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Parameterization of the Farquhar-von Caemmerer-Berry C_3 photosynthesis model for oil palm

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Abstract

The Farquhar-von Caemmerer-Berry C_3 photosynthesis (FvCB) model is used to model photosynthesis of oil palm. However, some model parameters and their temperature dependencies are not known for oil palm. Hence, the aim of this study was to determine the intercellular photocompensation point (C_i*), rate of leaf day respiration in the light (R_d), the chloroplastic photocompensation point (Γ*), mesophyll conductance (g_m), maximum rates of Rubisco carboxylation (V_{cmax}) and electron transport (J_{max}), triose phosphate utilization (TPU) and their temperature dependencies between 25 and 40°C in oil palm. Using leaf gas-exchange and chlorophyll fluorescence measurements, parameters such as R_d, C_i*, Γ*, g_m, V_{cmax}, J_{max}, and TPU were determined for oil palm. The parameters C_i*, R_d, Γ*, g_m, and V_{cmax} responded to temperature exponentially without thermal deactivation. In contrast, J_{max} and TPU responded to temperature exponentially up to 38°C before decreasing slightly at 40°C. Taken altogether, this study determined some key FvCB model parameters and their temperature dependencies for oil palm. This paves the way for more accurate modelling of photosynthetic carbon assimilation in oil palm particularly under future elevated temperatures and CO_2 concentrations.

Additional key words: carbon assimilation; chlorophyll; climate change; leaf respiration; maximum electron transport rate.

Introduction

The oil palm (*Elaeis guineensis* Jacq.) is an important oil crop cultivated extensively in the tropical regions, especially in Indonesia, Malaysia, Thailand, and Papua New Guinea (Padfield *et al*. 2019). Its oil is the most consumed vegetable oil in the world, accounted for 35% of total global demand of vegetable oil in 2016 (Chong *et al*. 2017). Due to its increasing importance as global major oil crop, many crop models of oil palm have been developed such as OPSIM (van Kraalingen 1989), SIMPALM (Dufrêne *et al*. 1990), OPRODSIM (Henson 2009), ECO-PALM (Combres *et al*. 2013), PALMSIM (Hoffmann *et al*. 2014), APSIM-Oil Palm (Huth *et al*. 2014), CLM-Palm (Fan *et al*. 2015), CLIMEX-Oil Palm (Paterson *et al*. 2015), and PySawit (Teh and Cheah 2018), among others, to predict effect of climate change on oil palm. But such models require a more precise and mechanistic photosynthesis model.

The C_3 photosynthesis model developed by Farquhar *et al*. (1980), otherwise also widely known as Farquhar-von Caemmerer-Berry model (FvCB) model and later modified by Harley and Sharkey (1991), is commonly used to predict the responses of net CO_2 assimilation rate to rising ambient air temperature and atmospheric CO_2. The FvCB model predicts that the rate of net CO_2 assimilation is limited by the smallest of three rates: (*1*) the maximum rate of Rubisco catalyzed carboxylation (Rubisco-limited); (*2*) the regeneration of ribulose-1,5-bisphosphate (RuBP), controlled by electron transport rate (RuBP-limited), and (*3*) the regeneration of RuBP, controlled by the rate of triose-phosphate utilization (TPU-limited).

Recently, the FvCB model was used to model CO_2 assimilation rate of oil palm leaves (Meijide *et al*. 2017, Teh and Cheah 2018, Nugroho 2018). The key FvCB model parameters, such as maximum rate of Rubisco carboxylation (V_{cmax}) and maximum rate of electron transport (J_{max}) used to estimate Rubisco-limited and RuBP-limited rate of CO_2 assimilation of oil palm, were derived differently. Meijide *et al*. (2017) and Nugroho

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Abbreviations: C_a – reference CO_2 concentrations; C_c – CO_2 concentrations at the sites of carboxylation; C_i – intercellular CO_2 concentrations; C_i* – intercellular photocompensation point; F_m' – maximum fluorescence during a saturating light pulse; F_s – the steady-state fluorescence; FvCB – Farquhar-von Caemmerer-Berry model; g_m – mesophyll conductance; g_{sc} – stomatal conductance to CO_2; g_{sw} – stomatal conductance to water vapour; J – rate of electron transport; J_F – electron transport rate estimated from chlorophyll fluorescence; J_{max} – maximum rate of electron transport; P_N – net CO_2 assimilation rate; Q – photosynthetic photon flux density; R_d – rate of leaf day respiration in the light; TPU – maximum rate of triose phosphate utilization; V_{cmax} – maximum rate of Rubisco carboxylation; Γ* – chloroplastic photocompensation point in the absence of leaf day respiration; Φ_{PSII} – electron transport efficiency of PSII.

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(2018) estimated V_{cmax} and J_{max} by assuming infinite mesophyll conductance (g_m), while Teh and Cheah (2018) estimated V_{cmax} by allowing g_m to vary between 0 and 30 mol(CO_2) m^{-2} s^{-1} MPa^{-1}, following Sharkey (2015). These differences in methodology increase the uncertainties in the estimated values of V_{cmax} and in turn the modelled rates of CO_2 assimilation in oil palm because the accuracy of the FvCB model in predicting responses of net CO_2 assimilation rate depends strongly on how accurately its model parameters are parameterized (Harley *et al.* 1992a, Bernacchi *et al.* 2001, 2002, 2003; Walker *et al.* 2013).

Among the model parameters required to estimate V_{cmax} and J_{max}, the parameter g_m has the greatest influence because g_m affects the CO_2 concentration at the carboxylation site (C_c) (von Caemmerer and Evans 1991). If g_m is overestimated, C_c will be higher, and this will underestimate V_{cmax} and J_{max} (Manter and Kerrigan 2004, Sun *et al.* 2014, Weise *et al.* 2015). Thus, the accurate estimation of g_m is required to determine V_{cmax} and J_{max}. The accurate estimation of g_m requires values of R_d (rate of leaf day respiration in the light) and Γ^* (CO_2 photocompensation point in the absence of leaf day respiration) for the species under consideration (Di Marco *et al.* 1990, Harley *et al.* 1992b, Pons *et al.* 2009). If reported values of R_d and Γ^* from other species were used, this will likely increase errors in estimating g_m because estimation of g_m is sensitive to R_d and Γ^* (Harley *et al.* 1992b, Weise *et al.* 2015). Γ^* is known to vary within (Walker *et al.* 2013, Weise *et al.* 2015) and between species (Betti *et al.* 2016) and R_d varies between different ages of leaves and between species (Warren and Dreyer 2006, Gong *et al.* 2018). Thus, for the purpose of modelling CO_2 assimilation rate of oil palm, it is clear that actual estimations of Γ^*, R_d, and g_m for oil palm should be used to parameterize the FvCB model.

The FvCB model was originally parameterized for a leaf temperature of 25°C (Farquhar *et al.* 1980). Using tobacco plants, the *in vivo* temperature response functions of FvCB model parameters were later developed by Bernacchi *et al.* (2001, 2002, 2003) to allow for more accurate prediction of net CO_2 assimilation rate at a wider range of leaf temperatures. They suggested that the derived temperature response functions would improve accuracy of predicting net CO_2 assimilation rate of other C_3 species considering the properties of Rubisco kinetics are conserved among higher plants (von Caemmerer 2000). However, recent experimental evidence suggests that temperature dependencies of Rubisco kinetics are species-specific and could result in significantly different modelled rates of leaf CO_2 assimilation (Walker *et al.* 2013). These findings highlight the importance of parameterizing FvCB model for the species under study when modelling the plant's temperature response of net CO_2 assimilation. To our best knowledge, the temperature dependencies of FvCB model parameters specifically for oil palm, such as V_{cmax}, J_{max}, g_m, R_d, and Γ^*, have not been determined.

This study was undertaken (*1*) to estimate intercellular CO_2 photocompensation point (C_i*), Γ^*, R_d, and g_m and their temperature responses and (*2*) to use these parameters to estimate V_{cmax}, J_{max} and triose-phosphate utilization rate (TPU) and their temperature responses for oil palm.

Materials and methods

Plant material: A total of 18 germinated oil palm seeds (*Elaeis guineensis* Jacq., Deli Dura × AVROS) were planted in black polybags (38 cm wide × 51 cm deep), filled with *Rengam Series* soil (Typic Kandiudults), at Ulu Remis Oil Palm Nursery, Layang (1.844°N 103.446°E). One germinated seed was planted per one polybag. Oil palm seedlings were raised according to standard nursery practices up to the seven months of planting. Six healthy seedlings of a similar size were then selected for leaf gas-exchange and chlorophyll (Chl) fluorescence measurements. The selected six seedlings represent six replicates used for estimating R_d, C_i*, Γ^*, g_m, V_{cmax}, J, and TPU.

Gas-exchange and Chl fluorescence measurements: All gas-exchange and Chl fluorescence measurements were performed using a *LI-6800-01A* portable photosynthesis system equipped with *Multiphase Flash*™ fluorometer (*Li-Cor Inc*., Lincoln, NE, USA). All measurements were conducted on the third bifoliate leaf of each seedling.

Measurements of C_i*, Γ^*, and R_d: The Laisk method (Laisk 1977) was followed to estimate C_i* and R_d. Net CO_2 assimilation rates (P_N) and intercellular CO_2 concentrations (C_i) were measured at four different light intensities [250, 150, 100, and 50 µmol(photon) m^{-2} s^{-1}] at seven reference CO_2 concentrations, C_a, *i.e.*, 400, 400, 200, 150, 100, 75, 50, and 0 µmol(CO_2) mol^{-1}(air). All P_N-C_i measurements were made at five different leaf temperatures of 25, 28, 30, 35, and 40°C. For each leaf temperature, P_N-C_i data collected from gas-exchange measurements made at four different light intensities were used to determine C_i* and R_d by the slope-intercept regression approach (Walker and Ort 2015).

Two approaches were used to determine Γ^*. In the first approach, Γ^* was determined from C_i* and R_d by solving iteratively with g_m using Eq. 1 and 7 because Γ^* can be related to C_i*, R_d, and g_m according to von Caemmerer *et al.* (1994) as

$$\Gamma^* = C_i^* + R_d/g_m \quad (1)$$

For this, C_i* was used as a proxy for Γ^* to solve for g_m using Eq. 7. The resulting g_m was then used to solve for Γ^* using Eq. 1. This iteration process was continued until constant values of g_m and Γ^* were attained (Pons *et al.* 2009).

The second approach used an empirical equation derived from carbon isotopic disequilibrium method (Gong *et al.* 2018) to estimate independent g_m since the range of stomatal conductance to CO_2 (g_{sc}) being studied in oil palm and that in Gong *et al.* (2018) was similar and the relationship between g_{sc} and g_m was linear (Fig. 1S, *supplement*). Thus g_m can be estimated from g_{sc} as

$$g_m = 1.3343g_{sc} - 0.003 \quad (2)$$

$$g_{sc} = g_{sw}/1.6 \quad (3)$$

where g_{sw} is stomatal conductance to water vapour which can be obtained from leaf gas-exchange measurements. Using g_m calculated from Eq. 2, C_c was calculated using Eq. 4 and subsequently P_N-C_i curves were converted to P_N-C_c curves to determine R_d and Γ^* following the slope-intercept regression approach:

$$C_c = C_i - (P_N/g_m) \tag{4}$$

Measurements of g_m, V_{cmax}, J, and TPU: Combined gas-exchange and Chl fluorescence measurement was used to determine g_m, V_{cmax}, J, and TPU. All P_N-C_c measurements were conducted at 400, 300, 200, 100, 50, 400, 400, 500, 600, 800; 1,000; 1,200; 1,400; 1,600; and 1,800 µmol(CO_2) mol^{-1}(air) under saturating light conditions of 1,500 µmol(photon) m^{-2} s^{-1}. Concurrently, Chl fluorescence measurements were performed using the multiphase flash (MPF) approach (Loriaux *et al.* 2013). All measurements were made at seven different leaf temperatures of 25, 28, 30, 33, 35, 38, and 40°C.

Estimating mesophyll conductance: Eq. 2 (Gong *et al.* 2018) and the variable J method were used to estimate g_m for each step of the P_N-C_i curves. Following the variable J method, g_m was estimated by first computing the electron transport rate (J_F [µmol(e^-) m^{-2} s^{-1}]) from Chl fluorescence measurements following Genty *et al.* (1989) as

$$J_F = \alpha \times \beta \times Q \times \Phi_{PSII} \tag{5}$$

where α is the fraction of incoming irradiance absorbed by photosystems which varies between 0.5 and 0.95 (Bauerle *et al.* 2004). β is the partitioning fraction of photons between PSI and PSII which varies between 0.45 and 0.6 (Laisk and Loreto 1996). Q is the photosynthetic photon flux density incident on the leaf [µmol(photon) m^{-2} s^{-1}]. The product $\tau = \alpha\beta$ which represents the fraction of I_{inc} harvested by PSII was estimated for each P_N-C_i measurement using P_N-C_i curve fitting utility developed by Moualeu-Ngangue *et al.* (2017). The upper limit of τ was set at 0.421 which is the default value used by *LI-6800-01A*. Using estimated τ for each P_N-C_i measurement minimises uncertainties between J_F and J calculated from gas exchange. Hence increases the robustness in using J_F as a proxy of J for estimating g_m in oil palm. Φ_{PSII} [mol(e^-) mol^{-1}(photon)] is the electron transport efficiency of PSII which can be estimated from Chl fluorescence measurements as

$$\Phi_{PSII} = (F_m' - F_s)/F_m' \tag{6}$$

where F_s is the steady-state fluorescence and F_m' is the maximum fluorescence during a saturating light pulse (Genty *et al.* 1989). Upon obtaining values of J, A, C_i, and R_d, the parameter g_m [mol(CO_2) m^{-2} s^{-1} MPa^{-1}] was solved iteratively with Γ^* using Eqs. 1 and 7 (Harley *et al.* 1992) as discussed previously:

$$g_m = \frac{P_N}{C_i - \left[\frac{(J + 8(P_N + R_d))}{J - 4(P_N + R_d)}\right]} \tag{7}$$

Since g_m declines with increasing C_i (Fig. 2S, *supplement*) and in order to minimize uncertainties associated with declining g_m as highlighted by Gu and Sun (2014), g_m was determined at reference CO_2 concentration of 400 µmol mol^{-1}(air) and g_m averaged over the reliable range of $10 < dC_c/dP_N < 50$ (averaged g_m) were compared. Averaged g_m was obtained following Harley *et al.* (1992b):

$$\frac{dC_c}{dP_N} = \frac{12\,\Gamma^* J}{[J - 4(P_N + R_d)]^2} \tag{8}$$

Estimating V_{cmax}, J_{max}, and TPU: P_N-C_i data obtained from gas-exchange measurements on 7-month-old oil palm at 25, 28, 30, 33, 35, 38, and 40°C were fitted to a *Microsoft Excel*-based P_N-C_i curve fitting utility (Sharkey 2015) to estimate V_{cmax}, J, and TPU using R_d, Γ^*, g_m and their respective temperature response functions determined in oil palm. J_{max} was then calculated using Eq. 9 (Farquhar and Wong 1984) as

$$\theta J^2 - (ØQ + J_{max})J + ØQJ_{max} = 0 \tag{9}$$

where Q is the photosynthetic photon flux density, Ø is the photon yield of electron transport, and θ is a dimensionless convexity parameter ($\theta \leq 1$). Following Buckley and Diaz-Espejo (2015), Ø and θ was taken as 0.331 mol(e^-) mol^{-1}(photon) and 0.825, respectively.

In order to assess the effects of palm age on V_{cmax}, J_{max}, and TPU, additional gas-exchange and Chl fluorescence measurements were made on 1-, 2-, 7-, and 12-year-old palms under field conditions with measuring temperature ranges between 30 and 36°C. The parameter g_m was estimated at a reference CO_2 of 400 µmol mol^{-1}(air) for each oil palm leaf following the iterative approach using fitted R_d and C_i^* determined in this study. The resulting g_m was then used to estimate V_{cmax}, J, and TPU using P_N-C_i curve fitting utility (Sharkey 2015). J_{max} was then calculated using Eq. 9. Since g_m, V_{cmax}, J_{max}, and TPU were estimated at different leaf temperatures, all values were normalized to 25°C using their respective temperature response function developed in this study.

Temperature response function: The temperature response of R_d, g_m, and V_{cmax} was modelled using a best fit of the data to Eq. 10 while the temperature response of C_i^* and Γ^* was modelled using Eq. 11.

$$(R_d, g_m, V_{cmax}) = \text{value at 25°C} \times \exp(c - \Delta H_a/RT_k) \tag{10}$$

$$(C_i^*, \Gamma^*) = \exp(c - \Delta H_a/RT_k) \tag{11}$$

where c is a scaling constant, ΔH_a is the energy of activation, R is the molar gas constant (8.314 JK^{-1} mol^{-1}), and T_k is the leaf temperature in Kelvin (Tenhunen *et al.* 1976, Bernacchi *et al.* 2001, 2002). The temperature response of J_{max} and TPU was modelled using a best fit of the data to the equation:

$$(J_{max}, \text{TPU}) = \frac{\exp\left(c - \frac{\Delta H_a}{RT_k}\right)}{1 + \exp\left(\frac{\Delta ST_k - \Delta H_d}{RT_k}\right)} \tag{12}$$

where ΔH_d is the energy of deactivation and ΔS is the entropy for the temperature response of J_{max} and TPU (Bernacchi *et al.* 2003).

Statistical analyses: Paired *Student*'s *t*-test was used to compare Γ* estimated from iterative and slope-intercept regression approaches, g_m estimated from Eq. 2 and iterative approach, and g_m determined at reference CO_2 concentration of 400 μmol mol^{-1}(air) and averaged g_m. One-way analysis of variance (*ANOVA*) was performed on V_{cmax}, J_{max}, and TPU estimated for different ages of palms. All *ANOVA* were followed with a *Tukey*'s Studentized Range Test and all statistical analyses were performed using *JMP® Statistical software version 14* (*SAS Institute*, Cary, North Carolina, USA). The Solver add-in program in *Excel® 2016* (*Microsoft Corporation*, Washington, USA) was used to fit measured parameter values for R_d, C_i*, Γ*, g_m, V_{cmax}, J_{max}, and TPU to their respective temperature response models. Coefficient of determination, r^2, was used to define goodness of fit between measured and modelled values and r^2 was calculated using the *CORREL* function in *Excel® 2016*.

Results

R_d, C_i*, and Γ* estimated from slope-intercept regression approach: The estimated C_i* and Γ* for oil palm averaged at 4.32 ± 0.19 and 4.56 ± 0.23 Pa(CO_2), respectively (Table 1). As expected, C_i* estimated from P_N-C_i curves was lower than Γ* estimated from P_N-C_c curves. R_d estimated either from P_N-C_i or P_N-C_c curves were similar, averaged between 0.25 ± 0.05 μmol(CO_2) m^{-2} s^{-1} and 0.26 ± 0.06 μmol(CO_2) m^{-2} s^{-1} (Table 1).

Comparing Γ* estimated from P_N-C_c curve and iterative approach: Γ* derived from P_N-C_c curve using independent g_m estimated by Eq. 2 was very close to the Γ* estimated by iterative approach (Table 2). Iterative approach estimated Γ* averaged at 4.54 ± 0.17 Pa(CO_2) while Γ* derived from P_N-C_c curve averaged at 4.56 ± 0.23 Pa(CO_2), suggesting Γ* estimated for oil palm is reliable.

Comparing g_m estimated from Eq. 2 and iterative approach: Averaged g_m estimated by iterative approach were slightly higher than averaged g_m determined by Eq. 2 but the differences were not significant while g_m determined at 400 μmol(CO_2) mol^{-1}(air) by both methods were identical (Table 3). Similarly, when comparing g_m estimated by the same method, either iterative approach or Eq. 2, no significant differences were observed between g_m determined at 400 μmol(CO_2) mol^{-1}(air) and averaged g_m. The results suggest that the estimated g_m is reliable and either g_m determined at 400 μmol(CO_2) mol^{-1}(air) or averaged g_m can be used to estimate V_{cmax}, *J*, and TPU in oil palm.

Temperature response of R_d, C_i*, Γ*, and g_m in oil palm: All three parameters R_d, C_i*, and Γ* responded to temperature exponentially without thermal deactivation even at high temperature of 40°C (Fig. 1) and all were

Table 1. Leaf day respiration (R_d), intercellular CO_2 photocompensation point (C_i*), and chloroplastic CO_2 photocompensation point in the absence of R_d (Γ*) determined from CO_2 assimilation curves measured under four sub-saturating photosynthetic photon flux densities and six intercellular CO_2 concentrations. The slope-intercept regression approach was used to determine R_d, C_i*, and Γ*. Values of g_m derived from Eq. 2 were used to convert P_N-C_i curves to P_N-C_c curves. Values are means (± SD) of six replicates. Measurements were made at a leaf temperature of 25°C.

Derived from P_N-C_i curves		Derived from P_N-C_c curves	
C_i* [Pa(CO_2)]	R_d [μmol(CO_2) m^{-2} s^{-1}]	Γ* [Pa(CO_2)]	R_d [μmol(CO_2) m^{-2} s^{-1}]
4.32 ± 0.19	0.26 ± 0.06	4.56 ± 0.23	0.25 ± 0.05

Table 2. Comparison of Γ* determined by iterative and slope-intercept regression approaches. Values of g_m derived from Eq. 2 were used to convert P_N-C_i curves to P_N-C_c curves, Γ* was subsequently determined using slope-intercept regression approach. Eqs. 1 and 7 were solved iteratively to determine g_m and Γ*. g_m – mesophyll conductance; Γ* – chloroplastic CO_2 photocompensation point in the absence of leaf day respiration. Values are means (± SD) of six replicates. Measurements were made at a leaf temperature of 25°C.

Model parameter	Slope-intercept regression	Iterative approach	*p*-value
Γ* [Pa(CO_2)]	4.56 ± 0.23	4.54 ± 0.17	0.695

Table 3. Mesophyll conductance (g_m) determined in oil palm using iterative approach and Eq. 2. In iterative approach, g_m was determined by solving Eqs. 1 and 7 iteratively. g_m determined at reference CO_2 concentration of 400 μmol mol^{-1} ($g_m[C_a]$) and averaged g_m (averaged over the reliable range of $10 < dC_c/dP_N < 50$) are means (± SD) of six replicates. All g_m values were determined at a leaf temperature of 25°C. na denotes not applicable.

Method	$g_m[C_a]$ [mol(CO_2) m^{-2} s^{-1} MPa^{-1}]	Averaged g_m [mol(CO_2) m^{-2} s^{-1} MPa^{-1}]	$g_m[C_a]$ × averaged g_m *p*-value
Iterative approach	1.25 ± 0.25	1.32 ± 0.30	0.661
Eq. 2	1.25 ± 0.27	1.28 ± 0.28	0.835
p-value	0.920	0.825	na

well described by the simple Arrhenius equation with r^2 value of > 0.98. C_i* and Γ* were less temperature sensitive than R_d as indicated by their lower activation energy (ΔH_a) (Table 4).

Oil palm g_m increased exponentially with temperature up to 40°C without thermal deactivation (Fig.1*D*). However, the response of g_m to temperature was rather insensitive. At the highest temperature of 40°C, g_m only increased to 1.60 ± 0.24 mol(CO_2) m^{-2} s^{-1} MPa^{-1}, representing a small increase of 0.35 mol(CO_2) m^{-2} s^{-1} MPa^{-1} despite a significant 15°C increase in temperature. The present study also demonstrated that the temperature responses of Γ* and g_m in oil palm differed from tobacco (Bernacchi *et al.* 2002) and *Arabidopsis* (Walker *et al.* 2013) (Fig. 1), suggesting the temperature dependencies of oil palm Γ* and g_m are likely species-specific.

***V_{cmax}*, *J_{max}*, TPU and their temperature responses**: At 25°C, V_{cmax}, J_{max}, and TPU determined in 7-month-old oil palms averaged at 74 ± 12, 94 ± 13, and 6.7 ± 0.7 µmol(CO_2) m^{-2} s^{-1}, respectively. V_{cmax} increased exponentially with temperature up to 226 ± 32 µmol(CO_2) m^{-2} s^{-1} at 40°C without deactivation of Rubisco (Fig. 2*A*, Table 5). However, inclusion of a thermal deactivation term improved its goodness of fit, indicating that V_{cmax} likely optimized at 40°C. Similarly, J_{max} and TPU increased exponentially with temperature but only up to 38°C, thereafter both parameters declined to lower values due to occurrence of thermal deactivation (Fig. 2*B*,*C*; Table 5). At 38°C, J_{max} and TPU averaged at 184 ± 30 and 11.3 ± 2 µmol(CO_2) m^{-2} s^{-1} but declined to 177 ± 17 and 10.4 ± 1.2 µmol(CO_2) m^{-2} s^{-1}, respectively, at 40°C. All three parameters were well described by the Arrhenius function except that J_{max} and TPU required a deactivation term (r^2 = 0.9971, 0.9885, 0.9352 for V_{cmax}, J_{max}, and TPU, respectively). In this study, temperature had a greater effect on V_{cmax} which increased about threefold between 25 and 40°C while J_{max} and TPU only increased about twofold over the same temperature range.

Using R_d, Γ*, and g_m determined in this study, V_{cmax}, J_{max}, and TPU were estimated for 7-month-, 1-, 2-, 7-, and 12-year-old oil palms, respectively (Table 6). Field-grown palms (2-, 7-, and 12-year-old palms) had significantly higher V_{cmax} than the nursery-grown palms (7-month- and 1-year-old palms). Similarly, J_{max} and TPU estimated from field-grown palms were higher than that of nursery-grown

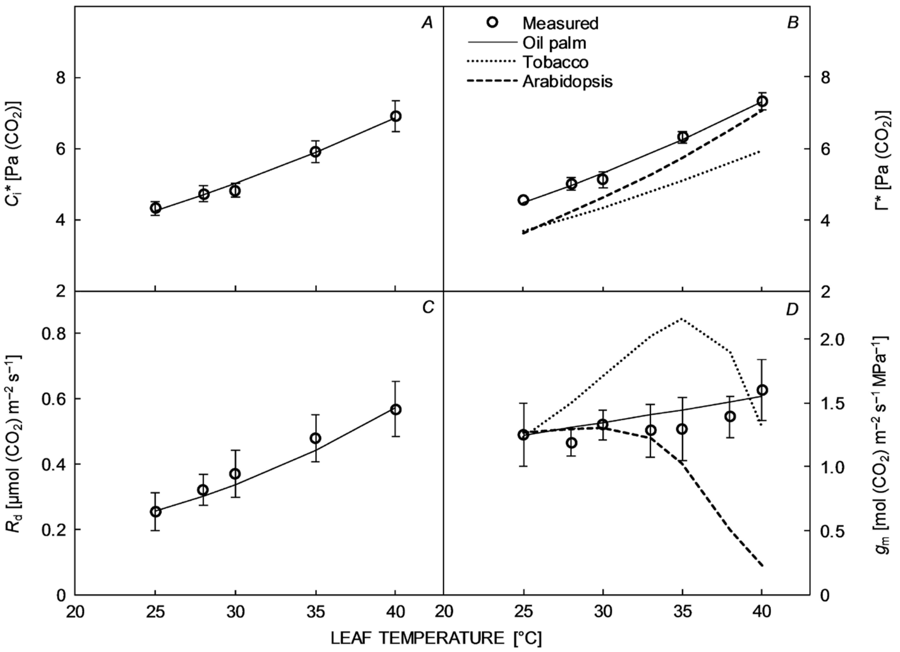

Fig. 1. Temperature response of intercellular CO_2 photocompensation point (C_i*) (*A*), chloroplastic CO_2 photocompensation point in the absence of R_d (Γ*) (*B*), leaf day respiration rate (R_d) (*C*), and mesophyll conductance (g_m) (*D*) in oil palm (*open circles*). *Solid line* represents best-fit temperature response of C_i*, Γ*, R_d, and g_m in oil palm. *Dotted* and *dashed lines* represent modelled Γ* and g_m derived from tobacco (Bernacchi *et al.* 2002) and *Arabidopsis* (Walker *et al.* 2013). Temperature responses of oil palm C_i*, Γ*, R_d, and g_m were calculated using ΔH_a and *c* given in Table 4. All measured values are means ± SD of six replicates. Γ* and g_m were determined by solving Eqs. 1 and 7 iteratively.

Table 4. The scaling constant (*c*) and energy of activation (ΔH_a [kJ mol^{-1}]) for oil palm. Equation Parameter = value at 25°C × exp($c - \Delta H_a/RT_k$) was used to estimate *c* and ΔH_a for R_d and g_m while equation Parameter = exp($c - \Delta H_a/RT_k$) was used to estimate *c* and ΔH_a for C_i* and Γ*. The scaling constant (*c*) has been corrected to give partial pressure in term of Pa as determined in Sharkey *et al.* (2007). R_d and g_m were normalized to 1 at 25°C. Γ* and g_m were determined by solving Eqs. 1 and 7 iteratively. na denotes not applicable.

	R_d [µmol(CO_2) m^{-2} s^{-1}]	C_i* [Pa(CO_2)]	Γ* [Pa(CO_2)]	g_m [mol(CO_2) m^{-2} s^{-1} MPa^{-1}]
Value at 25°C	1.00	4.32	4.54	1.0
c	16.78	11.43	11.65	4.5
ΔH_a	41.60	24.75	25.14	11.2

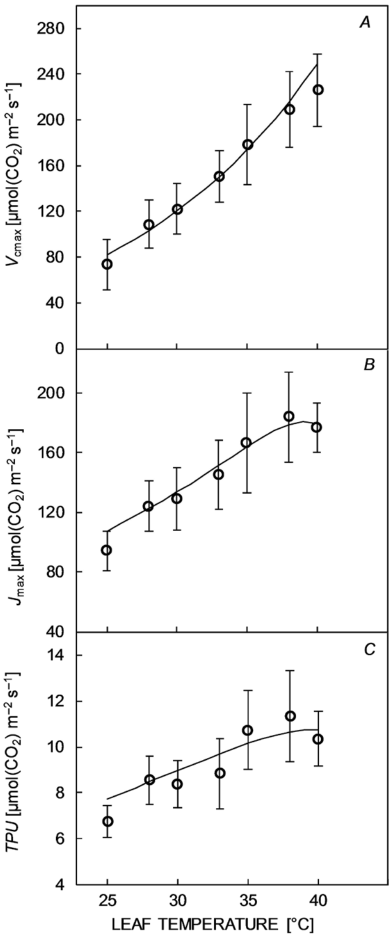

Fig. 2. Temperature response of maximum rate of Rubisco carboxylation (V_{cmax}) (*A*), maximum potential electron transport rate (J_{max}) (*B*), and triose phosphate utilization rate (TPU) (*C*) in oil palm (*open circles*). *Solid line* represents best-fit temperature response of V_{cmax}, J_{max}, and TPU in oil palm. Measured values are means ± SD of six replicates.

palms. However, no relationship was found between photosynthetic capacity (V_{cmax}, J_{max}, and TPU) and palm age in field-grown palms. On average, V_{cmax}, J_{max}, and TPU were 118 ± 26, 118 ± 16, and 7.9 ± 0.9 μmol(CO$_2$) m^{-2} s^{-1}, respectively, for field-grown palms aged between 2 and 12 years. Despite markedly different in V_{cmax}, J_{max}, and TPU between nursery- and field-grown palms, it is interesting to note that g_m determined in both groups of palms was statistically similar except for the 7-year-old palms which have significantly higher g_m. The higher g_m values did not seem to affect estimation of V_{cmax}, J_{max}, and TPU in the 7-year-old palms.

Discussion

R_d, C_i*, Γ*, and g_m determined in oil palm: Γ* is most commonly determined using the Laisk's method by first having C_i* and R_d determined, and then solve for Γ* by accounting for g_m using equation $\Gamma^* = C_i^* + R_d/g_m$ (von Caemmerer *et al.* 1994). The Laisk's method was, however, criticised for estimating a biased Γ* (Gu and Sun 2014, Gong *et al.* 2018). Using the slope-intercept regression approach, Walker and Ort (2015) demonstrated that biases associated with the Laisk's method could be minimized. Similar approach was used in this study to determine C_i* and R_d at different temperatures which were then used to solve for Γ* and g_m iteratively using equation $\Gamma^* = C_i^* + R_d/g_m$ (Eq. 1) and variable *J* method (Eq. 7). At 25°C, the estimated Γ* and g_m compares well with the Γ* and g_m estimated using Eq. 2 (Tables 2, 3), an empirical equation relating stomatal conductance to g_m (Gong *et al.* 2018). Eq. 2 was used as an independent approach to check on Γ* and g_m estimated from iterative approach. Both methods might compromise on the accuracy of g_m estimates and thus increases uncertainty in the estimates of Γ*. The use of more reliable g_m estimates such as g_m estimated from the carbon isotope discrimination method (Walker *et al.* 2013, von Caemmerer and Evans 2015) or carbon isotope disequilibrium method (Gong *et al.* 2018) was believed to allow more accurate estimation of Γ*. However, the same isotope discrimination method has yielded different g_m estimates in *Arabidopsis* (Walker *et al.* 2013, von Caemmerer and Evans 2015). Thus, oil palm Γ* and g_m estimated in this study can be used as the first approximation.

The rate of oil palm leaf day respiration, R_d, was generally lower than that of other C$_3$ species. Peisker and Apel (2001) estimated R_d for *Nicotiana tabacum* varying between 0.37–1.22 μmol(CO$_2$) m^{-2} s^{-1} while Gong *et al.* (2018) estimated R_d for six herbaceous C$_3$ species between 0.7–1.17 μmol(CO$_2$) m^{-2} s^{-1}. R_d has been shown to vary between different ages of leaves and between species (Warren and Dreyer 2006, Gong *et al.* 2018). It is thus possible that oil palm has low R_d. However, the low R_d observed might be attributed to palm age since 7-month-old seedlings instead of adult palms were used for measurements. Thus measurement on adult palms would be useful to confirm this finding. The estimates of C_i* and Γ* determined for oil palm were well within the range of C$_3$ species (Walker and Ort 2015) and C_i* was slightly lower than Γ* due to the effect of mesophyll conductance (von Caemmerer *et al.* 1994). Hence, it is biased to use C_i* as a proxy of Γ* for estimation of g_m. In this respect, using iterative approach to solve for Γ* and g_m or using Eq. 2 to get an independent estimate of g_m which was subsequently used to estimate Γ* appeared justifiable.

Mesophyll conductance estimated by the iterative approach and Eq. 2 was well within the range of woody C$_3$ species [0.05–1.89 mol(CO$_2$) m^{-2} s^{-1} MPa^{-1}] (Manter and Kerrigan 2004) but was much lower than that of herbaceous C$_3$ crops, such as paddy [3.9–5.0 mol(CO$_2$) m^{-2} s^{-1} MPa^{-1}], wheat [3.2–6.38 mol(CO$_2$) m^{-2} s^{-1} MPa^{-1}] (Ethier and Livingston 2004), and soybean [4.9 ± 0.5 mol(CO$_2$) m^{-2} s^{-1} MPa^{-1}] (von Caemmerer and Evans 2015). The apparently low g_m observed in oil palm indicates that g_m would likely impose considerable limitation to CO$_2$ assimilation by the oil palm leaves.

Temperature response of R_d, C_i*, Γ*, and g_m: Given the highly variable nature of R_d between plant species, ages

Table 5. The scaling constant (c), energies of activation (ΔH_a [kJ mol^{-1}]) and deactivation (ΔH_d [kJ mol^{-1}]) and entropy (ΔS) for the temperature response of maximum rate of Rubisco carboxylation (V_{cmax}), maximum potential electron transport rate (J_{max}), and triose phosphate utilization rate (TPU) in oil palm. V_{cmax} data was fitted to the equation Parameter = $\exp(c - \Delta H_a/RT_k)$ while J_{max} and TPU data was fitted to the equation Parameter = $\exp(c - \Delta H_a/RT_k)/1 + \exp(\Delta S \times T_k - \Delta H_d/RT_k)$. V_{cmax}, J_{max}, and TPU were all given in µmol(CO$_2$) m^{-2} s^{-1}. na denotes not applicable.

Parameter	Value at 25°C	c	ΔH_a	ΔH_d	ΔS
V_{cmax}	1	23.327	57.55	na	na
J_{max}	1	13.405	32.81	443.6	1.40
TPU	1	9.542	23.30	208.5	0.65

Table 6. Maximum rate of carboxylation of Rubisco (V_{cmax}), maximum rate of electron transport (J_{max}), and triose phosphate utilization rate (TPU) estimated from P_N-C_c curves. Mesophyll conductance (g_m) at reference CO$_2$ concentration of 400 µmol mol^{-1} was estimated for each oil palm leaf by solving Eqs. 1 and 7 iteratively. Using the estimated g_m, parameters V_{cmax}, J, and TPU were estimated using the P_N-C_i curve fitting utility (Sharkey 2015) with leaf day respiration (R_d) and g_m entered as a constant for each oil palm leaf. J_{max} was then calculated using Eq. 9. Values of g_m, V_{cmax}, J_{max}, and TPU were normalized to 25°C using their respective temperature response function determined in this study. Values of g_m, V_{cmax}, J_{max}, and TPU are means (± SD) of six replicates for 7-month-old palm and four replicates for 1-, 2-, 7-, and 12-year-old palm. Oil palms are normally field planted after growing one year in the nursery. Mean values with *different letters* within a same column are significantly different at $p<0.05$ by *Tukey*'s Studentized Range test.

Age of palm	g_m [mol(CO$_2$) m^{-2} s^{-1} MPa^{-1}]	V_{cmax} [µmol(CO$_2$) m^{-2} s^{-1}]	J_{max} [µmol(CO$_2$) m^{-2} s^{-1}]	TPU [µmol(CO$_2$) m^{-2} s^{-1}]
7 months	1.25 ± 0.25^{b}	78 ± 22^{b}	94 ± 13^{bc}	6.7 ± 0.7^{ab}
1 year	1.08 ± 0.14^{b}	72 ± 20^{b}	82 ± 15^{c}	5.8 ± 1.0^{b}
2 years	1.09 ± 0.17^{b}	115 ± 14^{a}	126 ± 7^{ab}	8.4 ± 0.7^{a}
7 years	1.78 ± 0.13^{a}	120 ± 32^{a}	134 ± 30^{a}	8.3 ± 1.2^{a}
12 years	1.25 ± 0.39^{b}	119 ± 33^{a}	115 ± 15^{abc}	7.1 ± 0.7^{ab}
p-value	0.004	0.018	0.002	0.002

of leaves, and growth conditions (Villar *et al.* 1994, Ayub *et al.* 2011, Gong *et al.* 2018), many studies have found no consistent relationship between R_d and temperature (Villar *et al.* 1994, Atkin *et al.* 2000, Warren and Dreyer 2006, Walker *et al.* 2013). Thus, the close relationship between R_d and temperature observed in oil palm suggests that the rate of R_d measured in this study is reliable though the rate of R_d is challenging to measure (Hanson *et al.* 2016, Tcherkez *et al.* 2017). From the modelling perspective, this study revealed that R_d temperature response function determined in this study can be used to model temperature response of R_d in oil palm.

The marked differences in temperature response of Γ^* between oil palm, tobacco, and *Arabidopsis* was not all unexpected. Similar observations were reported by Warren and Dreyer (2006), Walker *et al.* (2013), and Weise *et al.* (2015) when compared Γ^* temperature response between *Q. canariensis* and tobacco; between tobacco and *Arabidopsis*, and between *Arabidopsis* itself. These differences in temperature response could be attributable to species-specific variation in photorespiratory efficiency with temperature, suggesting variation in stoichiometry of CO$_2$ release per Rubisco oxygenation can cause Γ^* responds differently to temperature (Walker *et al.* 2017) even though Γ^* is relatively conserved among C$_3$ species (von Caemmerer 2000). Thus, it is best using Γ^* determined in oil palm to estimate Rubisco kinetics, g_m and CO$_2$ assimilation of oil palm particularly at elevated temperatures. Previous studies have shown that g_m (Harley *et al.* 1992b, Weise *et al.* 2015), V_{cmax}, and J (Weise *et al.* 2015) are very sensitive to changes in Γ^* thus its accuracy is critical.

Mesophyll conductance of oil palm is insensitive to temperature and responds to temperature differently compared to tobacco (Bernacchi *et al.* 2002) and *Arabidopsis* (Walker *et al.* 2013). These differences in the temperature response of g_m demonstrate variation in species-specific capacity to transfer CO$_2$ from the intercellular airspace to the site of carboxylation at chloroplast stroma at elevated temperatures. Thus, the present findings suggest that it is best to use temperature response function of g_m derived from oil palm to estimate g_m or Rubisco kinetics of oil palm at elevated temperatures.

Temperature insensitivity of g_m has also been seen in *Arabidopsis* between 15 and 27°C (Bunce 2008) and between 15 and 35°C (Walker *et al.* 2013), *Quercus canariensis* between 20 and 35°C (Warren and Dreyer 2006), *Eperua grandiflora* between 28 and 38°C (Pons and Welschen 2003), and *Triticum aestivum*, *Quercus engelmannii*, *Lophostemon confertus*, and *Arabidopsis* all between 15 and 40°C (von Caemmerer and Evans 2015). Thus, it is no surprise that oil palm g_m is insensitive to temperature.

V_{cmax}, J_{max}, TPU and their temperature responses: The FvCB model of C_3 photosynthesis has been used to scale CO_2 assimilation in oil palm from leaf to canopy and ecosystem levels (Fan *et al*. 2015, Teh and Cheah 2018, Meijide *et al*. 2017). Modelling oil palm CO_2 assimilation under natural environment requires that the temperature response of FvCB model parameters, such as V_{cmax}, J_{max}, and TPU, are parameterized for oil palm since response of leaf CO_2 assimilation to temperature is species-specific (Walker *et al*. 2013, von Caemmerer and Evans 2015). In this context, this study provides the first estimates of temperature response of V_{cmax}, J_{max}, and TPU in oil palm. The temperature dependency of V_{cmax}, J_{max}, and TPU observed in oil palm clearly showed that optimal temperatures for RuBP carboxylation, RuBP regeneration, and triose phosphate utilization were between 38 and 40°C, consistent with other studies on V_{cmax} and J_{max} (Díaz-Espejo *et al*. 2006, Warren 2008, Alonso *et al*. 2009, Greer and Weedon 2012) but the thermal optimum of oil palm TPU was higher than that of other species with thermal optimum varied between 33 and 35°C (Harley *et al*. 1985, 1992a; Wise *et al*. 2004, Yang *et al*. 2016).

In this study, V_{cmax} estimated from palms of different ages was much higher than the reported V_{cmax} for oil palms grown under field conditions. Teh and Cheah (2018) reported V_{cmax} declines with palm age, from a mean (± SE) of 91.1 ± 3.7 µmol(CO_2) m^{-2} s^{-1} at 1-year-old to 69.8 ± 2.6 µmol(CO_2) m^{-2} s^{-1} at 19-year-old, while Meijide *et al*. (2017) estimated V_{cmax} for 1-year-old and 12-year-old palms to be 51.97 ± 9.43 and 42.00 ± 2.42 µmol(CO_2) m^{-2} s^{-1}, respectively. Nugroho (2018), on the other hand, estimated V_{cmax} for shaded and sunlit leaves from 13-year-old palms to be 28.1 and 53.3 µmol(CO_2) m^{-2} s^{-1}, respectively. The discrepancies observed are likely related to R_d, Γ^*, and g_m and their temperature responses used to estimate V_{cmax}. In Teh and Cheah (2018), parameters, such as V_{cmax}, J, TPU, R_d, and g_m, were estimated simultaneously using P_N-C_i curve fitting utility (Sharkey 2015). This approach tends to overestimate g_m and underestimate V_{cmax} because the P_N-C_i curve fitting utility allows V_{cmax} and g_m to complement each other as to obtain a very good fit to the observed data (Sharkey 2015). High g_m overestimates CO_2 concentration at the site of carboxylation (C_c) and leads to lower estimates of V_{cmax} (Manter and Kerrigan 2004, Sun *et al*. 2014) as in the case of Teh and Cheah (2018). In Meijide *et al*. (2017) and Nugroho (2018), an *R* (*R Core team* 2013) toolkit for leaf gas exchange called *Plantecophys* (Duursma 2015) was used to estimate V_{cmax} in oil palm. In both cases, C_i was used to estimate V_{cmax} instead of C_c. This approach assumed infinite g_m and as such underestimated V_{cmax}.

On the other hand, J_{max} estimated in this study is consistent with Nugroho (2018) but higher than that of Meijide *et al*. (2017). Nugroho (2018) estimated J_{max} for sunlit leaves of highly fertilised 13-year-old palms to be 139 µmol(CO_2) m^{-2} s^{-1}, while J_{max} reported by Meijide *et al*. (2017) were 81 and 89 µmol(CO_2) m^{-2} s^{-1} for 1-year-old and 12-year-old palms, respectively. The present study provides the first estimates of TPU for oil palm and the estimated TPU were well within the range reported for woody plants (Wullschleger 1993), indicating that net CO_2 assimilation in oil palm will be limited by the utilization of triose phosphates in the Calvin-Benson cycle, particularly under high CO_2 partial pressure conditions.

No declining trend was found between photosynthetic capacity (V_{cmax}, J_{max}, and TPU) and palm age for field-grown palms. This is inconsistent with Teh and Cheah (2018) and Meijide *et al*. (2017). Many studies reported changes in V_{cmax} and J_{max} with stand age (McDowell *et al*. 2002, Law *et al*. 2003, Han *et al*. 2008, Kositsup *et al*. 2010) but many studies also reported V_{cmax} and J_{max} did not decline with the stand age (Hubbard *et al*. 1999, Barnard and Ryan 2003, Phillips *et al*. 2003, Delzon *et al*. 2005). Thus, the stand age alone could not explain the decline in V_{cmax} observed in Teh and Cheah (2018) and Meijide *et al*. (2017).

Modelling net photosynthesis: Leaf level CO_2 response of net photosynthesis in oil palm was modelled at 25 and 35°C using the FvCB model and its parameters for oil palm (determined in this study) and for tobacco (determined in Bernacchi *et al*. 2001, 2002, 2003) in order to discern how species-specific model parameters impact net photosynthesis. At 25°C, CO_2 assimilation rates were 5% higher when modelled using oil palm-specific parameters as compared with tobacco-specific parameters (Fig. 3S, *supplement*). At the higher temperature of 35°C, using oil palm-specific parameters produced higher assimilation rates by as much as 10% than that using tobacco-specific parameters (Fig. 3S). The differences in assimilation rates were most obvious at higher CO_2 partial pressure, where regeneration of RuBP most limits CO_2 assimilation. Similar species-specific responses of CO_2 assimilation rates to increasing CO_2 partial pressure at 25 and 35°C were reported by Walker *et al*. (2013) who compared CO_2 assimilation rates between *Arabidopsis* and tobacco. However, the differences between *Arabidopsis* and tobacco were mostly at CO_2 partial pressure close to the inflection point between Rubisco and RuBP-regeneration limited photosynthesis.

This simple simulation of CO_2 assimilation demonstrates the importance of using oil palm-specific parameter values to model CO_2 assimilation in oil palm at elevated temperature and atmospheric CO_2 partial pressure. A 10% difference in CO_2 assimilation rate at the leaf level is large enough to detrimentally affect the accuracy of estimating the photosynthetic carbon assimilation in oil palm at canopy and ecosystem levels.

Conclusion: Using leaf gas-exchange and chlorophyll fluorescence measurements, we were able to obtain estimates of R_d, C_i^*, Γ^*, g_m, V_{cmax}, J_{max}, and TPU for oil palm. Their temperature responses were also determined. Temperature responses of oil palm Γ^* and g_m were found to be species-specific and therefore should be used to estimate V_{cmax}, J_{max}, and TPU in oil palm. R_d, C_i^*, Γ^*, V_{cmax}, and g_m were found to respond to temperature exponentially without thermal deactivation between 25 and 40°C, while J_{max} and TPU also responded to temperature exponentially but only up to 38°C, thereafter declined slightly at 40°C. Taken altogether, this study determined some key FvCB model parameters and their temperature dependencies for oil palm. This is the way for more accurate modelling of photosynthetic carbon assimilation in oil palm particularly under future elevated temperatures and CO_2 concentrations.

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