Environmental Research Letters

LETTER • OPEN ACCESS

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

To cite this article: Zheng-Hong Tan *et al* 2017 *Environ. Res. Lett.* **12** 054022

Environmental Research Letters

OPEN ACCESS

RECEIVED
5 December 2016

REVISED
23 April 2017

ACCEPTED FOR PUBLICATION
26 April 2017

PUBLISHED
19 May 2017

LETTER

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

Zheng-Hong Tan[1,17], Jiye Zeng[2], Yong-Jiang Zhang[3], Martijn Slot[4], Minoru Gamo[5], Takashi Hirano[6], Yoshiko Kosugi[7], Humberto R da Rocha[8], Scott R Saleska[9], Michael L Goulden[10], Steven C Wofsy[11], Scott D Miller[12], Antonio O Manzi[13], Antonio D Nobre[14], Plinio B de Camargo[15] and Natalia Restrepo-Coupe[9,16]

1 Ecology Program, Institute of Tropical Agriculture and Forestry, Hainan University, Haikou 570228, People's Republic of China
2 National Institute for Environmental Studies, Tsukuba 305-0053, Japan
3 Department of Organismic and Evolutionary Biology, Harvard University, Cambridge 02138, United States of America
4 Smithsonian Tropical Research Institute, Apartado 0843–3092, Panama
5 National Institute of Advanced Industrial Science and Technology, Tsukuba 305–8569, Japan
6 Graduate School of Agriculture, Hokkaido University, Sapporo 060–8589, Japan
7 Forest Hydrology, Graduate School Agriculture, Kyoto University, Kyoto 606–8502, Japan
8 Department of Atmospheric Science, Universidade de Sao Paulo, Sao Paulo 05508-090, Brazil
9 Department of Ecology and Evolutionary Biology, University of Arizona, Tucson AZ, 85721, United States of America
10 Department of Earth System Science, University of California, Irvine 92697, United States of America
11 Division of Applied Science, Harvard University, Cambridge 02138, United States of America
12 Atmospheric Sciences Research Center, State University of New York at Albany, New York 12203, United States of America
13 Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus 69011, Brazil
14 Laboratório de Ecologia Isotópica, Universidade de São Paulo, São Paulo 05468, Brazil
15 Department of Biological Sciences, Macquarie University, Sydney 2109, Australia
16 Plant Functional Biology and Climate Change Cluster, University of Technology Sydney, Sydney, NSW, 2007, Australia
17 Author to whom any correspondence should be addressed.

E-mail: tanzh@xtbg.ac.cn

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. Paleoecological 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 floras (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 warning 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 CO_2 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 CO_2 uptake by the forests could in turn result in an increase in atmospheric CO_2, 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

Table 1. Site information.

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

'—', no data available; Lat., Latitude; Long., Longitude; Age, stand age (yr); Hc, canopy height (m); LAI, leaf area index; Ta, mean annual temperature (°C); ppt, precipitation (mm); System, the open (OP) or closed path (CP) eddy covariance system; IRGA, the infrared gas analyzer model.

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 (c_i) 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_{optE}) for seven tropical forests across different continents. We then analyzed the relationship between T_{optE} 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 located near the equator (latitude ~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 (~2°S or N) and the other two Thailand forests (MKL and SKR) are located at ~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 2. Terms (and their abbreviations) used at the leaf-level and the corresponding abbreviations used at ecosystem-level. P_g: leaf gross photosynthetic rate; G_{PP}: gross primary production of ecosystem; R_L: leaf respiration; R_E: ecosystem respiration, which is the sum of autotrophic and heterotrophic respiration; T_L: leaf temperature; T_a: air temperature near the top of the forest canopy; c_{iL}: leaf intercellular CO_2 concentration; c_{iE}: bulk canopy intercellular CO_2 concentration; D_L: leaf-to-air water vapour deficit; D_E: atmospheric water deficit; g_s: stomatal conductance; G_c: canopy conductance; P_n: net leaf photosynthesis rate, where $P_n = P_g - R_L$; N_{EE}: net ecosystem exchange, where $N_{EE} = G_{PP} - R_E$.

General description	Leaf	Ecosystem
Gross photosynthesis	P_g	G_{PP}
Dark respiration: R_d	R_L	R_E
Temperature	T	T_a
Intercellular CO_2 concentration: c_i	c_{iL}	c_{iE}
Water vapour deficit: D	D_L	D_E
Stomatal or canopy conductance: g	g_s	G_c
Maximum carboxylation rate: V_{cmax}	V_{cmaxL}	V_{cmaxE}
Maximum electronic transport rate: J_{max}	J_{maxL}	J_{maxE}
Conductance sensitivity: g_1	g_{1L}	g_{1E}
Temperature curve factor: S	S_L	S_E
Temperature curve factor: H	H_L	H_E
Net photosynthesis rate	P_n	N_{EE}
Optimal temperature: T_{opt}	T_{optL}	T_{optE}

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 CO_2 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 CO_2 exchange. The daytime CO_2 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 CO_2 exchange (N_{EE}, after storage flux correction), latent heat flux (L_E), sensible heat flux (H_s), net radiation flux (R_n), and soil heat flux (G). In addition to flux data, we also used meteorological measurements, including air temperature (T_a, °C), relative humidity (h_s, %), water vapour pressure deficit (D_E, 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/

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 inconsistence 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 CO_2 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):

$$N_{EEsat} = N_{EE25}\exp(b(T_K - 298)/(298RT_k))/[1 + \exp(c(T_k - T_{optE}))]^2, \quad (1)$$

where N_{EEsat} is the measured net ecosystem photosynthesis rate under light saturation (μmol 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} (μmol 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 CO_2 (c_i). The model was coded in the C++ environment and is available upon request.

The big-leaf analogy

The factors used in determining T_{opt} 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 analog to leaf chamber measurements do a small scale (table 2). Thus, daytime net ecosystem exchange (N_{EE}) 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_E), and canopy bulk intercellular CO_2 concentration (c_{iE}) corresponded to leaf temperature (T_L), leaf-to-air water vapour deficit (D_L) 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_{optE} of tropical forests

The temperature dependence of light-saturated ecosystem photosynthesis (N_{EEsat}) is shown in figure 1 general, there was a clear unimodal pattern for most of the sites. The T_{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_{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_{optE}. The slope of the linear relationship is close to one (1.12). T_{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_{optE} and mean air temperature under light saturated condition.

Contribution of physiological parameters to the change in T_{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_{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_{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_{optE} and stomatal sensitivity (g_{1E}): with the exception of PDF and MKL, the sites show a negative correlation between T_{optE} and g_{1E}. These two excluded sites have special water conditions which discussed latter in the discussion section.

The contribution of stomatal processes in determining T_{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_{optE}. The overall T_{optE} for the PSO site was 26.5 °C for the entire D_E range, as shown by the dashed line in figure 5(*a*) When the whole dataset was divided into different D_E levels, we found that the light-saturated

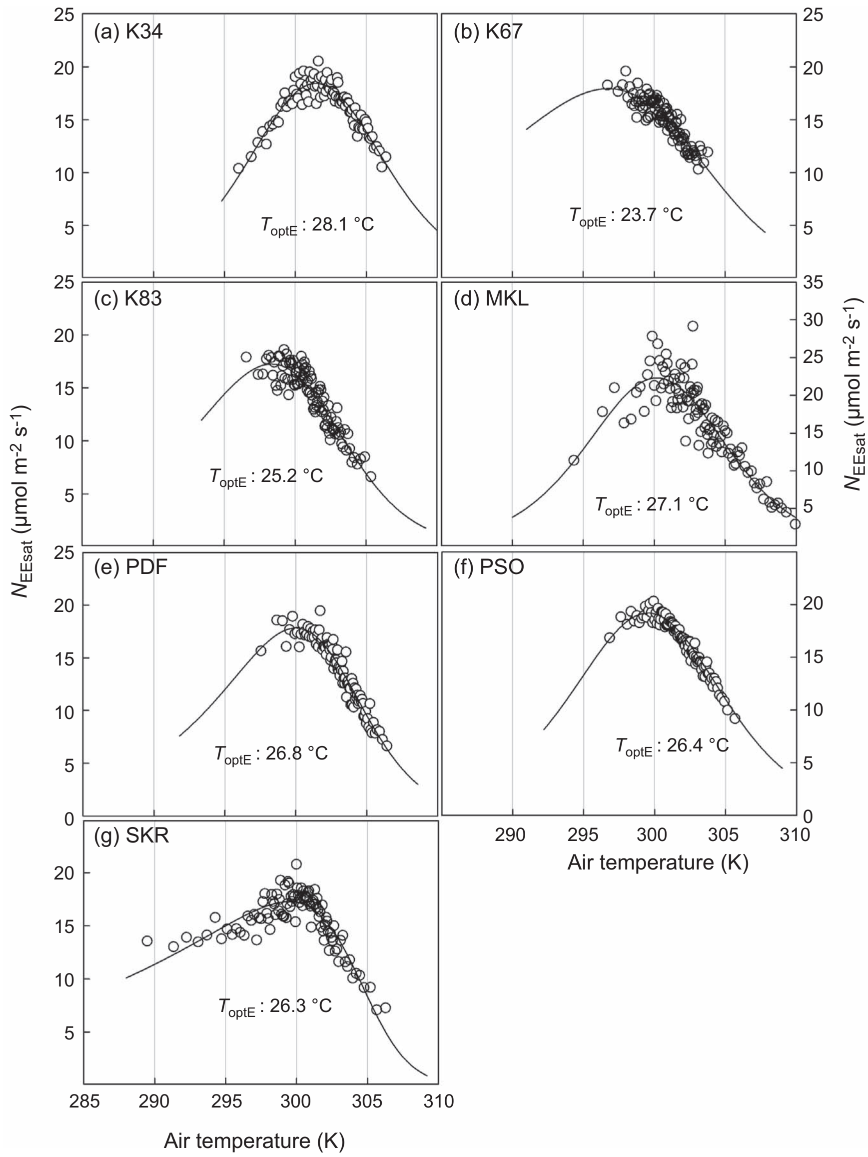

Figure 1. Temperature response of light saturated ecosystem photosynthesis (N_{EEsat}). A modified June *et al* (2004) function was fitted to the data point and optimum temperature (T_{optE}) was determined.

photosynthesis rate (N_{EEsat}) 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 NEE_{sat} found to decrease with T_a. In this regard, T_{optE} (when NEE_{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

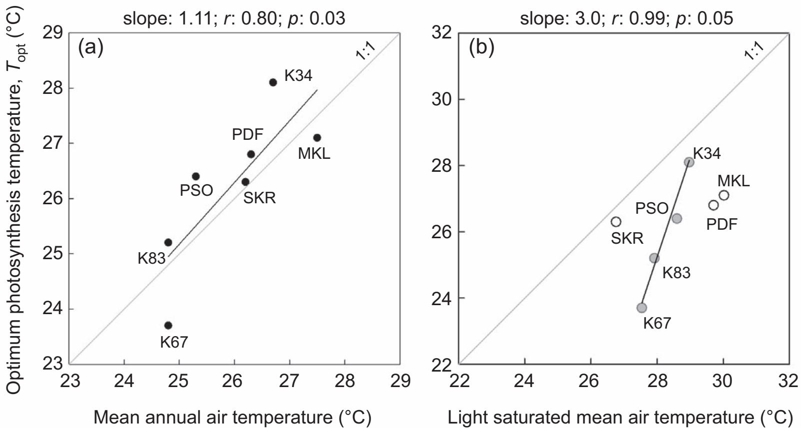

Figure 2. A comparison on photosynthesis optimum temperature (T_{optE}) with mean annual air temperature (T_a) (*a*) and mean light saturated air temperature (*b*). Black line is linear regression line, and grey line is 1:1 line. The open circles in subpanel (*b*) were not included in regression. The statistic information was shown in the top of figures.

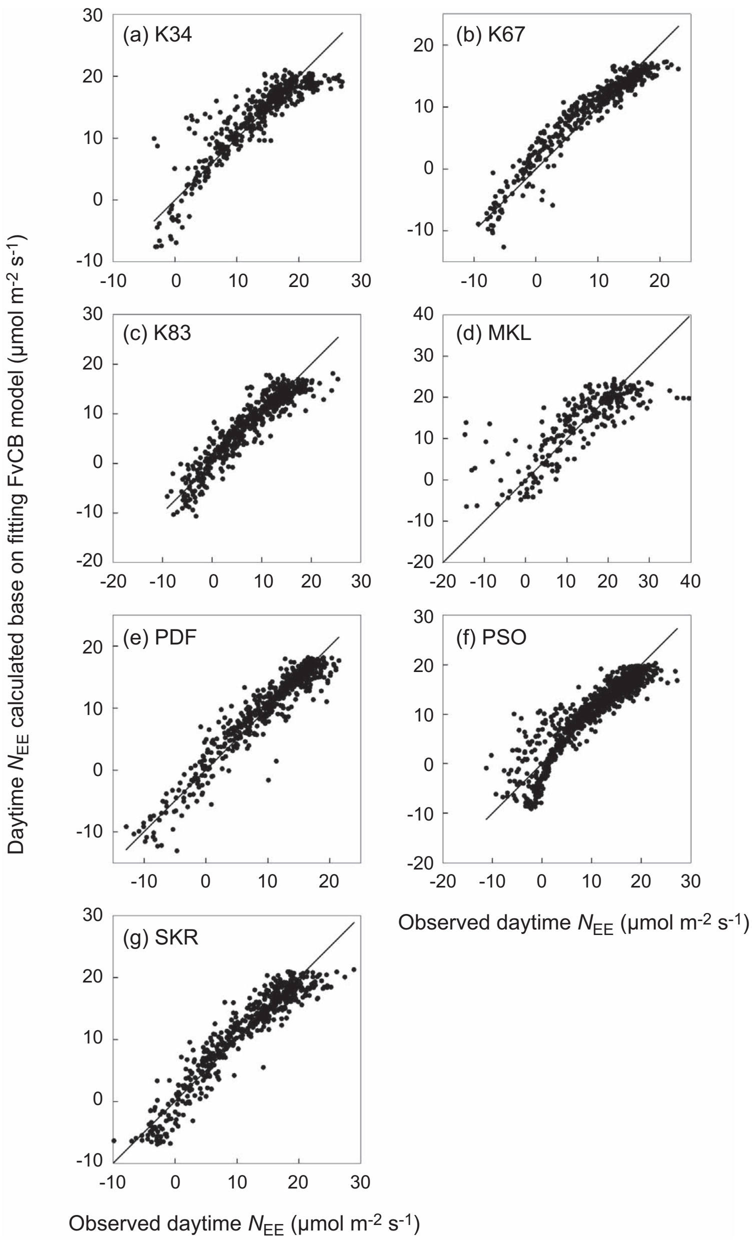

Figure 3. A comparison on observed and FvCB model fitted daytime net ecosystem exchange (N_{EE}) to illustrate the goodness-of-fit. The fitted parameters were listed in table 3. The solid line is 1:1 line.

Table 3. Parameters of a photosynthesis model inverted using a nonlinear regression method.

Site	Rate at 25 °C (μmol m^{-2} s^{-1})			Activation energy (J)			S_E	H_E	g_{1E}
	V_{cmaxE}	J_{maxE}	R_{dE}	V_{cmaxE}	J_{maxE}	R_{dE}			
K34	294	190	9.03	65 340	76 340	10 000	706	218 782	2.31
K67	297	212	10.00	60 503	35 255	66 673	702	217 451	3.27
K83	290	215	9.64	63 009	33 047	39 721	408	126 451	2.97
MKL	295	235	9.15	63 724	56 013	25 547	630	195 119	3.83
PDF	230	212	10.00	61 913	38 906	44 375	697	215 911	3.40
PSO	185	209	9.44	59 110	70 404	15 779	798	247 355	2.60
SKR	252	239	9.59	62 342	56 916	35 102	710	220 120	2.69

V_{cmax}, maximum Rubisco activity; J_{max}, maximum electron transport rate; R_d, dark respiration rate; S, a term similar to an entropy factor, H, the rate of decrease in the function above the optimum, g_1, stomatal sensitivity factor.

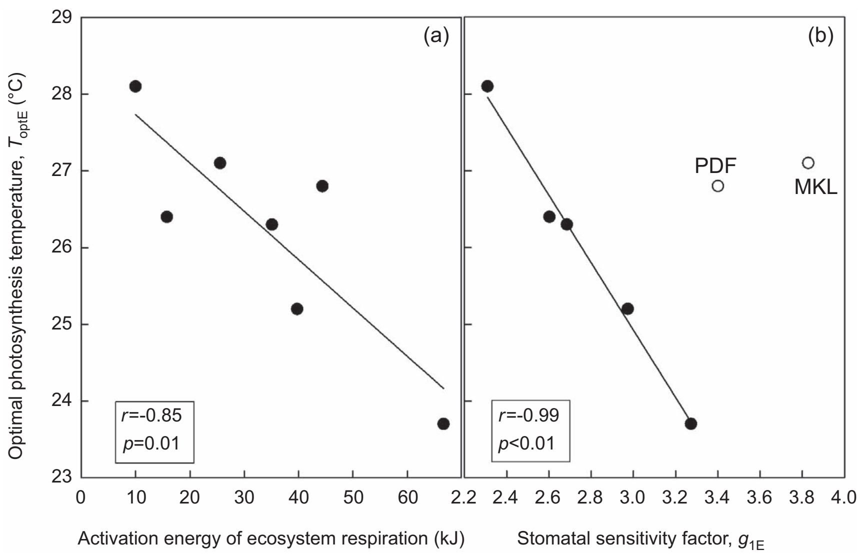

Figure 4. Optimum photosynthesis temperature (T_{optE}) was related to activation energy (E_a) of dark respiration (R_E) and stomatal sensitivity factor (g_{1E}). Two sites indicated by open circles were not included in regression for subfigure (*b*).

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_{optE} changes across sites, the contribution of stomatal processes to T_{optE}, and the implications of our findings.

The mechanisms of T_{optE} changes across sites

Our cross-site analysis shows that tropical forests growing in a warmer climate tend to exhibit higher T_{optE} (figure 2(*a*)). We separated the contributions of biochemical, respiratory, and stomatal processes to T_{optE} by means of parameter inversions. Respiratory process play a role in T_{optE}, as suggested by the significant relationship between T_{optE} and the activation energy (E_a) of 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_{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_{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:

$$Q_{10} = \exp\left(\frac{10E_a}{RT_a(T_a + 10)}\right). \qquad (2)$$

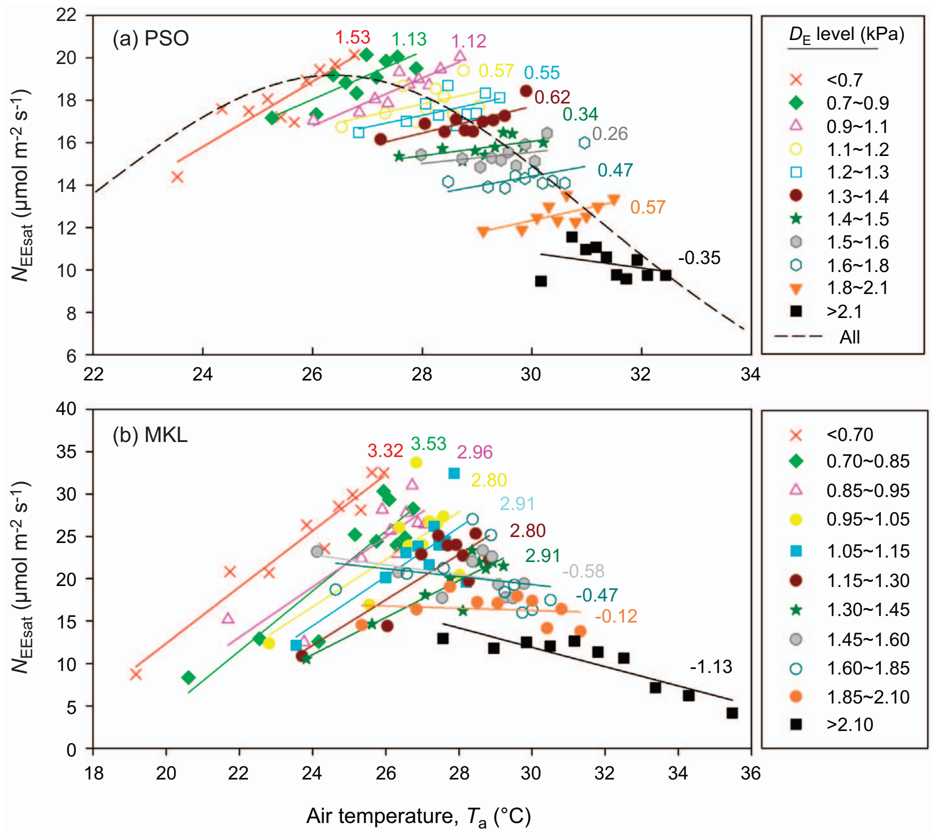

Figure 5. The temperature response of light saturated photosynthesis rate (N_{EEsat}) under different water vapor deficit (D_E) levels. (*a*) represents the per-humid environment collected from the PSO site; (*b*) represents seasonal climate collected from the MKL site. The symbols and regression line 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*).

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 levels (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 (μmol m^{-2} s^{-1})	V_{cmaxE}	91	100	114	254	288	289	273	268	165	279	101
	J_{maxE}	125	123	107	110	140	118	129	129	107	91	102
	R_{dE}	0.10	0.51	0.10	1.91	8.10	5.67	8.50	8.98	6.59	5.00	2.90
Activation energy (J)	V_{cmaxE}	62 714	59 957	60 577	64 505	68 994	70 017	66 453	66 916	63 578	66 943	59 348
	J_{maxE}	44 315	41 412	47 631	51 075	66 799	65 574	79 995	79 573	79 994	79 998	41 830
	R_{dE}	63 481	63 637	63 254	63 565	55 985	60 646	64 301	61 926	62 723	58 468	64 409
S_E		742	729	756	798	1052	1126	903	896	859	874	742
H_E		22 9765	22 5983	23 4348	24 7302	32 5870	34 8879	27 9685	27 7651	26 6097	27 0846	22 9800
g_{1E}		11.00	10.51	13.00	20.43	36.50	30.72	13.85	14.31	10.97	3.44	2.08

V_{cmax}, maximum Rubisco activity; J_{max}, maximum electron transport rate; R_d, dark respiration rate; *S*, a term similar to an entropy factor, *H*, the rate of decrease in the function above the optimum, g_1, stomatal sensitivity factor.

The relationship between decreasing T_{optE} and increasing Q_{10} suggests that the R_E of tropical forests with higher T_{optE} and mean T_a is less sensitive to T_a variations than forests with lower T_{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_{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_{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_{optE} (Leuning 1990, Medlyn *et al* 2011). Our numeric simulation also supports this theoretic expectation for a specific site by checking T_{optE} with varied g_{1E} (data not shown). Nevertheless, we found that at the ecosystem level for tropical forests, T_{optE} tends to decrease with increasing g_{1E} (figure 4(*b*)). Since g_{1E} is strongly correlated with the E_a 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_{1E} or whether it is merely an indirect reflection of the E_a–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_E range. However, when we divided the whole dataset into different D_E levels (as shown by the different colours in figure 5(*a*)), it was apparent that N_{EEsat} 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_E limitation on the stomatal response, which is considerably higher than the value estimated from the entire D_E 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_{optL} 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_E limitation on stomatal conductance, tropical forests could have a higher photosynthetic performance (N_{EEsat}) 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	$P_n = \min\{P_c, P_j, P_s\}$
2	$P_c = \frac{(c_i - \Gamma_*)V_{cmax}}{c_i + K_c(1 + O_i/K_o)} - R_d$
3	$P_j = \frac{(c_i - \Gamma_*)J}{4c_i + 8\Gamma_*} - R_d$
4	$P_s = 0.5V_{cmax} - R_d$
5	$0.7J^2 - J(I_{abs} + J_{max}) + I_{abs}J_{max}g_b = 0$
6	$I_{abs} = I^* f_{abs}(1 - f)/2$
7	$c_i = c_a - P_n\left(\frac{1}{g_b} + \frac{1}{g_s}\right)$
8	$g_b = 0.147^* \sqrt{\frac{W_s}{0.752^* L_w}}$
9	$g_s = \frac{g_1 h_s}{c_s} P_n + g_0$
10	$0.98P_v^2 - (P_c + P_j)P_v + P_cP_j = 0$ $0.98P_n^2 - (P_v + P_s)P_n + P_vP_s = 0$
11	$\{K_c, K_o, R_d, V_{cmax}, \Gamma_*\} = \{K_c, K_o, R_d, V_{max}, \Gamma_*\}_{25} e^{E_a\left(\frac{T_K - 298}{298^* R^* T_K}\right)}$
12	$\{J_{max}\} = \{J_{max}\}_{25} e^{E_a\left(\frac{T_K - 298}{298^* R^* T_K}\right)} \times \frac{1 + e^{(298S - H)/(298R)}}{1 + e^{(T_K S - H)/(T_K R)}}$

P_n: net photosynthetic rate, P_c: Rubisco-limited photosynthesis, P_j: electron transport-limited photosynthesis, P_s: export-limited photosynthesis, R_d: dark respiration rate, c_i: CO_2 partial pressure at the carboxylating site, O_i: O_2 partial pressure at the carboxylating site, K_c: Michaelis–Menten constant of Rubisco for CO_2, K_o: Michaelis–Menten constant of Rubisco for O_2, V_{cmax}: maximum Rubisco activity, Γ^*: CO_2 compensation point in the absence of R_d, J: electron transport rate, J_{max}: maximum electron transport rate, I_{abs}: absorbed light, f_{abs}: leaf absorbance (~0.85), I: light intensity, f: correction factor for the spectral quality of light (0.15), g_s: stomatal conductance, c_a: ambient CO_2 concentration, c_s: leaf surface CO_2 concentration, g_b: laminar boundary layer conductance, W_s: wind speed, L_w: leaf width, h_s: relative humidity, g_0 and g_1 are two model parameters, P_v is used for smoothing the transition between P_c, P_j, and P_s, E_a: activation energy, T_K: 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 CO_2 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_{optE} for tropical forests, which ranges from 23.7 to 28.1 °C. Moreover, we found that tropical forests with higher growth temperatures tend to have higher T_{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_{optE} changes across sites. Instead, respiratory processes, which are generally negligible at the leaf level, play an important role in explaining T_{optE} variation across sites. Consistent with leaf level studies, stomatal processes are also critical in determining T_{optE} at the ecosystem level. Strong D and stomatal limitation on T_{optE} suggests that increasing CO_2 concentrations may increase the T_{optE} of tropical forests.

Appendix

Acknowledgments

The study was supported by the C-project of Talent, Hainan University and National Natural Science Foundation of China (31660142). Brazil flux data was produced with funds from the NASA LBA-DMIP project (# NNX09AL52G) (NASA), NASA LBA investigation CD-32, and the National Science Foundation's Partnerships for International Research and Education (PIRE). We thank two reviewers and an editor board member for their insightful and constructive comments on this work. The AsiaFLUX was acknowledged for permission on accessing and using their dataset.

References

Anderegg W R L *et al* 2015 Tropical nighttime warming as a dominant driver of variability in the terrestrial carbon sink *Proc. Natl Acad. Sci.* **112** 15591–6

Baldocchi D D 2003 Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future *Glob. Change Biol.* **9** 479–92

Ball J T, Woodrow I E and Berry J A 1987 A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions *Progress in Photosynthesis Research* ed I Biggins (Dordrecht: Martinus-Nijhoff)

Berry J and Björkman O 1980 Photosynthetic response and adaptation to temperature in higher plants *Annu. Rev. Plant Physiol.* **31** 491–543

Campbell G S and Norman J M 1998 *An Introduction to Environmental Biophysics* (New York: Springer)

Carswell F E, Meir P, Wandelli E V, Bonates L C M, Kruijt B, Barbosa E M, Nobre A D, Grace J and Jarvis P G 2000 Photosynthetic capacity in a central Amazonian rain forest *Tree Physiol.* **20** 179–86

Cavaleri M A, Reed S C, Smith W K and Wood T E 2015 Urgent need for warming experiments in tropical forests *Glob. Change Biol.* **21** 2111–21

Corlett R T 2011 Impacts of warming on tropical lowland rainforests *Trends Ecol. Evol.* **26** 606–13

Damour G, Simonneau T, Cochard H and Urban L 2010 An overview of stomatal conductance at the leaf level *Plant Cell Environ.* **33** 1419–38

de Pury D G and Farquhar G D 1997 Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models *Plant Cell Environ.* **20** 537–57

Dixon R K, Brown S, Houghton R A, Solomon A M, Trexler M C and Wisniewski J 1994 Carbon pools and flux of global forest ecosystems *Science* **263** 185–90

Doughty C E 2011 An *in situ* leaf and branch warming experiment in the Amazon *Biotropica* **43** 658–65

Doughty C E and Goulden M L 2008 Are tropical forests near a high temperature threshold? *J. Geophys. Res. Biogeosci.* **113** G00B07

Duursma R A, Barton C V M, Lin Y S, Medlyn B E, Eamus D, Tissue D T, Ellsworth D S and McMurtrie R E 2014 The peaked response of transpiration rate to vapour pressure deficit in field conditions can be explained by the temperature optimum of photosynthesis *Agric. Meteorol.* **189–190** 2–10

Farquhar G D, von Caemmerer S and Berry J 1980 A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species *Planta* **149** 78–90

Gamo M *et al* 2005 Carbon flux observation in the tropical seasonal forests and tropical rain forest. *Proc. Int. Workshop on Advanced Flux Network and Flux Evaluation (AsiaFlux Workshop 2005) (Fujiyoshida, Japan)*

Goulden M L, Miller S D, da Rocha H R, Menton M C, de Freitas H C, Figureira A M E S and de Sousa C A D 2004 Diel and seasonal patterns of tropical forest CO_2 exchange *Ecol. Appl.* **14** s42–54

Hikosaka K, Ishikawa K, Borjigidai A, Muller O and Onoda Y 2006 Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate *J. Exp. Bot.* **57** 291–302

Hirano T, Seagh H, Harada T, Limin S, June T, Hirata R and Osaki M 2007 Carbon dioxide balance of a tropical peat swamp forest in Kalimantan, Indonesia *Glob. Change Biol.* **13** 412–25

Hirata R, Saigusa N, Yamamoto S, Ohtani Y, Ide R, Asanuma J, Gamo M, Hirano T, Kondo H and Kosugi Y 2008 Spatial distribution of carbon balance in forest ecosystems across East Asia *Agric. Meteorol.* **148** 761–75

Ishida A, Toma T, Matsumoto Y, Yap S K and Maruyama Y 1996 Diurnal changes in leaf gas exchange characteristics in the uppermost canopy of a rain forest tree, *Dryobalanops aromatic* Gaertn. f *Tree Physiol.* **16** 779–85

Jaramillo C *et al* 2010 Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation *Science* **330** 957–61

June T, Evans J R and Farquhar G D 2004 A simple new equation for the reversible temperature dependence of photosynthetic electron transport: a study on soybean leaf *Funct. Plant Biol.* **31** 275–83

Koch G W, Amthor J S and Goulden M L 1994 Diurnal patterns of leaf photosynthesis, conductance and water potential at the top of a lowland rain forest canopy in Cameroon: measurements from the Radeau des Cimes *Tree Physiol.* **14** 347–60

Kositsup B, Montpied P, Kasemsap P, Thaler P, Ameglio T and Dreyer E 2009 Photosynthetic capacity and temperature response of photosynthesis of rubber trees (*Hevea brasiliensis* Müll. Arg.) acclimate to changes in ambient temperatures *Trees* **23** 357–65

Lange O L, Schulze E-D, Evenari M, Kappen L and Buschbom U 1974 The temperature-related photosynthetic capacity of plants under desert conditions. I. Seasonal changes of the photosynthetic response to temperature *Oecologia* **17** 97–110

Lasslop G, Reichstein M, Papale D, Arneth A D, Barr A, Stoy A and Wohlfahrt P 2010 Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation *Glob. Change Biol.* **16** 187–208

Lenorman M, Jabot F and Deffuant G 2013 Adaptive approximate Bayesian computation for complex models *Comput. Stat.* **28** 2777–96

Leuning R 1990 Modelling stomatal behavior and photosynthesis of *Eucalyptus grandis Aust. J. Plant Physiol.* **17** 339–55

Lloyd J and Farquhar G D 2008 Effect of rising temperatures and $[CO_2]$ on the physiology of tropical forest trees *Phil. Trans. R. Soc.* B **363** 1811–17

Lin Y S, Medlyn B E and Ellsworth D S 2012 Temperature response of leaf net photosynthesis: the role of component processes *Tree Physiol.* **32** 219–31

Lombardozzi D L, Bonan G B, Smith N G, Dukes J S and Fisher R A 2015 Temperature acclimation of photosynthesis and respiration: a key uncertainty in the carbon cycle-climate feedback *Geophys. Res. Lett.* **42** 8624–31

Medlyn B E, Duursma R A, Eamus D, Ellsworth D S, Prentice C V M, Barton K Y, Crous P, Angelis M, Freeman M and Wingate L 2011 Reconciling the optimal and empirical approaches to modeling stomatal conductance *Glob. Change Biol.* **17** 2134–44

Niu S *et al* 2012 Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms *New Phytol.* **194** 775–83

Restrepo-Coupe N *et al* 2013 What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network *Agric. Meteorol.* **182** 128–44

Rowland L *et al* 2015 Modelling climate change responses in tropical forests: similar productivity estimates across five models, but different mechanisms and responses *Geosci. Model Dev.* **8** 1097–110

Sage R F and Kubien D S 2007 The temperature response of C_3 and C_4 photosynthesis *Plant Cell Environ.* **30** 1086–106

Slot M and Kitajima K 2015 General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types *Oecologia* **177** 885–900

Slot M and Winter K 2017 *In situ* temperature response of photosynthesis of 42 tree and liana species in the canopy of two Panamanian lowland tropical forests with contrasting rainfall regimes *New Phytol.* **214** 1103–17

Tjoelker M G, Oleksyn J, Lorenc-Plucinska G and Reich P B 2009 Acclimation of respiratory temperature response in northern and southern populations of *Pinus banksiana New Phytol.* **181** 218–29

Vargas G G and Cordero S R A 2013 Photosynthetic responses to temperature of two tropical rainforest tree species from Costa Rica *Trees* **27** 1261–70

Vårhammar A, Wallin G, McLean C M, Dusenge M E, Medlyn B E, Hasper T B, Dsabimana D and Uddling J 2015 Photosynthetic temperature response of tree species in Rwanda: evidence of pronounced negative effects of high temperature in montane rainforest climax species *New Phytol.* **206** 1000–12 von Caemmerer S, Farquhar G and Berry J 2009 Biochemical model of C_3 photosynthesis *Photosynthesis in Silico: Understanding Complexity from Molecules to Ecosystems* ed A Laisk, L Nedbal and Govindjee (New York: Springer) pp 209–30

Wang Y P, Baldocchi D, Leuning R, Falge E and Vesala T 2007 Estimating parameters in land-surface model by applying nonlinear inversion to eddy covariance flux measurements from eight Fluxnet sites *Glob. Change Biol.* **13** 652–70

Wright S J, Muller-Landau H C and Schipper A J 2009 The future of tropical species on a warmer planet *Conserv. Biol.* **23** 1418–26

Yi C, Davis K J, Bakwin P S, Berger B W and Marr L C 2000 Influence of advection on measurements of the net ecosystem-atmosphere exchange of CO_2 from a very tall tower *J. Geophys. Res. Atmos.* **105** 9991–9

Yi C *et al* 2004 A nonparametric method for separating photosynthesis and respiration components in CO_2 flux measurements *Geophys. Res. Lett.* **31** L17107

Yi C *et al* 2010 Climate control of terrestrial carbon exchange across biomes and continents *Environ. Res. Lett.* **5** 034007

Zeng J, Tan Z H and Saigusa N 2017 Using approximate Bayesian computation to infer photosynthesis model parameters *Chinese J. Plant Ecol.* **41** 378–85

Zhang Y J, Cristiano P M, Zhang Y F, Campanello P I, Tan Z H, Zhang Y P, Cao K and Goldstein G 2016 Tropical tree physiology *Carbon Economy of Subtropical Forests* ed G Goldstein and L S Santiago (Cham: Springer) pp 337–55