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To cite this article: Yue Chen *et al* 2024 *Environ. Res. Lett.* **19** 014052

ENVIRONMENTAL RESEARCH
LETTERS

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RECEIVED
21 July 2023

REVISED
14 November 2023

ACCEPTED FOR PUBLICATION
28 November 2023

PUBLISHED
18 December 2023

LETTER

The direct and indirect effects of the environmental factors on global terrestrial gross primary productivity over the past four decades

Yue Chen[1,2], Zaichun Zhu[1,2,*], Weiqing Zhao[1,2], Muyi Li[1,2], Sen Cao[1,2], Yaoyao Zheng[1,2], Feng Tian[1,2] and Ranga B Myneni[3]

1 School of Urban Planning and Design, Shenzhen Graduate School, Peking University, Shenzhen, People's Republic of China
2 Key Laboratory of Earth Surface System and Human-Earth Relations, Ministry of Natural Resources of China, Shenzhen Graduate School, Peking University, Shenzhen, People's Republic of China
3 Department of Earth and Environment, Boston University, Boston, MA, United States of America
* Author to whom any correspondence should be addressed.

E-mail: zhu.zaichun@pku.edu.cn

Keywords: gross primary productivity, leaf area index, climate change, CO_2 fertilization, random forests

Supplementary material for this article is available online

Abstract

Gross primary productivity (GPP) is jointly controlled by the structural and physiological properties of the vegetation canopy and the changing environment. Recent studies showed notable changes in global GPP during recent decades and attributed it to dramatic environmental changes. Environmental changes can affect GPP by altering not only the biogeochemical characteristics of the photosynthesis system (direct effects) but also the structure of the vegetation canopy (indirect effects). However, comprehensively quantifying the multi-pathway effects of environmental change on GPP is currently challenging. We proposed a framework to analyse the changes in global GPP by combining a nested machine-learning model and a theoretical photosynthesis model. We quantified the direct and indirect effects of changes in key environmental factors (atmospheric CO_2 concentration, temperature, solar radiation, vapour pressure deficit (VPD), and soil moisture (SM)) on global GPP from 1982 to 2020. The results showed that direct and indirect absolute contributions of environmental changes on global GPP were 0.2819 Pg C yr ^{2} and 0.1078 Pg C yr ^{2}. Direct and indirect effects for single environmental factors accounted for 1.36%–51.96% and 0.56%–18.37% of the total environmental effect. Among the direct effects, the positive contribution of elevated CO_2 concentration on GPP was the highest; and warming-induced GPP increase counteracted the negative effects. There was also a notable indirect effect, mainly through the influence of the leaf area index. In particular, the rising VPD and declining SM negatively impacted GPP more through the indirect pathway rather than the direct pathway, but not sufficient to offset the boost of warming over the past four decades. We provide new insights for understanding the effects of environmental changes on vegetation photosynthesis, which could help modelling and projection of the global carbon cycle in the context of dramatic global environmental change.

1. Introduction

Gross primary productivity (GPP), defined as the amount of organic matter produced by photosynthesis in an ecosystem over a given period, is the starting point of the terrestrial carbon cycle (Beer *et al* 2010, He *et al* 2013). The formation of GPP is driven by multiple factors, including the canopy structure of plants, physiological properties, and the surrounding environmental variables (Chen *et al* 2019, Smith *et al* 2019a, Song *et al* 2022, Zhao *et al* 2022). The canopy structure affects the photosynthesis of vegetation by influencing light interception and distribution. The physiological properties of vegetation determine the maximum efficiency of photosynthesis after sunlight is intercepted. Environmental variables constrain the whole photosynthesis process through temperature, light, water, and CO_2 conditions.

For past years, GPP contributions from the canopy structure and physiological properties have been extensively studied. It has been found that the canopy structure is the primary explanatory factor for the maximum productivity of an ecosystem (Long *et al* 2006, Zhu *et al* 2010, Ort *et al* 2015, Migliavacca *et al* 2021, Zhao *et al* 2021). As the amount and size of leaves largely determine the light interception by the canopy, leaf area index (LAI) has been a popular variable in studying GPP variations (Zhu *et al* 2013, 2016, Zhao *et al* 2021). A major advantage of LAI is that it could be retrieved from satellite-based remote sensing observations available since the early 1970s. This advantage enables the possibility of accurately estimating GPP at a global scale and on a regular basis (Myneni *et al* 2002), using process-based models, light-use efficiency models, and data-driven models (Ruimy *et al* 1994, Running *et al* 2004). The main physiological properties that influence photosynthesis include nitrogen (N), phosphorus (P), and the maximum rate of Rubisco carboxylation (V_{cmax}). N and P have been shown to strongly limit plant growth and productivity (Vitousek *et al* 2010, Yan *et al* 2018, Du *et al* 2020). V_{cmax} defines the capacity of leaves to utilize the energy excited by chlorophyll for photosynthesis (Chen *et al* 2022b). N, P, and V_{cmax} are thus closely related to the photosynthetic capacity of plants (LeBauer and Treseder 2008, Dong *et al* 2017, Yan *et al* 2022).

In the ever-changing global environment, there has been a growing recognition of the significance of environmental factors in influencing GPP variations. Current studies have highlighted the substantial impacts from atmospheric CO_2, temperature, water availability, and solar radiation, which are projected to persist in the coming decades (IPCC 2013, 2018, Friedlingstein *et al* 2019). The impacts can work in several pathways. First, the increasing atmospheric CO_2 concentration has a positive fertilization effect that promotes the photosynthesis rate while limiting leaf transpiration, producing a notably higher GPP at regional and global scales (Sitch *et al* 2015, Zhu *et al* 2021). Second, global warming can benefit vegetation productivity by further improving the maximum photosynthetic rate of plants and lengthening the active growing season in the northern latitudes (Nemani *et al* 2003, Thomas *et al* 2016). Third, recent studies have demonstrated the limitations of vegetation growth due to increasing atmospheric dryness and decreasing soil moisture (SM) caused by warming (Zhang *et al* 2016, Ballantyne *et al* 2017, Schwalm *et al* 2017, Liu *et al* 2018). Global warming could also lower GPP in tropical regions where the temperature is already close to optimal (Huang *et al* 2015, Zhu *et al* 2016, Bastos *et al* 2019, Gonsamo *et al* 2021, Song *et al* 2022). Furthermore, the abovementioned pathways could be complicated by a variety of processes operating at different time scales and in different directions (Denissen *et al* 2022). All current findings put forward the urgent need to thoroughly investigate the mechanisms of GPP regulation under climate change for future climate policies.

Environmental changes can not only directly act on the photosynthesis system (direct effects) but also indirectly affect photosynthesis by altering the canopy structure (indirect effects) (figure 1). Most GPP studies directly employed vegetation indices (VIs) that are related to canopy structure, such as LAI, normalized difference vegetation index (NDVI), or near-infrared reflectance of vegetation (Badgley *et al* 2017, Burrell *et al* 2020, Pierrat *et al* 2022), neglecting the fact that the canopy structure is also a function of environmental variables among others. The quantification of indirect effects can be difficult and has been rarely discussed (Smith *et al* 2019b). On the one hand, canopy structure and physiological properties of the vegetation jointly determine GPP, but their synergistic effect is still not well understood. On the other hand, strong coupling exists between key environmental factors, including temperature (Tmp), surface solar radiation downwards (SRAD), vapour pressure deficit (VPD), and SM. Identifying the direct and indirect effects of individual environmental variables requires comprehensively considering the collaborative regulation of vegetation productivity and carefully decoupling the constituting components in GPP.

In this context, this study aims to systematically investigate the direct and indirect effects of environmental factors on global GPP during 1982–2020. We propose a framework that combines a nested machine-learning model and a theoretical photosynthesis model so that direct and indirect effects of environmental factors (EN) including CO_2, Tmp, SRAD, VPD, and SM can be decoupled, compared, and evaluated.

2. Methods

As the CO_2 fertilization effect (CFE) may not be well explained in machine-learning-based (ML-based) models (Anav *et al* 2015, Fernández-Martínez *et al* 2018, Wang *et al* 2020, Chen *et al* 2022a), our methodology first removed CFE from LAI and GPP and evaluated the effects of other environmental factors. The evaluation was based on fixing the environmental variable, one at a time, in LAI and GPP estimation models. Then, CFE was added back to the predicted GPP to assess its contribution (figure 1(a)). A description of the satellite- and site-based data used in this study can be found in the supplementary materials.

2.1. Quantifying and removing the CFEs

We used the FvCB C3 photosynthesis model to quantify the LAI and GPP increments induced by CFE. The increments were then removed from the LAI reference data (the GIMMS Leaf Area Index,

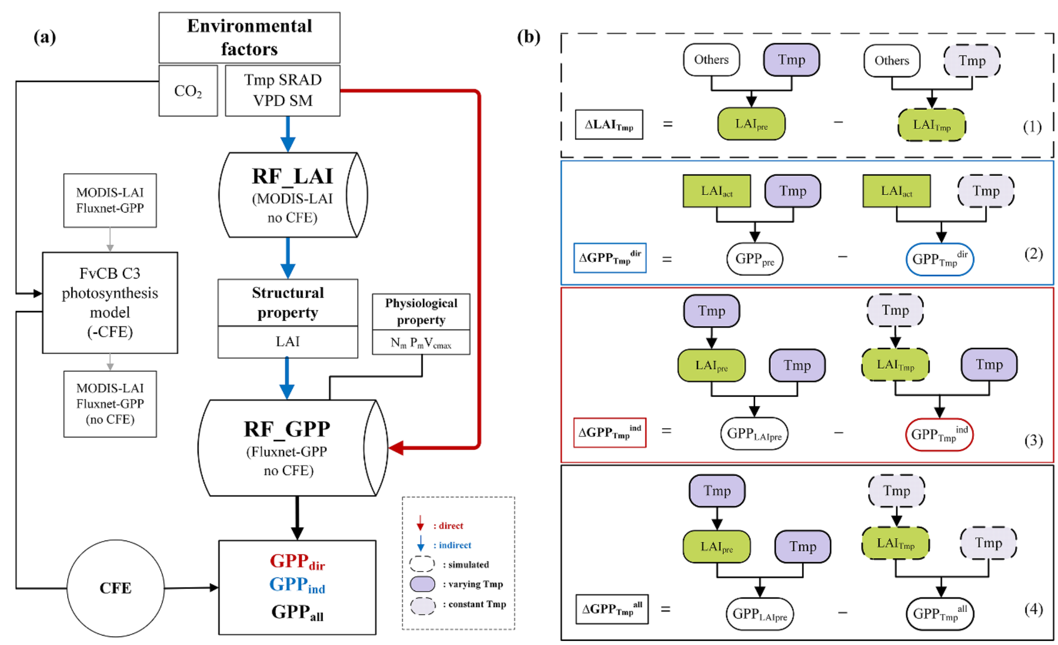

Figure 1. Schematic diagram of the methodology. (a) The direct (red) and indirect (blue) pathways by which environmental changes affect gross primary productivity (GPP). The workflow hierarchically nests the LAI and GPP models (RF_LAI and RF_GPP). (b) Schematic illustration for quantifying the direct, indirect, and total effects of environmental factors on GPP. Temperature (Tmp) was taken as an example. The dashed Tmp indicates a fixed value as the monthly average of the first five years (1982–1986), and the solid Tmp is the observed value. The dashed LAI_{pre} indicates the predicted value of LAI after fixing Tmp. For better illustration, other variables including the soil nutrient, plant vegetation type (PFT) in the LAI model, and the canopy physiological factors and PFT in the GPP model were hidden in the diagrams.

GIMMS LAI4g, Cao *et al* 2023; section S1.2) and GPP reference data (FLUXNET-GPP; figure S1; section S1.1.1), respectively. The FvCB C3 photosynthesis model describes the long-term response of plant photosynthesis to a changing atmospheric CO_2 concentration using relationships between the atmospheric CO_2 concentration, plant carbon uptake, and plant water use (Farquhar *et al* 1980, Franks *et al* 2013, Burrell *et al* 2020). More details are available in section S2.1. The LAI and GPP models below (section 2.2) thus would not account for the CFEs.

2.2. LAI and GPP estimation models

This study created random forest (RF) models to estimate global LAI and GPP (Breiman 2001, Pierrat *et al* 2022, Zhao and Zhu 2022). The RF model was chosen due to its interpretable and non-parametric nature, high accuracy and robustness, and the ability to estimate the feature contribution (Breiman 2001, Pierrat *et al* 2022). Our LAI models used GIMMS LAI4g data as the dependent variable and meteorological factors (MFs), (including Tmp, SRAD, VPD, and SM), soil nutrient factors (N_{soil} and P_{soil}; section S1.4), PFT (section S1.5), and temporal information (year and month (YrMon)) as the explanatory variables. We constructed pixel-wise RF models for LAI (RF_LAI; section S2.2), as global ones were less adequate in predicting interannual variation and trend benchmarking (Kelley *et al* 2013, Li *et al* 2016). In the GPP model (RF_GPP), the dependent variable was the FLUXNET-GPP, and the explanatory variables included canopy structure (LAI), canopy physiological factors (foliar nitrogen and phosphorus concentration per unit dry mass (N_m and P_m); and the maximum rate of Rubisco carboxylation (V_{cmax})), MFs, PFT, geographic location (latitude (Lat), longitude (Lon)), and temporal information (table S1). We used partial dependence plots to analyse and interpret the variations of RF modelled GPP with environmental factors (Friedman 2001, Hastie *et al* 2001; figure S3; section S2.2).

The RF_LAI and RF_GPP can be hierarchically nested because LAI was the dependent variable in the LAI model and the explanatory variable in the GPP model (figure 1(a)). For both LAI and GPP models, the data were divided into 70% for training and 30% for validation, where R^2 and RMSE were calculated. The LAI and GPP global maps were evaluated using the GIMMS LAI4g dataset (LAI_{act}, section S1.2) and the Global GPP dataset (GPP_{act}, see section S1.1.2). As both LAI_{act} and GPP_{act} included CFE, the CFE was added to predicted LAI and GPP exclusively in the evaluation.

2.3. Quantifying the environmental effects (except CO_2) on GPP

Based on the RF models, we used multiple simulation scenarios to disentangle and quantify the direct and indirect effects of key environmental factors on GPP (Chen 2023). Monthly data between 1982 and 2020 were used. The first simulation (S1) produced two GPP baselines. With the same physiological and environmental data, the difference between the baselines was the choice of LAI data. We used GPP_{pre} to represent the GPP baseline produced from GIMMS LAI4g and GPP_{LAIpre} to represent the GPP baseline produced from RF-modelled LAI (LAI_{pre}) (figure 1(a), table S2).

The second simulation (S2) was used to evaluate the effects of Tmp on GPP (figure 1(b), table S3). For the direct effect, GPP^{dir}_{Tmp} was derived from the RF_GPP with the Tmp value fixed as the monthly average of the first five years (1982–1986) and other variables (including LAI) from the observation. The five-year-average was used to mitigate potential climate fluctuations in a particular year (Song *et al* 2018, Sun *et al* 2018). For the indirect effect, GPP^{ind}_{Tmp} was also derived from the RF_GPP but with observed Tmp and estimated LAI from the RF_LAI (LAI_{Tmp}) where Tmp was fixed as the average. For the overall effect, GPP^{all}_{Tmp} was derived with Tmp fixed as the average in both RF_GPP and RF_LAI. Similar to S2, the effect of SRAD, VPD, and SM were evaluated by simulations S3 to S5. We also conducted simulation 6 (S6), where MFs were fixed, to analyse the total effects of four environmental factors on LAI and GPP. Based on the simulations and equations (1)–(4) (figure 1(b)), the contributions of the environmental factors on LAI (LAI_X) and their direct, indirect, and overall contributions on GPP (GPP^{dir}_X, GPP^{ind}_X, and GPP^{all}_X) can be obtained (figure 1(b)). Multiple linear regression was applied to annual averages of the contributions. Slopes of the regressions were used to determine contribution trends of the environmental factors, denominated as Con^{LAI}_X, Con^{dir}_X, Con^{ind}_X, and Con^{all}_X, respectively. The relative dominance of individual Con^{dir}_X and Con^{ind}_X was further evaluated via their absolute values and the sum (section S2.2).

2.4. Direct and indirect effects of CO_2 on global GPP

We used the nested machine-learning model and the FvCB C3 photosynthesis model (section S2.1) to calculate the predicted GPP that accounted for CFE, obtaining GPP^{+CFE}_{LAIpre} from GPP_{LAIpre}. We also derived GPP_{LAIact} using RF_GPP and LAI before removing the CFE (LAI_{act}). The direct effect of CO_2 ($Con^{dir}_{CO_2}$) was calculated as the trend of the difference between GPP^{+CFE}_{pre} and GPP_{pre}; the indirect effect ($Con^{ind}_{CO_2}$) was the trend of the difference between GPP_{LAIact} and GPP_{LAIpre}; and the overall effect was the trend of the difference between GPP^{+CFE}_{LAIact} and GPP_{LAIpre}.

3. Results

3.1. LAI and GPP from RF models

The LAI and GPP predicted by the hierarchical nested RF models (RF_LAI and RF_GPP) had high accuracies compared to the observed LAI from Cao *et al* (2023) and observed GPP from Zhao and Zhu (2022), with the fitting lines close to the 1:1 line (figure 2). The models were also considered robust with high Out-Of-Bag R^2 (LAI: 0.8841; GPP: 0.8488) and low RMSE (LAI: 0.1929 $m^2\ m^{-2}$; GPP: 43.5791 $g\ C\ m^{-2}\ mon^{-1}$) (figure 3).

In RF_LAI, MFs and temporal information were the dominant variables (figure 3(a)). In RF_GPP, LAI was more influential than others (figure 3(b)). The spatial distribution of RF-predicted LAI and GPP can be found in section S3.1 (figure S4). While our models boasted a high level of accuracy overall, they could be less accurate in predicting LAI/GPP trends over certain areas. For GPP, lower absolute values (underestimation) of the trend can be found in northeast and southern Africa, southern and eastern Australia, and southern North America (figures 4(d) and (e)).

3.2. Direct effects of environmental factors on global GPP

We found that warming has directly increased GPP by 0.0432 $Pg\ C\ yr^{-2}$, followed by the effects of enhanced radiation ($Con^{dir}_{SRAD} = 0.0227$ $Pg\ C\ yr^{-2}$, p 0.01). They accounted for 11.09% and 5.82% of the total effects. The largest negative effect observed was from elevated VPD with $Con^{dir}_{VPD} = -0.0082$ $Pg\ C\ yr^{-2}$ (2.10%, p 0.01), being stronger than the decreased SM ($Con^{dir}_{SM} = -0.0053$ $Pg\ C\ yr^{-2}$, p 0.01, 1.36%) (figure 5 and table S4). The overall direct effects of the four factors on GPP showed a significant positive trend ($Con^{dir}_{MF} = 0.0557$ $Pg\ C\ yr^{-2}$, p 0.01, figure 5(e)). The spatial distribution results showed that the direct effects of warming were mainly in the northern mid-high latitudes and, were especially, noticeable in evergreen needleleaf forests, deciduous needleleaf forests, deciduous broadleaf forests and wetlands (figure S7(a)).

The direct effect of changes in the atmospheric CO_2 concentration on GPP was 0.2025 $Pg\ C\ yr^{-2}$ (figure 5(f)), accounting for more than half (51.96%) of the total contribution (p 0.01, table S4). With the MFs being fixed (Con^{dir}_{MF}), GPP also responded positively to the combined effect of environmental factors (figure 5(e)). CFE in the last 40 years played a dominant role in directly promoting the GPP growth for all vegetation, particularly for evergreen deciduous forests (EBF) (figure S7(b)).

3.3. Indirect effects of environmental factors on global GPP

Warming was the factor that dominated the indirect effect on GPP. We also found that the rising VPD and declining SM impact GPP more through indirect pathway rather than direct pathway. The indirect effect of increased VPD (0.0093, 2.39%, p 0.01) was higher than its direct effect (0.0082, 2.10%, p 0.01) and was half of the indirect effect of warming (0.0197, 5.06%, p 0.01). It has also been found that the negative indirect effect due to

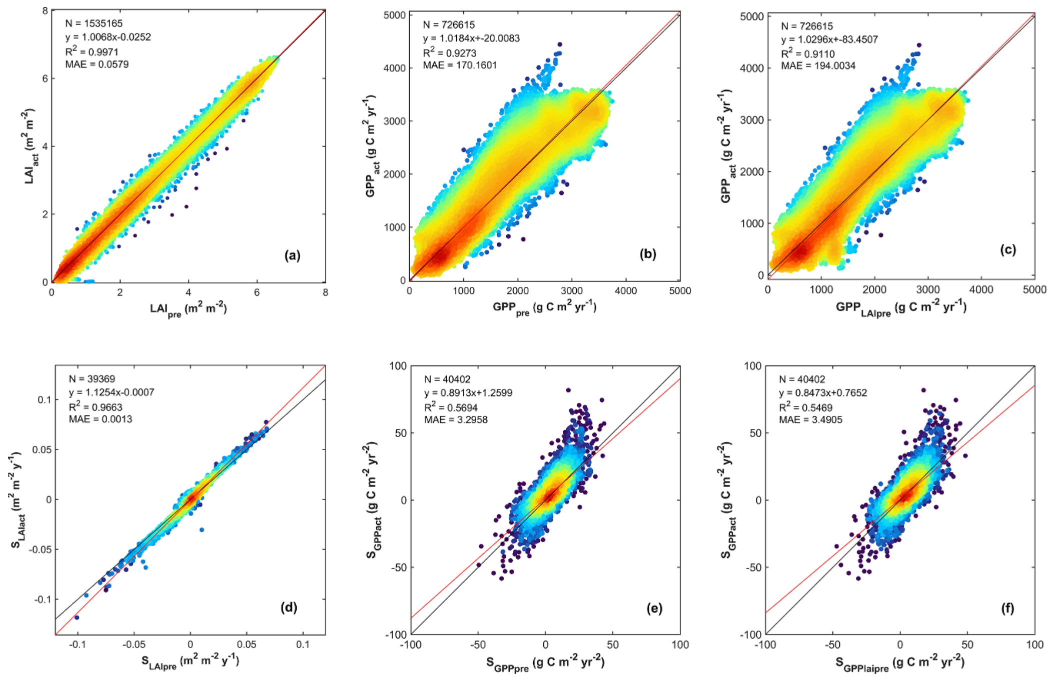

Figure 2. Performance evaluation of RF_LAI and RF_GPP. (a) and (d) show annual average LAI (LAI_{pre}) from RF_LAI and annual trends at validation sample locations (S_{LAIpre}) against those from the GIMMS LAI4g (LAI_{act};S_{LAIact}); (b) and (e) show the assessment of global GPP fluxes (GPP_{pre}) from RF_GPP and trends at sample locations (S_{GPPpre}) against the GPP_{act} andS_{GPPact}; (c) and (f) show the assessment of global GPP fluxes (GPP_{LAIpre}) from RF_LAI and RF_GPP and trends at sample locations ($S_{GPPlaipre}$) against the GPP_{act} and $S_{GPPlaiact}$. The black line is the 1:1 line.

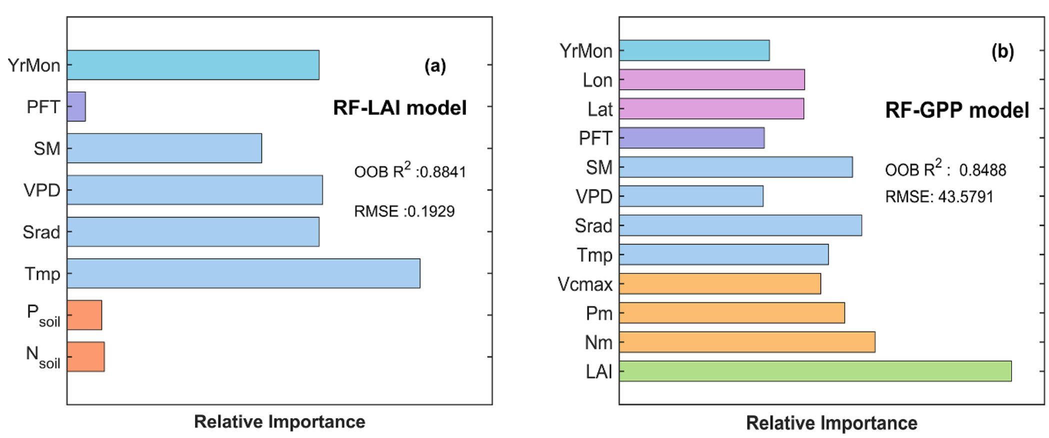

Figure 3. The relative importance of explanatory variables involved in (a) RF_LAI and (b) RF_GPP. For RF_LAI, the variables include soil nutrient factors (N_{soil} and P_{soil}), meteorological factors, PFT, and temporal information. (a) is averaged from the relative importance of all pixel models. For RF_GPP, the explanatory variables include the canopy structure, canopy physiological, environmental, geographic location, and temporal factors (see section 2.2).

elevated VPD was particularly significant in open shrublands and grasslands (figure S7(a)). At the same time, the indirect effect of SM was approximately equal to its direct effect ($\mathrm{Con}_{SM}^{dir} = \quad 0.0053$, $\mathrm{Con}_{SM}^{ind} = \quad 0.0050$). The total indirect effect of MFs on GPP indicated that the positive effect of Tmp offset the negative indirect effects of factors such as VPD ($\mathrm{Con}_{MF}^{ind} = 0.0097$ Pg C yr ^{2}, $p \quad 0.01$; table S4). Meanwhile, we found that warming could indirectly lead to GPP loss in EBF by lowering LAI (figure S7(a)). In addition, SRAD had a negative effect on GPP through LAI, but this effect was very slight (0.0022; table S4). The indirect negative response of GPP to radiation enhancement was observed in savannas (SAV) and closed shrublands (CSH) (figure S7(a)).

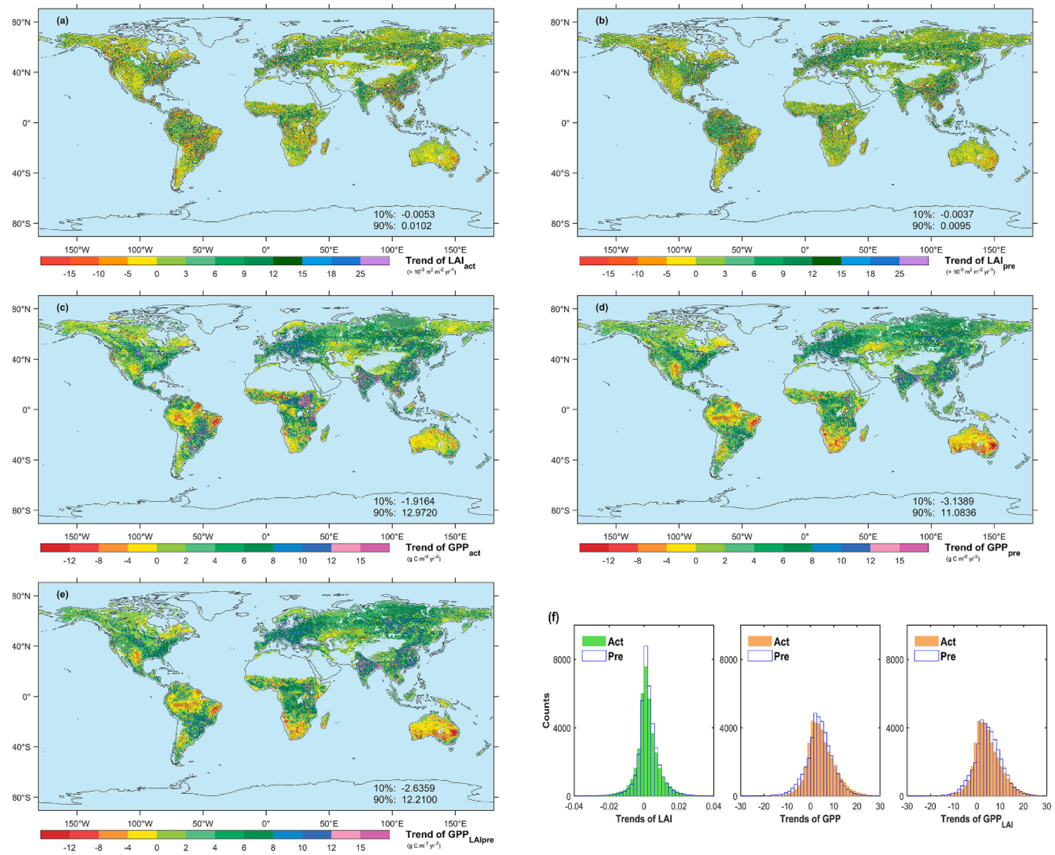

Figure 4. Spatial patterns of global LAI and GPP trends during 1982–2020. (a) is the GIMMS LAI4g (LAI$_{act}$); (b) is LAI predicted by RF_LAI (LAI$_{pre}$); (c) is GPP$_{act}$; (d) is GPP$_{pre}$; (e) is GPP$_{LAIpre}$. The two numbers in each subplot represent the 10th and 90th percentile values, respectively. (f) is the distribution of observed or modelled trends. Black dots indicate trends that are statistically significant ($p < 0.05$).

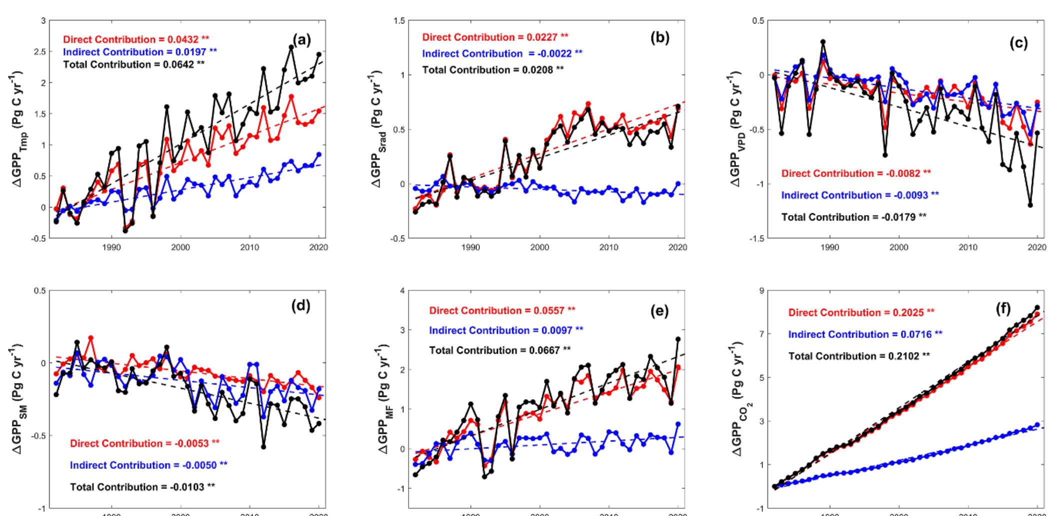

Figure 5. Effects of environmental change on GPP during 1982–2020. ΔGPP$_X$ represents the difference between the predicted GPP value after fixing the environmental factors (S2–S6) and the actual predicted GPP value (S1). The unit of contribution is Pg C yr^{-2}. (a)–(f) refers to Tmp, SRAD, VPD, SM, MF, and CO_2, respectively. ** represents significance at 99% confidence interval ($p < 0.01$).

The indirect effect of elevated atmospheric CO_2 concentration on GPP was higher than warming (figure 5(f)), accounting for 18.37% of the total effects. The percentage was much less than the direct effect yet still remarkable. The combined positive effects of elevated atmospheric CO_2 concentration and warming outweighed the negative effects of elevated VPD and decreased SM (table S4).

3.4. The overall effects of environmental factors on global GPP

During 1982–2020, overall GPP growth has been primarily driven by increased CO_2 concentration and warming, with the hidden negative effects dominated by rising VPD and decreasing SM (figure 7). The GPP trend decrease due to rising VPD (0.0179 Pg C yr ^{2}, 4.59%) was far smaller than the increase due to warming (0.0642 Pg C yr ^{2}, 16.47%); and both of them were much smaller than the increase due to elevated CO_2 concentration (0.2102 Pg C yr ^{2}, p 0.01, 53.94%; figure 7).

Overall, the direct contribution of elevated CO_2 concentration was higher than the indirect contribution (table S4; direct: 51.96%, indirect: 18.37%). The direct contribution of warming to global GPP trends was more than twice as large as the indirect contribution (direct: 11.09%, indirect: 5.06%). In contrast, the indirect pathways were more essential for VPD (direct: 2.10%, indirect: 2.39%) and SM (1.36%, 1.28%).

4. Discussion

4.1. The important role of temperature and VPD in regulating global GPP

The direct and indirect warming contributions to the GPP trend had a ratio of approximately 2:1. Climate warming directly promotes the increase of plant internal temperature, which promotes the activity of the enzymes (plant photosynthesis) and consequently increases the maximum photosynthetic rate (Nemani *et al* 2003, Thomas *et al* 2016). The results of large-scale leaf-level photosynthesis experiments in different biomes by Liang *et al* (2013) also showed that climate warming increased the net photosynthetic rate by 6.13%. At the same time, a higher temperature may extend the length of the growing season and alter photosynthetic carbon assimilation and increase vegetation production (Myneni *et al* 1997, Bastos *et al* 2019, Gu *et al* 2022). The early spring phenology of trees has been widely reported in response to the increasing temperature in recent decades. The lengthened growing season allowed plants to have longer time for photosynthesis. This aligns with the indirect pathway of warming. In addition, warming-induced GPP promotion was manifested in most parts of the globe, especially in the high latitudes of the northern hemisphere, mainly through the direct effect (figures 6 and S6). This is also consistent with previous findings that productivity in high northern latitudes is mainly limited by low temperatures (Liu *et al* 2018). However, warming may also exert a negative influence on terrestrial ecosystems. Leaf and canopy photosynthesis are inhibited when temperature reaches a certain threshold (Kattge and Knorr 2007, Lloyd and Farquhar 2008, Huang *et al* 2019). A recent study by Doughty *et al* (2023) showed that tropical forest leaves are more vulnerable to increasing temperatures, which may close stomata and cause leaf browning and necrosis (Wilson and Raven 1988, Doughty *et al* 2008, Hubau *et al* 2020). Meanwhile, we also found that warming could indirectly lead to GPP loss in EBF by lowering LAI (figure S7(a)).

Global warming generally leads to higher VPD and evaporation rates (Huang *et al* 2015). It has been found that there has been a significant increase in VPD globally over the last 40 years, due to an increase in saturated water vapor pressure and a decrease in actual vapor pressure (Willett *et al* 2014, Yuan *et al* 2019, Franklin *et al* 2020). The increase in VPD potentially limits vegetation photosynthesis at the leaf scale by reducing stomatal conductance and increasing nonphotochemical quenching (Flexas *et al* 2002, Lu *et al* 2018, Song *et al* 2022). This effect is primarily observed as negatively impacting LAI. In Yuan's study, VPD was negatively correlated with LAI when the effects of Tmp, SRAD, and atmospheric CO_2 concentration were excluded (Yuan *et al* 2019). On the one hand, increased VPD would trigger stomatal closure, leading to carbon starvation at the tissue level; on the other hand, reduced soil water supply coupled with high evaporation demand dry out plant tissues, both of which may lead to plant death (McDowell *et al* 2008, Yuan *et al* 2019, Hubau *et al* 2020). Above reasons explained the result that the indirect effect of rising VPD was higher than its direct effect in this study. Meanwhile, our results were also consistent with other studies that found global GPP was significantly controlled by a higher atmospheric VPD after 2000 (Madani *et al* 2020). This was confirmed by our funding that indirect negative effect of rising VPD on GPP over the last 20 years offset the indirect positive effect of warming over the last 20 years (figures S2 and S8). Warming could promote photosynthesis while exacerbating the water crisis to lessen GPP, especially in relatively arid ecosystems (e.g. CSH, SAV, and grasslands (GRA)), which is also found in this study (figure S7). In the northern high latitudes, however, we observed significant positive impact on GPP from elevated VPD, mainly because high VPD usually coincides with high temperature. Previous studies have confirmed their joint effect in increasing vegetation productivity in cold regions (Piao *et al* 2007, Xia *et al* 2014) (figure S6).

The correlation between SM and VPD arises because of the linkage and feedback between SM, plant stomatal conductance, and transpiration

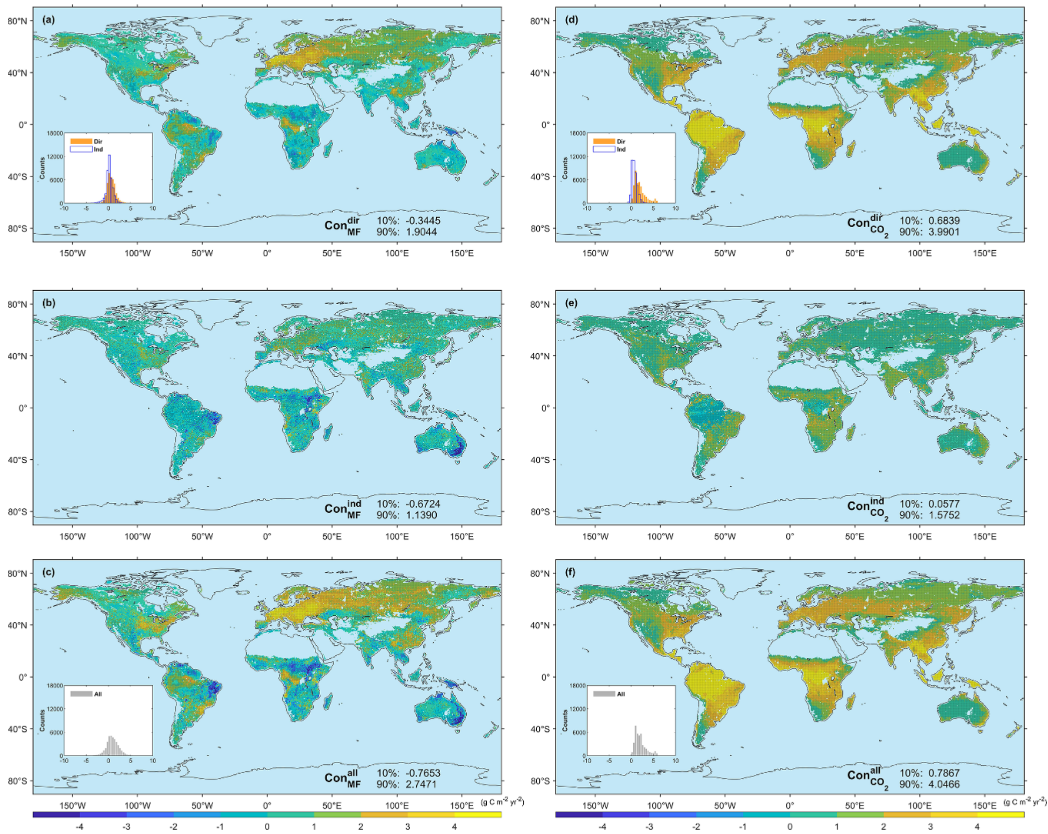

Figure 6. Spatial patterns of the contributions of environmental changes on GPP during 1982 2020. (a)–(c) are contributions of meteorological factors (including Tmp, SRAD, VPD, and SM); (d)–(f) are contributions of changes in the atmospheric CO_2 concentration on GPP. The two numbers in each subplot represent the 10th and 90th percentile values, respectively. The insets in (a), (c), (d), and (f) indicate the corresponding data distributions. Black dots indicate trends that are statistically significant (p 0.05).

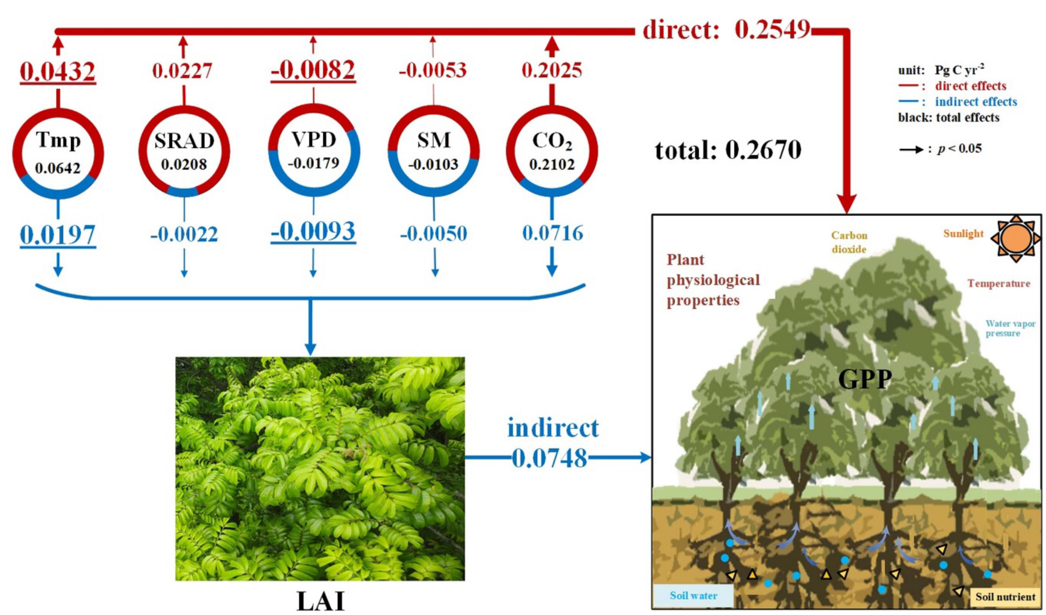

Figure 7. A comparison of contributions from environmental factors on GPP during 1982–2020. Red: direct effect; blue: indirect effect; black: total effect. See sections 2.3 and 2.4 for quantification of multi-pathway effects.

(Seneviratne *et al* 2010, Stocker *et al* 2018). An increasing VPD implies an increase in the amount of water vapour lost by plants to the atmosphere through transpiration and soil evapotranspiration. Stocker *et al* (2018) simulated lower SM on the reduction of light energy utilization, which reduced annual photosynthesis by about 15% globally. His results emphasized the limiting effect of SM on vegetation productivity, especially when drought occurs. In contrast, Yuan *et al* (2019) used different simulation models to show a significant VPD increase in the future. A recent study using flux tower observations also found that a decrease in GPP was not generally associated with a decrease in SM but was, rather, dominated by an increase in VPD (Fu *et al* 2022). Our study indicated that the increase in atmospheric dryness would have a greater impact on GPP than the decrease in SM, and the significant upward trend in VPD over the last 20 years reminds us to emphasize the critical impact of future changes in atmospheric dryness on GPP (Yuan *et al* 2019).

4.2. The contribution of increasing CO_2 concentration on global GPP

The highly significant upward trend in observed LAI and GPP over the 40 years, as shown in previous studies as well as in this study, prompted a continuous increase in vegetation greenness and productivity (Piao *et al* 2015, Zhu *et al* 2016, Haverd *et al* 2020, Fu *et al* 2022). Previous studies have emphasized the important role of atmospheric CO_2 concentration, Tmp, and VPD on vegetation productivity formation, but the results varied greatly across the globe. Haverd *et al* (2020) identified rising atmospheric CO_2 concentration as the dominant driver in global GPP, revealing a global CFE on photosynthesis of 30% since 1900. A small fraction (∼8.1%–15.0%) of the warming and CO_2-induced elevation in solar-induced fluorescence (SIF) (or GPP) was offset by the negative effect of increased VPD in more than 50% of vegetated areas globally over the last two decades (Song *et al* 2022). However, other studies showed that more than half of the CFE was offset by the strong effect of elevated VPD on GPP (Yuan *et al* 2019, He *et al* 2022). The comparative analysis by Song *et al* (2022) suggested that the inconsistent results in current studies, despite with similar methods, may be related to different proxies for vegetation productivity.

This study concluded that the effect of CO_2 changes occupies an absolutely important position compared to other environmental factors. The significant increase in the atmospheric CO_2 concentration over the last 40 years caused GPP to increase at a rate of 0.2102 Pg C yr ^{2}. In terms of direct effects, the increase in GPP driven by CFE far outweighed the multifaceted negative effects induced by the increased VPD and reduced SM. It has been reported that the effect of CO_2 fertilization accounted for 47.0% of the cumulative change in the terrestrial carbon sink (Chen *et al* 2019), which was consistent with our results for the direct response of GPP to an elevated CO_2 concentration. The increase in CO_2 could improve the water use efficiency of plants (Reich *et al* 2014), which compensates for the deficiency of water use to some extent. The CFE in semi-arid ecosystems also counteracted the negative effects of water stress. Meanwhile, elevated CO_2 concentration can increase vegetation biomass fixation and promote the expansion of leaf area. The indirect effect of increased CO_2 concentration in our results accounted for 34% of its total effect and accounted for 18.37% of total effects, confirming this essential indirect role. This was consistent with previous findings that 70% of the global greening trend was attributed to CFEs (Zhu *et al* 2016). The total effect of CFE accounted for 53.94% of the total effect of all factors, confirming the important driving role of rising CO_2 on vegetation productivity growth (figure 6 and table S4).

4.3. Uncertainty analysis

The sources of uncertainty in this study may include (1) the RF machine learning models that lack support for physiological mechanisms and the interaction between LAI and GPP requires further exploration (see supplementary section 4.1); (2) the FvCB C3 photosynthesis model that does not directly explore the indirect effect of the increased CO_2 concentration on GPP through LAI; (3) the unavailability of monthly or seasonal physiological data for the leaf nutrient and photosynthetic characterization (Yan *et al* 2022); and (4) the lack of sufficient FLUXNET sites for GPP modelling in certain regions such as East Asia, and the tropics.

5. Conclusion

This study quantified the direct and indirect effects of key environmental factors on global GPP by machine learning models and a theoretical photosynthesis model. The results showed that the direct contribution of environmental change on global GPP was 0.2819 Pg C yr ^{2}, with individual direct impact ranged from 1.36% to 51.96% of the total effects. Among the direct effects, the positive contribution of elevated CO_2 concentration on GPP was the highest. The direct promotion of GPP by warming was sufficient to offset the negative direct effect caused by the increased VPD and decreased SM. There were also notable indirect influences of environmental factors on global GPP (0.1078 Pg C yr ^{2}), which contributed 0.56%–18.37% of the total effects. In particular, the rising VPD and declining SM negatively impacted GPP more through the indirect pathway rather than the direct pathway, but these negative effects were counteracted by the boost of warming over the past four decades. Our results underscored the importance of evaluating the indirect effects of environmental factors on GPP and would benefit future studies of climate change's impacts on terrestrial vegetation.

Data availability statements

The data that support the findings of this study are openly available in the supplemental and at https://zenodo.org/records/10018475 (Chen 2023).

Acknowledgments

This work was supported by the National Natural Science Foundation of China (42271104), the Shenzhen Fundamental Research Program (GXWD20201231165807007-20200814213435001), the Shenzhen Science and Technology Program (JCYJ20220531093201004), and the Shenzhen Science and Technology Program (KQTD20221101093604016). The authors would like to thank the authors of the relevant public data in this study. The authors appreciate the editors and anonymous reviewers for their valuable comments and suggestions.

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