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Triose phosphate limitation in photosynthesis models reduces leaf photosynthesis and global terrestrial carbon storage

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Abstract

Triose phosphate utilization (TPU)-limited photosynthesis occurs when carbon export from the Calvin–Benson cycle cannot keep pace with carbon inputs and processing. This condition is poorly constrained by observations but may become an increasingly important driver of global carbon cycling under future climate scenarios. However, the consequences of including or omitting TPU limitation in models have seldom been quantified. Here, we assess the impact of changing the representation of TPU limitation on leaf- and global-scale processes. At the leaf scale, TPU limits photosynthesis at cold temperatures, high CO₂ concentrations, and high light levels. Consistent with leaf-scale results, global simulations using the Community Land Model version 4.5 illustrate that the standard representation of TPU limits carbon gain under present day and future conditions, most consistently at high latitudes. If the assumed TPU limitation is doubled, further restricting photosynthesis, terrestrial ecosystem carbon pools are reduced by 9 Pg by 2100 under a business-as-usual scenario. The impact of TPU limitation on global terrestrial carbon gain suggests that CO₂ concentrations may increase more than expected if models omit TPU limitation, and highlights the need to better understand when TPU limitation is important, including variation among different plant types and acclimation to temperature and CO₂.

Introduction

Photosynthesis is the largest gross carbon flux (~120 Pg C yr⁻¹) between Earth's surface and the atmosphere, enabling terrestrial sequestration of approximately one-third of anthropogenic carbon dioxide (CO₂) emissions (Le Quéré *et al* 2016). Models of leaf-level photosynthesis (e.g. Farquhar *et al* 1980) provide the foundation for estimating global CO₂ uptake by plants, yet there is considerable uncertainty associated with the structure and parameterization of

photosynthesis in these models (Arora *et al* 2013, Bonan *et al* 2012, Rogers 2014, Rogers *et al* 2017a). The recent CMIP5 ensemble of Earth system model (ESM) simulations showcases this uncertainty, with present day (1986–2005) estimates of Northern Hemisphere gross primary production (GPP) ranging from 6–16 Pg C in July (Anav *et al* 2013) and estimates of global cumulative land uptake between 1850 and 2005 spanning ~150 Pg C across all models (Ciais *et al* 2013).

One source of uncertainty in modeled estimates of carbon fluxes arises from differences in how

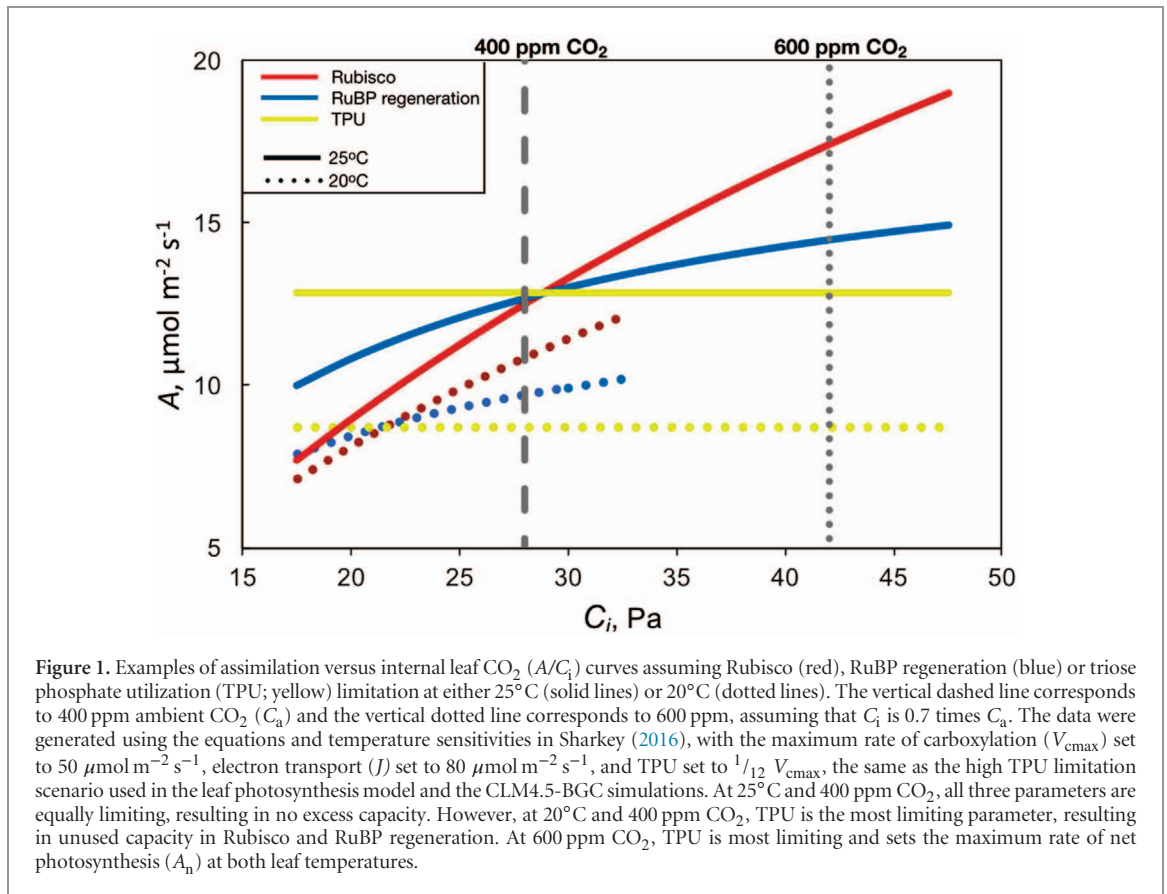


Figure 1. Examples of assimilation versus internal leaf CO_2 (A_n/C_i) curves assuming Rubisco (red), RuBP regeneration (blue) or triose phosphate utilization (TPU; yellow) limitation at either 25°C (solid lines) or 20°C (dotted lines). The vertical dashed line corresponds to 400 ppm ambient CO_2 (C_a) and the vertical dotted line corresponds to 600 ppm , assuming that C_i is 0.7 times C_a . The data were generated using the equations and temperature sensitivities in Sharkey (2016), with the maximum rate of carboxylation (V_{cmax}) set to $50\ \mu\text{mol m}^{-2}\text{ s}^{-1}$, electron transport (J) set to $80\ \mu\text{mol m}^{-2}\text{ s}^{-1}$, and TPU set to $1/12\ V_{\text{cmax}}$, the same as the high TPU limitation scenario used in the leaf photosynthesis model and the CLM4.5-BGC simulations. At 25°C and 400 ppm CO_2 , all three parameters are equally limiting, resulting in no excess capacity. However, at 20°C and 400 ppm CO_2 , TPU is the most limiting parameter, resulting in unused capacity in Rubisco and RuBP regeneration. At 600 ppm CO_2 , TPU is most limiting and sets the maximum rate of net photosynthesis (A_n) at both leaf temperatures.

models represent specific plant processes (e.g. Lovenduski and Bonan 2017, Rogers *et al* 2017a). For example, Rogers *et al* (2017a) evaluated how representation of C_3 photosynthesis at leaf and canopy scales varied across several global models and included recommendations for future research that may help to reduce model structural uncertainty and improve carbon cycle predictions. Here, we quantitatively assess one source of variation identified by Rogers *et al* (2017a)—structural uncertainty associated with the inclusion of triose phosphate utilization (TPU) limitation of photosynthesis (described below), which is only represented in a few Earth system models. In particular, we investigate the impact of TPU limitation on CO_2 assimilation at the leaf level and at the global scale for present-day and projected future carbon storage using the Community Land Model (CLM).

Typically, several physiological limitations to C_3 photosynthesis are represented in photosynthesis models, including biophysical constraints (e.g. stomatal and mesophyll conductance) that occur when CO_2 diffuses into and through the leaf, as well as biochemical constraints that occur during CO_2 fixation and utilization (Rogers *et al* 2017a). Two biochemical constraints that are commonly included in models are photosynthetic limitation by carboxylation and electron transport (see figure 1), which are calculated at the leaf-level using equations originally derived by Farquhar *et al* (1980). Carboxylation-limited photosynthesis (A_c) is often limiting under

low CO_2 partial pressure and is a function of V_{cmax} , which is the maximum carboxylation rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) assuming a saturating supply of ribulose 1,5-bisphosphate (RuBP). Electron transport-limited photosynthesis (A_j) describes photosynthesis limited by electron transport that supports the regeneration of RuBP and can also include limitations within the Calvin-Benson cycle other than Rubisco. It is often limiting under higher CO_2 partial pressures, but can be limiting over a broad range of CO_2 at low light (Sharkey 2016). Net photosynthesis (A_n ; $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$) is subsequently calculated as the minimum of A_c and A_j :

$$A_n = \min\{A_c, A_j\} - R_d \quad (1)$$

where R_d is non-photorespiratory respiration in the light,

$$A_c = \frac{V_{\text{cmax}}(C_i - \Gamma^*)}{C_i + K_C \left(1 + \frac{O_i}{K_o}\right)} \quad (2)$$

and

$$A_j = \frac{J(C_i - \Gamma^*)}{4C_i + 8\Gamma^*}. \quad (3)$$

In these equations, J ($\mu\text{mol electrons m}^{-2}\text{ s}^{-1}$) is based on the maximum potential electron transport rate (J_{max}), C_i is the intracellular concentration of CO_2 (Pa), K_c and K_o are the effective Michaelis-Menten

constants for CO₂ and O₂, O_i is the O₂ partial pressure (Pa), and Γ^* (Pa) is the CO₂ compensation point in the absence of mitochondrial respiration (Farquhar *et al* 1980).

When both carboxylation and electron transport rates are fast, a third biochemical constraint can limit the rate of photosynthesis. This occurs when carbon is not exported from the Calvin-Benson cycle as quickly as it is fixed and is known as TPU limitation, and TPU limited A is denoted (A_p). TPU limitation is typically assumed to be negligible if it is included in photosynthesis models and is therefore often omitted. However, TPU limitation may become more prevalent under future climate conditions. When the TPU limitation is included with the biochemical limitations discussed above, A_n can be calculated as:

$$A_n = \min\{A_C, A_j, A_p\} - R_d. \quad (4)$$

A detailed representation of A_p accounts for inefficiencies in carbon recycling during photorespiration:

$$A_p = \frac{(C_i - \Gamma^*) \times 3\text{TPU}}{C_i - (1 + 3 \times a_g) \times \Gamma^*} \quad (5)$$

where a_g is a unitless scalar from 0–1 based on glycolate recycling (with 1 being 100% recycling) within the chloroplast (Ellsworth *et al* 2015, Busch and Sage 2016, von Caemmerer 2000). The metabolic basis of equation (5) is thought to apply in many cases and describes the TPU limitation quite well (Harley and Sharkey 1991, Collatz *et al* 1991, Sellers *et al* 1996, Busch *et al* 2018). When glycolate recycling (a_g) is assumed to be 0, equation (5) simplifies to:

$$A_p = 3\text{TPU}. \quad (6)$$

This simpler version of the calculation for A_p is used in some global models, such as the CLM (see Oleson *et al* 2013) and the Joint UK Land Environment Simulator (JULES; Mercado *et al* 2007). In these equations,

$$\text{TPU} = 0.167V_{\text{cmax}} \quad (7)$$

so that by using equation (7) to calculate equation (6), $A_p = 0.5V_{\text{cmax}}$. The model formulation from which equation (7) is derived originates from work by Collatz *et al* (1991) and has been used in some land surface models for many years, even though no empirical data explicitly links TPU to V_{cmax} . Using observations available in Wullschleger (1993) for 16 C₃ plant species, we calculated the ratio of TPU to V_{cmax} to determine that $\text{TPU} = 0.132(\pm 0.038)^* V_{\text{cmax}}$, suggesting that the current calculation of TPU in models falls on the high end of the observed range, and is perhaps a conservative estimate.

Leaf- and global-scale photosynthetic models typically specify values of V_{cmax} used in equation (2) and sometimes J_{max} , which is used to calculate J in equation (3). Because these parameters are the foundation for photosynthesis models, it is important that the values are representative of the vegetation they

are simulating (Rogers 2014). For example, changes in the representation of V_{cmax} within the canopy of an Earth system model can cause estimates of global GPP to change as much as 30 Pg C yr⁻¹ (Bonan *et al* 2011). Field-based estimates of V_{cmax} , J_{max} , and TPU are frequently derived from measured photosynthetic CO₂ response curves (A/C_i curves), and the values used in many global-scale models are averages across species using data available from sources like the TRY database (Kattge *et al* 2011). However, TPU is not always included in curve fitting analyses. Nonetheless, studies using non-standard methods find that TPU limitation occurs frequently (Ellsworth *et al* 2015, Yang *et al* 2016).

Available research suggests that TPU limitation is most likely to occur under high CO₂ concentrations, high light, and/or low air temperature relative to growth temperature (Harley and Sharkey 1991, Busch and Sage 2016, Bernacchi *et al* 2009). Despite this basic understanding, the individual and interactive effects of environmental controls on TPU remain unknown for most species (Busch and Sage 2016), so model representations of TPU-limited photosynthesis are either necessarily over parameterized, represented non-mechanistically, or excluded (Gu *et al* 2010, Sharkey 2016, Maayar *et al* 2006, Rogers *et al* 2017a). The sensitivity of photosynthesis to TPU limitation has rarely been examined across global scales even though it could become an important limitation to carbon uptake under future environmental conditions.

Here, we explore the impact of TPU limitation under various climate conditions by quantifying the effect of including TPU limitation on photosynthesis across multiple scales. Because global scale models depend on leaf-scale photosynthesis calculations, we first use a leaf-scale photosynthesis model to high-light conditions under which modeled TPU would be expected to limit photosynthesis. We then scale the impact of including TPU-limited photosynthesis on global carbon uptake using the full global land model. We conclude by discussing research priorities for improving our understanding of TPU-limited photosynthesis using targeted field campaigns that will help to evaluate and constrain the representation of TPU in photosynthesis models and improve carbon cycle simulations in ESMs.

Methods

We used a global-scale land model and its embedded leaf-scale photosynthesis submodel to explore the sensitivity of A_n and ecosystem carbon storage to TPU limitation under changing environmental conditions. The global model used here is CLM4.5-BGC (Oleson *et al* 2013). Both the leaf submodel and the CLM4.5-BGC calculate TPU-limited A_n (i.e. A_p) using equation (4) above, and include export-limited photosynthesis based on TPU limitation as in equations (6) and

(7) above (Harley and Sharkey 1991). It should be noted that CLM4.5 solves for A_n (equation 4) as a rate colimited by Rubisco-, light-, and export-limitation (Collatz *et al* 1991, 1992, Bonan *et al* 2011) to account for variability in photosynthetic limitations across the canopy, which reduces A_n more than any single limitation (Bonan *et al* 2011) and may have a greater impact at low temperatures. Both the CLM4.5-BGC and the leaf submodel included photosynthetic temperature acclimation based on Kattge and Knorr (2007), with TPU acclimating in the same manner as V_{cmax} (Lombardozzi *et al* 2015). In CLM4.5-BGC, photosynthetic temperature acclimation occurs between leaf growth temperatures of 11°C–35°C, though the leaf submodel did not impose temperature restrictions on acclimation. The leaf submodel additionally assumed a V_{cmax} at 25°C ($V_{\text{cmax}25}$) of 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$, Rubisco kinetics from Bernacchi *et al* (2001), and an intracellular to extracellular CO_2 ratio (C_i/C_a) of 0.7.

We tested the sensitivity of leaf and global photosynthesis to TPU limitation by testing three different TPU limitation scenarios. The unmodified TPU used in CLM4.5, which we term here ‘standard TPU limitation,’ calculated TPU as one-sixth of V_{cmax} (equation 7) and the export-limited rate of photosynthesis as three times TPU (equation 6, leading to an export-limited rate = $0.5 V_{\text{cmax}}$; Collatz *et al* 1991). To test a scenario where plants are more limited by TPU limitation (‘high TPU limitation’), we modified TPU to be one-twelfth of V_{cmax} (e.g. equation 7 is updated to $\text{TPU} = 0.0835 V_{\text{cmax}}$, halving the TPU and doubling the TPU limitation by making the export-limited rate in equation 6 = $0.25 V_{\text{cmax}}$). The high TPU limitation scenario brackets the range of observations ($\text{TPU} = (0.132 \pm 0.038) * V_{\text{cmax}}$; Wullschleger *et al* 1993) and is close to the low-end estimate of this range ($\text{TPU} = 0.094 * V_{\text{cmax}}$). This simulation was anticipated to reduce carbon gain because TPU will more strongly limit photosynthesis. Finally, to test a scenario where plants are less limited by TPU, termed ‘low TPU limitation’, we modified TPU to be one-third of the V_{cmax} rate (e.g. equation 7 is updated to $\text{TPU} = 0.334 V_{\text{cmax}}$, doubling the TPU so that the export-limited rate in equation 6 = V_{cmax}), lessening the importance of TPU and reducing export-limited photosynthesis. The low TPU limitation scenario illustrates the impact of having very weak to no TPU limitation compared to the standard representation used in CLM.

Using the leaf photosynthesis model, we ran simulations with the high and standard representations of TPU limitation at combinations of varying C_a (1–2000 $\mu\text{mol mol}^{-1}$), photosynthetically active radiation (PAR; 50–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$), and leaf temperature (5°C–35°C). In our testing, the low TPU simulation that is used in the global simulations does not limit photosynthesis below a C_a value of 2000 $\mu\text{mol mol}^{-1}$ (data not shown) and is therefore not discussed in our leaf photosynthesis analysis. From these simulations,

we identified the C_a value at which modeled photosynthesis became TPU-limited under different light and leaf temperature conditions for ‘standard TPU’ and ‘high TPU’ limitations.

To test the implications of TPU limitation for the global carbon cycle, we ran the CLM4.5 with active biogeochemistry (BGC; Oleson *et al* 2013) at 2 degree resolution from 1850 through 2100 using atmospheric forcing data archived from a Community Earth System Model (CESM) simulation that used a historical forcing scenario through 2005 and the representative concentration pathway 8.5 (RCP8.5) forcing scenario through 2100 (Meehl *et al* 2012). Each of the TPU scenarios described above (standard, low, and high) was tested in a separate simulation. After the modifications were included to adjust TPU, each simulation was spun up using 1850 initial conditions until carbon pools stabilized. Analysis focused on the changes in GPP, as well as the integrated response of total ecosystem carbon, which sums total soil and vegetation carbon pools, to better understand the consequences of the accumulated changes in productivity on terrestrial carbon storage.

Results and discussion

Leaf-level photosynthesis

The results from the leaf model illustrate that the C_a value where leaves become TPU-limited increases with temperature and decreases with PAR (figure 2). TPU limitation occurs across a range of C_a values, from as low as 200 $\mu\text{mol mol}^{-1}$ at a leaf temperature of 5°C, to over 2000 $\mu\text{mol mol}^{-1}$ under high temperature and low light conditions (figure 2). Not surprisingly, assuming lower rates of TPU (i.e. high TPU limitation) limited photosynthesis more across the range of environmental conditions tested here, but the patterns remained the same (figure 2(b) compared to 2(a)).

Overall, this leaf-scale exercise suggests that Earth system models (ESMs) that include TPU limitation in photosynthesis calculations would predict large geographic areas where photosynthesis is limited by carbohydrate export, particularly cold regions during times of high radiation. It is important to note that the leaf submodel used here assumes a static $V_{\text{cmax}25}$ value, whereas observations indicate that $V_{\text{cmax}25}$ varies with environmental conditions such as temperature (Ali *et al* 2015), nitrogen in leaves (Walker *et al* 2014, Kattge *et al* 2009), water availability (Reich *et al* 2007, Ali *et al* 2015), day length (Bauerle *et al* 2012), or ozone exposure (Lombardozzi *et al* 2012). Additionally, the ratio of TPU to $V_{\text{cmax}25}$ can be decreased by factors such as water stress (Vassey and Sharkey 1989, Lawlor 2002), changes in leaf respiration capacity (Dahal *et al* 2014), and increased leaf nitrogen (Sage *et al* 1990).

We assumed that the temperature sensitivity of TPU is the same as that of V_{cmax} . Although evidence

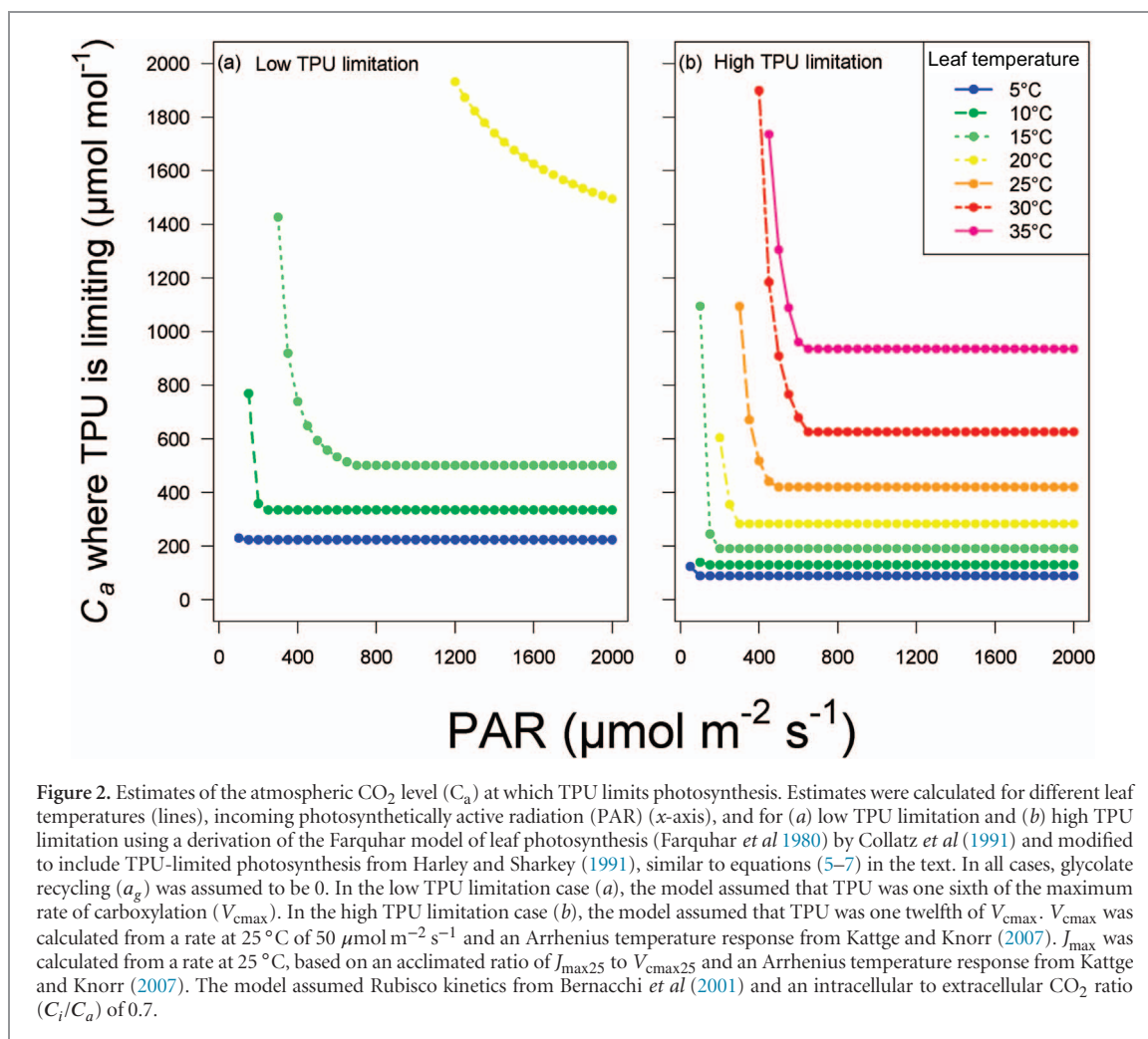


Figure 2. Estimates of the atmospheric CO_2 level (C_a) at which TPU limits photosynthesis. Estimates were calculated for different leaf temperatures (lines), incoming photosynthetically active radiation (PAR) (x -axis), and for (a) low TPU limitation and (b) high TPU limitation using a derivation of the Farquhar model of leaf photosynthesis (Farquhar *et al* 1980) by Collatz *et al* (1991) and modified to include TPU-limited photosynthesis from Harley and Sharkey (1991), similar to equations (5–7) in the text. In all cases, glycolate recycling (a_g) was assumed to be 0. In the low TPU limitation case (a), the model assumed that TPU was one sixth of the maximum rate of carboxylation (V_{cmax}). In the high TPU limitation case (b), the model assumed that TPU was one twelfth of V_{cmax} . V_{cmax} was calculated from a rate at 25 °C of $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ and an Arrhenius temperature response from Kattge and Knorr (2007). J_{max} was calculated from a rate at 25 °C, based on an acclimated ratio of $J_{\text{max}25}$ to $V_{\text{cmax}25}$ and an Arrhenius temperature response from Kattge and Knorr (2007). The model assumed Rubisco kinetics from Bernacchi *et al* (2001) and an intracellular to extracellular CO_2 ratio (C_i/C_a) of 0.7.

suggests that physiological processes in plants may acclimate (Ainsworth and Rogers 2007, Sage *et al* 1989) or even adapt (Watson-Lazowski *et al* 2016) to elevated CO_2 and may therefore change photosynthetic limitations in the future, the leaf model used here, and most Earth System models, do not account for these processes. The introduction of prognostic V_{cmax} (e.g. Xu *et al* 2012, Ali *et al* 2016), as planned for CLM5, may alleviate these limitations. Nonetheless, the occurrence of simulated TPU-limited photosynthesis should increase as C_a levels rise, though increasing leaf temperatures could offset this increase. Thus, it is important to improve our understanding of how photosynthesis acclimates to the combination of CO_2 and temperature changes expected in the future.

Global photosynthesis and carbon cycle

Compared to the standard (unmodified) simulation, reducing TPU limitation increased simulated GPP slightly by 2100 under low TPU limitation compared to the standard TPU limitation (+1 Pg C, ~2%), whereas high TPU limitation more clearly decreased simulated GPP by 2100 (−3 Pg C, ~6%; figures 3(c) and (d)). Similarly, low TPU limitation increased simulated total ecosystem C gain (+4.5 Pg, ~4%) by 2100, while

high TPU limitation reduced simulated total ecosystem C gain (−9.0 Pg, ~9%; figures 3(a) and (b)). The changes in total ecosystem carbon reflect the integrated C fluxes from changes in productivity.

In CLM4.5 simulations, TPU limits GPP (and the accumulated ecosystem carbon storage, see SI figure 1 available at stacks.iop.org/ERL/13/074025/mmedia) most in the high latitudes (figure 4), particularly in 2100, which is consistent with the results from the leaf photosynthesis submodel that suggests TPU limits photosynthesis more frequently at low temperatures and higher CO_2 (figures 1 and 2). The CLM4.5 simulations also illustrate that high limitation of TPU suppresses GPP by 2000, and increasingly more by 2100. Rogers *et al* (2017b) showed that V_{cmax} in Arctic vegetation was markedly higher than the values used in current ESMs and approximately double the value used here. Because of the assumed relationship between V_{cmax} and TPU, higher Arctic V_{cmax} might lead to TPU limitation at higher (CO_2) than we found here, resulting in higher GPP and carbon storage. It is important to note that figure 4 shows the change of a change ($\Delta\Delta$) for the low (figures 4(a) and (c)) and high (figures 4(b) and (d)) TPU limited scenarios. Thus, differences plotted in figure 4 are a result of both the temporal change in TPU limitation (2100 or 2000–1850) as

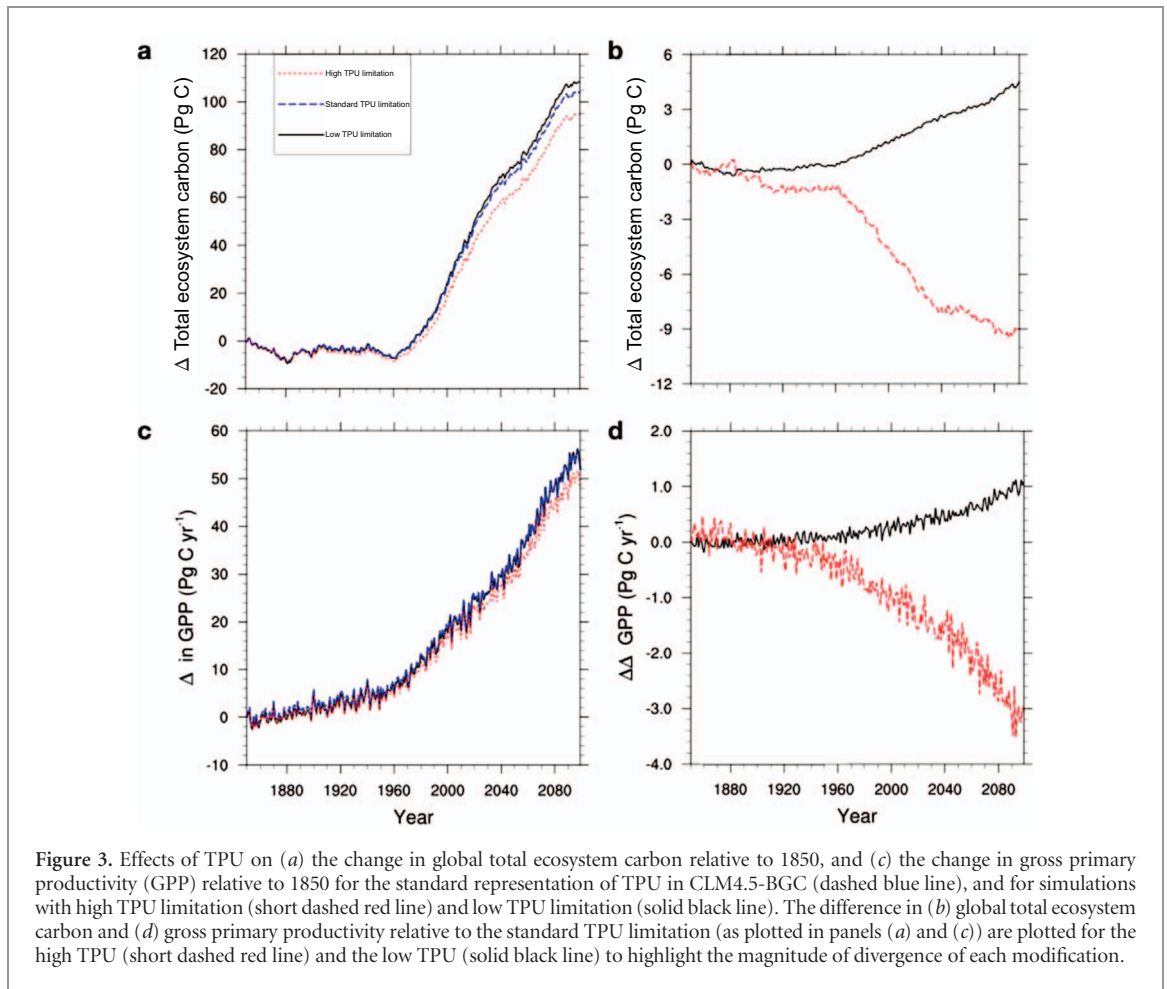


Figure 3. Effects of TPU on (a) the change in global total ecosystem carbon relative to 1850, and (c) the change in gross primary productivity (GPP) relative to 1850 for the standard representation of TPU in CLM4.5-BGC (dashed blue line), and for simulations with high TPU limitation (short dashed red line) and low TPU limitation (solid black line). The difference in (b) global total ecosystem carbon and (d) gross primary productivity relative to the standard TPU limitation (as plotted in panels (a) and (c)) are plotted for the high TPU (short dashed red line) and the low TPU (solid black line) to highlight the magnitude of divergence of each modification.

well as the change in TPU scenario (high or low TPU limitation—standard TPU limitation). Though the spatial patterns of change are similar in the low- and high-TPU limited scenarios, the magnitude of the decrease in GPP (and ecosystem carbon, SI figure 1) is much larger in many regions with high TPU limitation (e.g. $>100 \text{ g C m}^{-2} \text{ yr}^{-1}$) than the increase in GPP due to reducing TPU limitation. The increased GPP in the low TPU simulation illustrate that the standard parameterization used in CLM4.5-BGC is TPU limited in high latitudes by the end of the twenty-first century.

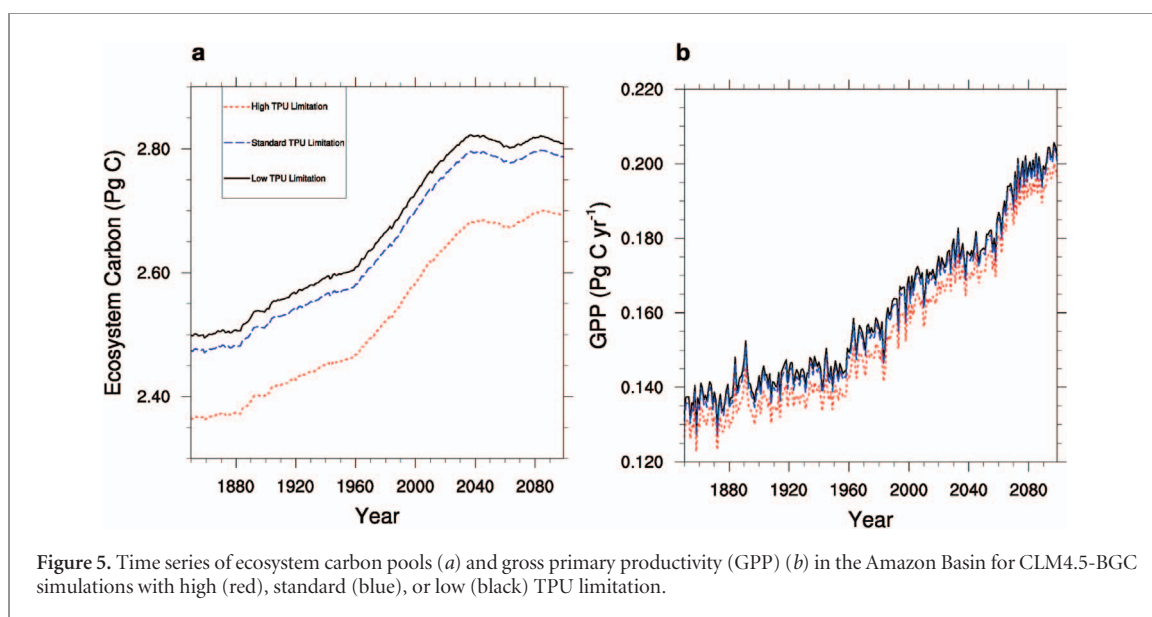
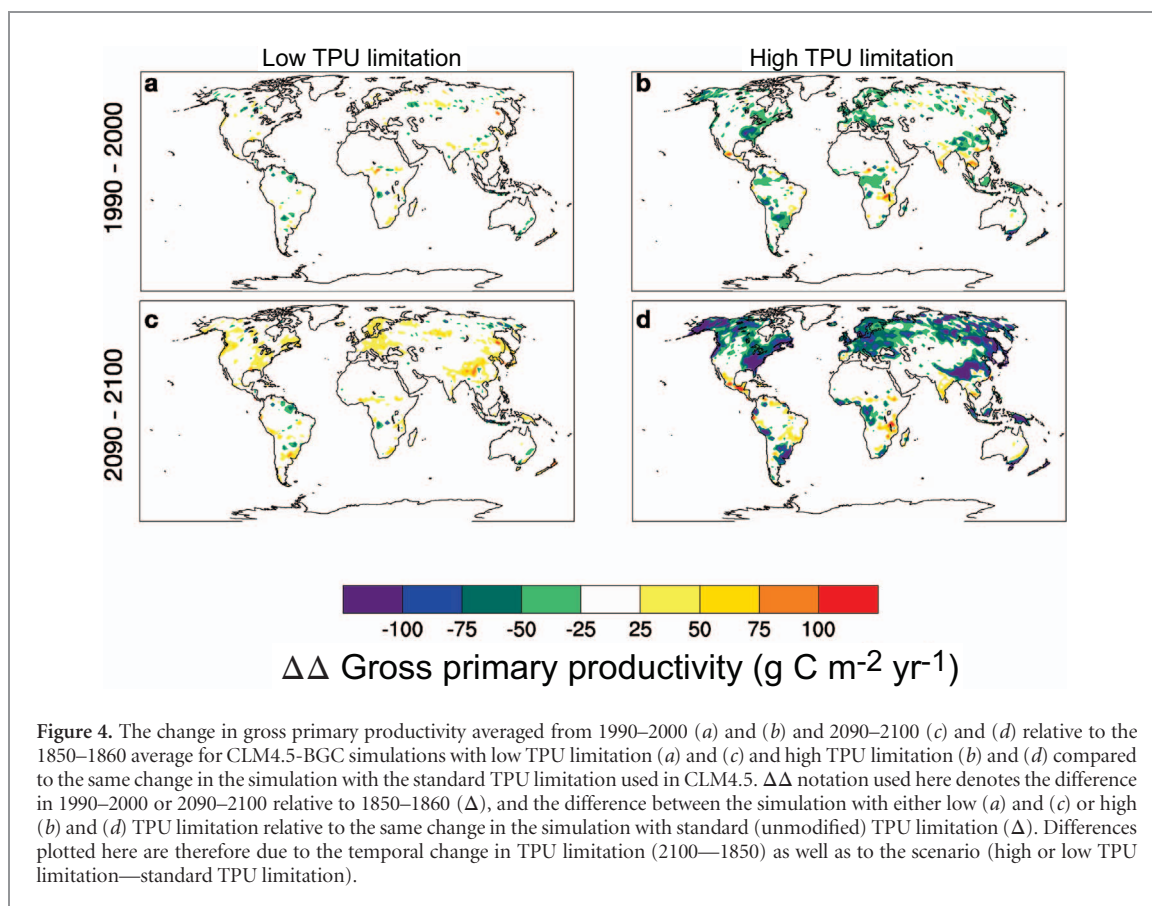
Regional responses of photosynthesis to changes in TPU limitation may be partly affected by the representation of TPU acclimation to short-term (10-day) changes in mean temperature in CLM (Lombardozzi *et al* 2015). Though few data are available to verify whether TPU acclimates, TPU is thought to be temperature dependent, and is perhaps more sensitive to temperature changes than V_{cmax} (Yang *et al* 2016), even though it is often modeled without a temperature function. Temperature is an important determinant of TPU limitation (figure 2), so understanding whether TPU acclimates to temperature changes remains a key research priority. Limitation of photosynthesis under the standard TPU representation in CLM4.5 suggests that TPU limitation likely occurs in models that represent it, espe-

cially if acclimation to temperature is not accounted for.

The decrease in global (figure 3) and high latitude (figure 4) GPP and ecosystem carbon between the standard and high TPU limitation simulations compared to the low TPU limitation are more intuitive than the relative increases in GPP and ecosystem carbon that occur in tropical regions and a few other locations like Central Europe (figure 4, SI figure 1). In fact, a time-series of GPP and ecosystem carbon in the Amazon Basin illustrates that the absolute values of GPP and ecosystem carbon were lower in simulations that included standard or high TPU limitation throughout the duration of the simulation compared to the low TPU limitation simulation (figure 5). Therefore, the relative increases in response to high TPU limitation (figure 4) result from a larger net carbon gain between 1850 and 2100. It is possible that the maximum GPP and ecosystem carbon gain in tropical regions, for example, is limited by another ecosystem driver like nitrogen availability (see Lombardozzi *et al* 2015).

Conclusions and future research priorities

Overall, our work illustrates that model estimates of net photosynthesis in leaf- and global-scale models are likely limited by TPU under some environmental



conditions (figures 2 and 3), with TPU limitation having the largest impact under high CO_2 in cold regions (figure 4), similar to current theoretical understanding and available observations. Using a global-scale model, we add to current understanding of TPU limitation by identifying times when and regions where TPU limitation may be important. As represented in CLM4.5, the present-day carbon cycle is currently limited by TPU, and the limitation increases under the future RCP8.5 climate scenario (figures 3 and 4). Given

the few available data on TPU, it is difficult to assess the realism of the TPU limitation exerted within the models we tested. The calculation of TPU we use equation (7) is within the range of measured estimates ($(0.132 \pm 0.038) * V_{\text{cmax}}$; Wullschlegel 1993) and may be a conservative estimate. The observational estimates suggest that TPU limitation is more likely to fall between the standard and high TPU limitation scenarios, so even the ESMs that currently include TPU limitation using the standard formulation may

underestimate its impact. If TPU limitation is underestimated or omitted from photosynthesis calculations in ESMs, then projections of future CO₂ concentration increases are likely also underestimated.

Currently, we lack a robust theoretical understanding of the drivers of TPU limitation under different environmental conditions and over large spatial and temporal scales. Estimates of TPU limitation from *in situ* measurements may help to constrain carbon cycle uncertainty in model simulations, and measurements collected under environmental manipulations, such as elevated CO₂ experiments, can help to better understand whether model projections of future changes in TPU limitation are at all realistic. Our modeling results identify high latitudes as regions where TPU limitation is most likely to occur in the future, and these regions should have the highest priority for measurement campaigns. We recognize that measuring TPU limitation is challenging, but the advent of new techniques, such as combining gas exchange and fluorescence measurements of leaf O₂ and CO₂ sensitivities (Busch and Sage 2016, Busch *et al* 2018) may help with collecting more accurate estimates of TPU, as well as other photosynthetic parameters.

Measurement campaigns should also consider the potential for acclimation of export-limited photosynthesis to environmental conditions thought to be particularly susceptible to high TPU limitation, such as high CO₂, high light, and low temperatures. For example, the temperature sensitivity of TPU documented by Yang *et al* (2016) suggests that TPU is more sensitive to temperature than V_{cmax} . Additionally, recent work using the coordination theory of photosynthesis (e.g. Wang *et al* 2017, Quebbeman and Ramirez 2016) suggests that plants adjust carboxylation- and electron transport-limited photosynthetic processes such that neither is strongly limiting at current growth conditions. It is possible that similar acclimation of export-limited photosynthesis occurs, though more measurements are needed to fully assess this response. Gaining a better process understanding of TPU limitation through the targeted measurements recommended above is necessary to improve the representation of TPU limitation in photosynthesis models. Ultimately, improved process understanding of TPU limitation may help to constrain the uncertainty in carbon cycle projections in the future, when TPU limitation is expected to more frequently limit photosynthesis.

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