Recent Amplified Global Gross Primary Productivity Due to Temperature Increase is offset by Reduced Productivity Due to Water Constraints

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**Key points:**
- We used a new dynamic LUE model to estimate global GPP for 1982-2016.
- Increasing GPP in northern high latitudes is offset by GPP decline in the tropics.
- Global GPP is shifting from being temperature limited to VPD limited.

**Key words:** Climate change, Ecosystem productivity, GPP, LUE, SIF, VPD
Abstract

Satellite remote sensing observations show an increased greenness trend over land in recent decades. While greenness observations can indicate increased productivity, estimation of total annual productivity is highly dependent on vegetation response to climate and environmental conditions. Models have been struggling to determine how much carbon is taken up by plants as a result of increased atmospheric CO$_2$ fertilization. Current remote sensing light use efficiency (LUE) models contain considerable uncertainty due to the lack of spatial and temporal variability in maximum LUE parameter and climate sensitivity defined for global plant functional types (PFTs). We used the optimum LUE (LUE$_{opt}$) previously derived from the global FLUXNET network to improve estimation of global gross primary productivity (GPP) for the period 1982–2016. Our results indicate increasing GPP in northern latitudes owing to reduced cold temperature constraints on plant growth, thereby suggesting increasing negative carbon-climate feedback in high latitudes. In the tropics, by contrast, our results indicate an emerging positive climate feedback, mainly due to increasing atmospheric vapor pressure deficit (VPD). Further pervasive VPD increase is likely to continue to reduce global GPP and amplify carbon emissions.

Plain language summary

In light use efficiency (LUE) models, plant production is linearly related to canopy absorbed photosynthetically active radiation (APAR), based on the assumption that plants absorb and convert solar radiant energy into vegetation biomass with a given efficiency rate. Here, we used an enhanced LUE model driven with remote sensing observations to estimate plant productivity for 1982-2016. We found that over the study period, plant photosynthetic activity has increased over northern latitudes, which may partially offset the CO$_2$ emissions from fossil fuel consumption. However, our results show that productivity in the tropical zones is declining rapidly due to increased water stress. With increased warming, water limitations are expected to increasingly limit global plant productivity.
1 Introduction

Life on Earth is supported by plant photosynthesis through gross primary productivity (GPP), which represents the largest annual carbon flux linked directly linked to environmental conditions and atmospheric CO$_2$ concentrations (Beer et al., 2010). Human reliance on plant photosynthesis includes GPP allocation to food, fiber, and fuel production, as well as ecosystem services provided by offsetting atmospheric CO$_2$ emissions from fossil fuel consumption (Norby et al., 2010; Quéré et al., 2018; Schimel et al., 2015). For the past three decades, global satellite remote sensing has provided direct observations of the amount of photosynthetic leaf area (Myneni et al., 1999). These observations serve as primary inputs for satellite-driven diagnostic models of GPP such as light use efficiency (LUE) models (Running et al., 2004). Satellite observations from the Advanced Very High Resolution Radiometer (AVHRR) and the MODerate resolution Image Spectrometer (MODIS) sensors provide consistent global measurements of changes in photosynthetic leaf area starting in June 1981 (Zhu et al., 2013).

During this period, the global mean atmospheric CO$_2$ concentration has increased by 20%, from 340 ppm in 1981 to 407 ppm in 2016 (Etheridge et al., 1996; Keeling et al., 2005). This increase has coincided with widespread increase in leaf area (Zhu et al., 2016) and changes in vegetation phenology, including earlier spring green-up (Cleland et al., 2007; Cong et al., 2013; Zhu et al., 2016). Conversely, anomalous changes in global productivity associated with climate extremes driven by the El Niño Southern Oscillation (ENSO) have also been observed and modeled (Liu et al., 2017; Nemani et al., 2003; Zhao & Running, 2010; Zhu et al., 2018). In addition to ENSO, other factors coinciding with water scarcity, high temperatures and large fires (Reichstein et al., 2013) have significantly impacted the global carbon cycle over the past few decades. Some of these satellite-observed events, including large-scale wind throw, biotic events, pest outbreaks, and deforestation, have significantly impacted global vegetation cover (Reichstein et al., 2013; Zscheischler et al., 2013, 2014). Extreme events associated with cold temperature events and heavy rain are also known to impact the global carbon cycle (Zscheischler et al., 2014). However, the current generation of remote sensing driven LUE models have several key limitations that make it difficult to properly estimate long-term GPP trends.

The biome property lookup table approach is a well-known shortcoming of LUE models (Madani et al., 2014; Turner et al., 2002; Wang et al., 2010; Way et al., 2005). In this approach, photosynthetic rate is constrained by biome-specific, predefined thresholds to represent optimum
climatic conditions for plant productivity. In addition, the maximum LUE rate, which defines potential GPP, is typically assumed to be temporally constant (e.g., Running et al., 2004; Kimball et al., 2017). Improving these basic GPP model limitations will reduce uncertainty in global GPP estimates and advance the understanding of the terrestrial biosphere response to environmental change and climate extremes.

The variability in CO$_2$ sources and sinks in natural environments including ocean and land ecosystems is driven by the variability in atmospheric CO$_2$ accumulation rate (Keenan et al., 2016). However, estimation of the carbon sources and sinks in land ecosystems remains challenging, where the range of variability in estimated annual GPP and its inter-annual variability and trend is large among Earth system, LUE and machine learning based models (Anav et al., 2015). Even though all of the global models reviewed by Anav et al. (2015) show positive annual GPP trends over the last few decades, there are large discrepancies in the estimated magnitude of GPP trends and inter-annual variability. Previous studies noted that global ecosystem net primary productivity models that use a satellite data driven LUE modeling approach show an increasing trend for the period 1982–1999 (Nemani et al., 2003), but this productivity trend diverged after 2000 due to climatic changes, including severe droughts (Zhao & Running, 2010).

Here, we provide a quantitative and mechanistic multi-decadal assessment of global GPP trends and anomalies using an enhanced remote sensing LUE model. Our primary goal is to identify the most important factors driving long-term GPP change across key bioclimatic regions. We model global monthly GPP using the third-generation Global Inventory Modeling and Mapping Studies (GIMMS3g) fraction of photosynthetically active radiation (FPAR) record for the period 1982–2016 (Zhu et al., 2013) as a primary model input. By building upon our previous experience (Madani et al., 2014; Madani, et al. 2017a; Madani, et al., 2017b), our enhanced LUE model provides temporally and spatially explicit dynamic optimum LUE (LUE$_{opt}$) information that supports improved estimates of long-term (1982-2016) GPP trends across the globe.

2 Methods

2.1 Geospatial data

We acquired the global semi-monthly GIMMS3g FPAR data (Zhu et al., 2013) for the 35-year (1982–2016) study period. GIMMS3g FPAR is created based on the relationship between the
new improved GIMMS3g normalized difference vegetation index (NDVI) and best-quality MODIS leaf area index (LAI) and FPAR products for the overlapping period 2000-2009 using a neural network algorithm (Zhu et al., 2013). We obtained meteorological and other geospatial information, including monthly minimum air temperature, dew point temperature, incoming shortwave solar radiation, and surface-to-root-zone soil moisture from the Modern-Era Retrospective analysis for Research and Applications, Version 2 (MERRA-2; Gelaro et al. 2017). We aggregated FPAR semi-monthly data to monthly scales by averaging the FPAR values over each month and resampled the MERRA-2 ½° latitude by 5/8° longitude spatial resolution meteorological data using nearest neighboring approach to match the FPAR 0.08° spatial resolution for modeling GPP at monthly time scale for the entire GIMMS3g record. Adopting the finer FPAR resolution for the GPP model simulations, rather than the coarser resolution of the meteorological data, allowed us to better capture the effect of land cover and land use change on GPP (Robinson et al., 2018).

2.2 Spatially explicit LUE_{opt} data
Global, spatially distributed LUE_{opt} values were derived from the flux tower-based estimates of LUE_{opt} (Madani, et al., 2017b). The tower eddy covariance CO_{2} flux measurement sites presented in Madani et al. (2017b) represent a broad range of global biomes (Table S1 in the supplementary material) with at least two years of daily ecosystem CO_{2} exchange measurement records at each site. In this approach, the upper 98-99.5% bin of FLUXNET tower daily gap-filled GPP values for each tower site are selected to represent the maximum daily GPP (GPP_{max}). It is assumed that in the upper bin of GPP, plant productivity is not restricted by climate constraint factors (Kergoat et al., 2008; Madani et al., 2014). The FPAR data collocated with FLUXNET tower site locations are temporally matched with the tower GPP records, and PAR is resampled to FPAR resolution using nearest neighboring approach. For each tower site, LUE is defined as:

\[ LUE = \frac{GPP_{\text{max}}}{\text{APAR}} \quad (1) \]

In Eq. (1), APAR is the absorbed photosynthetically active radiation (PAR), which is derived from the product of FPAR defined from the GIMMS3g record and the daily PAR, estimated as half of the global incoming shortwave solar radiation derived from the MERRA-2 global
reanalysis (Gelaro et al. 2017). For each of the tower sites the averaged daily LUE observations from Eq. (1) are used to represent the $LUE_{opt}$ value of that specific site.

We extrapolated the tower-based $LUE_{opt}$ values to the global domain based on a generalized additive model (GAM) framework (Hastie & Tibshirani, 1990). The model used several explanatory variables for $LUE_{opt}$ including: average annual long-term temperature from MERRA-2 to determine climate sensitivity, the satellite observed solar induced chlorophyll fluorescence (SIF) from the Global Ozone Monitoring Experiment-2 (GOME-2) (Köhler et al., 2015) to represent biome heterogeneity in productivity within the land cover classifications defined by MODIS MOD12-type-2 (Friedl et al., 2010) classes, maximum and minimum annual FPAR to represent annual changes in land cover as well as the potential effect of the atmospheric CO$_2$ concentration growth rate on plant leaf area (Zhu et al., 2016). We used the GAM model to provide annual $LUE_{opt}$ information distributed over the global vegetated land areas from 1982–2016 at 8-km spatial resolution. (Refer to Table S2 for the parametric and smoothed coefficient functions of selected environmental predictors used to extrapolate tower estimated $LUE_{opt}$) Our model was trained on measurements from a subset of global tower sites from the La Thuile FLUXNET synthesis dataset (Baldocchi, 2008) and was tested using independent tower sites from the 2015 FLUXNET record (Pastorello et al., 2020; Refer to Figure S1 for location of tower sites). The trained model was then used along with dynamic annual FPAR observations to generate corresponding spatially explicit $LUE_{opt}$ data from 1982-2016.

2.3 Modeling global GPP

The LUE model used here is similar to the NASA Soil Moisture Active Passive (SMAP) mission’s level 4 carbon model algorithm (L4C) (Jones et al., 2017), which uses soil moisture (SM) as a water supply constraint factor, enabling improved GPP accuracy in water limited regions (Jones et al., 2017; Kimball et al., 2012; Stocker et al., 2019). Our model also accounts for changes in atmospheric vapor pressure deficit (VPD), which we modeled following Murray (1967):

$$VPD = 611 \times e^{\frac{17.502 \times T_a}{T_a + 240.97}} - 611 \times e^{\frac{17.502 \times T_d}{T_d + 240.97}}$$  \text{Eq. 1}

where $T_a$ is the average daily temperature in degrees Celsius and $T_d$ is the dew point obtained from MERRA2.

Our LUE model provides enhanced GPP estimates (hereinafter termed GPP$_{Enh}$) as follows:
**GPP\textsubscript{Enh}** = \( FPAR \times PAR \times LUE_{opt} \times f_{VPD} \times f_{SM} \times f_{T_{min}} \) \hspace{1cm} \text{Eq. 2}

where \( f_{VPD}, f_{SM}, \) and \( f_{T_{min}} \) represent dimensionless environmental constraint functions ranging from zero (fully constrained) to one (no effect) that describe reductions from optimal GPP due to water and temperature stress:

\[
0, \quad T_{min} \leq T_{M_{min}}
\]

\[
f{T} = \frac{T_{min} - T_{M_{min}}}{T_{M_{max}} - T_{M_{min}}}, \quad T_{M_{min}} < T_{min} < T_{M_{max}} \hspace{1cm} \text{Eq. 3}
\]

\[
1, \quad T_{min} \geq T_{M_{max}}
\]

\[
0, \quad VPD \geq VPD_{Max}
\]

\[
f_{VPD} = 1 - \frac{VPD_{Max} - VPD_{Min}}{VPD_{Min} - VPD_{Max}}, \quad VPD_{Min} < VPD < VPD_{Max} \hspace{1cm} \text{Eq. 4}
\]

\[
1, \quad VPD \leq VPD_{Min}
\]

The Min and Max subscripts in equations (4) and (5) represent the minimum and maximum defined thresholds for minimum daily air temperature (\( T_{min} \)) and VPD functions derived from the bioclimatic factors controlling productivity at global scales (Madani et al., 2017b), in addition to ecosystems phenological patterns indicated from flux tower observations. In this regard, we used global tower sites to acquire minimum and maximum thresholds for the \( T_{min} \) and VPD bioclimatic variables. \( T_{min} \) in the LUE model defines the length of plant activity. We defined \( T_{M_{min}} \) and \( T_{M_{max}} \) as 10 and 20 quantiles of the daily GPP climatology and recorded SIF value of the corresponding time for a given tower location. We used a similar technique to establish the VPD thresholds with the exception of using the upper 90 daily GPP quantiles to assess the negative impact of high VPD on stomatal conductance. We then used the observed SIF seasonality to generate spatial maps of environmental constraint factors and used the constraint factors only for regions where seasonality in productivity, confirmed by SIF observations, was shown to be controlled by the specific constraint factor (Madani, et al., 2017b).

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Daily SM for the global simulations was normalized as a daily proportion of the maximum and minimum reported local SM values from the long-term (1982–2016) record for
each pixel. The resulting normalized SM values were aggregated to monthly time steps and used in the following nonlinear constraint function built upon a non-linear relationship between SM and LUE (Stocker et al., 2018) to estimate GPP in Eq. 2:

\[ f_{SM} = 1 - (SM - 1)^2 \]  Eq. 5

2.3 Validation and analysis

We validated GPP_{Enh} against flux tower GPP observations for the 2007 to 2014 period obtained from the 2015 FLUXNET record, where the tower validation sites were independent from the sites used for model training (Figure S1). The tower sites used for model training and validation were selected on the basis of being representative of the major global biomes and having at least two years of CO₂ flux measurements. To assess different factors contributing to changes in GPP, we executed the GPP_{Enh} model on a monthly basis with static APAR (APAR climatology) and variable climatic factors \((f_{VPD} \times f_{SM} \times f_{T_{min}})\), and once again with static climatic factors (climatology of \(f_{VPD} \times f_{SM} \times f_{T_{min}}\)) and dynamic APAR data. We extended our analysis by detrending GPP and underlying factors controlling productivity, including annual FPAR, SM, PAR, \(T_{min}\) and VPD, and performed annual and multi-decadal assessment of GPP anomalies at regional and global scales. We calculated the anomalies in time series data by removing the linear trend. In this regard, residuals \(e_t\), or the differences between the data values \((y)\) and the corresponding linearly fitted values over time \(x_t\), are defined as:

\[ e_t = y_t - \beta_0 - \beta_1 x_{1,t} - \beta_2 x_{2,t} - \ldots - \beta_k x_{k,t} \]  Eq. 6

For comparison, we used the GIMMS FPAR data and MERRA-2 meteorology to model GPP using fixed LUE_{max} values used by the MODIS MOD17 operational (Collection 6) GPP product (Zhao & Running, 2010). We also compared our GPP_{Enh} key findings with the TRENDY ensemble mean GPP, atmospheric CO₂ inversion model results and SIF observations.

We used the ensemble mean GPP of ten dynamic global vegetation models (DGVMs; Table S3) from the TRENDY-v7 project (Quéré et al., 2018; Sitch et al., 2015) for comparison with our GPP model results. The selected models with spatial resolutions of 0.5 to 2° for the period 1982–2016 use climate, land use, and CO₂ forcing effects on ecosystem productivity. We also acquired net biome productivity (NBP) data from CO₂ inversion model results with 1° monthly spatiotemporal resolution from six inversion models, including CT2017, CTE2018, CarboScope s76_v4.2, CarboScope s85_v4.2, JAMSTEC, and CAMS (see Table S4 for references and details) to compare with our LUE model findings. In addition to modeled
ecosystem productivity data, we used SIF from the scanning imaging absorption spectrometer for atmospheric chartography (SCIAMACHY) for 2003–2011 (Joiner et al., 2012) and GOME-2 (Köhler et al., 2015) for 2007–2016 as remote sensing indicators of ecosystem productivity. To mitigate artifacts in the GOME-2 SIF retrievals after mid-2012 due to sensor degradation (Zhang et al., 2018), we corrected the drift in time series data by matching the mean of observations after mid-2012 to the mean values from 2007 to mid-2012. We generated the anomalies in annual GPP_{Enh}, NBP, TRENDY GPP and SIF by calculating the departure from long-term average and normalized the values using:

\[ z_i = 2 \times \frac{x_i - \text{min}(x)}{\text{max}(x) - \text{min}(x)} - 1 \]  

Eq. 7

Where \( x = (x_1, \ldots, x_n) \) and \( z_i \) denotes \( i^{th} \) normalized data. We compared these data over tropical and northern high latitudes, the two highly important regions for carbon cycle dynamics.

3 Results

The new GPP_{Enh} model explains 80% of the variation in annual GPP across flux tower sites, with an RMSE of 331 gC m^{-2} yr^{-1}. The variance explained declines to 75%, and RMSE increases to 506 gC m^{-2} yr^{-1} for the model with constant LUE_{max} (and otherwise the same meteorology and FPAR data; Figure S2; Refer to Figure S3 for comparison between GPP_{Enh} with the conventional LUE model over independent test sites). The improvement in the GPP estimate was a result of the environmental explanatory variables that explained ~56% of the spatial variation (p < 0.0001) among tower observed LUE_{opt} values. However, the fixed LUE_{max} parameters defined for each land cover type could only explain ~36% of the variance in tower observed LUE_{opt}. 
Figure 1. Trends in global gross primary productivity (GPP) for 1982–2016. Thirty-five-year linear trends in GPP demonstrate that, in ~50% of the vegetated land areas, GPP is increasing by up to 20 gC m$^{-2}$ yr$^{-1}$, whereas the GPP of tropical regions is declining at the same rate. Black dots represent pixels with statistically significant trends ($p < 0.05$).

Our estimated global average GPP over the last three decades is 130±1.6 Pg yr$^{-1}$. The lowest GPP is estimated for 1983 (126 Pg yr$^{-1}$), and the highest GPP is for 2011 (133 Pg yr$^{-1}$). Over the study period, annual GPP trends indicate that GPP in Amazonia and the Southeast Asian tropics decreased at rates of up to 20 g C m$^{-2}$ yr$^{-1}$ (at grid scale), while GPP in the northern latitudes increased at the same rate (Figure 1). To further assess the regional GPP trends, we performed a multi-decadal GPP assessment for selected latitudinal zones.

In the northern high latitudes (> 45ºN) GPP began to increase by 0.07 Pg yr$^{-1}$ from 1982 onward, which represents about 0.4% increase in GPP per year relative to the 35-year mean (17.9 Pg C). In contrast, equatorial GPP (10ºS–10ºN) has steadily declined since the 1980s, leading to a reduction of 0.5–1 Pg over 35 years compared to the long-term average (Figure 2).
Figure 2. **a**: Zonal plot showing global GPP anomalies (departure from mean) binned by latitude and decade. Solid lines and shaded envelopes around each line denote the mean and standard deviation. While GPP steadily increased across the decades in mid-latitudes and northern high latitudes, equatorial GPP steadily decreased. **b**: Bar plots showing anomalies in annual GPP in Tg C averaged per decade. **c**: PFT classification modified from MODIS-MOD12 Type 5 (Friedl et al., 2010) for Evergreen Broadleaf Forests (EBF), Deciduous Broadleaf Forests (DBF), shrub lands (SHR), grasslands (GRA), and croplands (CRO).

We further analyzed the main factors affecting global annual GPP anomalies. VPD contributes the highest variability to GPP in tropical regions. In arid environments, water
restrictions defined by SM and VPD are the primary limiting factors. In the northern latitudes, where the growing season is short, seasonal cold temperatures primarily limit productivity (Figure 3).

Figure 3. Climatic factors affecting GPP. Dominant environmental constraint factors influencing changes in GPP for the period 1982–2016 derived from the Pearson correlations of minimum daily temperature (Tmin), vapor pressure deficit (VPD), soil moisture (SM) and photosynthetically active radiation (PAR) to this study’s long-term estimated annual GPP. Productivity is primarily related to soil moisture availability and VPD in arid regions and tropics, whereas low temperatures primarily limit productivity in the high northern latitudes. In far northern latitudes and rainforests, ecosystem GPP is positively correlated with the amount of PAR. Nonsignificant correlations are masked out.

In the Amazon forest, western and central United States, southern Australia, and Africa, GPP limitation is more related to water constraints (VPD and SM) through the negative impact of high VPD and the positive impact of SM availability. In tropical rainforest, GPP is controlled by the amount of incoming radiation and the negative impact of high VPD (Figure 3).

We analyzed the relationships between GPP anomalies at decadal time scales and underlying environmental factors affecting plant activity by detrending the long-term annual data. During the 1980s, global GPP was most strongly correlated with PAR and FPAR, indicating that the water and temperature constraints had a relatively smaller influence on interannual variability in GPP (Figure 4). Since in the LUE model the cold temperature constraint factor controls the length of the growing season, it exerts the strongest control in seasonally cold environments such as temperate forests and northern high latitude ecosystems. On the other hand, the sensitivity of productivity to SM, which has a stronger influence on the productivity in arid environments, has
not significantly changed in 2000s compared to previous decades. However, with increasing
temperature, the cold temperature constraint effect declines, while correlations with VPD, which
limits the productivity during the growing season, increased after the 1980s, indicating that
global GPP is shifting from being temperature-limited to VPD-limited (Figure 4, S4).

Because GPP reductions occur primarily in tropical zones (Figure 2), we performed an
anomaly analysis for GPP in the tropics. Horizon plots (Figure 5) show how annual GPP in each
tropical region has changed relative to the average of annual GPP for 1982–2016. GPP
significantly declined after the early 2000s in the Amazon and, to a lesser degree, in Africa,
whereas GPP in the Asian rainforests began to decline almost a decade earlier than on other
continents. GPP in the Amazon has been declining since the 2005 drought, so its mean annual
GPP was ~0.13 Pg C lower during the 2000s (compared to the 35-year average) and has
continued to drop by up to -1.2 Pg C yr\(^{-1}\) after the 2010 drought. The annual average GPP of the
African tropics was 8.14 Pg C for the study period; it began to slightly decline after 2000 by
about 0.06 Pg C and increased by about 0.03 Pg C after 2010. In the Asian tropics after the
1990s, average GPP indicates a decline of 0.3–2 % per decade (0.03-0.17 Pg C).
Figure 4. The correlation between interannual GPP anomalies with FPAR, PAR, SM, Tmin, and VPD. The plot shows the spatial average of such time series correlations in $R^2$ between anomalies in annual GPP (Pg C yr$^{-1}$) with average detrended FPAR, PAR, SM, Tmin, and VPD values for the corresponding decade. Inter-annual GPP before 2000 was highly correlated with FPAR and PAR variations, but global GPP was significantly controlled by higher atmospheric VPD after 2000.

To unravel the underlying mechanism driving tropical GPP change, we performed a VPD anomaly analysis that directly influenced our modeled GPP results for the tropics. Figure 5b demonstrates that VPD in the Amazon began to increase in the early 2000s. In the African tropics, VPD increased from the mid-1990s to mid-2000s, resulting in decreased GPP compared to the 1982–2016 average. In the Asian tropics, where inter-annual VPD variability is much lower than in Africa and the Amazon, PAR is a larger limiting factor than VPD (Figure 3).
Figure 5. Horizon plot of anomalies in GPP and VPD time series for tropical forests in the Amazon, Africa, and Asia. The plot shows anomalies as departure from a: average annual GPP (Pg C yr\(^{-1}\)) and b: percent change in annual VPD. In the Amazon, GPP anomalies were positive through 2004 and then began to decline thereafter, whereas the GPP of the African forests showed a slight decline in the 2003–2007 period. The Asian tropics showed a declining trend after 1992. Plots divide the data on the y-axis based on different bands shown in the legend, and assign a different color to each band. Negative values are mirrored and values farther from 0 have more intense colors. Bands with higher values are drawn above the bands with lower values. For more information related to the horizon plots, refer to the supplementary materials (SI2).

The correlations between inter-annual GPP variability and environmental factors that constrain our LUE model in the tropics indicate that, in the Amazon, GPP variability is significantly \((p < 0.05)\) correlated with variability in VPD \((R^2 = 0.43)\) and PAR \((R^2 = 0.47)\), but has no significant correlation with FPAR variability over the 35-year record. However, FPAR showed a low but statistically significant correlation \((p < 0.05)\) with GPP after 2005 in the Amazon \((R^2=0.16)\). Over the 35-year period, the African tropics showed a significant correlation with VPD \((R^2=0.21)\), but not with PAR and FPAR. GPP in the Asian tropics showed a
significant correlation with VPD ($R^2=0.49$), a very high correlation with PAR ($R^2=0.8$), and a non-significant correlation with FPAR.

We further compared anomalies as a departure from long-term mean values of GPP from the TRENDY models, inversion model CO$_2$ fluxes, and SIF from the GOME-2 and SCIAMACHY (Figure 6) for tropical and northern northern mid and high latitudes. Our results indicate that, unlike the TRENDY GPP, the GPP$\text{Enh}$ model shows a recent variable response of northern ecosystem productivity to climatic changes. GOME-2 SIF also shows a variable annual signal despite focusing on a shorter period compared to GPP$\text{Enh}$, TRENDY, and net biome production (NBP) data from the inversion models. The NBP data show increasing net CO$_2$ uptake after 2000, even though there is more inter-annual variation compared to the TRENDY data.

![Image of Figure 6 showing regional anomalies in long-term ecosystem productivity metrics and estimates.](image)

**Figure 6. Regional anomalies in long-term ecosystem productivity metrics and estimates.** Ecosystem productivity metrics include GOME-2 (2007–2016, Joiner et al., 2012) and SCIAMACHY (2003–2011, Köhler et al., 2015) SIF; GPP models included the enhanced GPP (GPP$\text{Enh}$; this study) and TRENDY GPP (ensemble mean of ten ecosystem models Quéré et al., 2018; Sitch et al., 2015), compared with net biome productivity (NBP; ensemble mean from six inversion models, see Table S4 for references) for a northern latitudes (> 45ºN) and b tropical zones (10ºS–10ºN). Anomalies as departures from the mean are calculated at regional scales for each year and normalized for visualization and comparisons.

### 4 Discussion

Our results indicated increasing trends in annual GPP in mid to high latitudes. The GPP increase shown in the northern tundra and boreal ecosystems (> 45ºN) supports previous evidence of
greening trends observed from long-term satellite records (Myers-Smith et al., 2015; Zhu et al., 2016). Our results also provided evidence of a link to warming and longer growing seasons consistent with recent climate change (Mao et al., 2016; Zhu et al., 2016).

The rapidly changing arctic and boreal ecosystems are crucial components of the Earth system that store more than 30% of terrestrial carbon stocks (Apps et al., 1993; Pan et al., 2011). While boreal ecosystems have remained a persistent terrestrial carbon sink (Ciais et al., 2010), recent models and observations predict that increasing air temperatures will reduce the carbon uptake capacity of these biomes over the next century (Liu et al., 2019; Natali et al., 2019). Longer growing seasons and earlier observed photosynthesis from climate warming (Assmann et al., 2019; Box et al., 2019; Parazoo et al., 2018) lead to increased rate and duration of evapotranspiration which can deplete soil moisture and plant available water in the late growing season (Buermann et al., 2013, 2018; Lian et al., 2019; Parida & Buermann, 2014; Yi et al., 2014; Zhang et al., 2020). Prevalence of warming and browning in the Arctic (Bhatt et al., 2013; Phoenix & Bjerke, 2016; Treharne et al., 2019) also increases the risk of fire occurrences (Hu et al., 2010). All of these factors can affect satellite observed FPAR and SIF, while our model results also confirm recent high inter-annual variability in productivity in the northern high latitudes consistent with variability in temperature and water constraints.

Although the GPP increase in the northern high latitudes indicates a persistent, increasing negative carbon-climate feedback, our results suggest an emerging positive feedback to climate in the tropics. The negative GPP trend in the tropics suggests that the increased atmospheric water demand is not balanced by increased available water supply. The changes in rainfall patterns and recent increase in forest mortality in the Amazon forest (Brienen et al., 2015; Phillips et al., 2009; Wigneron et al., 2020) is a clear example of the severe impact of episodic drought and changes in patterns of water supply on these critical ecosystems. These changes in water supply and precipitation forcing in the Amazon influence VPD through land-atmosphere feedback and the trends in PAR.

In contrast to the declining trends seen in \( GPP_{\text{Enh}} \) in the tropical zones, the TRENDY models show an increase in GPP. LUE models have the advantage over prognostic vegetation models of a direct FPAR observational constraint and can thus potentially reflect anthropogenic effects such as deforestation and human pressure on the tropical hydro-climate system (Khanna et al., 2017) and indirectly impact ecosystem productivity. Like other LUE models, our model is
directly constrained by remote sensing observed vegetation indices that have been at the center of debates, especially over dense tropical forests (Bi et al., 2015; Huete et al., 2006; Morton et al., 2014; Saleska et al., 2016). However, our model revealed that there is no significant correlation between inter-annual variability of GPP in tropical South America with FPAR variability. Instead, we report a strong sensitivity of tropical GPP to VPD variability, which has also been shown for spaceborne SIF (Lee et al., 2013). We analyzed monthly VPD and GPP climatology observed at a CO$_2$ flux tower site in the Amazon and found a reduction in GPP when VPD increased beyond 800 Pa (Figure S5). Our results are consistent with other reports of increasing VPD at a global scale after the mid-1990s (Yuan et al., 2019) and highlight the potential constraining impact of increasing water limitations on global ecosystem productivity. This is especially true in the tropics, where changes in water constraints can lead to variable responses in net carbon exchange (Liu et al., 2017). However, this VPD impact on productivity seems to be less emphasized in Earth system models (Smith et al., 2016), which show increasing vegetation activity in the tropical zones after 2000 (Figure 7).

In tropical zones, where TRENDY models show increased GPP after 1997, GPP\textsubscript{Enh} estimates show divergent results, including a reduction in annual GPP after 2004. NBP obtained from inverse models generally indicates enhanced carbon uptake in the tropical zones after 2004 with some variation. It should be noted that inversion models have difficulty modeling the distribution of carbon sources and sinks in the tropics given the intensity of tropical convection, which can affect the spatial distribution of CO$_2$ concentration (Malhi & Phillips, 2004). In addition, the divergence in productivity estimates between DGVMs and LUE models can be related to DGVM oversensitivity to trends in atmospheric CO$_2$ fertilization (Smith et al., 2016) including lack of nutrient limitations, as these models tend to have higher sensitivity to CO$_2$ increase in tropical ecosystems than temperate and boreal ecosystems (Hickler et al., 2008; Schimel et al., 2015). However, it has been argued that most LUE models underestimate the CO$_2$ fertilization effect, as they do not explicitly account for atmospheric CO$_2$ concentrations (De Kauwe et al., 2016). LUE models are parametrized using carbon flux towers that have been operational since the late 1990s (Baldocchi et al., 2001). The dynamic effect of CO$_2$ fertilization on traditional LUE models is only reflected in FPAR observations that show long-term sensitivity to CO$_2$ trends (Chen et al., 2019; Zhu et al., 2016). Even though we used dynamic maximum and minimum annual FPAR for LUE\textsubscript{opt} extrapolation to represent changes in the
atmospheric CO$_2$ growth rate and the effects of land use change on photosynthetic efficiency, it is likely that the long-term trend in our LUE based GPP is underestimated.

As we addressed, our study was limited by the LUE$_{opt}$ estimated for the majority of the flux towers that were operational mostly during the 2000s. However, water and temperature constraints also play a significant role in controlling the growing season length and vegetation phenology. Our results indicate that when climate remained static, the APAR-only model, driven implicitly by leaf area and CO$_2$ fertilization, increased global GPP for the period 1982–2016 at a rate of 0.1 Pg C yr$^{-1}$ (Figure S6). The addition of climate constraints reduces the global APAR driven GPP trend by 10% to 0.09 Pg C yr$^{-1}$. However, it is important to note that the long-term trends here are affected by nonstationarity in time series. For example, large ENSO events affect these trends, but our results indicate that climate warming and drying in the tropics is gradually reducing the GPP growth rate at global scale. This estimated annual GPP trend is significantly lower than the TRENDY estimated GPP trend of 0.57 Pg C yr$^{-1}$, which optimistically follows the atmospheric CO$_2$ growth rate pattern (Figure S7).

Our GPP approach of using spatially and temporally variable LUE$_{opt}$ shows significant improvements over using fixed predefined LUE$_{max}$ values per biome type (Figure S2, S3). The LUE$_{opt}$ model is based on the concept that ecosystem processes differ based on plant community compositing, and that consideration of the geographic location and key life history traits of plants better accounts for the range of plant functional relationships with climate (Madani et al., 2014). Improving the LUE concept should also lead to better understanding of the response of plant productivity to climate change, despite the limitations associated with our LUE model approach as a whole.

Here, we focused only on the uncertainties related to extrapolated LUE (Figure S8) that were caused by random errors. At the global scale, these errors correspond to less than 10% of the LUE values for PFTs (Figure S9) and 6 Pg C standard deviation in annual GPP estimates. The resulting standard deviation around GPP estimates (Figure S10) does not affect our key findings. Nonetheless, uncertainties are involved in each of the LUE model inputs (Zhao et al., 2005) including the MERRA-2 surface meteorological data. Like all reanalysis data, MERRA-2 estimates may be impacted adversely by discontinuities in the assimilated satellite observing system record that impact the modeled water and energy fluxes (Robertson et al., 2016; Gelaro et al., 2017). Moreover, the use of gauge-based precipitation forcing in MERRA-2 can likewise
result in discontinuities, especially in poorly observed regions such as the Amazon (Reichle et al., 2017; their Figure 8).

Even though CO$_2$ fertilization and nutrient effects are indirectly considered in the remote sensing derived FPAR observations and the spatially explicit estimation of LUE$_{opt}$ model, future work should more directly account for these effects. Further improvement in the LUE models by including higher spatiotemporal resolution meteorological information capturing local variations in soil moisture (due to topography) and incoming shortwave radiation (due to clouds, diffuse and direct fraction), better representation of disturbance events such wildfires, and full representation of plant water availability, such as the inclusion of surface-to-groundwater information and the assimilation of satellite data (Madani et al., 2020; Smith et al., 2019), may further improve the model correspondence with productivity benchmark observations derived from the satellite SIF and global carbon flux tower record. These improvements will enable more accurate assessments and attribution of long-term climate and CO$_2$ effects and improved benchmarking of DGVMs, giving us better insight into future productivity changes.

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Data availability

The data produced from this study are accessible to the public through the ORNL DAAC and NTSG public portal at http://files.ntsg.umt.edu. All data used in this research are publicly available from the cited literature and the links below:

MERRA-2 data are available at: https://gmao.gsfc.nasa.gov/reanalysis/MERRA-2/data_access/.

GIMMS 3g FPAR data can be accessed from: http://sites.bu.edu/cliveg/. SIF data can be accessed from GODDARD Space Flight Center data portal at https://avdc.gsfc.nasa.gov/pub/data/satellite/. TRENDY data can be obtained from
FLUXNET data are available on ORNL DAAC https://daac.ornl.gov/cgi-bin/dataset_lister.pl?p=9 and at: https://fluxnet.org/data/fluxnet2015-dataset/.

Carbon tracker is obtained from NOAA Earth System Research Laboratory (https://www.esrl.noaa.gov/gmd/ccgg/carbontracker/), Carbon Tracker Europe from Wageningen University (http://www.carbontracker.eu/), Jena CarboScope is from MPG (http://www.bgc-jena.mpg.de/CarboScope/), and CAMS from ECMWF (http://apps.ecmwf.int/datasets/data/cams-ghg-inversions/). MODIS data are available to download from https://lpdaac.usgs.gov/

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