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A test of the “one-point method” for estimating maximum carboxylation capacity from field-measured, light-saturated photosynthesis

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Summary
Simulations of photosynthesis by terrestrial biosphere models typically need a specification of the maximum carboxylation rate ($V_{cmax}$). Estimating this parameter using $A$-$C_i$ curves (net photosynthesis, $A$, vs. intercellular CO$_2$ concentration, $C_i$) is laborious, which limits availability of $V_{cmax}$ data. However, many multi-species field data sets include $A_{sat}$ (net photosynthetic rate at saturating irradiance at ambient atmospheric CO$_2$ concentration) measurements, from which $V_{cmax}$ can be extracted using a “one-point method”.

We used a global data set of $A$-$C_i$ curves (564 species from 46 field sites, covering a range of plant functional types) to test the validity of an alternative approach to estimate $V_{cmax}$ from $A_{sat}$ via this “one-point method”.

If leaf respiration during the day ($R_{day}$) is known exactly, $V_{cmax}$ can be estimated with an $r^2 = 0.98$ and root mean squared error (RMSE) of 8.19 µmol m$^{-2}$ s$^{-1}$. However, $R_{day}$ typically must be estimated. Estimating $R_{day}$ as 1.5% of $V_{cmax}$, we found that $V_{cmax}$ could be estimated with an $r^2 = 0.95$ and RMSE of 17.1 µmol m$^{-2}$ s$^{-1}$.

The one-point method provides a robust means to expand current databases of field-measured $V_{cmax}$, giving new potential to improve vegetation models and quantify the environmental drivers of $V_{cmax}$ variation.

**Keywords:** $V_{cmax}$, photosynthesis, one-point method, $A_{sat}$, $A$-$C_i$ curve, $R_{day}$. 
Introduction

Photosynthesis is a primary driver of the terrestrial carbon cycle (Prentice et al., 2001; Beer et al., 2010) and accurate modelling of this process is critical for projecting the response of the terrestrial biosphere to environmental change (Friedlingstein et al., 2014). Terrestrial biosphere models (TBMs; including ecosystem, land surface and vegetation models) almost universally simulate photosynthesis following the leaf biochemical model of Farquhar et al., (1980), or a variant of this approach (e.g. Collatz et al., 1991). This approach relies on the accurate estimation of two key model parameters: $V_{\text{cmax}}$, the maximum carboxylation rate, and $J_{\text{max}}$, the maximum rate of electron transport (von Caemmerer, 2000). A third term, triose-phosphate utilisation, is often ignored as it is thought to seldom limit photosynthesis under field conditions (Sharkey et al., 1985; but see Ellsworth et al., 2015). In many cases both $V_{\text{cmax}}$ and $J_{\text{max}}$ scale linearly with leaf nitrogen (N) (Field & Mooney, 1986; Hirose & Werger 1987), although the scaling with N can differ among biomes (e.g. Meir et al., 2002; Domingues et al., 2015). $V_{\text{cmax}}$ and $J_{\text{max}}$ also tend to be closely correlated, a fact that some models exploit by assuming $J_{\text{max}}$ can be determined through a fixed relationship with $V_{\text{cmax}}$ (see Niinemets & Tenhunen (1997) for a critique), or, at least, assuming that variation in the two properties is tightly coordinated (Chen 1993; Maire et al., 2012). Nevertheless, $V_{\text{cmax}}$ and $J_{\text{max}}$ both vary considerably among species (up to a 30-fold variation; Walker et al. 2014; Ali et al. 2015), among and within plant functional types (PFTs) (Wullschleger 1993; Kattge et al 2009; Maire et al., 2012; Ali et al 2015), and within individual species. Given this large variability it is perhaps unsurprising that TBMs have demonstrated considerable sensitivity in simulated carbon fluxes due to uncertainty in these parameters (Bonan et al., 2011; Piao et al., 2013). As a consequence these parameters are often used as a method of model “tuning” to obtain more accurate fluxes (which we consider as obtaining the ‘right answer for the wrong reasons’), rather than as a means of characterising a PFT-specific trait (Rogers, 2014).

Traditionally, the photosynthesis model parameters $V_{\text{cmax}}$ and $J_{\text{max}}$ have been estimated by fitting the Farquhar et al., (1980) photosynthesis model directly to photosynthetic CO$_2$ response curves, where photosynthesis is measured at several CO$_2$ concentrations and under saturating irradiance (net photosynthesis, $A$ (µmol m$^{-2}$ s$^{-1}$), vs. intercellular CO$_2$ concentration, $C_i$ (µmol mol$^{-1}$); so-called $A$-C$_i$ curves). However, accurately determining these parameters from such measurements is not a straightforward process (see Long & Bernacchi et al., 2003). Firstly, $A$-
$C_i$ data are time consuming to collect: each CO$_2$ response curve may take an hour to set up and measure, particularly in stressed plants where stomatal closure may even prohibit such measurements. Secondly, a number of competing methods exist for fitting the data (Sharkey et al., 2007; Dubois et al., 2007; Patrick et al., 2009; Gu et al., 2010; Feng & Dietze, 2013) and, depending on the chosen method, parameter estimates may vary even for the same datasets (Miao et al., 2009; Niinemets et al., 2009). Many individual experimental studies tend to focus just on a small number of species and, more often than not, they concern plants grown and measured in controlled environments (laboratory or glasshouse). As a result, compared to many plant traits, there is a general paucity of field-measured $V_{\text{cmax}}$ and $J_{\text{max}}$ data, which likely undermines the accuracy of model simulations of terrestrial photosynthesis. The largest data compilations to date included $V_{\text{cmax}}$ data based on $A$--$C_i$ curve analysis for 127 species (Ali et al., 2015), 114 species (Walker et al., 2014), 130 species (Sun et al., 2014) and 109 species (Wullschleger 1993), but it is unclear what proportion of these data were for field-grown plants, nor what total species number these represent, with many individual datasets appearing in more than one compilation. Currently in the TRY database (www.try-db.org; accessed 7 July 2015) there are geo-referenced $V_{\text{cmax}}$ data for 353 species (of which c. 250 were obtained from $A$--$C_i$ curves).

In contrast to the relatively limited number of field-measured $A$--$C_i$ curves, there is a plethora of net photosynthesis measurements obtained in the field at ambient [CO$_2$] and at saturating irradiance ($A_{\text{sat}}$) – e.g. 1500 species were included in the compilation by Maire et al., (2015; dataset assembled in 2008), the TRY database currently contains geo-referenced photosynthesis data for 2192 species (8522 individual observations), and in recent years there have been a number of large field campaigns, from which the data are yet to make it into these types of databases. Together, these $A_{\text{sat}}$ data represent species from large parts of the globe, and all PFTs (Kattge et al 2011), but are currently left out of analyses of $V_{\text{cmax}}$. By virtue of their global coverage, analyses of $A_{\text{sat}}$ have included quantification of latitudinal, climate- and soil-related trends, including modulation of relationships between $A_{\text{sat}}$ and other leaf traits (Reich et al., 1997, 2009; Wright et al 2005; Ordonez & Ollf 2013; Maire et al., 2015). When corresponding values of $C_i$ and leaf temperature are reported with each $A_{\text{sat}}$ measurement, and if one assumes: (1) that photosynthesis at saturating irradiance is Rubisco-limited (rather than being limited by RuBP regeneration); and (2) that the value of leaf mitochondrial respiration in the light (i.e. ‘day’ respiration, $R_{\text{day}}$) can be estimated, then the $V_{\text{cmax}}$ value required to
support the observed rate of $A_{sat}$ can be estimated. This estimated quantity is hereafter referred to as $\tilde{V}_{cmax}$, and the method as the “one-point method” (Wilson et al. 2000). However, whether $A_{sat}$-dependent estimates of $\tilde{V}_{cmax}$ are an accurate reflection of the $V_{cmax}$ values obtained from full $A$-$C_i$ curves remains uncertain. In the absence of measurements of $C_i$, values may be estimated from data reported for stomatal conductance and ambient [CO$_2$]. Values for $R_{day}$ may be estimated from either a relationship with dark respiration, $R_{darks}$, or by assuming a relationship with $V_{cmax}$, see below).

Although several studies have indeed done this – used measurements of $A_{sat}$ and associated parameters to estimate $\tilde{V}_{cmax}$ (Niinemets et al., 1999; Wilson et al., 2000; Kosugi et al., 2003; Grassi et al., 2005; Kattge et al., 2009; Uddling et al., 2009; Niinemets et al., 2015) – a thorough examination of the issues associated with this approach has not been made. That said, preliminary tests of the approach were encouraging. For five tree and five understory species Wilson et al., (2000) estimated $V_{cmax}$ from $A$-$C_i$ curves as well as from independent measurements of the assimilation rate, $C_i$ at the ambient external CO$_2$ concentration (360 μmol mol$^{-1}$) and a constant value of $R_{day}$ (~0.5 μmol m$^{-2}$ s$^{-1}$). The two sets of estimates were tightly correlated ($r^2 = 0.97$) with an intercept not statistically different from zero, but with a small bias in the slope (1.08). Grassi et al., (2005) demonstrated that this method could be used to accurately estimate $V_{cmax}$ for three deciduous forest species ($r^2 = 0.97$; slope = 0.96). Given the global coverage of $A_{sat}$ data, there could be great potential for deriving $\tilde{V}_{cmax}$ from datasets such as that of Maire et al. (2015), or the TRY database (Kattge et al., 2011), providing a means to dramatically expand the species- and geographic coverage of $V_{cmax}$ estimates from field-grown plants in global databases. Nevertheless, employing this approach may result in errors and/or bias, which leads to the question and the focus of this study: “How robust is the so-called one-point method for estimating $V_{cmax}$?” Errors in estimation are principally likely to occur if (1) the biochemical limitation to $A_{sat}$ is not Rubisco activity or (2) if the estimate of $R_{day}$ is biased (Figure 1).

We tested how well the one-point method works, by estimating $V_{cmax}$ from complete $A$-$C_i$ response curves and comparing these values with $V_{cmax}$ estimated using the one-point method applied to the $A_{sat}$ data extracted from these curves. To this end, we compiled 1,394 $A$-$C_i$
response curves, from 564 species. These data represent by far the largest compilation of field-measured photosynthetic CO₂-response data to date. These data are taken from all vegetated continents – from the Arctic to the tropics – and so represent a broad spread of site climates (Fig S1). Using this dataset, we sought to test the following hypotheses:

i. That under ambient CO₂ and saturating irradiance, \( A_{sat} \) is normally Rubisco-limited, or co-limited by Rubisco and electron transport (a requirement for the one-point method to be valid). There are environmental conditions where this is less likely to be true, leading to the following additional hypotheses:

a. In mesophytic leaves growing in wet and/or humid environments, the effective operational \( C_i \) for leaves is likely to be high, meaning, the leaf is more likely to be electron-transport limited, and thus \( V_{cmax} \) values are more likely to be underestimated.

b. The \( J_{max} \) to \( V_{cmax} \) ratio at 25 °C has been found to decline with increasing growth temperature (Dreyer et al. 2001; Medlyn et al., 2002a; Kattge & Knorr, 2007; Lin et al., 2013). As a result, the leaf is more likely to be electron-transport limited at higher growth temperatures; thus we also hypothesise an underestimation of \( V_{cmax} \) at higher growth temperatures.

ii. Estimates of \( V_{cmax} \) would in general be less accurate for leaves operating at low \( A_{sat} \) and/or low \( g_s \) because the cumulative effect of errors in the various underlying assumptions would contribute to a lower signal-to-noise ratio.

iii. Uncertainties in \( R_{day} \) can contribute to greater bias for estimating \( V_{cmax} \) using the one-point method.

In this study we provide a thorough analysis of the one-point method for estimating carboxylation capacity from point measurements of light-saturated photosynthesis, and indicate the conditions under which it works best or may be subject to greater errors. Our primary purpose is to find out whether it would be viable to markedly expand plant trait databases of maximum carboxylation capacity, \( V_{cmax} \), by supplementing those data acquired from \( A-C_i \) curves with values derived from \( A_{sat} \) by the one-point method.
Material and Methods

Datasets

We collated 1,394 A-Ci curve measurements from 564 C3 species (91 families) and 46 field sites across various ecosystems, including Arctic tundra, boreal and temperate forest, semi-arid woodlands and tropical forest (Table 1, Figure S1). In most cases measurements were made using the LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE, USA), except for one data set obtained in Estonia which was measured using a customised open system (Niinemets et al., 1998). We selected data where measurements were first conducted at ambient CO2 concentration (360–400 µmol mol−1, depending on the year of collection) and saturating irradiance conditions (photosynthetic photon flux density, PPFD, between 1000 and 2000 µmol m−2 s−1). The measurements then progressed through a series of step-wise changes in CO2 concentration spanning sub-ambient (40–400 µmol mol−1) and super-ambient saturating CO2 concentration (typically > 700 µmol mol−1). During each A-Ci response curve measurement, leaf temperatures were maintained close to the site ambient temperature, ranging from 6 to 40°C. Any measurements obtained which did not follow this protocol, e.g. in cases where the first measurement was recorded at sub-ambient CO2, were not used in our analyses.

Estimation of apparent Vc,max, Jmax and Rd,ay from A-Ci response curves

We first estimated apparent Vc,max, Jmax and Rd,ay by fitting each field-measured A-Ci curve using the C3 photosynthesis model of Farquhar et al., (1980). Several different estimates for the temperature-dependence of Kc, the Michaelis constant for CO2 (µmol mol−1), Ko, the Michaelis constant for O2 (mmol mol−1), and Γ*, the CO2 compensation point in the absence of mitochondrial respiration (µmol mol−1), can be found in the literature (Badger & Collatz, 1977; Jordan & Ogren, 1984; Brooks & Farquhar, 1985; Bernacchi et al., 2001; Crous et al., 2013). We chiefly use values taken from Bernacchi et al. (2001), hereafter denoted B01, in common with many TBMs. To test whether the choice of values for these parameters affects the success of the one-point method, we also used two alternative sets of these parameters, namely those advanced by Badger & Collatz (1977) (denoted BC77) and Crous et al., (2013) (denoted C13): see Table 2 for details. The Γ* temperature dependencies of tobacco (B01) and eucalypt (C13) represent two extremes of the most and least temperature-sensitive Γ* responses respectively,
using *in vivo* gas exchange methods (Crous, unpublished data). To contrast with *in vitro* methods, we also considered the temperature response of $I^*$ in *Atriplex glabrriuscula* (BC77).

The intercellular concentration of oxygen ($O_i$) was assumed to be 210 mmol mol$^{-1}$ for all data collected at sea level. In other datasets, $O_i$, $C_i$ and $I^*$ were corrected for the effect of elevation on partial pressure by multiplying by the observed pressure readings and correcting units to µbar, mbar and mbar, respectively. For calculations with the B01 and C13 temperature dependencies, $K_o$ and $K_c$ were converted to units of µbar and mbar, respectively. This was done by assuming that the original measurements were obtained at an average atmospheric pressure of 987 mbar in Urbana, Illinois (von Caemmerer et al., 2009). $K_o$ and $K_c$ values from BC77 were simply converted from concentration to partial pressure assuming a standard pressure of 1011.35 mbar.

We assumed an infinite mesophyll conductance ($g_{na}$); therefore the estimated $V_{cmax}$ and $J_{max}$ values should be regarded as apparent values (Evans 1986; Sun et al., 2013), as generally used in TBMs and reported in most of the ecophysiological literature. A closer match to *in vitro* enzyme activity of Rubisco can be obtained by considering the mesophyll conductance to CO$_2$ to the sites of carboxylation (Flexas et al., 2007; Rogers et al., 2001); however, as $g_{na}$ values are available for so few of the sampled species, we assumed that $C_i$ is equal to $C_c$, the CO$_2$ concentration at the chloroplast. The $C_i$ at which photosynthesis is co-limited by both carboxylation and RuBP regeneration was calculated for each $A$-$C_i$ curve based on the apparent $V_{cmax}$, $J_{max}$ and $R_{day}$ using the C$_3$ photosynthesis model. As the temperature responses of $V_{cmax}$, $J_{max}$ and $R_{day}$ are not the focus of our study, we did not adjust the estimated parameter values to a standard temperature. Therefore, all the parameters were estimated at their corresponding measured leaf temperatures. All parameter fits were carried out using the Levenberg–Marquardt least squares approach (Levenberg, 1944; Marquardt, 1963); the source code is freely available from GitHub (De Kauwe et al. 2015). Of the 1,394 measured $A$-$C_i$ curves, the data used to estimate $V_{cmax}$ were screened to exclude “bad” measurement curves based on the traditional $A$-$C_i$ fitting approach, “bad” being defined as: (i) if the first obtained measurement was at an ambient CO$_2$ concentration < 300 or > 400 µmol mol$^{-1}$; (ii) if the fitted function had $r^2 < 0.9$; or (iii) if the relative error of fitted $V_{cmax}$ values is > 40%. After screening this resulted in 1318 measurements; filtering criteria (i), (ii) and (iii) removed ~4%, 1% and 1%, respectively.
respectively. The fitting method used makes no assumption about the $C_i$ value at which the leaf transitions between carboxylation and RuBP regeneration limitations ($C_i$ transition point), but it does use a hyperbolic minimum function to smooth the transition between the carboxylation and RuBP regeneration limitations (Kirschbaum & Farquhar, 1984).

$\bar{V}_{c,max}$ estimation from the one-point method

The main underlying assumption of the one-point method is that leaf net photosynthesis under ambient CO$_2$ and saturated irradiance conditions is limited by Rubisco carboxylation rather than by RuBP regeneration (Wilson et al., 2000; Rogers & Humphries, 2000). As such, $\bar{V}_{c,max}$ can be estimated from the carboxylation-limited portion of the photosynthetic-CO$_2$ response curve, given by:

$$\bar{V}_{c,max} = \left( A_{sat} + R_{day} \right) \frac{(C_i + K_m)}{(C_i - I^*)}$$  (1)

where $K_m$ is the Michaelis-Menten constant, given by:

$$K_m = K_c \left( 1 + \frac{O_i}{K_0} \right)$$  (2)

$K_c$, $K_0$ (and $I^*$) were estimated following the equations in Table 2. We used the first measurement point of each $A-C_i$ curve as the $A_{sat}$ value required to estimate $V_{c,max}$. One difficulty with this approach is that it requires an estimate of $R_{day}$. In the first instance we used the fitted value for $R_{day}$ obtained from the $A-C_i$ curve (hereafter called ‘known’ $R_{day}$). This approach may be viewed as a “best-case” test of the method, since these values will not be known when only $A_{sat}$ is measured. In order to estimate $V_{c,max}$ in the situation where $R_{day}$ is not known, we assumed that $R_{day}$ was 1.5% of $V_{c,max}$ (hereafter called ‘estimated’ $R_{day}$), following Collatz et al., (1991). Under this assumption, the estimation equation is:

$$\bar{V}_{c,max} = A_{sat} \left( \frac{C_i + K_m}{C_i - I^*} - 0.015 \right)$$  (3)

The fixed proportion between $R_{day}$ and $V_{c,max}$ was proposed by Collatz et al. (1991) to hold at 25°C. We further assumed that this ratio would remain constant with varying leaf temperature, thus assuming similar temperature dependences for $R_{day}$ and $V_{c,max}$. This assumption is reasonable because leaf respiration and $V_{c,max}$ both typically have increasing temperature...
dependences with Q10 values close to 2 at temperatures up to 35°C (Collatz et al., 1991; Medlyn et al., 2002; Atkin et al., 2015).

Assessing the robustness of the one-point method

We compared $\hat{V}_{\text{cmax}}$ values to $V_{\text{cmax}}$ values estimated from each full $A$-$C_i$ curve in order to assess the performance of the one-point method. We also analysed the residuals as a function of a range of variables to identify the circumstances under which the method is most (or least) successful.

As there were 1318 data points we opted in a number of comparison plots to (i) group (colour) species by PFT and also (ii) to bin these data (Fig. 2, 4, 5, 7, S1 and S2). Binning the data (with all values within a ‘bin’ being averaged out to a single value), allows us to better visualise the underlying main trends in large datasets, rather than being distracted by the small number of points towards the edges of any bivariate distribution. Regression lines however were fitted to raw data, not to the binned data. Bin sizes are shown in all figure captions.

Other datasets

Using 0.5° resolution Climate Research Unit climatology data (CRU CL1.0; New et al. 1999) over the period 1961 to 1990, we derived for each site: mean annual temperature (MAT; a proxy for growth temperature); mean annual precipitation (MAP); a moisture index (representing an indirect estimate of plant water availability, calculated as the ratio of mean annual precipitation to the equilibrium evapotranspiration as described in Gallego-Sala et al., 2010); and the number of growing degree days above 0 and 5 degrees C, respectively. We also obtained site elevation estimates from data from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (GDEM V2) at 1.0° resolution.

Results
The $C_i$ transition point of each $A-C_i$ curve was located by fitting both the Rubisco-limited and RuBP-limited net CO$_2$ assimilation rates and then identifying the point at which the two limitations intersected (transition point) (Fig. 2a). In our dataset c. 94% of the measured $A_{sat}$ values were found to be Rubisco-limited under saturated irradiance and ambient CO$_2$. This result supports the key underlying assumption of the one-point approach: that in field datasets at current $C_a$ and (importantly) at light saturation, carboxylation usually limits $A$ (hypothesis i).

Among the wide range in estimated transition points there was some distinct patterning according to plant functional type (PFT; Fig. 2b); namely, higher median transition points for evergreen needleleaf species than in broadleaf species (whether evergreen or deciduous; post hoc Tukey test: $p < 0.001$), and higher median transition points in herbaceous species than in deciduous shrubs (post hoc Tukey test: $p = 0.08$) (note the deciduous needleleaf forests PFT only has three sample curves).

When $R_{day}$ was known, $\tilde{V}_{c_{\text{max}}}$ values were in excellent agreement with $V_{c_{\text{max}}}$ derived from traditional $A-C_i$ curve fitting (Fig. 3). Across all species, $\tilde{V}_{c_{\text{max}}}$ values were estimated with a positive bias of 0.99 µmol m$^{-2}$ s$^{-1}$; $r^2 = 0.98$; root mean squared error (RMSE) = 8.19 µmol m$^{-2}$ s$^{-1}$. Error and bias varied somewhat among PFTs (bias = $-4.02$ to $-2.26$ µmol m$^{-2}$ s$^{-1}$; $r^2 > 0.95$; RMSE: 4.33 to 10.34 µmol m$^{-2}$ s$^{-1}$) but were still rather modest even in the worst case, deciduous shrubs (RMSE = 10.34 µmol m$^{-2}$ s$^{-1}$).

Residuals between $V_{c_{\text{max}}}$ and $\tilde{V}_{c_{\text{max}}}$ were examined as a function of several factors, namely: $V_{c_{\text{max}}}$ estimated from traditional $A-C_i$ curves (Fig. 4a), ambient $g_s$ (Fig. 4c), estimated $R_{day}$ (via $A-C_i$ curve; Fig. 4e) and ambient $C_i$ (Fig. 4g); leaf temperature, mean annual temperature (MAT); a proxy for growth temperature) and mean annual precipitation (MAP) (Fig. 5); and a selection of other common indices of site climate (site moisture index, elevation, growing degree days; Figs. S2-3). The plot of residuals against the “true” $V_{c_{\text{max}}}$ values (Fig. 4a) shows considerable scatter in individual $\tilde{V}_{c_{\text{max}}}$ values. When using a known $R_{day}$, this spread in errors largely disappears in the binned data, suggesting that it results from a small number of individual measurements. There was a positive trend in the residuals that indicates increasing error with
increasing \( V_{\text{cmax}} \) values, but importantly, most (~10% of binned data) errors are small (within 10%, denoted by dotted lines in Fig. 4a).

We originally hypothesised that we would observe larger biases between \( \hat{V}_{\text{cmax}} \) and \( V_{\text{cmax}} \) at high ambient \( C_i \) and in species sampled from very wet and/or humid environments, due to a greater stomatal aperture (hypothesis i(a)). When using a known \( R_{\text{day}} \) our dataset did not support this hypothesis (Fig 4c): at high \( g_s \), there was a weak trend for over-estimation of \( V_{\text{cmax}} \), rather than the hypothesised under-estimation expected if the error resulted from being above the operating \( C_i \). Whilst there was a small trend with MAP, the slope was negligible (Fig. 5c) and there were no trends when examining the residuals as a function of \( C_i \) (Fig. 4g). We also hypothesised that we might see greater bias at high growth temperatures (hypothesis i(b)). When using a known \( R_{\text{day}} \), our results do indeed show a significant trend with increasing MAT (proxy for growth temperature; Fig 5c), and the annual number of growing degree-days (Fig. S3), but again the slope of this trend was negligible. We also hypothesised that we may see larger error (both absolute and relative) in the residuals at low \( g_s \) values due to a low signal-to-noise ratio (hypothesis ii). To test this prediction, we divided the measurements into two groups: those at low \( g_s \) (<0.2 mol m\(^{-2}\)s\(^{-1}\)) and those at higher \( g_s \) (>0.2 mol m\(^{-2}\)s\(^{-1}\)). The RMSE was similar in both groups (8.07 \( \mu \)mol m\(^{-2}\)s\(^{-1}\) vs. 8.37 \( \mu \)mol m\(^{-2}\)s\(^{-1}\) at low and high \( g_s \), respectively), but the percentage error was greater (8.4% vs. 4.5%), supporting our prediction.

Estimated \( R_{\text{day}} \)

Errors were noticeably greater when \( R_{\text{day}} \) was estimated as a fixed fraction of \( V_{\text{cmax}} \). Overall (all species) there was a negative bias: -2.2 \( \mu \)mol m\(^{-2}\)s\(^{-1}\); \( r^2 = 0.95 \); RMSE: 17.1 \( \mu \)mol m\(^{-2}\)s\(^{-1}\). When grouping by PFT these errors increased further (biases -8.18 – 10.93 \( \mu \)mol m\(^{-2}\)s\(^{-1}\); \( r^2 > 0.85 \); RMSE: 8.30 – 26.46 \( \mu \)mol m\(^{-2}\)s\(^{-1}\)). Examining the residuals between \( V_{\text{cmax}} \) and \( \hat{V}_{\text{cmax}} \) as a function of the “true” \( V_{\text{cmax}} \) values (Fig. 4b) showed a negative trend suggesting an over-estimation of \( V_{\text{cmax}} \) at higher values. Errors were greatest for species grouped into the deciduous broadleaf forest PFT; here \( \hat{V}_{\text{cmax}} \) values are systematic over-estimates.
These results provide strong support for the hypothesis that uncertainties in $R_{\text{day}}$ would contribute to bias in estimating $V_{\text{cmax}}$ values (hypothesis iii). Overall, errors were greater across all comparisons when using an estimated $R_{\text{day}}$ compared to errors with a known $R_{\text{day}}$. $V_{\text{cmax}}$ values also showed a positive trend with increasing $R_{\text{day}}$ (Fig. 4f), suggesting a modest but systematic under-estimation of $V_{\text{cmax}}$ at $R_{\text{day}}$ values < 2 µmol m$^{-2}$ s$^{-1}$, and an over-estimation at higher $R_{\text{day}}$ values.

To enable the estimation of $V_{\text{cmax}}$ without an independent estimate of $R_{\text{day}}$, we assumed a fixed relationship with $V_{\text{cmax}}$ that is commonly used in TBMs. However, there was a strong negative relationship between $V_{\text{cmax}} - V_{\text{cmax}}$ residuals and leaf temperature (Fig. 5b) and a notable positive trend in errors with increasing estimates of $R_{\text{day}}$ (Fig. 4f), both of which suggest that the relationship between $R_{\text{day}}$ and $V_{\text{cmax}}$ is not constant. Figure 6a shows the $R_{\text{day}}:V_{\text{cmax}}$ ratio obtained from fitting our $A$-$C_{\text{i}}$ response curves as a function of leaf temperature for the B01 temperature dependencies for $K_{c}$, $K_{o}$ and $I^{*}$. The data show a strong negative trend with increasing temperature. This strong negative trend arises because the fitted $R_{\text{day}}$ values decline with leaf temperature (Fig. 6b), rather than increasing in line with $V_{\text{cmax}}$ as we assumed. Figure 6b indicates that fitted $R_{\text{day}}$ values commonly hit the lower bound of zero above 25°C. As $R_{\text{day}}$ is estimated as the value of $A$ where $C_{\text{i}} = I^{*}$, this may indicate that the values of $I^{*}$ used are inappropriate for these datasets.

Sensitivity to temperature dependencies of $K_{c}$, $K_{o}$ and $I^{*}$

We repeated the exercise of comparing $V_{\text{cmax}}$ and $V_{\text{cmax}}$ using two alternative temperature dependencies of $K_{c}$, $K_{o}$ and $I^{*}$ for the case where $R_{\text{day}}$ was estimated (Fig. 7; Figs S4-5). The accuracy of estimated values was largely insensitive to our three tested assumptions. $V_{\text{cmax}}$ values estimated with the C13 paramaterisation had the lowest RMSE values (average across all PFTs 13.85 µmol m$^{-2}$ s$^{-1}$) and those estimated with BC77 had the largest (average across all PFTs 15.42 µmol m$^{-2}$ s$^{-1}$). However, grouping by PFTs, the mean absolute difference between the different parameterisations was small, c. 2 µmol m$^{-2}$ s$^{-1}$. It is also notable that using the BC77 parameterisation resulted in greater errors for herbaceous species, RMSE = c. 19 vs. c. 11 µmol m$^{-2}$ s$^{-1}$ for B01 and C13 parameterisations. Figures S4-S5 demonstrate that the assumption of a fixed ratio of 0.015 for $R_{\text{day}}$: $V_{\text{cmax}}$ is still relatively poor for BC77 and C13.
parameterisations, particularly at low leaf temperatures; the approximation is marginally better for the C13 parameterisation, explaining the lower RMSE values obtained with this parameterisation.
In this study we have examined an alternative approach to traditional $A$-$C_i$ curve analysis for estimating $V_{\text{cmax}}$, an approach that holds promise for greatly expanding the set of species represented in global $V_{\text{cmax}}$ datasets. One of the principal concerns about the use of this approach has been that typical measurements of $A_{\text{sat}}$ may be limited by RuBP-regeneration rates, rather than Rubisco activity, and hence would yield underestimates of $V_{\text{cmax}}$, especially in wet or warm conditions. Here we have demonstrated that, for photosynthesis measurements taken at ambient CO$_2$ and under saturating irradiance conditions, values are normally Rubisco-limited and as such, $\hat{V}_{\text{cmax}}$ values are in good agreement with $V_{\text{cmax}}$ determined from $A$-$C_i$ curves. Residual analysis when using a known $R_{\text{day}}$ did not show any bias in $V_{\text{cmax}}$ estimation with environmental conditions such as mean annual temperature or precipitation. As a result, our results suggested that the one-point method is likely to be a robust means to resolve $V_{\text{cmax}}$ from light-saturated photosynthesis.

That said, our analysis did identify other, non-trivial sources of error in using the one-point approach. First, we found support for our hypothesis that increased errors would occur at low $g_s$ due to a lower signal-to-noise ratio (hypothesis ii), suggesting that rates of $A_{\text{sat}}$ that are not subject to severe stomatal limitation are most suited to this approach. Secondly, poor estimation of the day respiration rate, $R_{\text{day}}$, led to a notable increase in the RMSE of estimates, approximately doubling RMSE from 7.18 to 14.71 µmol m$^{-2}$ s$^{-1}$. The proportional error in $V_{\text{cmax}}$ when estimating $R_{\text{day}}$ (i.e. Fig 4b) was on average around 20% for most datasets when grouped by PFT. These errors were larger because we estimated $R_{\text{day}}$ using a fixed $R_{\text{day}}$-$V_{\text{cmax}}$ relationship, and this relationship did not capture variation in values of fitted $R_{\text{day}}$. There was strong bias at low and high temperatures, leading to a clear pattern in residuals. In addition, there was higher estimation error ($V_{\text{cmax}} - \hat{V}_{\text{cmax}}$ residuals) at higher $V_{\text{cmax}}$, higher leaf temperatures or at hotter sites (though it should be noted $V_{\text{cmax}}$ is typically greater at higher temperatures), and at either very high or very low $R_{\text{day}}$. Having identified and quantified these apparently systematic biases it would of course then be up to individual researchers using this method to decide for themselves what magnitude of error (or bias) was acceptable for the purpose at hand.
$R_{\text{day}}$ is as yet not well understood in terms of responses to environmental variation or temperature dependence and hence is difficult to model (Tcherkez et al., 2012; Heskel et al., 2013; Way & Yamori 2014). It is widely understood that estimates of $R_{\text{day}}$ obtained from $A$-$C_i$ curves are inaccurate. One reason for the inaccuracy is that the values are extrapolated from small fluxes at low $C_i$ conditions, and hence are subject to noise and possibly gasket-leak effects (Bruhn et al. 2002; Hurry et al. 2005). In this study we also show that there is a systematic bias in $R_{\text{day}}$ estimates with temperature (Figs. 5 and 6), which leads to bias in estimates of $P_{\text{cmax}}$. This bias could be potentially due to a number of factors. Firstly, fluxes are lower at lower temperature, so errors due to noise may be greater. Secondly, it is likely that our assumptions for the temperature dependence of either, or both, $R_{\text{day}}$ and $\Gamma^*$ are incorrect. Fitted estimates of $R_{\text{day}}$ showed either no temperature dependence, or a negative temperature dependence, depending on what $\Gamma^*$ was assumed (Figs 6, S4 and S5). In contrast, most studies of $R_{\text{day}}$ suggest a positive temperature dependence, as is assumed in most TBMs (KC - refs?).

The issue may lie with $\Gamma^*$: the most widely-used parameterisation for $\Gamma^*$ (B01) resulted in fitted values of $R_{\text{day}}$ going to zero at higher temperatures, suggesting this parameterisation may in fact be too temperature-sensitive for many species. This issue also affects photosynthesis values estimated by TBMs using estimates of $V_{\text{cmax}}$ obtained from $A$-$C_i$ curves, because such models commonly use a fixed ratio in $R_{\text{day}}$: $V_{\text{cmax}}$. The estimates of $V_{\text{cmax}}$ are dependent on the fitted values of $R_{\text{day}}$ (i.e. our known $R_{\text{day}}$). If models estimate photosynthesis with fitted $V_{\text{cmax}}$ but a fixed $R_{\text{day}}$: $V_{\text{cmax}}$ ratio, the resulting estimates of photosynthesis will be in error.

Addressing this problem requires that we develop better empirical parameterisations of the temperature dependences of both $\Gamma^*$ and $R_{\text{day}}$, which are applicable across species and climates, rather than the single-species, single-site relationships currently used.

An alternative approach to using a fixed $R_{\text{day}}$: $V_{\text{cmax}}$ ratio would be to base estimates of $R_{\text{day}}$ on measured values of dark respiration rate, $R_{\text{dark}}$. For example, it could be assumed that $R_{\text{day}} = 0.6 \times R_{\text{dark}}$ (Kirschbaum and Farquhar 1984) or, alternatively, one might simply set $R_{\text{day}} = R_{\text{dark}}$, as was done by Atkin et al., (2015) when employing the one-point method. However, we note that such approaches would still result in errors when estimating $P_{\text{cmax}}$ because they both assume a similar temperature dependence for $R_{\text{day}}$ and $R_{\text{dark}}$, whereas the fitted temperature...
dependence of $R_{\text{day}}$ does not resemble the exponential response typically found for $R_{\text{dark}}$ (Figs 6, S4 and S5).

**New research avenues**

Despite the error introduced by inaccuracies in $R_{\text{day}}$, the one-point method nevertheless has the potential to provide new insight into variability of $V_{c_{\text{max}}}$ across and within species, PFTs and in relation to other plant traits. Due to logistical constraints, studies measuring $V_{c_{\text{max}}}$ using $A$-$C_{i}$ curves typically focus on a relatively small number of species, and are biased towards both controlled environments and temperate regions (e.g. Wullschleger 1993; Kattge et al., 2009; Sun et al., 2014; Walker et al., 2014). The results of this paper suggest that measurements of $A_{\text{sat}}$, which are more readily made on a wide range of species under field conditions, can also be used to estimate $V_{c_{\text{max}}}$ using the one-point method. An expanded global $V_{c_{\text{max}}}$ database would greatly facilitate testing of ecophysiological theories of plant trait distribution based on environmentally driven traits (Verheijen et al., 2013, Reich, 2014, van Bodegom et al., 2014), trait-trade offs (Wright et al., 2010, Reu et al., 2011) and optimality concepts (Xu et al., 2012; Prentice et al., 2014; Wang et al., 2014; Ali et al., 2015b). Larger datasets for $V_{c_{\text{max}}}$ would also allow insights into the true scaling of photosynthetic capacity with leaf structural and chemical traits, with the caveat that we have identified some systematic biases in the approach, suggesting it would be best to constrain analysis to data < 30°C (Fig 5b).

From a modelling perspective, additional data would serve to improve the underlying evidence base used to constrain model simulations of photosynthesis. For example, Bonan et al., (2011) found that uncertainty due to $V_{c_{\text{max}}}$ was equivalent to uncertainties due to structural errors (e.g. scaling photosynthesis and stomatal conductance from the leaf to the canopy), accounting for a ~30 Pg C year$^{-1}$ variation in modelled gross primary productivity in CLM4. A number of models (e.g. CABLE, JULES, CLM4) assume that the $J_{\text{max}}$ parameter and/or the autotrophic respiration are proportional to $V_{c_{\text{max}}}$. Therefore, this single parameter has a marked impact on modelled carbon flux and improvements in the $V_{c_{\text{max}}}$ parameter have the potential to constrain multiple facets of current TBM. For example, Dietze et al., (2014a) showed that inclusion of even small observational datasets of $V_{c_{\text{max}}}$ could adequately constrain the parameterisation of the Ecosystem Demography (ED2) model across a range of biomes. Furthermore, it is now
commonplace in some modelling studies to simulate vegetation fluxes considering the full uncertainty of key parameters, rather than assuming a PFT can be described by a single value (Ziehn et al., 2011; Wang et al., 2012).

It should be noted that our analysis calls into question the modelling assumption that $J_{\text{max}}$ is proportional to $V_{\text{cmax}}$, as shown by the high variability in $C_i$ transition points observed across our data set (Figure 2). These transition points can be used to estimate the ratio of $J_{\text{max}} / V_{\text{cmax}}$. We estimated this ratio at 25°C from the transition points, and found a mean value of 1.9 with a large inter-quartile range, stretching from 1.68 to 2.14. As noted above, there was some difference in the median transition point (and hence $J_{\text{max}} / V_{\text{cmax}}$ ratio) among PFTs, but the variability within a PFT is considerably larger than between PFTs. While the one-point method can provide insights into variation in $V_{\text{cmax}}$, it does not enable us to develop better parameterisations for other key photosynthetic parameters. There remains a need for full $A$-$C_{\text{i}}$ curves to also quantify the variability in $J_{\text{max}} / V_{\text{cmax}}$ ratio, or as an alternative, cluster sampling approaches (e.g. extensively sampling of the photosynthesis-light response curve) as proposed by Dietze (2014b).

There is also the potential for a complementary set of parameter estimates to be obtained through a re-examination of existing $A_{\text{sat}}$ datasets. Large quantities of field-measured $A_{\text{sat}}$ data currently exist in global databases, for example ~1500 species in Maire et al., (2015) and 2192 species in TRY (Kattge et al., 2011). By putting together $V_{\text{cmax}}$ data derived from $A$-$C_{\text{i}}$ curves with $V_{\text{cmax}}$ values determined from the one-point method (i.e., $\hat{V}_{\text{cmax}}$), there is potential to generate a database consisting of data for thousands of species, for many hundred sites around the world. Consistent conversion of $A_{\text{sat}}$ to $V_{\text{cmax}}$ values in worldwide datasets would be strongly beneficial, enabling a wider characterisation of $V_{\text{cmax}}$ variations across the globe, and better quantification of relationships between $V_{\text{cmax}}$ and other leaf traits (Walker et al., 2014) and with site climate (Ali et al., 2015). However, it is important to note that application of the one-point method to these datasets may involve additional sources of error. For example, Kattge et al. (2009) estimated $\hat{V}_{\text{cmax}}$ using a one-point method applied to $A_{\text{sat}}$ data that did not include complementary values of $C_{\text{i}}$, and thus estimated $C_{\text{i}}$ as a constant fraction (0.8) of $C_{\text{a}}$. In our dataset, the 25th and 75th quartiles for the $C_{\text{i}};C_{\text{a}}$ ratio were 0.60 – 0.75; use of a constant value
would thus have introduced considerable additional error. Application of the one-point method to species-mean values of $A_{sat}$ and $g_s$, such as those collated by Maire et al. (2015), would also be subject to systematic error from averaging a non-linear function. Thus, application of the one-point method in these circumstances needs to be done with caution.

This manuscript presents an empirical justification for using the one-point method, which we conclude can be used to estimate accurate values of $V_{cmax}$, for an estimate that we labelled $\hat{V}_{cmax}$ for distinction from intensively measured curves. We stress that continued measurement of plant behaviour using detailed $A-C_i$ response curves is still invaluable and, indeed, “best-practice”. Fitting the model of Farquhar et al., (1980) to data has provided a tried and tested way to evaluate and interpret plant physiological behaviour in the field and lab alike. The one-point method tested here complements the traditional approach, potentially allowing us to greatly expand plant trait datasets of maximum carboxylation efficiency.
Acknowledgements

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All data analysis and plots were written in Python; in particular we made use of the Scipy (Jones et al., 2001), LMFIT (Neville et al. 2014) and Matplotlib libraries (Hunter, 2007).
Figure Captions

Figure 1: Conceptual figure demonstrating how errors could arise when estimating $V_{\text{cmax}}$ using the one-point method. When $R_{\text{day}}$ is correct (dark yellow point) and $A_{\text{sat}}$ is Rubisco limited (black point) $V_{\text{cmax}}$ is correctly estimated (dashed purple line). When $A_{\text{sat}}$ is RuBP-regeneration limited (blue point) $V_{\text{cmax}}$ will be under-estimated (dashed blue line). If $R_{\text{day}}$ is over-estimated (green point) $V_{\text{cmax}}$ will be over-estimated (dashed green line).

Figure 2: Relationship between ambient $C_i$ and the $C_i$ value at the transition point obtained from $A$-$C_i$ curve fitting. In panel (a) data shown are for individual species, but have been grouped (coloured) by plant functional type: EBF - evergreen broadleaved forest, DBF - deciduous broadleaved forest, ENF - evergreen needle leaved forest, DNF - deciduous needle leaved forest, DSB - deciduous shrubs and HRB - herbaceous species. The data have also been binned (bin size = 10), with the original data shown in a matching semi-transparent colour. In panel (b) the box and whisker plots show the $C_i$ value at the transition point (line, median; box, inter-quartile range), with bars extending to 1.5 times the inter-quartile range. Dots outside of the box and whiskers show outlying points.

Figure 3: Comparison between $V_{\text{cmax}}$ values estimated from traditional $A$-$C_i$ curve fitting and $V_{\text{cmax}}$ estimated from one-point method, $\tilde{V}_{\text{cmax}}$. Panel (a) and (b) show the effect of using a known and an estimated $R_{\text{day}}$ (1.5% of $V_{\text{cmax}}$), respectively. Data shown are for all 1318 species but have been coloured as in Figure 2 to match representative plant functional types. Regression lines have been fit to the raw data (1318 species measurements) and coloured to match plant functional types.

Figure 4: Residuals ($V_{\text{cmax}} - \tilde{V}_{\text{cmax}}$) shown as a function of $V_{\text{cmax}}$, ambient $g_s$, estimated $R_{\text{day}}$ and $C_i$. Data were binned (panels (a) and (b) bin size = 10; panel (c) and (d) bin size = 0.05; panels (e) and (f) bin size = 0.25), panels (e) and (f), bin size = 10), with the original data shown in a matching semi-transparent colour. Data shown are for all 1318 species but have been coloured as in Figure 2 to match representative plant functional types. A significant (p<0.05) trend in the residuals is shown by a solid black line. Trend lines have been fit to the raw data (1318 species measurements).
species measurements). In panels (a) and (b) the grey dashed lines represent 5 (dot-dash) and 10% (dot-dot) error, respectively.

Figure 5: Residuals ($V_{cmax} - \hat{V}_{cmax}$) shown as a function of leaf temperature, mean annual temperature and mean annual precipitation. Data in the residual panels have been binned (panels (a), (b), (c) and (d) bin size = 0.5; panels (e) and (f), bin size = 100), with the original data shown in a matching semi-transparent colour. Data shown are for all 1318 species, but have been coloured as in Figure 2 to match representative plant functional types. A significant ($p<0.05$) trend in the residuals is shown by a solid black line. Trend lines have been fit to the raw data (1318 species measurements).

Figure 6: Fitted $R_{day}:V_{cmax}$ ratio (a) and (b) $R_{day}$ as a function of leaf temperature using the Bernacchi et al. (2001) parameters. Data shown are for all 1318 species, but have been coloured as in Figure 2 to match representative plant functional types. The horizontal red line shows the $R_{day}:V_{cmax}$ commonly assumed by terrestrial biosphere models following Collatz et al. (1991).

Figure 7: Relationship between $V_{cmax}$ values estimated from the traditional approach and $\hat{V}_{cmax}$ values using three different sets of $K_c$, $K_o$, and $I^*$ parameters. Data shown are for all 1318 species, but have been coloured as in figure 2 to match representative plant functional types. Regression lines have been fit to the raw data (1318 species measurements) and coloured to match plant functional types.

Supplementary Figure 1: Climatic space covered by this study shown by density hexagons. Over-plotted colour symbols represent sampled species, grouped by plant functional type.

Supplementary Figure 2: Residuals ($V_{cmax} - \hat{V}_{cmax}$) shown as a function of a moisture index and elevation. Data in the residual panels have been binned ((panels (a) and (b) bin size = 0.1; panels (c) and (d), bin size = 100), with the original data shown in a matching semi-transparent...
colour. Data shown are for all 1318 species, but have been coloured as in figure 2 to match representative plant functional types. A significant (p<0.05) trend in the residuals is shown by a solid black line. Trend lines have been fit to the raw data (1318 species measurements).

Supplementary Figure 3: Residuals $V_{\text{cmax}} - \hat{V}_{\text{cmax}}$ shown as a function of the number annual growing degree days above > 0°C and > 5°C. Data in the residual panels have been binned (panels (a), (b), (c) and (d) bin size = 0.5), with the original data shown in a matching semi-transparent colour. Data shown are for all 1318 species, but have been coloured as in figure 2 to match representative plant functional types. Significant (p<0.05) trends in absolute and non-absolute residuals are shown by the solid red and black lines, respectively. These trends lines have been fit to the raw data (1318 species measurements).

Supplementary Figure 4: Fitted $R_{\text{day}}:V_{\text{cmax}}$ ratio (a) and (b) $R_{\text{day}}$ as a function of leaf temperature using the Badger & Collatz (1977) parameters. Data shown are for all 1318 species, but have been coloured as in figure 2 to match representative plant functional types. The horizontal red line shows the $R_{\text{day}}:V_{\text{cmax}}$ commonly assumed by terrestrial biosphere models following Collatz et al. (1991).

Supplementary Figure 5: Fitted $R_{\text{day}}:V_{\text{cmax}}$ ratio (a) and (b) $R_{\text{day}}$ as a function of leaf temperature using the Crous et al. (2013) parameters. Data shown are for all 1318 species, but have been coloured as in figure 2 to match representative plant functional types. The horizontal red line shows the $R_{\text{day}}:V_{\text{cmax}}$ commonly assumed by terrestrial biosphere models following Collatz et al. (1991).

References


Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1: Climatic space covered by this study shown by density hexagons.

Fig. S2: Residuals ($V_{\text{max}} - \hat{V}_{\text{max}}$) shown as a function of a moisture index and elevation.

Fig. S3: Residuals $V_{\text{max}} - \hat{V}_{\text{max}}$ shown as a function of the number annual growing degree days above $>0^\circ\text{C}$ and $>5^\circ\text{C}$. 
Fig. S4: Fitted $R_{\text{day}}/V_{\text{cmax}}$ ratio (a) and (b) $R_{\text{day}}$ as a function of leaf temperature using the Badger & Collatz (1977) parameters.

Fig. S5: Fitted $R_{\text{day}}/V_{\text{cmax}}$ ratio (a) and (b) $R_{\text{day}}$ as a function of leaf temperature using the Crous et al. (2013) parameters.
Table 1: List of the data sets, site locations, vegetation types and associated references used in this study.

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<td>Unpublished</td>
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<tr>
<td>Cuzco Amazonico, Peru</td>
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<td>-3.37</td>
<td>-72.97</td>
<td>Malhi &lt;em&gt;et al.&lt;/em&gt;, 2014; Anderson &lt;em&gt;et al.&lt;/em&gt;, 2009</td>
<td>Forests over alluvial terrain</td>
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<tr>
<td>Esperanza, Peru</td>
<td></td>
<td>-2.48</td>
<td>-71.97</td>
<td></td>
<td>Upper limit of the cloud forest</td>
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<td>Jenaro Herrera, Peru</td>
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<td>-4.88</td>
<td>-73.63</td>
<td>del Aguila-Pasquel &lt;em&gt;et al.&lt;/em&gt;, 2014</td>
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<td>San Pedro, Peru</td>
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<td>-6.54</td>
<td>-77.71</td>
<td>Huasco &lt;em&gt;et al.&lt;/em&gt;, 2014</td>
<td>Cloud forest</td>
</tr>
<tr>
<td>Sucusari, Peru</td>
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<td>-3.25</td>
<td>-72.91</td>
<td>Atkins &lt;em&gt;et al.&lt;/em&gt;, 2015</td>
<td>Humid Amazonian lowland forest</td>
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<tr>
<td>Tambopata, Peru</td>
<td></td>
<td>-13.02</td>
<td>-69.60</td>
<td>Huasco &lt;em&gt;et al.&lt;/em&gt;, 2014</td>
<td>Humid Amazonian lowland forest</td>
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<tr>
<td>Trocha Union, Peru</td>
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<td>-13.03</td>
<td>-71.49</td>
<td>Huasco &lt;em&gt;et al.&lt;/em&gt;, 2014</td>
<td>Montane cloud forest</td>
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<tr>
<td>Wayquecha, Peru</td>
<td></td>
<td>-13.12</td>
<td>-71.58</td>
<td>Girardin &lt;em&gt;et al.&lt;/em&gt;, 2014</td>
<td>Upper limit of the cloud forest</td>
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<tr>
<td><strong>Togashi (51 species)</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Great Western Woodland, WA, Australia</td>
<td></td>
<td>-30.25</td>
<td>-30.25</td>
<td>Unpublished</td>
<td>Temperate eucalyptus woodland</td>
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<tr>
<td>Robson Creek, QLD, Australia</td>
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<td>-17.25</td>
<td>145.75</td>
<td>Unpublished</td>
<td>Tropical rainforest</td>
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<td><strong>TROBIT</strong> (44 species)</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Bissiga, Burkina Faso</td>
<td></td>
<td>12.73</td>
<td>-1.16</td>
<td>Domingues &lt;em&gt;et al.&lt;/em&gt; (2010)</td>
<td>Tropical woody savanna</td>
</tr>
<tr>
<td>Bissiga, Burkina Faso</td>
<td></td>
<td>12.73</td>
<td>-1.11</td>
<td>Domingues &lt;em&gt;et al.&lt;/em&gt; (2010)</td>
<td>Tropical woody savanna</td>
</tr>
<tr>
<td>Boabeng-Fiema, Ghana</td>
<td></td>
<td>7.71</td>
<td>-1.69</td>
<td>Domingues &lt;em&gt;et al.&lt;/em&gt; (2010)</td>
<td>Seasonal tropical forest</td>
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<tr>
<td>Dano, Burkina Faso</td>
<td></td>
<td>10.94</td>
<td>-3.15</td>
<td>Domingues &lt;em&gt;et al.&lt;/em&gt; (2010)</td>
<td>Open tropical savanna</td>
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<tr>
<td>Hombori, Mali</td>
<td></td>
<td>15.34</td>
<td>-1.47</td>
<td>Domingues &lt;em&gt;et al.&lt;/em&gt; (2010)</td>
<td>Dry grass savanna</td>
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<tr>
<td>Kogyae, Ghana</td>
<td></td>
<td>7.30</td>
<td>-1.48</td>
<td>Domingues &lt;em&gt;et al.&lt;/em&gt; (2010)</td>
<td>Tropical woody savanna</td>
</tr>
<tr>
<td><strong>Serbin (21 species)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coachella Valley Agricultural Research Station, CA, USA</td>
<td></td>
<td>33.52</td>
<td>-116.16</td>
<td>Serbin &lt;em&gt;et al.&lt;/em&gt;, (2015)</td>
<td>Vineyard and date palm</td>
</tr>
<tr>
<td>Loma Ridge Coastal Sagescrub EC site, CA, USA</td>
<td></td>
<td>33.73</td>
<td>-117.70</td>
<td>Unpublished</td>
<td>Coastal sage-scrub</td>
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<tr>
<td>Site Description</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Notes</td>
<td>Location</td>
<td>Unpublished</td>
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<td>Sierra Mixed Conifer EC site, CA, USA</td>
<td>37.07</td>
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<td>Mixed conifer/broadleaf forest</td>
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<td>San Joaquin Experimental Range, CA, USA</td>
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<td>-119.73</td>
<td>Unpublished</td>
<td>Semi-arid woodland</td>
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<tr>
<td>San Jacinto James Reserve EC tower site, CA, USA</td>
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<td>-116.77</td>
<td>Unpublished</td>
<td>Mixed conifer/broadleaf forest</td>
<td></td>
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<tr>
<td>UW-Madison Arboretum, WI, USA</td>
<td>43.04</td>
<td>-89.43</td>
<td>Unpublished</td>
<td>Temperate broadleaf deciduous forest</td>
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<tr>
<td>Domingues (24 species) Tapajós, Brazil</td>
<td>-3.75</td>
<td>-56.25</td>
<td>Domingues et al., (2005)</td>
<td>Humid Amazonian lowland forest</td>
<td></td>
</tr>
<tr>
<td>Niinemets (3 species) Ulenurme, Estonia</td>
<td>58.30</td>
<td>26.70</td>
<td>Niinemets (1998)</td>
<td>Temperate broadleaf deciduous forest</td>
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<tr>
<td>Rogers (7 species) Barrow Environmental Observatory, Barrow, AK, USA</td>
<td>71.32</td>
<td>156.62</td>
<td>Unpublished</td>
<td>Tundra</td>
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<td>Tarvainen (1 species) Skogaryd, Sweden</td>
<td>58.23</td>
<td>12.09</td>
<td>Tarvainen et al., (2013)</td>
<td>Hemi-boreal coniferous forest</td>
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</tbody>
</table>
Table 2: Three sets of temperature dependencies for the Michaelis constant for CO₂, $K_c$ (µmol mol⁻¹) and the Michaelis constant for O₂, $K_o$ (mmol mol⁻¹) and the CO₂ compensation point, $I^*$ (µmol mol⁻¹). $T_k$ is the leaf temperature in Kelvin, $R$ is universal gas constant (8.314 J mol⁻¹ K⁻¹) and $O_i$ is the intercellular concentrations of O₂ (210 mmol mol⁻¹).

<table>
<thead>
<tr>
<th>Reference</th>
<th>Environment</th>
<th>Species</th>
<th>$K_c$</th>
<th>$K_o$</th>
<th>$I^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Badger and Collatz (1977)</td>
<td><em>in vivo</em></td>
<td>Bracted orache <em>(Atriplex glabrisscula)</em></td>
<td>If $T_k &gt; 288.15$: 460 $\cdot$ exp(\left(\frac{59536(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right)) else if $T_k &lt; 288.15$: 920 $\cdot$ exp(\left(\frac{10970(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right))</td>
<td>330 $\cdot$ exp(\left(\frac{35948(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right))</td>
<td>42.75 $\cdot$ exp(\left(\frac{37830(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right))</td>
</tr>
<tr>
<td>Bernacchi et al. (2001)</td>
<td><em>in vivo</em></td>
<td>Tobacco <em>(Nicotiana tabacum)</em></td>
<td>404.9 $\cdot$ exp(\left(\frac{79403(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right))</td>
<td>278.4 $\cdot$ exp(\left(\frac{36380(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right))</td>
<td>38.892 $\cdot$ exp(\left(\frac{20437(T_k - 298.15)}{298.15 \cdot R \cdot T_k}\right))</td>
</tr>
<tr>
<td>Crous et al. (2013)</td>
<td><em>in vitro</em></td>
<td>Tasmanian blue gum <em>(Eucalyptus globulus)</em></td>
<td>Same as Bernacchi et al. (2001)</td>
<td>Same as Bernacchi et al. (2001)</td>
<td>Same as Bernacchi et al. (2001)</td>
</tr>
</tbody>
</table>

\[I^* = \frac{K_c \cdot O_i - 0.21}{2 \cdot K_o}\]