol⁻¹, 52.75 kJ mol⁻¹, 704.98 J K⁻¹ mol⁻¹ and 21.77, according to Veroustraete (2002).

S_{CO_2} is defined by Veroustraete (1994) (0,+∞), due to CO₂ concentration levels above the reference level enhancing the carbon assimilation rate, as follows.

$$S_{CO_2} = \frac{[CO_2] - [O_2] \times (2s)^{-1}}{[CO_2]^{ref} - [O_2] \times (2s)^{-1}} \times \frac{K_m \times (1 + [O_2] \times K_0^{-1}) + [CO_2]^{ref}}{K_m \times (1 + [O_2] \times K_0^{-1}) + [CO_2]} \quad (\text{Equ-S6})$$

where the parameters of s , K_m , K_0 , $[CO_2]^{ref}$ are 2550, 948, and 30 and the CO₂ mixing ratio for the reference year is 1833 (281ppm). $[CO_2]$ is the atmospheric CO₂ concentration (for 1982-1999, we used the global averaged monthly mean value; for 2000-2015, we used the spatial continuous monthly grid data). In this study, $[O_2]$ was set to 209,500 ppm according to Zimmer (2013).

SM 2. Ancillary descriptions of the results

SM 2.1 Comparison with MTE GPP and MODIS Product

Table S1 the parameters of linear regression lines of GPP comparisons (p_value < 0.0001).

Year	MTE GL GPP		MTE MR GPP		MODIS GPP	
	Correlation coefficient	Slope	Correlation coefficient	Slope	Correlation coefficient	Slope
Average	0.9269	1.0977	0.9266	1.1008	0.9205	1.3089
1982	0.9267	0.9909	0.9267	0.9943	-	-
1983	0.9107	0.9540	0.9108	0.9567	-	-
1984	0.9270	1.0000	0.9265	1.0038	-	-
1985	0.9317	1.0443	0.9311	1.0477	-	-
1986	0.9293	1.0529	0.9285	1.0561	-	-
1987	0.9196	1.0137	0.9192	1.0164	-	-
1988	0.9251	1.0266	0.9247	1.0294	-	-
1989	0.9293	1.0761	0.9291	1.0795	-	-
1990	0.9241	1.0620	0.9243	1.0664	-	-
1991	0.9221	1.0314	0.9224	1.0348	-	-
1992	0.9238	1.0382	0.9230	1.0414	-	-
1993	0.9266	1.0637	0.9262	1.0678	-	-
1994	0.9235	1.0761	0.9228	1.0789	-	-
1995	0.9291	1.0857	0.9284	1.0886	-	-
1996	0.9271	1.0955	0.9265	1.0983	-	-
1997	0.9241	1.0829	0.9265	1.0983	-	-
1998	0.9153	1.0645	0.9155	1.0656	-	-
1999	0.9320	1.0993	0.9321	1.1029	-	-
2000	0.9325	1.1324	0.9324	1.1355	0.9242	1.2429
2001	0.9312	1.1501	0.9313	1.1525	0.9239	1.2634
2002	0.9269	1.1553	0.9264	1.1578	0.9178	1.2603
2003	0.9281	1.1635	0.9264	1.1578	0.9201	1.2630
2004	0.9308	1.1522	0.9303	1.1543	0.9189	1.2650
2005	0.9290	1.1321	0.9285	1.1340	0.9162	1.2856
2006	0.9325	1.1807	0.9322	1.1833	0.9206	1.3155
2007	0.9319	1.1927	0.9319	1.1958	0.9222	1.3232
2008	0.9299	1.1983	0.9296	1.2019	0.9225	1.3246
2009	0.9302	1.2000	0.9294	1.2029	0.9170	1.3268
2010	0.9274	1.1915	0.9273	1.1931	0.9229	1.3631
2011	0.9280	1.2254	0.9278	1.2287	0.9200	1.3602
2012	-	-	-	-	0.9218	1.3179
2013	-	-	-	-	0.9201	1.3623
2014	-	-	-	-	0.9188	1.3603

Fig. S1 Scatter plots of estimated GPP values (y axis) vs. MTE_GL GPP values (x axis) from 1982 to 2011. Only pixels over vegetated areas are shown. The parameters of the linear regression line in all panels are shown in Table S1.

Fig. S2 Scatter plots of estimated GPP values (y axis) vs. MTE_MR GPP values (x axis) from 1982 to 2011. Only pixels over vegetated areas are shown. The parameters of the linear regression line in all panels are shown in Table S1.

Fig. S3 Scatter plots of estimated GPP values (y axis) vs. MODIS Product (x axis) from 1982 to 2011. Only pixels over vegetated areas are shown. The parameters of the linear regression line in all panels are shown in Table S1.

Fig. S4 Relationship between the slopes of the estimated GPP to MODIS product and atmospheric CO₂ concentration.

SM 2.2 Comparison with process-based model

Table S2 the parameters of linear regression lines of GPP comparisons

	GSWP3		PGMFD		WATCH	
	Slope	R	Slope	R	Slope	R
CARAIB	1.0268	0.8544	1.0451	0.8619	1.0422	0.8590
DLEM	1.0188	0.8241	1.0055	0.8290	1.0542	0.8266
JULES-B1	0.7151	0.7565	0.7005	0.7633	-	-
LPJml	1.1017	0.8500	1.0843	0.8475	1.1225	0.8399
ORCHIDEE	0.9963	0.8727	0.9452	0.8785	1.0201	0.8766
VEGAS	-	-	1.2797	0.8720	1.2984	0.8792
VISIT	0.8661	0.8051	0.9571	0.8195	1.0231	0.8012

models: CARAIB- CARbon Assimilation In the Biosphere; DLEM- Dynamic Land Ecosystem Model; JULES-B1- formerly JULES_UoE; LPJml- Lund Potsdam Jena model with managed Land; ORCHIDEE- Organizing Carbon and Hydrology in Dynamic EcosystEms; VEGAS- VEgetation - Global - Atmosphere - Soil; VISIT- Vegetation Integrative Simulator for Trace Gases; Climate dataset: G- GSWP3; P- PGMFD v.2 (Princeton); W- WATCH (WFD). The GPP datasets used in this study were obtained from The Inter-Sectoral Impact Model Intercomparison Project (ISIMIP2a) (<https://www.isimip.org/>).

SM 2.3 Spatial Distribution of GPP trend in each month of a year

All drivers considered in this study have the overall effect of increasing GPP for each month for the whole terrestrial ecosystems (Units: $\text{gCm}^{-2}\text{yr}^{-1}$; Jan: 0.3918; Feb: 0.3818; Mar: 0.3999; Apr: 0.5234; May: 0.6968; Jun: 1.0340; Jul: 1.0418; Aug: 0.8255; Sep: 0.6338; Oct: 0.4390; Nov: 0.3869; Dec: 0.3680). Fig. S6 shows considerable seasonal variations, especially in the Northern Hemisphere, with larger increases in later spring and summer and low increases or decreases in earlier spring and autumn. Regarding the ITCZ regions, GPP trends in Amazon and Asian rainforests are continuously increasing throughout the year; on the contrary, the GPP trends in the Congo rainforest is reduced. The GPP trends in Southern South America, southern Africa and Australia also have seasonal change characteristics. The GPP trends in two regions, southern Amazon and Congo Basin, have trends that reflect the most significant changes more obviously following the subsolar point from the equator moving northward. The GPP trends correctly captured patterns at the global scale, such as the trends over North America showing considerable East-West differences and a typical longitudinal gradient in Northern Eurasia.

Fig. S5 The monthly spatial distributions of linear trends in GPP during the period 1982-2015.

SM 2.4 Spatial distribution of monthly trends in GPP drivers

Fig. S6 The monthly spatial distributions of linear trends in atmospheric CO₂ concentrations during the period 1982-2015.

Fig. S7 The monthly spatial distributions of linear trends in radiation during the period 1982-2015.

Fig. S8 The monthly spatial distributions of linear trends in water conditions during the period 1982-2015.

Fig. S9 The monthly spatial distributions of linear trends in temperature during the period 1982-2015.

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