



COMMENTARY

Converging towards a common representation of large-scale photosynthesis

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At its simplest, photosynthesis can be regarded as how trees and plants draw down carbon dioxide (CO₂) from the atmosphere and use this to grow. The mechanisms behind this process have fascinated research scientists for many centuries. Photosynthesis represents a major exchange of carbon between the atmosphere and the land surface, and with a magnitude of ~120 Pg C/year, this flux is key to the global carbon cycle. Although most photosynthesis is offset by respiration (i.e. the release by vegetation of CO₂ back to the atmosphere), the difference between these fluxes is sufficiently large that the land surface currently draws down nearly one-third of CO₂ emissions from anthropogenic activity (Le Quéré et al., 2015). Relatively small changes to photosynthesis under climate change could have a disproportionately large impact on whether the land surface can continue to accumulate a substantial fraction of CO₂ emissions. Hence, given the potential implications for climate policy, the land surface part of Earth system models (ESMs) is under particular scrutiny. ESMs are the main tool used by climate researchers to understand climate-carbon cycle interactions and their response to fossil fuel burning. However, projections of future photosynthetic carbon uptake by ESMs have high uncertainty (Friedlingstein et al., 2014) and reducing this uncertainty is paramount to improve the forecasts of global climate change upon which policy and impact assessments are based. A good starting point is a process at the very heart of the simulated land surface in ESMs—photosynthesis.

The 'Farquhar' (Farquhar et al., 1980) and 'Collatz' (Collatz et al., 1991, 1992) models are both well-recognized mechanistic representations of photosynthesis, and ESMs commonly use either one. Yet are these models fully understood? In this issue of *Global Change Biology*, Walker et al. (2020) provide a highly detailed assessment of

these two photosynthesis schemes and use novel multi-hypothesis models to quantify both parameter and process-level uncertainty. The commonality between the two schemes is highlighted through unifying parameter definitions and units. Both schemes contain a CO₂-limited (i.e. carboxylation capacity) component and a light-limited (i.e. electron transport) component, both of which are sensitive to temperature. A third limitation (Sharkey, 1985) is that of triose phosphate utilization, which is related to the capacity of the leaf to use photosynthates. Developed subsequent to the Farquhar model, this third limiting rate is only included in the Collatz model. For most temperature, light and CO₂ levels, photosynthesis is limited by one of these three drivers. Key, however, is the transition from one limiting rate to the other. For example, the transition between light-limited and CO₂-limited assimilation under conditions of increasing light can be modelled with a smoothing function requiring empirical co-limitation parameters, as is used in the Collatz model. This method contrasts with a simple switch between the two photosynthetic limitations, as is employed in the Farquhar model. Following the notation of Walker et al. (2020), we refer to this transitioning as the 'fourth limitation' on photosynthesis.

Previous studies noted that parametric differences lead to high variability between models of photosynthesis, and particularly those associated with carboxylation, such as $V_{c,max}$ (the maximum rate of Rubisco carboxylation). Rogers et al. (2017), for example, highlight the problem that the values of these parameters, as derived from measurements, are highly dependent on the form of the equation in which they sit. Consequently, it is easy for such model-dependent parameters to be misused or misinterpreted. As an example, Walker et al. (2020) discuss how $V_{c,max}$ estimates are not independent of the limiting rate selection assumption. This means that $V_{c,max}$, a parameter of identical meaning in the two photosynthesis models, can have

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a different value in each model, even though it has been derived from the same set of measurements. Unfortunately, this means that in order to make accurate estimates of photosynthesis, model parameters may need to be adjusted to compensate for the alternative co-limitation descriptions. Furthermore, in quantifying parameter versus process-level uncertainty, Walker et al. (2020) demonstrate that the variation in modelled photosynthesis associated with parameter variability is exceeded by the empirical fourth limitation process of limiting rate selection. Global simulations using three terrestrial biosphere models show that quadratic smoothing between the limiting rates of photosynthesis lowers global photosynthesis by a substantial 4%–10% compared to the simpler Farquhar approach.

It is apparent that we need a data-driven approach to derive a more mechanistic understanding of what drives any transition between different limiting rates of photosynthesis, and to constrain any related parameters. Walker et al. (2020) ask the fundamental first question: What is any smoothed transition intended to represent? In Figure 1a, we show a simple switch between limiting factors, as is used in the Farquhar model. In this case, there is no smoothing, and photosynthesis is modelled at its upper bound (i.e. the lowest upper bound of the limiting factors). Then, in Figure 1b, we present a schematic that captures three transition possibilities using the smoothing approach applied in the Collatz model. The first (blue curve) is for individual leaves: in this case, the change between photosynthetic limitations might occur over a short range of changing meteorological conditions, demonstrated here with an increase in light. The second broader curve (orange) might capture the average behaviour within a full canopy. The transition between the two limitations to photosynthesis occurs over a larger range of irradiances, as it aggregates the within-canopy switches for different leaves, all of which experience slightly different micro-meteorological conditions. The third, even broader curve (red) represents where different biomes might be present within the same modelled plant function type, all of which have a range of photosynthetic responses leading to alternative transition points between the limiting factors. The ability to aggregate into plant functional types is important for ESMs, which can only represent terrestrial ecosystems by a limited

number of discrete vegetation types. As an aside, for numerical reasons, there is a preference to avoid abrupt switches in ESMs, and instead to employ smooth transitions, even if over small ranges. Walker et al. (2020) argue that the simpler minimum rate assumption of the Farquhar model is a more defensible assumption. We suggest, though, that there can be process meaning to co-limitation functions, especially when used to aggregate across canopies and biomes (Figure 1b). However, as presented in Figure 1, the larger the range of co-limitation, the more photosynthesis is suppressed, likely requiring compensation elsewhere in any model.

Arguably the use of just one model structure is dangerous for any component of ESMs, at least at their early stages of development. Simulation differences in parameterization or format encourage new analyses and measurement campaigns that advance understanding. In climate change research, the popular use of the technique of Emergent Constraints to reduce inter-ESM differences actually relies on a spread of projections by climate model ensembles (Hall et al., 2019). Specifically, Emergent Constraints use regression to relate the spread in estimation of a quantity of relevance to future climatic states for raised atmospheric greenhouse gas concentrations to a quantity that is measured for the contemporary period. Emergent Constraints use the present-day measurement to constrain the future estimate, via the regression. However, ecosystem models are quite mature, and now their convergence is needed to support ESM simulation frameworks that are accurate. Robust ESM predictions provide assessments of the evolving global climate-carbon cycle system as perturbed by fossil fuel burning, and their projections of regional change enable adaptation planning. Reliable descriptions of photosynthetic CO₂ drawdown play a vital role in both requirements, especially as under climate change, warming over most land points is expected to be larger than global average temperature changes (Huntingford & Mercado, 2016). If the land ESM subcomponents are too simple, then they will not characterize expected changes to the terrestrial part of the global carbon cycle under climate change. If there is too much complexity, an overly large number of parameters cannot be evaluated based on the available measurements. As land surface modellers strive to

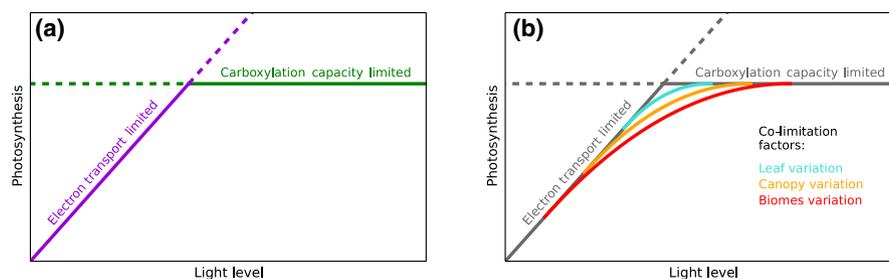


FIGURE 1 Schematic of the response of photosynthesis to changes in light availability. In (a), electron transport (i.e. light-limited) and carboxylation-limited photosynthesis are shown in the purple and green straight lines respectively. The Farquhar model uses an abrupt transition between the two limitations, corresponding to the parts of the lines presented in solid format (elsewhere as dashed). The Collatz model includes a smoothing function that allows for co-limitation by electron transport and carboxylation at intermediate light intensities. In (b), the blue, yellow and red curves represent such possible transitions between the two limiting cases for increasing light levels. The curves are illustrative of how photosynthesis may behave at the individual leaf level, for a complete canopy, or aggregating across multiple biomes that might exist together at any particular location. For completeness, the lines of (a) are repeated in (b), in grey

satisfy this balance, the paper of Walker et al. (2020) makes a significant contribution. Walker et al. (2020) illustrate common features between the two most frequently used models of photosynthesis. They demonstrate the importance of simultaneously evaluating parameter and process uncertainty, providing a quantified assessment of both. Crucially they add insight to the two common models of photosynthesis and the impact of their assumptions on simulated photosynthesis from the leaf to the global scale. The paper provides a fascinating illustration of the importance of the understudied co-limitation parameters that some use to characterize the transition between factors that limit photosynthesis.

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AUTHOR CONTRIBUTION

C.H. designed the format of the commentary and created the figure. R.J.O. provided support on the current knowledge of photosynthesis. Both authors contributed to writing the paper.

DATA AVAILABILITY STATEMENT

A script of the python code leading to Figure 1 is available upon request from C.H. (chg@ceh.ac.uk).

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