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Optimum air temperature for tropical forest photosynthesis: mechanisms involved and implications for climate warming

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Introduction

Tropical forests are characterized by a warm and humid climate (Corlett 2011); however, there is currently little consensus on whether climate change will affect tropical forests. Paleocological studies show that neotropical vegetation largely persisted after a 3 to 5 °C warming during the Paleocene–Eocene Thermal Maximum (Jaramillo et al 2010). However, this historical warming was short-lived and considerably slower than current warming and future warming predicted for the next century. A survey of the temperatures of broad-leaved forest land cover suggests that climatic warming could have severe consequences for tropical florals (Wright et al 2009). Closed-canopy forests are found in areas with a mean annual temperature below 28 °C, whereas areas with mean temperatures above 28 °C support shrubs and grasses instead of broad-leaved evergreen trees. Given that excessively high temperatures are typically associated with a high evaporative demand and dry climate, the absence of closed-canopy forests in areas with temperatures above 28 °C could also be a consequence of water limitation. This past record and the distribution of tropical forests suggest a temperature limit, and therefore the ecosystem sensitivity to this threshold needs to be further studied.

Photosynthetic performance, the basis for carbon sequestration and ecosystem production, is temperature dependent. In general, the light-saturated photosynthetic rate increases with temperature to a peak, which is followed by a decline (Sage and Kubien 2007). It has been suggested that current temperatures in regions supporting tropical forests are very close to or even exceed their photosynthetic optimum temperature ($T_{opt}$) (Doughty and Goulden 2008). This is a potentially ominous warming sign for our warming Earth. Tropical forests store large amounts of carbon in biomass (Dixon et al 1994). Consequently, a slight perturbation in tropical carbon fluxes could have wide-ranging effects on global atmospheric CO2 concentrations (Anderegg et al 2015). Temperatures in excess of $T_{opt}$ could result in a sharp decline in photosynthetic carbon sequestration in tropical forests (Doughty and Goulden 2008, Vårhammar et al 2015). A decline in CO2 uptake by the forests could in turn result in an increase in atmospheric CO2, which would further accelerate warming through positive feedback.

Model simulations indicate that tropical forests are currently not at their high-temperature threshold. With the aid of widely-used process models, Lloyd and Farquhar (2008) showed that the temperature of tropical forests was still well below $T_{opt}$. They argue that the apparent decrease in photosynthetic rate with
increasing temperature is predominantly an indirect effect of stomatal closure (30%) and not a direct effect of warming on mesophyll processes (2%). Temperature increases could reduce photosynthesis, either directly through inhibiting the activity of photosynthetic enzymes and electron transport, or indirectly through decreasing stomatal conductance (Farquhar et al. 1980). A linear increase in temperature could lead to an exponential growth of water vapour pressure deficit (D) (Campbell and Norman 1998), whereas stomatal aperture (conductance) decreases with increased D (Damour et al. 2010). Since CO$_2$ enters the mesophyll through stomata, intercellular CO$_2$ ($\delta$) and photosynthesis decrease when stomatal conductance (g) declines (Farquhar et al. 1980). In contrast to the direct effects of temperature on the photosynthetic apparatus, a reduction in photosynthesis caused by increased stomatal resistance could be offset, at least partly, by elevated CO$_2$ (Lloyd and Farquhar 2008). Elevated CO$_2$ increases $T_{opt}$ by reducing photorespiration and stomatal resistance, which has a positive effect on the acclimation potential of photosynthesis. Moreover, stomatal closure reduces transpiration and subsequently reduces its cooling effect (Doughty 2011). This could in turn lead to excessively high temperatures at the leaf level, which could cause irreversible damage to the photosynthetic machinery (Berry and Björkman 1980, Doughty 2011).

In this study, to examine the potential effects of climate change on forest photosynthesis, we first quantified the $T_{opt}$ of ecosystem photosynthesis ($T_{opt}$) for seven tropical forests across different continents. We then analyzed the relationship between $T_{opt}$, and mean growing season air temperature ($T_a$) to confirm the widely held consensus that these parameters increase simultaneously. Ecosystem physiological parameters were then inverted using a big-leaf analogized process model driven by ecosystem photosynthesis measurements. Further, we tested the hypothesis proposed by Lloyd and Farquhar (2008), which suggests that stomatal processes play a prominent role in determining $T_{opt}$, and that increasing ambient CO$_2$ concentrations will increase tropical forest $T_{opt}$, which would imply that these forest are not as vulnerable to climate change as may have been indicated by Doughty and Goulden (2008). Finally, we discuss the implications of different climate warming scenarios on ecosystem photosynthesis in tropical forests.

### Material and methods

#### Studied sites

Tropical rainforests are primarily distributed in the Amazon, Southeast Asia, and Africa. In the present study, we investigated seven tropical forests, four of which are located in Southeast Asia and three are in the Amazon (table 1). All three Amazonian sites are near the equator (latitude $\sim$3°S): from west to east K34, K67, and K83. The four Asian rainforests are in two different locations: two sites (PDF and PSO) are near the equator (\sim$2^\circ$S or N) and the other two Thailand forests (MKL and SKR) are located at $\sim$14°N. The selected Asian rainforests are dominated by trees in the Dipterocarpaceae; the exception being the peat swamp forest of the PDF site. Canopy height typically exceeds 30 m, although in the peat forest the maximum height is approximately 26 m. The forest at the K83 site has previously been selectively logged.

### Table 1. Site information.

| Lat.                  | Long.                  | Age      | Hc     | LAI     | $T_a$ (°C) | $T_{opt}$ (°C) | System | Anemometer | IRGA | Period       | Country |
|-----------------------|------------------------|----------|--------|---------|------------|--------------|--------|-------------|------|--------------|---------|
| **Amazonian**         |                        |          |        |         |            |              |        |             |      |              |         |
| K34 2° 36’ S         | 60° 12’ W              | Primary  | 30–35  | 4.7     | 26.7       | 2286         | CP     | Wind master, | Li-6262 | 1999–2006    | Brazil  |
| K67 2° 51’ S         | 54° 58’ W              | Primary  | 35–40  | 6.0     | 24.8       | 1811         | CP     | CSAT3, Campbell | Li-6262 | 2002–2006    | Brazil  |
| K83 3° 3’ S          | 54° 56’ W              | Selective | 35–40  | 4.9     | 24.8       | 1811         | CP     | CSAT3, Campbell | Li-7000/ | 2000–2004    | Brazil  |
| **SE Asia**           |                        |          |        |         |            |              |        |             |      |              |         |
| MKL 14° 34’ N        | 98° 50’ E              | ~30 (2008)| 30     | 2–3     | 27.5       | 1650         | CP     | Wind master, | Li-6262 | 2003–2004    | Thailand |
| PDF 2° 20’ N         | 114° 2’ E              | ~26      | 5      | 26.3    | 2231      | CSAT3, Campbell | OP     | CSAT3, Campbell | Li-5000, | 2002–2005    | Indonesia |
| PSO 2° 58’ N         | 102° 18’ E             | Primary  | 35–45  | 6.52    | 25.3       | 1804         | OP     | SAT550, Kajio | Li-7500, | 2003–2009    | Malaysia |
| SKR 14° 29’ N        | 101° 55’ E             | Mature   | 35     | 3.5–4.0 | 26.2       | 1240         | CP     | Wind master, | Li-6262 | 2001–2003    | Thailand |

$'-$: no data available; Lat., Latitude; Long., Longitude; Age, stand age (yr); Hc, canopy height (m); LAI, leaf area index; $T_a$, mean annual temperature (°C); ppt, precipitation (mm); System, the open (OP) or closed path (CP) eddy covariance system; IRGA, the infrared gas analyzer model.
Table 2. Terms (and their abbreviations) used at the leaf-level and the corresponding abbreviations used at ecosystem-level. \( P_e \): leaf gross photosynthetic rate; \( G_{PP} \): gross primary production of ecosystem; \( R_e \): leaf respiration; \( R_{EC} \): ecosystem respiration, which is the sum of the autotrophic and heterotrophic respiration; \( T_e \): leaf temperature; \( T_c \): air temperature near the top of the forest canopy; \( c_i \): leaf intercellular CO2 concentration; \( g_i \): bulk canopy intercellular CO2 concentration; \( D_h \): leaf-to-air water vapour deficit; \( g_o \): stomatal conductance; \( g_s \): canopy conductance; \( P_n \): net leaf photosynthesis rate, where \( P_n = P_e - R_e - N_{EE} \); \( N_{EE} \): net ecosystem exchange, where \( N_{EE} = G_{PP} - R_{EC} \).

| General description | Leaf | Ecosystem |
|---------------------|------|-----------|
| Gross photosynthesis | \( P_e \) | \( G_{PP} \) |
| Dark respiration: \( R_d \) | \( R_e \) | \( R_{EC} \) |
| Temperature | \( T \) | \( T_c \) |
| Intercellular CO2 concentration: \( c_i \) | \( c_i \) | \( c_i \) |
| Water vapour deficit: \( D_h \) | \( D_h \) | \( D_h \) |
| Stomatal or canopy conductance: \( g_s \) | \( g_s \) | \( g_s \) |
| Maximum carboxylation rate: \( V_{cmax} \) | \( V_{cmax} \) | \( V_{cmax} \) |
| Maximum electronic transport rate: \( J_{max} \) | \( J_{max} \) | \( J_{max} \) |
| Conductance sensitivity: \( g_o \) | \( g_o \) | \( g_o \) |
| Temperature factor: \( S_h \) | \( S_h \) | \( S_h \) |
| Temperature factor: \( H \) | \( H_h \) | \( H_h \) |
| Net photosynthesis rate | \( P_n \) | \( N_{EE} \) |
| Optimal temperature: \( T_{opt} \) | \( T_{optE} \) | \( T_{optE} \) |

Determining the optimum temperature \( T_{opt} \) of photosynthesis

Determining of \( T_{opt} \) could be done based on gross photosynthesis \( (G_{PP}) \) dataset. The advantage of this way is reducing uncertainties related to respiratory processes which are most significant in eddy flux cases \((Yi \ et \ al \ 2000, Yi \ et \ al \ 2004)\). However, a reliable method to obtain \( G_{PP} \) by portioning \( N_{EE} \) is currently unavailable either because light inhibition of leaf respiration or inconstancy of temperature dependency of autotrophic respiration \((cf. \ Yi \ et \ al \ 2004 \ and \ reference \ therein)\).

\( T_{opt} \) could also be determined by fitting a peak function to the temperature response of light-saturated photosynthesis \((Lange \ et \ al \ 1974)\). In leaf-level studies, temperature is specified to leaf temperature \((T_l)\), and light in the leaf chamber is set to a saturating level during CO2 exchange measurements. There are, however, some modifications required when these equations are applied at the ecosystem level. Instead of leaf temperature, we used air temperature near the canopy level \((Niu \ et \ al \ 2012)\). Therefore, in the present study, the ecosystem photosynthesis \( T_{opt} \) \((T_{optE})\) was determined in terms of optimum air temperature. To determine values for light-saturated photosynthesis, we omitted all data points below site-specific saturating light levels. The site-specific light saturation point was calculated by applying a non-rectangular hyperbola to the stand-level photosynthesis–light response curve \((Lasslop \ et \ al \ 2010)\).

There are several peak functions that could be used to fit the temperature response curve to determine \( T_{opt} \). We adopted a modified function of the model proposed by \( June \ et \ al \ (2004)\): \( N_{EEsat} = N_{EE25}\exp(b(T_K - 298)/(298RT_K))/[1 + \exp(c(T_K - T_{optE}))]^2 \), \( (1) \)

\( N_{EEsat} \) is the measured net ecosystem photosynthesis rate under light saturation \((\mu mol \ m^{-2} \ s^{-1})\) (note that a positive \( N_{EE} \) indicates photosynthesis uptake, in order to make it comparable to that of leaf-level conventions). \( T_K \) is the ambient temperature in degrees Kelvin, \( R \) is the gas constant, and \( N_{EE25} \) \((\mu mol \ m^{-2} \ s^{-1})\), \( b, c \), and \( T_{optE} \) (Kelvin) are fitted parameters.

The Farquhar–von Caemmerer–Berry (FvCB) model

A process-based photosynthesis model was used in this study. The model is a combination of the Farquhar–von Caemmerer–Berry photosynthesis (FvCB) model \((Farquhar \ et \ al \ 1980)\) and the Ball–Berry stomatal conductance model \((Ball \ et \ al \ 1987)\), with some additional parameterization information provided by von Caemmerer \( et \ al \ (2009)\). The detailed model equations are listed in table A1 in the appendix. We used an iteration method to solve intercellular CO2 \((c_i)\). The model was coded in the C++ environment and is available upon request.

for experimental purposes \((Goulden \ et \ al \ 2004)\). All the studied forests have a year-round growing season, with the exception of MKL, in which a proportion of the trees shed their leaves during the late dry season. For additional detailed information on these sites and instrumentation please refer to the previously published studies of Hirata \( et \ al \ (2008)\) and Restrepo-Coupe \( et \ al \ (2013)\).

Eddy flux observations and data processing

The CO2 movement in the lower atmospheric boundary layer is primarily driven by turbulence that can be measured using the eddy covariance technique \((EC)\) \((Baldocchi \ 2003)\). Photosynthetic rates were quantified by examining the ecosystem–atmosphere CO2 exchange. The daytime CO2 exchange measured using EC apparatus is conceptually equal to net ecosystem photosynthesis \((table \ 2)\).

We collected EC flux data for the seven forests from flux networks. The fluxes have a temporal resolution of 30 min or 1 h, and span at least two years. The major flux data used in this study include the following: net CO2 exchange \( (N_{EE}, \ after \ storage \ flux \ correction) \), latent heat flux \( (L_h) \), sensible heat flux \( (H_h) \), net radiation flux \( (R_{nr}) \), and soil heat flux \( (G) \). In addition to flux data, we also used meteorological measurements, including air temperature \( (T_{a}, \ ^\circ \ C) \), relative humidity \( (h_h, \ %) \), water vapour pressure deficit \( (D_h, \ kPa) \), and soil water content \( (SWC, \ m^3 \ m^{-3}) \). For reproducibility, the data are available at the following sites:

AsiaFLUX dataset: https://db.cger.nies.go.jp/asiafluxdb/
BrasilFLUX dataset: www.climatemodeling.org/lba-mip/
The big-leaf analogy
The factors used in determining $T_{\text{optE}}$ can be summarized as photosynthetic biochemical (biochemical hereafter), respiratory, and stomatal processes (Hikosaka et al 2006, Lin et al 2012). In order to separate the relative contributions of each process, we implemented the FvCB model with a big-leaf analogy.

Firstly, the ecosystem as a whole was abstracted into a ‘big leaf’. This is consistent with the philosophy of the EC method and enabled us to directly use the leaf-level FvCB model at an ecosystem-level. The EC system measures the gas exchange at ecosystem level analogous to leaf chamber measurements do a small scale system measures the gas exchange at ecosystem level. The EC system measures the gas exchange at ecosystem level analogous to leaf chamber measurements do a small scale system measures the gas exchange at ecosystem level (figure 2). Thus, daytime net ecosystem exchange ($N_{\text{EEda}}$) was regarded as equivalent to net photosynthesis rate ($P_n$) at the leaf level. At the ecosystem level, the air temperature near the canopy ($T_a$), air water vapour deficit ($D_h$), and canopy bulk intercellular CO$_2$ concentration ($c_{ib}$) corresponded to leaf temperature ($T_1$), leaf-to-air water vapour deficit ($D_i$) and intercellular CO$_2$ concentration ($c_{il}$) at the leaf level, respectively. Critically, ecosystem respiration ($R_E$) at the ecosystem level was considered analogous to leaf respiration ($R_l$) at the leaf level. After analogizing, ecosystem terms were derived that corresponded to the leaf terms, and the FvCB model was applied at the ecosystem level and driven by ecosystem measurements.

This type of big-leaf analogy differs from that of the big-leaf model (de Pury and Farquhar 1997), in that here the ecosystem as a whole was treated as a big leaf. Therefore, the parameters derived here for the ecosystem are not directly comparable to those used in leaf studies. The overall motivation for us in conducting this analogy was to make the parameter inversion as simple as possible but with necessary physiological considerations. Parameter inversion is very sensitive to initial parameter values because of many non-linear processes, and consequently it is more practical and helpful to construct simple models with certain assumptions than to execute a complex multi-layer model (Wang et al 2007).

Inverting photosynthesis parameters by combining the FvCB model and ecosystem fluxes
Parameters of the FvCB model at the ecosystem level were inverted from eddy flux observations after abstracting. For inversion, we used the Levenberg–Marquardt optimization algorithm. We also examined whether the inversion method would have a strong impact on the inverted parameters. A Bayesian statistical method, the ‘adaptive population Monte Carlo approximate Bayesian computation’ method (Lenormand et al 2013), was included for comparison. The algorithm pseudo-code of the Bayesian method was presented in Zeng et al (2017).

Results
The $T_{\text{optE}}$ of tropical forests
The temperature dependence of light-saturated ecosystem photosynthesis ($N_{\text{EEda}}$) is shown in figure 1. In general, there was a clear unimodal pattern for most of the sites. The $T_{\text{optE}}$ determined by fitting equation 1 to the observations varied from 23.7 to 28.1 °C across sites.

A close relationship was found between mean annual air temperature ($T_a$) and $T_{\text{optE}}$ (figure 2(a)). Since most tropical forests maintain a year-round growing season, the mean annual $T_a$ could roughly be treated as the growth temperature. Therefore, tropical forests growing under higher growth temperature tend to have a higher $T_{\text{optE}}$. The slope of the linear relationship is close to one (1.12). $T_{\text{optE}}$ was also related to mean air temperature under light saturated condition (figure 2(b)). When the sites with seasonally climate were omitted, a very close relationship was found between $T_{\text{optE}}$ and mean air temperature under light saturated condition.

Contribution of physiological parameters to the change in $T_{\text{optE}}$ across sites
The goodness-of-fit was shown in figure 3 when implemented the FvCB model to these datasets. In general, the model fitted results have a good relationship with that of observations. It suggests high reliability of these inverted parameters (table 3). Principal component analysis of these parameters identified three components that could explain over 86% of the variance. However, none of the three components were significantly correlated with $T_{\text{optE}}$ (data not shown). A further correlation analysis showed that the activation energy of ecosystem respiration ($R_E$) was the only parameter significantly correlated with $T_{\text{optE}}$ (figure 4(a)). We found that two sites (PDF and MKL indicated by open circles in figure 4(b)) differ from the remaining sites with respect to the relationship between $T_{\text{optE}}$ and stomatal sensitivity ($g_{ib}$): with the exception of PDF and MKL, the sites show a negative correlation between $T_{\text{optE}}$ and $g_{ib}$. These two excluded sites have special water conditions which discussed latter in the discussion section.

The contribution of stomatal processes in determining $T_{\text{optE}}$
The PSO site, which has eight years’ continuous flux data, was taken as an example of per-humid site to illustrate the contribution of stomatal processes in determine $T_{\text{optE}}$. The overall $T_{\text{opt}}$ for the PSO site was 26.5 °C for the entire $D_h$ range, as shown by the dashed line in figure 5(a). When the whole dataset was divided into different $D_h$ levels, we found that the light-saturated
photosynthesis rate ($N_{EE_{sat}}$) increased with $T_a$ even at values greater than 30 °C (see data points and regression line in different colours, figure 5(a)). Only at the highest $D_E$ level was $N_{EE_{sat}}$ found to decrease with $T_a$. In this regard, $T_{optE}$ (when $N_{EE_{sat}}$ starts to decrease with an increase in $T_a$) should at least be 30 °C when $D_E$ is controlled. This contrasts with the value of 26.5 °C obtained using the full $D_E$ range and implies strong stomatal control of $T_{optE}$. We also inferred parameters of FvCB model for all $D_E$ sub-ranges (table 4). Most of these parameters showed a unimodal pattern along with increase of $D_E$. A similar case was found in a site with strongly seasonal climate (figure 5(b)).

**Discussion**

The ecosystem $T_{optE}$ we quantified differs from leaf $T_{optL}$ in several aspects. Leaf $T_{optL}$ is specified to leaf temperature, not air temperature. The leaf surface is a direct light interceptor, which leads to stronger temperature variations in leaves than in ambient air, i.e. the transitional leaf temperature can easily reach 40 °C under full light (Doughty and Goulden 2008). In addition, the dark respiration term ($R_d$) at the ecosystem level ($R_E$) is the sum of respirations from different organisms, litter, woody debris, and soil organic matter, whereas at the leaf level, the respiration term ($R_L$) is specified to leaf respiration. Despite these differences, however, the ecosystem $T_{optE}$ obtained in our study is very close to that of leaf $T_{optL}$. For example, two Costa Rican tropical forest species grown under a daily temperature of 27 °C showed a leaf $T_{optL}$ of 27 °C (Vargas and Cordero 2013), which is close to the ecosystem $T_{optE}$ value we determined for tropical forests. Similarly, Slot and Winter (2017) reported mean $T_{optE}$ values of 30.4 °C and 29.2 °C for the upper-canopy leaves of 42 species in two lowland forests in Panama, which were close to the mean afternoon air temperature. The higher $T_{optL}$ values

Figure 1. Temperature response of light saturated ecosystem photosynthesis ($N_{EE_{sat}}$). A modified June et al (2004) function was fitted to the data point and optimum temperature ($T_{optE}$) was determined.
Figure 2. A comparison on photosynthesis optimum temperature ($T_{\text{opt}}$) with mean annual air temperature ($T_a$) (a) and mean light saturated air temperature (b). Black line is linear regression line, and grey line is 1:1 line. The open circles in subpanel (b) were not included in regression. The statistic information was shown in the top of figures.

Figure 3. A comparison on observed and FvCB model fitted daytime net ecosystem exchange ($N_{\text{EE}}$) to illustrate the goodness-of-fit. The fitted parameters were listed in table 3. The solid line is 1:1 line.
reported by Slot and Winter (2017), compared with the values reported in the present study and those reported by Vargas and Cordero (2013), could be explained by the fact that upper canopy leaves experience higher light intensity and leaf temperatures compared to the whole canopy mean values. In the following sections, we discuss the possible mechanism of \( T_{\text{optE}} \) changes across sites, the contribution of stomatal processes to \( T_{\text{optE}} \), and the implications of our findings.

The mechanisms of \( T_{\text{optE}} \) changes across sites

Our cross-site analysis shows that tropical forests growing in a warmer climate tend to exhibit higher \( T_{\text{optE}} \) (figure 2(a)). We separated the contributions of biochemical, respiratory, and stomatal processes to \( T_{\text{optE}} \) by means of parameter inversions. Respiratory process play a role in \( T_{\text{optE}} \) as suggested by the significant relationship between \( T_{\text{optE}} \) and the activation energy (\( E_a \)) of dark respiration (\( R_E \)) (figure 4(a)). This finding differs from those of leaf level studies, which indicate that leaf respiration plays a negligible role in \( T_{\text{optL}} \) (Lin et al 2012). At the ecosystem level, \( R_E \) is the sum of the autotrophic respiration of all organisms (above- and below-ground) and heterotrophic respiration of soil organic matter and litter. At the leaf-level, however, \( R_L \) reflects only leaf respiration, which typically represents a small fraction of net photosynthesis. These differences emphasize the importance of respiratory processes in studying \( T_{\text{optE}} \) at the ecosystem level, even though it is negligible at the leaf level.

It is known that activation energy (\( E_a \)) can represent the temperature sensitivity (\( Q_{10} \)) of \( R_E \), the relationship of which can be expressed as follows:

\[
Q_{10} = \exp \left( \frac{10E_a}{RT_a(T_a + 10)} \right). \tag{2}
\]
The relationship between decreasing $T_{\text{optE}}$ and increasing $Q_{10}$ suggests that the $R_{E}$ of tropical forests with higher $T_{\text{optE}}$ and mean $T_a$ is less sensitive to $T_a$ variations than forests with lower $T_{\text{optE}}$. This is consistent with previous reports showing that $Q_{10}$ decreases with rising temperature, as a consequence of thermal acclimation (Tjoelker et al 2009, Slot and Kitajima 2015).

When we excluded PDF and MKL (two secondary forests with unique hydrological conditions) from the analysis, we identified a strong correlation between $g_{1E}$ and $T_{\text{optE}}$ (figure 4(b)). The forest in the PDF site is drained peat swamp forest (Hirano et al 2007), which is generally waterlogged. By contrast, the MKL site experiences seasonal water deficits (Gamo et al 2005). Since stomatal conductance or $g_{1E}$ is highly sensitive to water availability, it seems appropriate to treat these two secondary forests as outliers when investigating $T_{\text{optE}}$–$g_{1E}$ relationships.

Theoretically, $g_{1E}$, which is a stomatal sensitivity factor, would be expected to increase with increasing growth temperature, as does $T_{\text{optE}}$ (Leuning 1990, Table 4. The inverted parameters under different water vapor pressure deficit ($D_E$) levels. This was carried out in the per-humid Pasoh site. This table could correspond to figure 4(a).

| $D_E$ level (kPa) | <0.7 | 0.7–0.9 | 0.9–1.1 | 1.1–1.2 | 1.2–1.3 | 1.3–1.4 | 1.4–1.5 | 1.5–1.6 | 1.6–1.8 | 1.8–2.1 | >2.1 |
|------------------|------|---------|---------|---------|---------|---------|---------|---------|---------|---------|------|
| Rate at 25 °C ($\mu$mol m$^{-2}$ s$^{-1}$) | $V_{\text{max}}$ | $I_{\text{max}}$ | $R_{E}$ | $V_{\text{max}}$ | $I_{\text{max}}$ | $R_{E}$ | $V_{\text{max}}$ | $I_{\text{max}}$ | $R_{E}$ | $V_{\text{max}}$ | $I_{\text{max}}$ | $R_{E}$ |
| <0.7 | 91 | 100 | 114 | 254 | 288 | 289 | 273 | 268 | 165 | 279 | 101 |
| 0.7–0.9 | 125 | 123 | 107 | 110 | 140 | 118 | 129 | 129 | 107 | 91 | 102 |
| 0.9–1.1 | 0.10 | 0.31 | 0.10 | 1.91 | 8.10 | 5.67 | 8.50 | 8.98 | 6.59 | 5.00 | 2.90 |
| 1.1–1.2 | 62.714 | 59.957 | 60.577 | 64.505 | 68.994 | 70.017 | 66.453 | 66.916 | 63.578 | 66.943 | 59.348 |
| 1.2–1.3 | 44.315 | 41.412 | 47.631 | 51.075 | 66.799 | 65.574 | 79.995 | 79.573 | 79.994 | 79.998 | 41.830 |
| 1.3–1.4 | 63.481 | 63.637 | 63.254 | 63.565 | 55.985 | 60.646 | 64.301 | 61.926 | 62.723 | 58.468 | 64.409 |
| 1.4–1.5 | 74.2 | 72.9 | 756 | 798 | 1052 | 1126 | 903 | 896 | 859 | 874 | 742 |
| 1.5–1.6 | 22.9765 | 22.5983 | 23.4348 | 24.7302 | 32.5870 | 34.8879 | 27.9685 | 27.7651 | 26.6097 | 27.0846 | 22.9800 |
| 1.6–1.8 | 11.00 | 10.51 | 13.00 | 20.43 | 36.50 | 30.72 | 13.85 | 14.31 | 10.97 | 3.44 | 2.08 |
| 1.8–2.1 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 |
| >2.1 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 | 9.787 |

$V_{\text{max}}$, maximum Rubisco activity; $I_{\text{max}}$, maximum electron transport rate; $R_{E}$, dark respiration rate; $S$, a term similar to an entropy factor, $H$, the rate of decrease in the function above the optimum, $g_{1E}$, stomatal sensitivity factor.

Figure 5. The temperature response of light saturated photosynthesis rate ($N_{\text{Esat}}$) under different water vapor deficit ($D_E$) levels. (a) represents the per-humid environment collected from the PSO site; (b) represents seasonal climate collected from the MKL site. The symbols and regression line with different colours represent different $D_E$ levels. Values of different color represent the corresponding slope of the regression line. The dashed line in subpanel (a) is fully in the $D_E$ range which is the same as figure 1(f).
Medlyn et al (2011). Our numeric simulation also supports this theoretic expectation for a specific site by checking $T_{optE}$ with varied $g_{IE}$ (data not shown). Nevertheless, we found that at the ecosystem level for tropical forests, $T_{optE}$ tends to decrease with increasing $g_{IE}$ (figure 4(b)). Since $g_{IE}$ is strongly correlated with the $E_D$ of $R_E$ (Pearson’s $r = 0.96$), it is would be difficult to state that the strong correlation shown in figure 4(b) is solely attributable to $g_{IE}$ or whether it is merely an indirect reflection of the $E_D$–$T_{optE}$ relationship shown in figure 4(a). In situ warming experiments at both leaf and ecosystem levels might be helpful in reconciling these contrasts (Cavaleri et al 2015).

Interestingly, we found that biochemical processes did not play a significant role in $T_{optE}$ changes across sites. Traditionally, $T_{opt}$ acclimation studies have primarily focused on biochemical processes (Hikosaka et al 2006). However, in the present study these key processes were found to make a negligible contribution to $T_{optE}$ changes across sites. Subsequent to further confirmation that thermal acclimation of respiration rather than biochemical processes is a more important determinant of $T_{optE}$, these findings should be implemented in global change models (Lombardozzi et al 2015).

The role of stomatal processes in determining $T_{optE}$

Previous studies have shown that stomatal processes are potentially important (Lin et al 2012, Duursma et al 2014, Slot and Winter 2017), or even the most important factors determining $T_{optL}$ (Lloyd and Farquhar 2008, Rowland et al 2015). Nevertheless, how stomatal processes control $T_{opt}$ is still not well understood. This uncertainty is partly caused by the confounding effects of temperature and water factors on $T_{opt}$.

Relative humidity ($h_s$) and vapour pressure deficit ($D$) are strongly dependent on temperature (Campbell and Norman 1998). When temperature rises, the saturated water vapour pressure will increase exponentially. This, in turn, will alter both $h_s$ and $D$, and hence stomatal conductance. Therefore, there is an indirect effect of temperature on $T_{opt}$ through its effect on stomatal conductance. This effect is illustrated in figure 5. The dashed line in figure 5(a) shows the temperature response curve represented in figure 1(f) under the full $D_B$ range. However, when we divided the whole dataset into different $D_B$ levels (as shown by the different colours in figure 5(a)), it was apparent that $N_{EEma}$ increases with temperature within these subsets until the temperature exceed 30 °C. This indicates that the $T_{optE}$ should be at least 30 °C if there is no $D_B$ limitation on the stomatal response, which is considerably higher than the value estimated from the entire $D_B$ range (26.4 °C). This analysis lends support to the idea that stomatal processes play a significant role in determining $T_{optE}$, as temperature may indirectly influence photosynthesis through changing $D$.

The implications under future climate change

In the future, the Earth’s surface air is predicted to become richer in CO$_2$ and higher in mean temperature (Corlett 2011). At present, however, there seems little consensus on how tropical forest ecosystem will respond under such a climatic scenario (see the review by Lloyd and Farquhar (2008)). Our findings, however, provide certain insights into how tropical forest ecosystems might respond and could serve as complement to previous studies in our pursuit of a more complete understanding future changes in forest photosynthesis.

Firstly, we revealed the role of stomatal limitation in determining $T_{optE}$ at the ecosystem level, which is largely consistent with leaf-level findings. The role of stomatal effects in shaping $T_{opt}$ have been well demonstrated in leaf-level measurements (Koch et al 1994, Ishida et al 1996, Carswell et al 2000, Slot and Winter 2017) and have been verified by a leaf-level model (Lloyd and Farquhar 2008). Our ecosystem flux analysis showed that without $D_B$ limitation on stomatal conductance, tropical forests could have a higher photosynthetic performance ($N_{EEma}$) under high $T_a$ as indicated by their increased $T_{optE}$ (figure 5). The direct implication of this finding is that factors affecting stomatal conductance will contribute substantially to the modification of $T_{optE}$. Among these factors, the most prominent is ambient air CO$_2$ concentration. Given unchanged moisture conditions (e.g. soil water or $D$), $T_{optE}$ is expected to increase with CO$_2$ and will decrease stomatal limitation on photosynthesis (Lloyd and Farquhar 2008). Accordingly, this can be considered as a positive signal for tropical forests given the prospect of increasing CO$_2$ levels.

Secondly, tropical forests in environments with higher $T_a$ tend to have higher $T_{optE}$ (figure 2), which is consistent with growth chamber cultivation experiments (Kositsup et al 2009) and cross-season observations (Lange et al 1974). This pattern suggests potential acclimation of tropical forests to $T_a$, which is a further adaptive strategy that will increase the resilience of tropical forest given the predicted climate warming scenarios.

Thirdly, the significant relationship between the activation energy of respiration and $T_{optE}$ implies the possible thermal acclimation of $R_E$ (figure 4(a)). The temperature acclimation of ecosystem respiration, i.e. the decrease in the sensitivity of respiration to temperature changes as growth temperature increases, would have a positive effect on net photosynthesis and lead to increases in $T_{optE}$.
Table A1. Equations used for the leaf photosynthesis biochemical model (FvCB).

| Number | Equation |
|--------|----------|
| 1      | \( P_n = \min\left( P_c, P_i, P_s \right) \) |
| 2      | \( P_c = \frac{\gamma_c - V_{\text{max}}}{K_c + \frac{V_{\text{max}}}{P} + R_d} \) |
| 3      | \( P_i = \frac{\left( c_i - V_{\text{max}} / I \right)}{K_i + \frac{\gamma_i}{I}} \) |
| 4      | \( P_s = 0.5V_{\text{max}} - R_d \) |
| 5      | \( 0.7I - f I_{\text{abs}} + I_{\text{abs}} + \frac{Q_{\text{max}}}{I_{\text{abs}}} = 0 \) |
| 6      | \( I_{\text{abs}} = \frac{I}{f I \left( 1 - f \right) / 2} \) |
| 7      | \( \psi = c_i - P_i \left( \frac{g + L}{g} \right) \) |
| 8      | \( \sigma_n = 0.147 \sqrt{\frac{J_0}{\lambda R_g}} \) |
| 9      | \( K_i = \frac{P_c + P_i}{2} \) |
| 10     | \( 0.94P_c^2 - (P_c + P_i)P_c + P_iP_c = 0 \) |
| 11     | \( \{ K_c, K_i, R_d, V_{\text{max}}, \Gamma'_s \} = \{ K_c, K_i, R_d, V_{\text{max}}, \Gamma_s \} \times \frac{K_{\text{max}}}{V_{\text{abs}}} \) |
| 12     | \( \{ I_{\text{max}} \} = \{ I_{\text{max}} \} \times \frac{1 + e^{q(298.15 - \Gamma)/298.15}}{1 + e^{q(298.15 - \Gamma)/298.15}} \) |

- \( P_c \): net photosynthetic rate, \( P_i \): Rubisco-limited photosynthesis, \( P_s \): electron transport-limited photosynthesis, \( P_r \): export-limited photosynthesis, \( R_d \): dark respiration rate, \( c_i \): CO₂ partial pressure at the carboxylating site, \( O_2 \): O₂ partial pressure at the carboxylating site, \( K_c \): Michaelis–Menten constant of Rubisco for CO₂, \( K_i \): Michaelis–Menten constant of Rubisco for O₂, \( V_{\text{max}} \): maximum Rubisco activity, \( \Gamma' \): CO₂ compensation point in the absence of \( R_d \), \( J \): electron transport rate, \( I_{\text{max}} \): maximum electron transport rate, \( I_{\text{abs}} \): absorbed light, \( f_{\text{abs}} \): leaf absorbance (≈0.85), \( I \): light intensity, \( f \): correction factor for the spectral quality of light (0.15), \( g_c \): stomatal conductance, \( c_i \): ambient CO₂ concentration, \( c_j \): leaf surface CO₂ concentration, \( g_b \): laminar boundary layer conductance, \( W_g \): wind speed, \( L \): leaf width, \( h_i \): relative humidity, \( \gamma_i \): water vapor pressure deficit, \( g_b \) and \( g_s \) are two model parameters, \( P_c \) is used for smoothing the transition between \( P_c \), \( P_i \), and \( P_s \), \( E \): activation energy, \( T_c \): temperature in degrees Kelvin, \( R \): gas constant, \( S \): term similar to an entropy factor, \( H \): describes the rate of decrease in the function above the optimum.

Collectively, our findings indicate an optimistic future for tropical forests under the predicted conditions of global climate change. Nevertheless, some uncertainties remain. Firstly, increasing CO₂ will reduce stomatal conductance and water losses and hence the cooling effect of transpiration. This could potentially result in excessively high leaf temperatures and consequently heat damage and declines in photosynthesis and carbon sequestration. Furthermore, because ecosystem respiration in the tropics and subtropics is generally more sensitive to warming than that of photosynthesis (Yi et al. 2010, Zhang et al. 2016), it remains unclear to what extent the warming-induced increase in night-time ecosystem respiration would offset the positive effect of thermal acclimation in photosynthesis on net carbon sequestration.

Conclusions and implications

In conclusion, we quantified ecosystem \( T_{\text{optE}} \) for tropical forests, which ranges from 23.7°C to 28.1°C. Moreover, we found that tropical forests with higher growth temperatures tend to have higher \( T_{\text{optE}} \), suggesting the acclimation potential for many tropical forests. In contrast to previous studies, however, our results show that biochemical processes make only a minor contribution to the \( T_{\text{optE}} \) changes across sites. Instead, respiratory processes, which are generally negligible at the leaf level, play an important role in explaining \( T_{\text{optE}} \) variation across sites. Consistent with leaf level studies, stomatal processes are also critical in determining \( T_{\text{optE}} \) at the ecosystem level. Strong \( D \) and stomatal limitation on \( T_{\text{optE}} \) suggests that increasing CO₂ concentrations may increase the \( T_{\text{optE}} \) of tropical forests.

Appendix

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