Letters

Triose phosphate utilization limitation: an unnecessary complexity in terrestrial biosphere model representation of photosynthesis

Introduction

Triose phosphates are the principal product of photosynthesis. They are used within the chloroplast for starch synthesis, or translocated to the cytosol where they are used to fuel sucrose synthesis. Use of triose phosphate releases inorganic phosphate, and is under strict metabolic control that matches the supply of triose phosphate from the Calvin–Benson cycle to the demand for carbon by sinks (Heldt & Piechulla, 2011; McClain & Sharkey, 2019). However, a low rate of triose phosphate utilization (TPU) can deplete the phosphate pool, restrict adenosine triphosphate (ATP) synthesis and reduce the availability of ATP to power the Calvin–Benson cycle, thereby limiting photosynthesis (Sharkey, 1985).

Recent work has demonstrated the sensitivity of terrestrial biosphere models (TBMs) to TPU (Lombardozzi et al., 2018) and showed that models predict limitation of photosynthesis by TPU most consistently at high latitudes and future elevated CO_2 concentration ([CO_2]). However, a global scale analysis provided empirical evidence that TPU limitation rarely limits photosynthesis under present day growth conditions and is unlikely to limit photosynthesis at elevated [CO_2], even at the low temperatures typical at high latitudes (Kumarathunge et al., 2019a). Additionally, Walker et al. (2021) revealed an artifact in TBM representation of photosynthesis that exaggerates the limitation of TPU on modeled CO_2 assimilation. This artifact arises from quadratic smoothing of the transition among the potential limiting processes governing photosynthesis and is closely associated with TBM representation of TPU limitation. Collectively, these recent advances, highlight the need for an examination of the representation of TPU in TBMs.

Representation of triose phosphate utilization rate in terrestrial biosphere models

The Farquhar, von Caemmerer and Berry model of photosynthesis, is at the heart of many TBMs that seek to understand the global carbon cycle and project the response of the terrestrial biosphere to global change (Farquhar et al., 1980; Rogers et al., 2017a). In its simplest form the Farquhar et al. (1980) model represents net photosynthesis (A) as gross photosynthesis (A_g) minus the day-time respiration rate (R_{day}, Eqn 1), where A_g is the minimum of ribulose-1,5-bisphosphate (RuBP) saturated, or rubisco limited, photosynthesis (A_c) and RuBP limited photosynthesis (A_j). However, several TBMs (Table 1) also include representation of the TPU limited rate of photosynthesis (A_p) as a third potential limitation of A_g (Eqn 2; Sharkey, 1985; Rogers et al., 2017a).

$$A = A_g - R_{day} \qquad \text{Eqn 1}$$

$$A_g = \min \left\{ A_c, A_j, A_p \right\} \qquad \text{Eqn 2}$$

Since Calvin cycle intermediates must be conserved, 3 mol CO_2 must be fixed in order to produce 1 mol triose phosphate (3 carbon). Therefore, A_g will become limited by TPU when the rate of CO_2 assimilation is equal to three times the rate at which triose phosphates are used (Sharkey, 1985).

$$A_p = 3TPU \qquad \text{Eqn 3}$$

During photorespiration glycollate exported from the chloroplast is returned as glycerate and ATP is required to convert that glycerate to 3-phosphoglycerate. Therefore, when photosynthesis is limited by the TPU rate, the use of photorespiratory intermediates by other pathways, e.g. nitrate synthesis (Busch et al., 2018), will reduce the fraction of glycerate returned to the chloroplast, increase the availability of ATP in the stroma, and alleviate TPU limitation. This process has been described mathematically (Harley & Sharkey, 1991, Eqn 4) where C_i is the intercellular [CO_2], Γ^* is the CO_2 compensation point in the absence of non-photorespiratory mitochondrial respiration in the light and α_g describes the fraction (0–1) of glycollate not returned to the chloroplast during photorespiration.

$$A_p = \frac{(C_i - \Gamma^*)3TPU}{C_i - (1 + 3\alpha_g)\Gamma^*} \qquad \text{Eqn 4}$$

However, current TBM formulations only consider scenarios whereby carbon is maximally conserved by the photorespiratory cycle, i.e. three quarters of the carbon translocated to the peroxisome as glycollate is returned to the chloroplast as glycerate, and $\alpha_g = 0$. Under this assumption Eqn 4 can be simplified to Eqn 3, as originally proposed by Sharkey (1985).

To enable parameterization of models including representation of TPU limitation Collatz et al (1991), described A_p as a function of leaf temperature and the maximum carboxylation capacity of RuBP saturated photosynthesis ($V_{c,max}$) at a reference temperature, and considered A_p to equal the value of A at saturating [CO_2] and

Table 1 Terrestrial biosphere models that include representation of triose phosphate utilization (TPU) rate.

Model	TPU rate	Temperature response	Thermal acclimation	Limitation of A_n (θ, β)	TPU formulation
CLMv.5.0	0.167 $V_{c,max}$	Same as $V_{c,max}$	Kattge & Knorr (2007)[a]	Eqns 6 and 7 (0.98, 0.95)	Collatz *et al*. (1991)
ELMv.1	0.167 $V_{c,max}$	Same as $V_{c,max}$	Kattge & Knorr (2007)[a]	Eqns 6 and 7 (0.98, 0.95)	Collatz *et al*. (1991)
FATES	0.167 $V_{c,max}$	Independent	No	Eqns 6 and 7 (0.999, 0.999)[b]	Harley *et al*. (1992)
IBIS	0.122 $V_{c,max}$	Same as $V_{c,max}$	No	Eqns 6 and 7 (0.9, 0.9)	Foley *et al*. (1996)
JULES	0.167 $V_{c,max}$	Same as $V_{c,max}$	No	Eqns 6 and 7 (0.83, 0.93)	Collatz *et al*. (1991)
LM3	0.122 $V_{c,max}$	Same as $V_{c,max}$	No	Eqn 1 (na)	Foley *et al*. (1996)

Terrestrial biosphere models that include representation of TPU were identified from the CMIP6 model families. CLMv.5.0, Community Land Model v.5.0 (Lawrence *et al*., 2019); ELMv.1 E³SM (Energy Exascale Earth System Model) Land Model (Oleson *et al*., 2013; Golaz *et al*., 2019); FATES, Functionally Assembled Terrestrial Ecosystem Simulator (Koven *et al*., 2019); IBIS, Integrated Biosphere Simulator (Foley *et al*., 1996); JULES, Joint UK Land Environment Simulator (Harper *et al*., 2016); LM3, Geophysics Fluid Dynamics Laboratory Land Model. θ and β are the parameters in Eqns 7 and 8 used to set the convexity of the smoothing functions described by Collatz *et al*. (1991).
Note: na, not applicable.
[a]Thermal acclimation is restricted over the temperature range 11–35°C.
[b]Within FATES θ and β associated with Collatz *et al*. (1991) quadratic smoothing have been set to 0.999 to minimize artificial reductions in A_g and more closely resemble the strict minimum limitation in the original Farquhar *et al*. (1980) model.

irradiance which they approximated to be one half of $V_{c,max}$ i.e.

$$A_p = 0.5 V_{c,max} \qquad \text{Eqn 5}$$

Combining Eqn 5 with Eqn 3 yields Eqn 6, which is the most commonly used formulation for the TPU rate in TBMs.

$$\text{TPU} = 0.167 V_{c,max} \qquad \text{Eqn 6}$$

Therefore, in many TBMs, representation of the capacity for TPU is based on a speculative relationship with $V_{c,max}$. Note that two models (IBIS and LM3) use a different ratio (Table 1) to describe the TPU rate that was derived from a synthesis of photosynthetic CO_2 response (A–C_i) curves (Wullschleger, 1993).

Under what conditions does triose phosphate utilization limit photosynthesis?

There is good evidence for the occurrence of TPU limitation of photosynthesis when leaves are exposed to high irradiance and high $[CO_2]$ (Sage *et al.*, 1989; von Caemmerer, 2000; Ellsworth *et al.*, 2015; Busch & Sage, 2017; see blue line Fig. 1a) but also at current $[CO_2]$ when plants are measured at a low temperature relative to their growth temperature (Yang *et al.*, 2016; Busch & Sage, 2017), or following an abrupt modification of source–sink balance (Fabre *et al.*, 2019). Recent work suggests that TPU rate is typically poised just above the prevailing rate of photosynthesis (Yang *et al.*, 2016; Fabre *et al.*, 2019), highlighting the importance of understanding the short-term dynamics associated with TPU. However, once A_g becomes limited by TPU, adjustments result in a shift to limitation by RuBP regeneration, or more commonly rubisco (Sharkey, 2019). For example, the work of Busch & Sage (2017) considered plants that were grown at current $[CO_2]$ and 25°C (F. A. Busch, pers. comm.). When measured at low temperature they observed TPU limited A. However, they did not investigate the effect of photosynthetic acclimation to lower growth temperature that increases investment in carboxylation capacity and the ratio of $J_{max} : V_{c,max}$ (Kumarathunge *et al.*, 2019b), reducing the

likelihood of TPU limitation. When plants are measured in their natural growth environment TPU limitation of photosynthesis is rarely observed (Sage & Sharkey, 1987). Recent work (Kumarathunge *et al.*, 2019a) comprehensively demonstrated that TPU limitation of photosynthesis is a rare phenomenon in natural ecosystems. Kumarathunge *et al.* (2019a) used a large global dataset of A–C_i curves representing 141 species that ranged from the Arctic tundra to tropical rainforests and demonstrated that TPU did not limit light saturated photosynthesis at current atmospheric $[CO_2]$ when plants were measured under natural growth conditions, including plants growing at low temperature. Furthermore, they showed that TPU limitation is unlikely to limit photosynthesis until $[CO_2]$ is greater than 800 μmol mol^{-1}.

TPU limitation has been incorrectly linked to phosphate deficiency (McClain & Sharkey, 2019). Limitation of photosynthesis by TPU is a highly dynamic process influenced by rapid turnover of Calvin–Benson cycle intermediates and is not influenced by whole plant phosphate acquisition. Potential marked variation in leaf level phosphate status resulting from different phosphate nutrition is also unlikely to influence TPU. Acting over a period of hours the vacuole buffers inorganic phosphate concentration in the cell, maintaining cytosolic and plastidic phosphate concentration within a relatively narrow operational range (McClain & Sharkey, 2019). Therefore, plants with a lower total foliar phosphate level are not more susceptible to TPU limitation. As TBMs begin to include representation of the P-cycle (Yang *et al.*, 2014; Goll *et al.*, 2017; Thum *et al*, 2019; Wang *et al.*, 2020) consideration of TPU limitation of photosynthesis should not be a motivating factor.

Sensitivity of terrestrial biosphere models to the limitation of photosynthesis by triose phosphate utilization rate

A recent investigation (Lombardozzi *et al.*, 2018) provided the first assessment of the impact of TPU limitation in a TBM (The Community Land Model, CLMv.4.5). They demonstrated that CO_2 assimilation and ecosystem carbon gain were limited by TPU
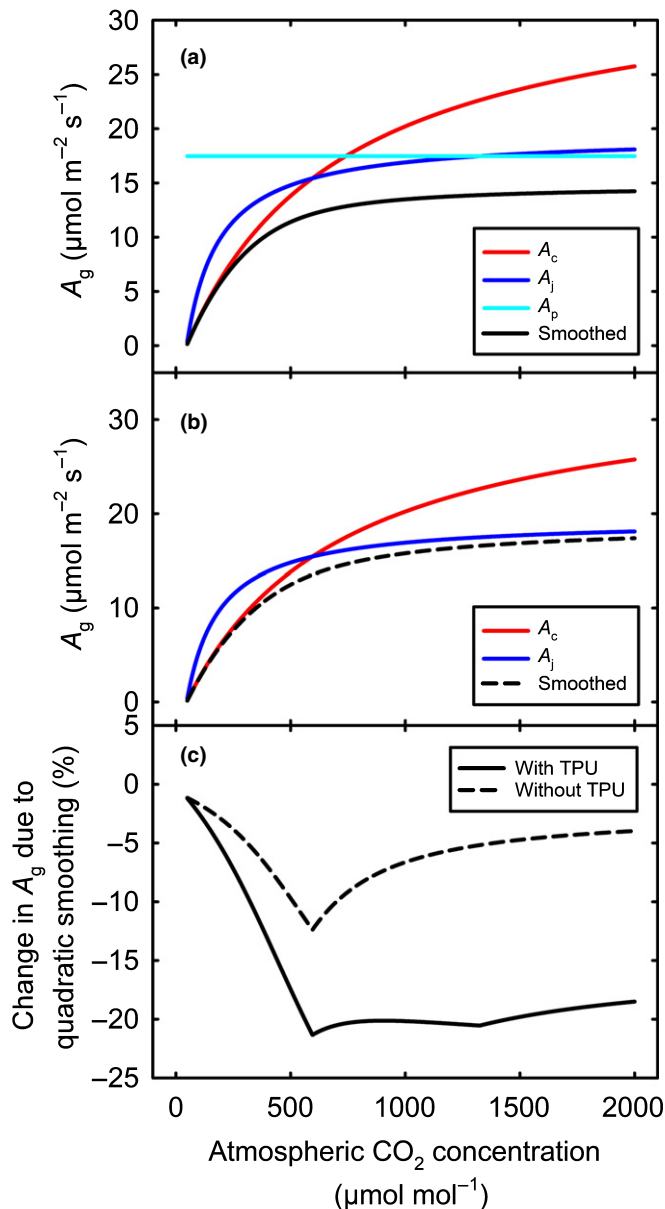
Fig. 1 The impact of applying Collatz *et al*. (1991) quadratic smoothing to the transitions between rubisco limited (A_c), ribulose-1,5-bisphosphate (RuBP) limited (A_j) and triose phosphate utilization (TPU) limited (A_p) rates of gross photosynthesis (A_g) with rising atmospheric CO_2 concentration [CO_2]. Panel (a) shows the three limiting processes of photosynthesis (A_c – red line, A_j – blue line, A_p – cyan line). Following Eqn 2, when modeled using the Farquhar *et al*. (1980) formulation, A_g would be limited by the minimum of either A_c, A_j or A_p. The quadratic smoothing of Collatz *et al*. (1991), shown in panels (a) and (b) as black lines, smooths the transition between A_c and A_j and then smooths the transition between the intermediate smoothed rate (A_{cj}) and A_p (see Eqns 7 and 8). Panel (b) shows the A_c and A_j rates of gross photosynthesis and the result of omitting A_p and the secondary smoothing function (Eqn 8) from the quadratic smoothing formulation (broken black line). Panel (c) shows the percent reduction in modeled A_g resulting from inclusion of the quadratic smoothing function in model formulations with TPU (solid black line) and without TPU and associated smoothing functions (broken black line). Photosynthesis was modeled following Farquhar *et al*. (1980) as implemented in CLMv.4.5 where the three potential limiting rates of *A* were modeled following Oleson *et al*. (2013), where $V_{c,max} = 50$ µmol m^{-2} s^{-1}, $T_{leaf} = 20°C$, Irradiance = 2000 µmol m^{-2} s^{-1}, the ratio between C_i and atmospheric [CO_2] was assumed to be 0.7. The A_g was modeled without using the option to account for thermal acclimation of $V_{c,max}$, J_{max} and their ratio to growth temperature (25°C). As implemented in CLMv.4.5 quadratic smoothing was applied to modeled rates of A_c, A_j, and A_p using values of $\theta = 0.98$ and $\beta = 0.95$. Note that process representation of photosynthesis and implementation of quadratic smoothing in CLMv.4.5 is essentially identical to the approach used in CLMv.5.0.

(Eqn 6), TPU limitation would be markedly greater when models are parameterized with a lower value of $V_{c,max}$. With the exception of FATES, all TBMs that include TPU assume that the temperature response of TPU is identical to $V_{c,max}$ (Table 1). However, there is evidence that the temperature response of TPU is independent of $V_{c,max}$, although the community lacks consensus on whether the TPU rate is more or less sensitive to temperature than $V_{c,max}$ (Harley *et al*., 1992; Yang *et al*., 2016; Kumarathunge *et al*., 2019a).

The basal rate of triose phosphate utilization

The extensive analysis conducted by Kumarathunge *et al*. (2019a) showed that the ratio of the basal rate of TPU to $V_{c,max}$ at 25°C was 0.09. This estimate is close to the low ratio (0.0835) Lombardozzi *et al*. (2018) used in their sensitivity analysis, almost half the rate originally assumed by Collatz *et al*. (1991) and 26% lower than the ratio used by LM3 and IBIS (Eqn 6, Table 1). Note that the ratio used by LM3 and IBIS was derived from just 23 A–C_i curves, from 16 species, grown mostly in controlled environments, and fitted with what are now arguably outdated kinetic constants (Wullschleger, 1993). Importantly, and in contrast to the key TBM assumption of a fixed ratio between TPU and $V_{c,max}$, Kumarathunge *et al*. (2019a) also showed that the ratio between TPU and $V_{c,max}$ decreases with rising growth temperature dropping from c. 0.2 at 5°C to c. 0.09 at 25°C.

Quadratic smoothing exacerbates triose phosphate utilization limitation in photosynthetic models

In the Farquhar *et al*. (1980) model A_g is limited by the strict minimum of A_c, A_j and A_p (Eqn 2). Collatz *et al*. (1991), introduced

in a future climate, and that by 2100, TPU limitation could reduce global terrestrial carbon gain by 4.5%. When evaluated with a lower TPU rate (0.0835 $V_{c,max}$) Lombardozzi *et al*. (2018) showed a markedly greater TPU limitation of gross primary productivity, particularly at high latitudes, clearly demonstrating the sensitivity of TBM outputs to decreasing the TPU rate (Lombardozzi *et al*., 2018).

Although CLMv.4.5 does include a formulation for photosynthetic acclimation to growth temperature (Lombardozzi *et al*., 2015), acclimation in CLMv.4.5 is not implemented below 11°C due to the limited temperature range of the underlying study (Kattge & Knorr, 2007), effectively limiting *in silico* acclimation at high latitudes (Oleson *et al*., 2013) and exacerbating potential TPU limitation. Furthermore, as noted in Lombardozzi *et al*. (2018), the prescribed $V_{c,max}$ at high latitudes was approximately half the rate recently reported for plants growing in the high Arctic (Rogers *et al*., 2017b) and since TPU is modeled as a fixed fraction of $V_{c,max}$

a formulation (Eqns 7 and 8) to quadratically smooth the transitions between A_c, A_j and A_p and to allow for some colimitation of A_g.

$$0 = \theta A_{cj}^2 - (A_c + A_j)A_{cj} + A_c A_j \qquad \text{Eqn 7}$$

$$0 = \beta A_g^2 - (A_{cj} + A_p)A_g + A_{cj}A_p \qquad \text{Eqn 8}$$

The term θ describes the degree of smoothing of the transition between A_c and A_j. When $\theta = 1$ the transition between A_c and A_j is abrupt, and as θ is reduced, progressively greater smoothing is simulated. The resulting term (A_{cj}) represents the smoothed intermediate rate. The transition between A_{cj} and A_p is described by Eqn 8 where β substitutes for θ. This quadratic smoothing is present only in TBMs that implement TPU limitation of photosynthesis, and of those, is present in all but one model (LM3, Table 1). Walker *et al.* (2021) demonstrated that including quadratic smoothing in model representation of photosynthesis introduces an artifactual fourth limitation that results in a modeled A_g that is always below A_c, A_j and A_p, sometimes markedly so (Fig. 1). Most TBMs that include a formulation for TPU also include quadratic smoothing (Eqns 7 and 8, Table 1), and therefore exaggerate the impact of TPU limitation on A (Fig 1c). In the original formulation θ and β were set to 0.98 and 0.95, respectively (Collatz *et al.*, 1991). However, some models use values for θ and β which are considerably lower (Table 1), further exacerbating the impact of TPU limitation (Friend, 1995; Walker *et al.*, 2021). In combination, inclusion of TPU limitation and quadratic smoothing results in a reduction in A at all [CO_2] values and most markedly so at high [CO_2] (Fig. 1c; Walker *et al.*, 2021).

Will triose phosphate utilization limit photosynthesis in a future elevated CO_2 concentration climate?

Projections from models, and consideration of observations, suggest that photosynthesis could become TPU limited at high [CO_2] (Busch & Sage, 2017; Lombardozzi *et al.*, 2018). However, these assessments do not account for reductions in $V_{c,max}$ that result from acclimation of photosynthesis to rising [CO_2] that have been well documented in Free-Air CO_2 Enrichment studies (Leakey *et al.*, 2009). As a result of photosynthetic acclimation, light saturated photosynthesis will continue to be limited predominantly by A_c in plants grown at elevated [CO_2] (Rogers & Humphries, 2000; Ainsworth & Rogers, 2007). However, with the exception of optimality approaches (e.g. Smith *et al.*, 2019; Stocker *et al.*, 2020), formulations for the representation of photosynthetic acclimation to elevated [CO_2] are absent from TBMs.

Conclusion

TPU limitation of A is an important phenomenon to understand but it has received little attention compared to the processes of carboxylation and electron transport. There is a need for further research to better understand the short-term dynamics of TPU, its

temperature response, the role TPU might play in signaling source–sink balance (McClain & Sharkey, 2019; Sharkey, 2019), and circumstances where glycollate might not be maximally conserved by the photorespiratory cycle (Ellsworth *et al.*, 2015; Busch *et al.*, 2018). It also remains important for physiologists to continue to consider TPU when analyzing A–C_i curves to avoid potential underestimation of J_{max} (Busch & Sage, 2017; Sharkey, 2019). However, when plants are grown in their natural environment the best current evidence shows that TPU does not limit A below a [CO_2] of 800 µmol mol^{-1} (Kumarathunge *et al.*, 2019a) and photosynthetic acclimation of plants to rising [CO_2] suggests that TPU limitation of A is also unlikely at higher [CO_2] (Leakey *et al.*, 2009) questioning the value of including representation of TPU in TBMs.

Current TBM formulations of TPU are founded on uncertain assumptions, most models do not account for the independent temperature sensitivity of TPU, or capture the temperature dependence of the ratio between the basal rate of TPU and $V_{c,max}$. The inclusion of TPU in combination with quadratic smoothing, results in an artificial reduction in CO_2 assimilation (Walker *et al.*, 2021) that increases the limitation of A by TPU (Fig. 1) and changes the fundamental mechanistic description of how plants respond to rising [CO_2].

Collectively these issues suggest that inclusion of TPU limitation of A in TBMs has introduced additional parameter uncertainty which has, or could, result in compensatory tuning of $V_{c,max}$. Given that $V_{c,max}$ is linked to several other important processes in many TBMs through simple multipliers, (e.g. respiration), more mechanistic approaches (e.g. nitrogen allocation), and has a strong influence on diverse model outputs (Rogers, 2014; Ricciuto *et al.*, 2018; Walker *et al.*, 2021), the resulting tuning will have a pervasive influence on the veracity of model projections. We advocate for the removal of current formulations of TPU from TBMs.

Author contributions

AR wrote the manuscript with valuable contributions from DPK, DLL, BEM, SPS and APW.

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