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Viewpoint

Extending the 'one-point method' for estimations of leaf photosynthetic capacity to a broader temperature range

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The 'one-point method' (OPM) is a quick approach to estimate the maximum apparent carboxylation rate of Rubisco (V'_{cmax}) based on a single measurement of leaf carbon assimilation rate taken under saturating light and ambient CO_2, lately equal to 400 ppm (De Kauwe *et al.*, 2016). However, the OPM overestimates V'_{cmax} at high temperatures (Burnett *et al.*, 2019). This overestimation results from the reliance of the method on a linear relationship between V'_{cmax} and leaf respiration rates under light (R_{day}), as a fixed R_{day}:V_{cmax} ratio equal to 1.5%, while these parameters have different temperature dependencies. Here, we highlight the importance of the adoption of a temperature-dependent scaling factor for the R_{day}:V_{cmax} ratio as a way to prevent the overestimation of the photosynthetic capacity at temperatures >35 °C.

The maximum carboxylation rate of Rubisco (V_{cmax}) is a key photosynthetic enzyme characteristic that reflects plant individual fitness. It is also a prescribed variable of global vegetation models (GVMs), which calculate primary productivity of terrestrial vegetation. This parameter is usually estimated from CO_2 response curves (A–C_{i} curves, where C_{i} is intercellular [CO_2]) (e.g. Farquhar *et al.*, 1980—the FvCB model). Recently, the OPM was proposed as a fast alternative to standard full biochemical curve-fitting methods (De Kauwe *et al.*, 2016). Against the gold-standard A–C_{i} curves, the OPM has proven to be very useful as it allows for the characterization of a large number of species and individual leaves in a short period of time (5–10 min per individual), enabling a better parameterization of highly diverse tropical vegetation communities within GVMs. Another alternative available is the rapid A–C_{i} technique (RACiR) (Stinziano *et al.*, 2017), which upon any change in conditions, such as leaf temperature, requires some data processing after the measurements are taken. Apart from being fast, another advantage of the OPM is the minimization of negative effects of performing multiple full A–C_{i} curves on the same leaf in order to obtain the temperature dependency of photosynthetic parameters. Therefore, providing measurements are taken with the proper care and allowing enough time for stabilization of gas exchange fluxes, the OPM has the potential to significantly improve our ability to describe the carbon uptake strategies of highly diverse plant communities.

According to De Kauwe *et al.* (2016), V'_{cmax} can be calculated as:

$$V'_{\mathrm{cmax}} = \left(A_{\mathrm{sat}} + R_{\mathrm{day}}\right) \times \frac{(C_{\mathrm{i}} + K_{\mathrm{m}})}{(C_{\mathrm{i}} - \Gamma^{*})} \qquad (1)$$

Where C_{i} is the intercellular CO_2 concentration, $\Gamma^{\star}$ is the CO_2 compensation point in the absence of mitochondrial respiration, K_{m} is the Michaelis–Menten constant of Rubisco, and R_{day} is the leaf mitochondrial respiration in the light. When R_{day} is not determined experimentally, the authors suggest the use of an estimated R_{day} ratio equal to 1.5% of V'_{cmax} (0.015 in Equation 2).

$$V'_{\mathrm{cmax}} = \frac{A_{\mathrm{sat}}}{\left(\frac{C_i - \Gamma^*}{C_i + K_m} - 0.015\right)} \tag{2}$$

However, the OPM provides an overestimation of V'_{cmax}, especially at high temperatures above 30 °C (De Kauwe *et al.* 2016; Slot and Winter, 2017; Burnett *et al.* 2019). As the temperature dependencies of R_{day} and V_{cmax} differ considerably from each other (Wang *et al.* 2020), assuming a linear relationship between these parameters as a constant ratio results in the overestimation of V'_{cmax}, as R_{day} peaks at a much higher leaf temperature. A better accuracy of the OPM is needed to improve its performance at higher leaf temperatures. In this sense, we propose here the adoption of a temperature-dependent scaling factor for the $R_{\mathrm{day}}:V'_{\mathrm{cmax}}$ ratio in order to improve predictions of V'_{cmax}.

The temperature dependencies of both R_{day} and V_{cmax} may be defined by standard Arrhenius functions, following Kumarathunge *et al.* (2019) as:

$$\frac{R_{\mathrm{day}}{}^{\mathrm{T}}}{R_{\mathrm{day}}{}^{\mathrm{R}}} = e\ \frac{Ea_{\mathrm{R}} \times (T_{\mathrm{k}} - 298.15)}{298.15 \times \mathrm{R} \times T_{\mathrm{k}}} \tag{3}$$

and

$$\frac{V_{\mathrm{cmax}}{}^{T}}{V_{\mathrm{cmax}}{}^{\mathrm{R}}} = e\ \frac{Ea_{\mathrm{V}} \times (T_{\mathrm{k}} - 298.15)}{298.15 \times \mathrm{R} \times T_{\mathrm{k}}} \times \left[\frac{1 + e^{\left(\frac{298.15 \times \Delta S_{\mathrm{V}} - \mathrm{Hd}_{\mathrm{V}}}{298.15 \times R}\right)}}{1 + e^{\left(\frac{T_{\mathrm{k}} \times \Delta S_V - Hd_V}{T_k \times R}\right)}}\right] \tag{4}$$

where $R_{\mathrm{day}}{}^{\mathrm{T}}$ and $V_{\mathrm{cmax}}{}^{\mathrm{T}}$ are respiration and carboxylation rates at a given leaf temperature (T_{k} in Kelvin), $R_{\mathrm{day}}{}^{\mathrm{R}}$ and $V_{\mathrm{cmax}}{}^{\mathrm{R}}$ are the rates at a reference leaf temperature of 25 °C, R is the universal gas constant (8.314 J mol^{-1} K^{-1}), $\mathrm{Ea_R}$ (kJ mol^{-1}) is the activation energy for respiration, and $\mathrm{Ea_V}$ (kJ mol^{-1}), $\Delta \mathrm{S_V}$ (J mol^{-1} K^{-1}), and $\mathrm{Hd_V}$ (kJ mol^{-1}) are respectively the activation energy, entropy, and deactivation energy of V_{cmax}. The adopted values for model constants are available in Supplementary Table S1.

Our new suggested model modifies Equation 2 for:

$$V'_{\mathrm{cmax-\rho}} = \frac{A_{\mathrm{sat}}}{\left(\frac{C_i - \Gamma^*}{C_i + K_m} - 0.015 \times \rho\right)} \tag{5}$$

where ρ is the temperature-dependent scaling on the R_{day} ratio (1.5% of V'_{cmax}), which is calculated by dividing Equation 3 by Equation 4.

The robustness of this approach was tested using 278 unpublished A–C_i curves (12 CO_2 concentration steps) under saturating light (2000 µmol m^{-2} s^{-1}), collected from 31 tropical species naturally occurring in savannas and Amazon rainforest in Brazil (Supplementary Table S2) using two portable gas exchange systems (LI-6800, Li-Cor Inc., Lincoln, NE, USA). Leaf temperatures were kept constant during each curve, but ranged from 25 °C to 45 °C among curves, and the leaf chamber relative humidity was not controlled. Over the whole dataset, the leaf-to-air vapor pressure deficit ranged from 1.08 kPa to 7.71 kPa (3.84 ± 1.65), while stomatal conductance ranged from 0.05 mol m^{-2} s^{-1} to 0.34 mol m^{-2} s^{-1} (0.134 ± 0.06). To estimate V'_{cmax} and $V'_{\mathrm{cmax-\rho}}$ values, we selected a single point measurement from each A–C_i curve, corresponding to ambient CO_2 concentrations (C_a) between 390 µmol mol^{-1} and 410 µmol mol^{-1}. The Kc, Ko, and $\Gamma^\star$ values used in Equations 2 and 3 were calculated according to the temperature dependencies listed in Bernacchi *et al.* (2002) and De Kauwe *et al.* (2016). Linear regressions were used to compare both V'_{cmax} and $V'_{\mathrm{cmax-\rho}}$ with V_{cmax} from full A–C_i curves (Duursma, 2015). The slopes between the two linear regressions were compared using ANOVA. Moreover, the distribution of the residuals of the regression models as a function of leaf temperature were used for method accuracy comparisons. Additionally, a multivariate sensitivity analysis was performed to investigate the role of temperature over the range values of the Arrhenius constants regarding the model outputs. All analyses we performed on R environment (R Core Team, 2020).

The temperature-dependent scaling factor provided a substantially better correspondence between V_{cmax} values from FvCB fits against the $V'_{\mathrm{cmax-\rho}}$ values, when compared with V'_{cmax} values from the original OPM (Fig. 1) (slope=1.10; r^2=0.93). The ANOVA test revealed that the outputs from the two models were statistically different (P<0.005). The evaluation of the distribution of the residuals from the two regression models highlights how the overestimation of V'_{cmax} by the original version of the OPM increases with leaf temperature (Fig. 2A), where overestimations of ~25% were observed above 35 °C. In contrast, no trend was observed for the residuals from the new model in relation to leaf temperature (Fig. 2B). The adoption of the Arrhenius temperature dependency

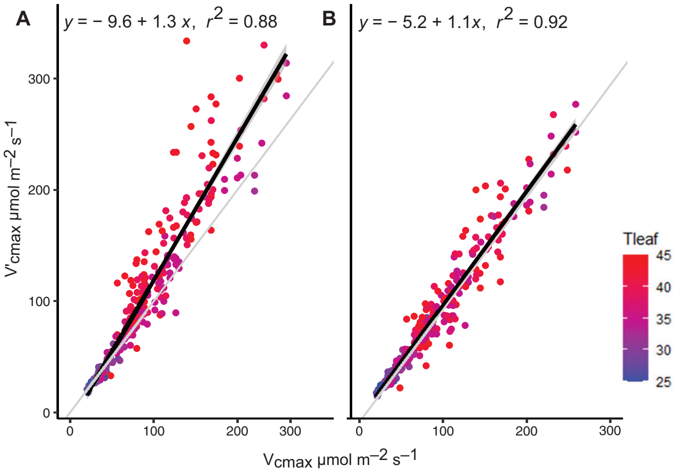

Fig. 1. Comparison of linear regression models between V_{cmax} estimated from full A–C_i curves against apparent photosynthetic capacity estimated by the 'one-point method' (V'_{cmax}; Equation 2) (A), and the modified version including the temperature dependency ($V'_{\mathrm{cmax-\rho}}$; Equation 5) (B). The light gray line is the 1:1 relationship.

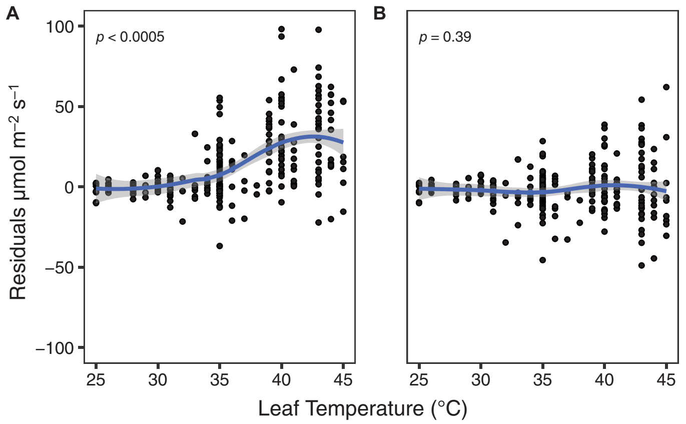

Fig. 2. Residuals of maximum carboxylation rate, V_{cmax}, estimated from A–C_{i} curves estimated from apparent maximum carboxylation capacity, V'_{cmax} (Equation 2) using the estimated R_{day}:V_{cmax} ratio (A), and using the temperature-dependent scaling factor (B) as a function of leaf temperature.

for R_{day} (Equation 3) was preferred over a Q_{10} temperature coefficient (Atkin *et al.*, 2015), the latter resulting in an overestimation of $V'_{\mathrm{cmax-\rho}}$ values of ~25% (slope=1.29, r^2=0.85) (Supplementary Fig. S1), with a non-significant difference between its slope against the model using the the original OPM approach (P=0.69). The sensitivity analysis revealed that the temperature-dependent scaling factor is strongly influenced by both Ea_{R} and Ea_{V} above 25°C (Supplementary Fig. S2). As temperature increases, their relative importance decreases, while ΔS_{V} and the interaction among parameters become the main factors determining R_{day}:V_{cmax}.

The adoption of a temperature-dependent scaling is indeed an important adjustment of the OPM, producing accurate estimations of V'_{cmax} at high temperatures where there is proportionality of V'_{cmax} and R_{day} responses to temperature (Wang *et al.*, 2020), as demonstrated empirically in Supplementary Fig. S3. Therefore, the temperature-dependent scaling factor proposed here should allow for better determinations of the temperature response of V'_{cmax}. However, providing reliable data for derivations of the Arrhenius constants is needed, as these constants vary among functional types of plants and species (Kumarathunge *et al.*, 2019). Apart from the difficult task of adopting appropriate values for the Arrhenius constants for R_{day} and V_{cmax}, other aspects might be important as well. The application of biochemical models of photosynthesis often disregards the influence of g_{m} over estimations of V'_{cmax}, assuming it to be large enough to cause C_{i} to be equal to chloroplastic CO_2 concentration (C_{c}). However, g_{m} varies with leaf temperature as a result of both enzymatic dynamics and CO_2 diffusion, resulting in an overestimation of V_{cmax} when assuming an infinite g_{m} (von Caemmerer and Evans, 2015), therefore directly impacting the R_{day}:V_{cmax} ratio. Similarly, the temperature dependency of the $\Gamma^\star$ is assumed to be invariant among plant species, and a single function is often used to scale this parameter to a specific leaf temperature (Bernacchi *et al.*, 2002). However, depending on the $\Gamma^\star$ assumption, the relationship between temperature and the R_{day}:V_{cmax} ratio may change (De Kauwe *et al.*, 2016); this is because the stoichiometry of CO_2 release by Rubisco oxygenation depends on how $\Gamma^\star$ responds to temperature (Bernacchi *et al.*, 2002). Therefore, a better understanding of possible variations of the temperature dependencies of both g_{m} and $\Gamma^\star$ is still needed in order to improve the understanding of temperature influence on the estimations of V'_{cmax}, irrespective of the estimation method used.

In conclusion, the inclusion of a temperature-dependent scaling factor in the 'one-point method' extends its applicability to leaf temperatures >35 °C. Therefore, this approach should contribute to the characterization of vegetation communities and provide data for the estimation of Arrhenius parameters without stressing leaves by performing repeated CO_2 response curves. Efforts should be directed to the understanding of the variation of temperature dependencies of the photosynthetic parameters, specifically the entropy and the activation and deactivation energies of V_{cmax}, R_{day}, and also the maximum electron transport rate (J_{max}).

Supplementary data

The following supplementary data are available at *JXB* online.

Table S1. Dataset of primary parameters and their temperature dependency used to estimate R_{day} and V'_{cmax} temperature response in Equations 3 and 4.

Table S2. Species studied with the biome, their family, number of individuals (N individuals) and curves (N curves), and temperature range curves.

Fig. S1. Comparison of linear regression models between V_{cmax} estimated from full A–C_{i} curves against apparent photosynthetic capacity estimated by the 'one-point method'.

Fig. S2. Normalized partitioning of the variation of the influence of individual coefficients over model output at a broad leaf temperature range (sensitivity analysis).

Fig. S3. Estimated R_{day} (R_{day}:V_{cmax} ratio) as a function of leaf temperature using the De Kauwe *et al.* (2016) model.

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Author contributions

TCSO, TFD, and MNG: design; TCSO and MNG: data collection. TCSO: data analysis; TCSO, TFD, EV, and MNG: interpreting the analysis and results; TCSO: writing—first draft; TFD, EV, and MNG: contributing to writing.

Conflict of interest

The authors have no conflicts to declare.

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Data availability

The data supporting the findings of this study are available from the corresponding author, Tony de Oliveira, upon request.

Keywords: Global vegetation models, global warming, photosynthesis, temperature response, V_{cmax}.

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