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Joint control of terrestrial gross primary productivity by plant phenology and physiology

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Terrestrial gross primary productivity (GPP) varies greatly over time and space. A better understanding of this variability is necessary for more accurate predictions of the future climate–carbon cycle feedback. Recent studies have suggested that variability in GPP is driven by a broad range of biotic and abiotic factors operating mainly through changes in vegetation phenology and physiological processes. However, it is still unclear how plant phenology and physiology can be integrated to explain the spatiotemporal variability of terrestrial GPP. Based on analyses of eddy–covariance and satellite-derived data, we decomposed annual terrestrial GPP into the length of the CO₂ uptake period (CUP) and the seasonal maximal capacity of CO₂ uptake (GPP_{max}). The product of CUP and GPP_{max} explained >90% of the temporal GPP variability in most areas of North America during 2000–2010 and the spatial GPP variation among globally distributed eddy flux tower sites. It also explained GPP response to the European heatwave in 2003 ($r^2 = 0.90$) and GPP recovery after a fire disturbance in South Dakota ($r^2 = 0.88$). Additional analysis of the eddy–covariance flux data shows that the interbiome variation in annual GPP is better explained by that in GPP_{max} than CUP. These findings indicate that terrestrial GPP is jointly controlled by ecosystem-level plant phenology and photosynthetic capacity, and greater understanding of GPP_{max} and CUP responses to environmental and biological variations will, thus, improve predictions of GPP over time and space.

ecosystem carbon uptake | growing season length | photosynthetic capacity | spatiotemporal variability | climate extreme

Large variability exists among estimates of terrestrial carbon sequestration, resulting in substantial uncertainty in modeled dynamics of atmospheric CO₂ concentration and predicted future

climate change (1). The variability in carbon sequestration is partially caused by variation in terrestrial gross primary productivity (GPP) (2), which is the cumulative rate over time of gross plant

Significance

Terrestrial gross primary productivity (GPP), the total photosynthetic CO₂ fixation at ecosystem level, fuels all life on land. However, its spatiotemporal variability is poorly understood, because GPP is determined by many processes related to plant phenology and physiological activities. In this study, we find that plant phenological and physiological properties can be integrated in a robust index—the product of the length of CO₂ uptake period and the seasonal maximal photosynthesis—to explain the GPP variability over space and time in response to climate extremes and during recovery after disturbance.

Author contributions: J.X., S.N., and Y.L. designed research; J.X. performed research; I.A.J., J.C., C.A., A.A., P.D.B., A.C., D.B., N.B., P.S.C., S.C., J.D., L.B.F., T.G., C.M.G., G.K., M.L., V.M., B.M., L. Merbold, L. Montagnani, E.J.M., J.E.O., A.R., O.R., A.E.S., M.U., F.P.V., A.V., T.V., M.W., G.W., and Y.L. contributed new reagents/analytic tools; J.X., D.H., L. Montagnani, and E.V. analyzed data; and J.X., S.N., P.C., I.A.J., J.C., C.A., P.D.B., A.C., D.B., N.B., S.C., L.B.F., C.F., T.G., C.M.G., D.H., G.K., J.L., M.L., V.M., B.M., L. Merbold, L. Montagnani, E.J.M., J.E.O., S.P., A.R., O.R., A.E.S., M.U., F.P.V., A.V., T.V., M.W., E.W., G.W., L.Y., and Y.L. wrote the paper.

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photosynthesis at the ecosystem level. Plant photosynthesis has been successfully modeled at the biochemical level (3, 4). When leaf-level biochemical models of photosynthesis are scaled up to estimate annual GPP over a region and the globe, however, great uncertainty arises from both vegetation properties, such as biome-dependent leaf parameters (5, 6), and environmental factors, such as climate variability (7–9) and episodic disturbances (10–12). As a consequence, estimated present day global GPP varies from 105 to 177 Pg C y^{-1} in the fifth phase of the Coupled Model Intercomparison Project (13). Additionally, spatiotemporal patterns of GPP (2, 14), their responses to extreme climate events (12) and disturbances (10), and the underlying mechanisms are still not well-understood. Previous studies have indicated that vegetation properties and environmental factors shape annual GPP of an ecosystem directly or indirectly through affecting plant physiological activities (15) and/or phenology (16–21). Thus, integrating plant physiological and phenological properties may provide a unified approach to explain the variability of GPP over time and space and in response to disturbance.

In this study, we show that annual GPP in grams C meter $^{-2}$ year $^{-1}$, the rate at which terrestrial ecosystems take up CO $_2$ from the atmosphere in a given year, can be quantitatively decomposed into

$$\text{GPP} = \alpha \cdot \text{CUP} \cdot \text{GPP}_{\text{max}}, \quad [1]$$

where the carbon dioxide uptake period (CUP; number of days per year) is a phenological indicator of the duration of ecosystem CO $_2$ assimilation within a given year. GPP $_{\text{max}}$ (grams C meter $^{-2}$ day $^{-1}$) is

the maximal daily rate of gross photosynthesis during the CUP and represents a property of plant canopy physiology. The ratio between annual GPP and the product of CUP and GPP $_{\text{max}}$ is represented by α . We estimated α , CUP, and GPP $_{\text{max}}$ for 213 globally distributed terrestrial sites with daily GPP from the global network of micrometeorological tower sites (FLUXNET; La Thuile Database) (22) (*SI Appendix, section S1.1.1 and Table S1*) and all $0.1^\circ \times 0.1^\circ$ land grid cells in North America during 2000–2010 with an 8-d GPP product from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the National Aeronautics and Space Administration Terra satellite (23) (*Materials and Methods*). Here, we show how CUP and GPP $_{\text{max}}$ jointly control the spatiotemporal variability of GPP and its response to and recovery from disturbances in different terrestrial ecosystems.

Results and Discussion

Using regression analysis, we first evaluated to what extent the product of CUP and GPP $_{\text{max}}$ (CUP \times GPP $_{\text{max}}$) explained the variability of satellite-derived GPP over broad temporal and spatial scales. CUP \times GPP $_{\text{max}}$ explained 94.9% of the interannual variability of the averaged MODIS GPP across North America from 2000 to 2010, with the minimum annual GPP (678 g C m $^{-2}$ y $^{-1}$) in 2000 and the maximum (748 g C m $^{-2}$ y $^{-1}$) in 2010 (Fig. 1A). The joint control of CUP and GPP $_{\text{max}}$ on the interannual variability of GPP was robust in most MODIS grid cells across North America but weak in tropical and Mediterranean climates, such as the

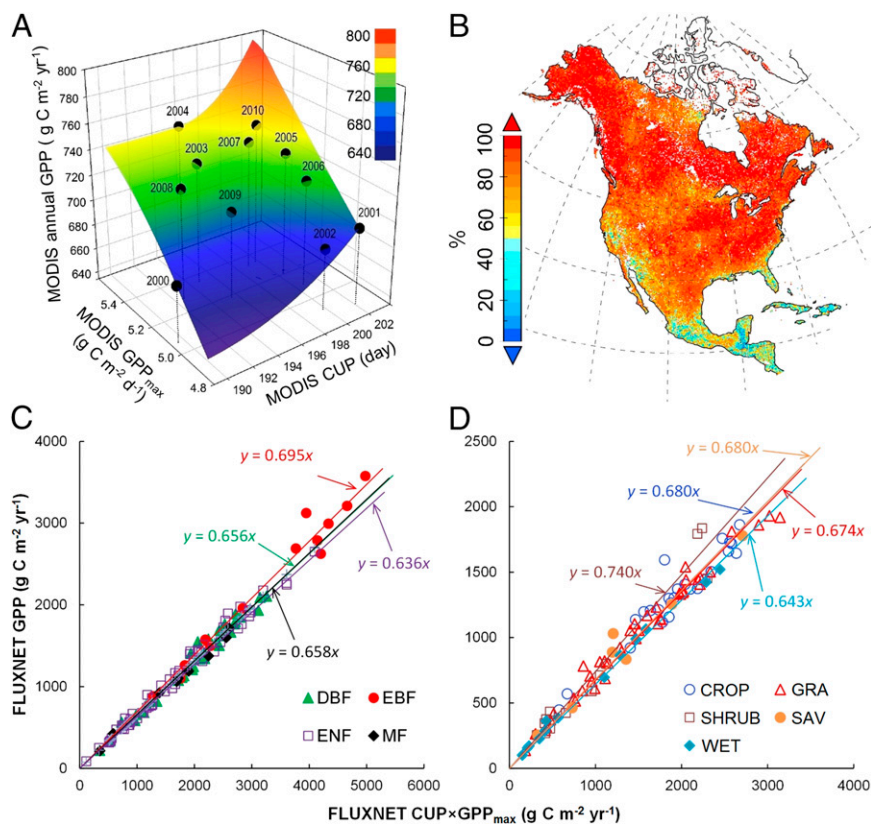


Fig. 1. Joint control of the temporal variability of satellite-derived annual GPP and the spatial variability of FLUXNET annual GPP by CUP and GPP $_{\text{max}}$. (A) The temporal variability of GPP in North America from 2000 to 2010 can be better understood by splitting annual GPP into GPP $_{\text{max}}$ and CUP. The flat color interpolated surface reflects a good relationship between annual GPP and GPP $_{\text{max}} \times$ CUP ($R^2 = 0.95$, $P < 0.001$). Vertical lines were added to improve readability. (B) Contribution of GPP $_{\text{max}} \times$ CUP to GPP temporal variability over 2000–2010. The contribution in each grid cell was derived from the R^2 in the linear regression analysis between GPP and GPP $_{\text{max}} \times$ CUP. C and D show relationships between GPP and GPP $_{\text{max}} \times$ CUP across FLUXNET sites in forest and nonforest biomes, respectively. Each data point in C and D represents one flux site with average data over different years. CROP, cropland; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRA, grassland; MF, mixed forest; SAV, savanna; SHRUB, shrubland; WET, wetland.

Caribbean region and California (Fig. 1B). Spatially, across all FLUXNET sites, although there was no relationship between CUP and GPP_{max} (SI Appendix, Fig. S1), $CUP \times GPP_{max}$ explained >95% of the spatial variation of annual observed GPP in all biomes (all $P < 0.001$) (Fig. 1C and D).

The product of CUP and GPP_{max} also explains the impact of a climate extreme on ecosystem CO_2 uptake. Linear regression analysis showed that the GPP reduction caused by the European heatwave in 2003 (12) across FLUXNET sites was well-explained by $CUP \times GPP_{max}$ ($R^2 = 0.90$, $P < 0.001$) (Fig. 2A, Inset). However, CUP and GPP_{max} played different roles in heatwave-induced GPP reduction among sites. For example, the reduction in annual GPP mainly resulted from a decrease of GPP_{max} (−37%) for a beech forest in Sarrebourg, France but a shortening of CUP (−11%) for a spruce site in Tharandt, Germany (Fig. 2A).

We also analyzed the dynamics of satellite-derived annual GPP, CUP, and GPP_{max} during recovery from a wildfire that occurred on August 24, 2000 in the Black Hills National Forest in South Dakota (24) (SI Appendix, Fig. S2). Although GPP_{max} and CUP followed contrasting postfire trajectories, the recovery trajectory of annual GPP was well-captured by the product of CUP and GPP_{max} ($R^2 = 0.88$, $P < 0.001$) (Fig. 2B). Immediately after the fire, GPP was sharply reduced by 27% in 2001 ($624 \text{ g C m}^{-2} \text{ y}^{-1}$) and 26% in 2002 ($636 \text{ g C m}^{-2} \text{ y}^{-1}$) relative to GPP before the disturbance in 2000 ($858 \text{ g C m}^{-2} \text{ y}^{-1}$). Thereafter, annual GPP gradually recovered to $816 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2010 (Fig. 2B). The dynamics of GPP_{max} after the fire paralleled those of annual GPP, with 40% and 36% reduction in 2001 and 2002, respectively, and then gradual recovery to 89% of prefire levels in 2010. In contrast, the CUP was extended by 30 to 60 days from 2000 (219 d) and then gradually shortened and returned to predisturbance values (Fig. 2B). The rapid extension of the CUP may have resulted from the return of grass in spring after fire disturbance (25).

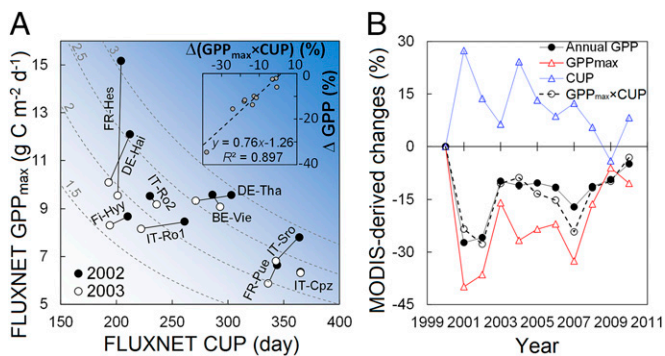


Fig. 2. Applications of the convergence of α (the ratio between annual GPP and $GPP_{max} \times CUP$) to explain GPP response to and recovery from disturbances. (A) Determination of the annual GPP reduction during the European heatwave in 2003 (12) by GPP_{max} and CUP. The dashed hyperbolic curves represent constant values (shown near the curves) of $GPP_{max} \times CUP$ (kilograms C meter⁻² year⁻¹), and the darker background blue color means a larger $GPP_{max} \times CUP$. Inset shows the dependences of the relative changes in annual GPP (ΔGPP ; percentage) in 2003 from those in 2002 on the relative changes in $GPP_{max} \times CUP$ [$\Delta(GPP_{max} \times CUP)$; percentage; black circles]. The ten sites are: BE-Vie (Vielsalm, Belgium), DE-Hai (Hainich, Germany), DE-Tha (Tharandt, Germany), Fi-Hyy (Hyytiälä, Finland), FR-Hes (Hesse Forest- Sarrebourg, France), FR-Pue (Puechabon, France), IT-Cpz (Castelporziano, Italy), IT-Ro1 and IT-Ro2 (Roccarespanpani, Italy), IT-Sro (San Rossore, Italy). Detailed information about each FLUXNET site can be found in SI Appendix, Fig. S9 and Table S1. (B) Contrasting dynamics of GPP_{max} and CUP after an extensive wildfire in the Black Hills National Forest in South Dakota. The data were extracted from a burned $0.1^\circ \times 0.1^\circ$ grid cell (43.85° N , 103.95° W) (original data are plotted in SI Appendix, Fig. S2). The ratio α was close to 0.62 during the 11-y span (SI Appendix, Fig. S10).

Not only did the product of CUP and GPP_{max} capture the variability in annual GPP over space and time and after disturbances, but the ratio α between annual GPP and $CUP \times GPP_{max}$ also converged across a broad range of vegetation types and environmental conditions (Fig. 3). The most frequent value of α was 0.62, with 90% of α -values falling within a range from 0.61 to 0.76 (Fig. 3A) based on an analysis of 213 FLUXNET sites. Those sites with $\alpha > 0.76$ were mainly located in tropical and subtropical climate zones (Fig. 3A and SI Appendix, Fig. S3). The analysis of the MODIS product showed a similar convergence of α over North America (Fig. 3B), with the most frequent value of 0.62 and a 90% range from 0.61 to 0.83. To explore the spatial distribution of α , we mapped the mean annual GPP, CUP, GPP_{max} , and α over 2000–2010. Although annual GPP, CUP, and GPP_{max} showed great spatial variability (SI Appendix, Fig. S4), α was relatively constant around 0.62 in most areas at a latitude of 37° N northward and gradually approached 1.0 toward the tropical regions of North America (Fig. 3C). Across North America, the temporal linear correlation between $CUP \times GPP_{max}$ and annual GPP was the highest in regions with α around 0.62 and gradually reduced with the ratio α approaching 1.0 (Fig. 3D).

High α -values were mainly distributed in tropical evergreen forest and regions with multiple growing seasons, where GPP_{max} and CUP exert weak controls over GPP variability (Fig. 3A, Inset). Values of α were high in tropical evergreen ecosystems, because GPP seasonality and amplitude were minimal, with plants assimilating CO_2 all year round. For example, daily GPP varied minimally across seasons in a tropical rain forest in Brazil (SI Appendix, Fig. S1.3.1), with α ranging between 0.77 and 0.80 from 2001 to 2003. The nontropical regions with high α -values usually have two or more peaks of daily GPP within a single year. For example, the Le Bray site in France, which is comprised of a maritime pine forest, had two separate GPP peaks in late May and September of 2005 (SI Appendix, Fig. S5). This phenomenon may also occur in Mediterranean regions with hot and dry summers (26) or double/triple cropping systems, where two or more crops are grown within a single year, such as winter wheat during winter and maize during summer in the North China Plain (27). Seasonally water-limited regions where two growing season peaks are present are widely distributed in the southern part of North America, leading to an abrupt increase in α at latitudes lower than about 30° N (Fig. 3C).

The decomposition of annual GPP into GPP_{max} and CUP allowed us to investigate the relative importance of GPP_{max} and CUP individually in regulating annual GPP variability among/within biomes (Fig. 4A). The linear correlation analysis across eight noncrop biomes showed that the biome-level GPP variability was significantly correlated to the variations in both GPP_{max} ($r^2 = 0.79$, $P = 0.003$) (Fig. 4B) and CUP ($r^2 = 0.64$, $P = 0.017$) (Fig. 4C). The partial correlation analysis across noncrop biomes revealed a larger contribution of GPP_{max} (partial $r^2 = 0.78$, $P = 0.004$) than CUP (partial $r^2 = 0.21$, $P < 0.001$) to GPP variability. A more important role of GPP_{max} than CUP in explaining the spatial variability of FLUXNET GPP was found within most biome types, including grassland (partial $r^2 = 0.70$, $P = 0.005$), shrubland (partial $r^2 = 0.52$, $P = 0.005$), savanna (partial $r^2 = 0.89$, $P = 0.001$), wetland (partial $r^2 = 0.91$, $P < 0.001$), and all forest types (partial $r^2 = 0.79$ – 0.87 , all $P < 0.01$) (SI Appendix, Fig. S6 and Table S2). A recent analysis has found that temperature and precipitation changes impact the net primary productivity of woody plant ecosystems mainly through their effects on growing season length, standing biomass, and stand age (28). Thus, standing biomass and stand age might be very important determinants of GPP_{max} in forest ecosystems.

The joint control of GPP_{max} and CUP on GPP variability indicates that environmental changes influence annual GPP by simultaneously affecting vegetation phenology and photosynthetic capacity. For example, climate warming leads to greater ecosystem CO_2 uptake by extending CUP in most cold regions (7, 17, 29) but could reduce ecosystem CO_2 uptake when

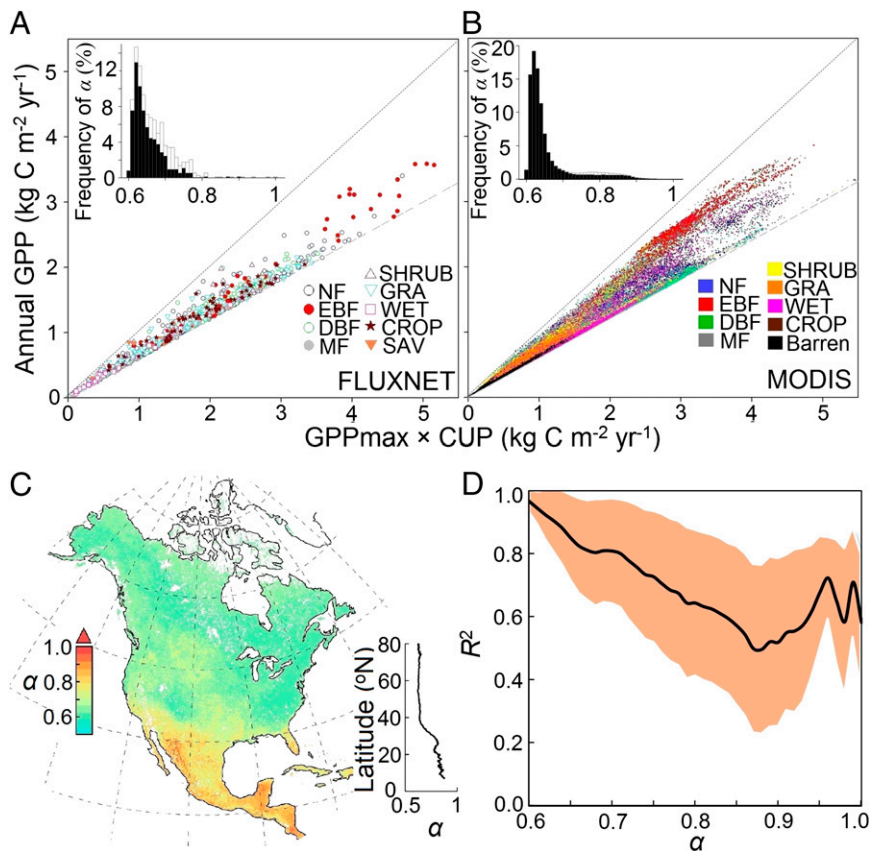


Fig. 3. The relationship between annual GPP and the product of CUP and GPP_{\max} (i.e., α) from FLUXNET and satellite-derived data. The relationship between annual GPP and $CUP \times GPP_{\max}$ is shown across (A) all FLUXNET site-years and (B) all $0.1^\circ \times 0.1^\circ$ land grids in North America. C shows spatial distributions of satellite-derived α , and D shows the relationship between α and the explanation of $GPP_{\max} \times CUP$ on temporal variability of annual GPP (R^2) (Fig. 1B) in North America. A, Inset and B, Inset show the relative frequency distribution of estimated α from all FLUXNET site-years and MODIS GPP data, respectively. The white bars are data from tropical and subtropical climate (including Mediterranean) zones and site-years with multiple GPP peaks, whereas the black bars are data from the rest of the site-years. C, Inset shows the latitudinal pattern of α with a 0.1° interval. CROP, cropland; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; GRA, grassland; NF, needleleaf forest; MF, mixed forest; SAV, savanna; SHRUB, shrubland; WET, wetland.

the GPP_{\max} is suppressed by the reduced snow melt water in spring (30, 31). Similarly, a recent analysis showed that warming-induced earlier springs reduced summer peak productivity during 1982–2008 in the North American boreal forests (32), which may have contributed to the declining trend of vegetation productivity associated with the climatic warming at northern high latitudes in the past few decades (33).

Given that simulated global GPP and its sensitivity to environmental factors vary substantially among current terrestrial biosphere models (13, 34), the findings in this study suggest that such uncertainty could largely stem from the different representations of vegetation phenology and photosynthetic capacity in the models. For example, although numerous vegetation phenology models have been developed for different biomes over the past few decades (35, 36), some existing terrestrial biosphere models poorly represent vegetation phenology in North America (8). Moreover, in those models, vegetation photosynthetic capacity may be unrealistically limited by the fixed parameterization of maximum rate of carboxylation (37), with observations indicating substantial temporal and spatial variations in maximum carboxylation (38, 39). Broadly collected vegetation phenology data derived from observations (40, 41), remote sensing (42, 43), and digital repeat photography (44, 45) as well as additional mechanistic understanding of canopy photosynthetic capacity (39, 46–48) could be useful to diagnose or benchmark model performances of simulating GPP (49).

Because the GPP_{\max} and CUP estimates were derived from existing data, our approach cannot be used for GPP prediction

unless GPP_{\max} and CUP can be inferred from other indicators. We first examined whether GPP_{\max} derived from MODIS GPP data was comparable with that measured by the flux towers in North America. We found that, although the two datasets had different spatial and temporal scales, the GPP_{\max} estimates from MODIS data were close to those from FLUXNET data at most sites with low GPP_{\max} (SI Appendix, Fig. S7). The FLUXNET data had much higher GPP_{\max} than MODIS data, mainly in the cropland sites with high GPP_{\max} (SI Appendix, Fig. S7). In addition to FLUXNET data, the maximum monthly sun-induced chlorophyll fluorescence data could be useful to estimate GPP_{\max} globally (50). We also examined whether the MODIS-derived CUP can be inferred from other types of satellite-derived datasets, such as the daily record of freeze/thaw status across North America (SI Appendix, section 1.8). We found that the MODIS-derived CUP is strongly correlated with the photosynthetically active period estimated from the freeze/thaw status data at most latitudes (SI Appendix, Fig. S8). The freeze/thaw status data can only provide information where the soil actually freezes in winter, partially leading to the disagreement between the two datasets in tropical regions (SI Appendix, Fig. S8). Thus, Eq. 1 could be useful for estimating and predicting annual GPP if both GPP_{\max} and CUP can be inferred from biotic and abiotic drivers measured at a global scale, the topic of a substantial body of ongoing research (15, 51).

In summary, we found a simple proximate cause to explain variation in annual GPP (i.e., Eq. 1) over space and time, in response to a climate extreme, and during recovery after disturbance.

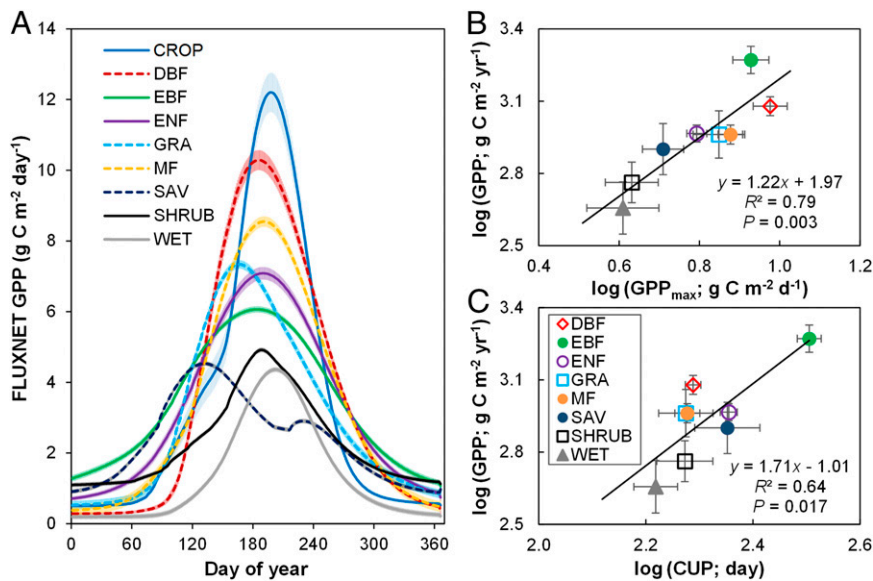


Fig. 4. (A) Dynamic of daily GPP in different biomes based on the FLUXNET dataset. The curves are obtained by averaging daily GPP over all site-years of each biome type, with the shaded areas representing SEs on GPP. *B* and *C* show dependence of annual FLUXNET GPP variability on GPP_{max} and CUP, respectively, among biomes. Note that there were, in total, 12 EBF sites in this analysis, and 7 of them were distributed in the temperate zone according to the MODIS IGBP (International Geosphere-Biosphere Programme) land cover classification (glcf.umd.edu/data/1c/) (*SI Appendix, Table S1*). CROP, cropland; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRA, grassland; MF, mixed forest; SAV, savanna; SHRUB, shrubland; WET, wetland.

The representation of interannual and spatial variations in GPP by the product of CUP and GPP_{max} was strong in those ecosystems with α -values close to 0.62 but weaker toward the tropics or in seasonally water-limited regions, where α -values approached 1.0. The strong correlation of annual GPP with the product of CUP and GPP_{max} in several different ecosystem types may be useful in detecting shifts in vegetation state and for monitoring short- and long-term response of GPP to extreme climate conditions and disturbances. Given that GPP_{max} better explains GPP variability than CUP, future studies need to emphasize the regulatory mechanisms for the dynamics of ecosystem photosynthetic capacity in terrestrial ecosystems.

Materials and Methods

GPP estimates (positive GPP means CO_2 uptake) from 213 FLUXNET sites from the La Thuile Database (www.fluxdata.org/default.aspx) (*SI Appendix, Table S1*) and the MODIS aboard National Aeronautics and Space Administration Terra satellites (MOD17A2 GPP) (23) were used in the analyses (*SI Appendix, section S1.1*). For FLUXNET sites, only those site-years with >300 daily estimates were chosen from the database. Because the MODIS GPP product was well-evaluated in North America (52), we only performed our analysis on MODIS GPP in this region from 2000 to 2010.

The determinations of CUP and GPP_{max} were from the method introduced by Gu et al. (53, 54) (*SI Appendix, section S1.2*). The CUP, GPP_{max} , and the ratio between annual GPP and $CUP \times GPP_{max}$ (i.e., α) were estimated for each selected FLUXNET site and each $0.1^\circ \times 0.1^\circ$ land grid cell of the MODIS product by the following steps (*SI Appendix, section S1.3*). (i) We judged if the site-year or grid cell is evergreen or not by counting the number of days with larger daily GPP than a given value (a site or land grid cell was defined as evergreen if there were more than 360 d with daily GPP > $1 \text{ g C m}^{-2} \text{ d}^{-1}$ within 1 y). (ii) The number of seasons in the non-evergreen site-years or land grid cells was determined by a model function (*SI Appendix, section S1.3 and Eq. S6*) suggested by the TIMESAT software (55). For those site-years and grid cells with one season, we fitted a five-parameter Weibull function to the data from that year. For those site-years or land grid cells with more than one season, we fitted the Weibull function to each season.

The nonlinear data fitting was performed with the function nls in R (www.r-project.org/) (*SI Appendix, section S1.4*). The robustness of the method was carefully validated by various approaches, including an evaluation with the data from all long-term FLUXNET sites (*SI Appendix, section S1.5*), a parameter sensitivity analysis of the Weibull function (*SI Appendix, section S1.6*), and a

random resampling test of the Weibull function (*SI Appendix, section S1.7*). Linear regression analysis was used to examine the contribution of $CUP \times GPP_{max}$ to the temporal and spatial variations of annual GPP. The global daily record of landscape freeze/thaw data from January 1, 2000 to December 31, 2010 was analyzed for an additional indicator of CUP (*SI Appendix, section S1.8*).

To further identify the relative contribution of GPP_{max} and CUP to GPP variability, we first linearized Eq. 1 by replacing all variables with their logarithms (base 10) as

$$\log(\text{GPP}) = \log(\alpha) + \log(\text{CUP}) + \log(\text{GPP}_{max}). \quad [2]$$

Then, we applied the partial correlation analysis to examine the relative contributions of CUP and GPP_{max} to FLUXNET GPP variability among and within biomes.

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