

Temperature response of CO₂ exchange in three tropical tree species

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Abstract. Tropical forests play a critical role in the global carbon cycle, but our limited understanding of the physiological sensitivity of tropical forest trees to environmental factors complicates predictions of tropical carbon fluxes in a changing climate. We determined the short-term temperature response of leaf photosynthesis and respiration of seedlings of three tropical tree species from Panama. For one of the species net CO₂ exchange was also measured *in situ*. Dark respiration of all species increased linearly – not exponentially – over a ~30°C temperature range. The early-successional species *Ficus insipida* Willd. and *Ochroma pyramidale* (Cav. ex Lam.) Urb. had higher temperature optima for photosynthesis (T_{opt}) and higher photosynthesis rates at T_{opt} than the late-successional species *Calophyllum longifolium* Willd. The decrease in photosynthesis above T_{opt} could be assigned, in part, to observed temperature-stimulated photorespiration and decreasing stomatal conductance (g_s), with unmeasured processes such as respiration in the light, Rubisco deactivation, and changing membrane properties probably playing important additional roles, particularly at very high temperatures. As temperature increased above T_{opt} , g_s of laboratory-measured leaves first decreased, followed by an increase at temperatures >40–45°C. In contrast, g_s of canopy leaves of *F. insipida* in the field continued to decrease with increasing temperature, causing complete suppression of photosynthesis at ~45°C, whereas photosynthesis in the laboratory did not reach zero until leaf temperature was ~50°C. Models parameterised with laboratory-derived data should be validated against field observations when they are used to predict tropical forest carbon fluxes.

Additional keywords: carbon balance, gas exchange, global warming, photosynthetic temperature response, stomatal conductance, tropical forest.

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Introduction

Given the large amount of carbon that tropical forests exchange with the atmosphere (Saugier *et al.* 2001) and store in live biomass (Pan *et al.* 2013), understanding the photosynthetic and respiratory responses of tropical forest trees to environmental drivers is critical for our ability to predict tropical and global carbon dynamics in the face of global warming. Lack of understanding of the potential feedbacks between the terrestrial biosphere and the atmosphere represents one of the largest sources of uncertainty in current coupled climate–vegetation models (Huntingford *et al.* 2013; Piao *et al.* 2013), with plant responses to temperature being recognised as a key uncertainty (Booth *et al.* 2012).

Temperature has a strong immediate effect on foliar physiology, both directly through its effect on enzyme activity and metabolic fluxes in plant cells, and indirectly through the tight coupling of temperature and atmospheric relative humidity. Carbon release from foliar dark respiration (R_{dark}) increases strongly with short-term temperature rise and peaks at ~50–55°C (e.g. O’Sullivan *et al.* 2013). This instantaneous temperature response generally takes the form of an exponential rise over biologically relevant temperatures (e.g. Amthor 1984; Ryan

1991). The sensitivity of R_{dark} to warming can be expressed using parameters derived from the exponential curve, e.g. a Q_{10} – the proportional increase in R_{dark} with 10°C warming. Respiration rates at ambient temperature are higher in the tropics than in higher latitudes (Atkin *et al.* 2015), but Q_{10} values reported for tropical forest vegetation are similar to those of higher latitude vegetation, with median values slightly >2.0 (Meir *et al.* 2001; Cavaleri *et al.* 2008; Slot *et al.* 2013, 2014).

Photosynthetic temperature-response curves are not well documented for tropical forest trees, in part because of instrumental restrictions and limitations in access to canopy trees. Temperature response curves of leaves of the tropical tree species *Zygia longifolia* (Willd.) Britton & Rose and *Dipteryx oleifera* Benth. measured *in situ* in Costa Rica showed similar optimum temperatures for photosynthesis of ~28°C, close to mean ambient temperature of the site (Vargas and Cordero 2013). The optimum temperature of photosynthesis in seedlings of *Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg. was also close to mean ambient growth temperature (Kositsup *et al.* 2009). These results are consistent with other measurements at the leaf and stand level that suggest that warming of tropical forest vegetation above current mean ambient temperatures will

decrease photosynthetic carbon gain (Doughty and Goulden 2008; Doughty 2011). Similarly, warming seedlings of tropical tree species above their optimum growth temperature significantly decreased net photosynthesis at all temperatures in two of three species tested by Cheesman and Winter (2013). The decrease in net photosynthesis above optimal temperatures is the result of temperature-dependent biochemical changes, including increased rates of photorespiration as both the relative solubility of CO₂ versus O₂ and the specificity of Rubisco for CO₂ decreases with increasing temperature (von Caemmerer and Quick 2000); a reduction of Rubisco activase functioning at high temperature (Salvucci and Crafts-Brandner 2004; Sage *et al.* 2008); and/or disruption of electron transport due to leaky thylakoid membranes (Wise *et al.* 2004). In addition, the vapour pressure deficit (VPD) of leaves increases with warming at a given absolute moisture content of the air, which may reduce stomatal conductance.

Tropical forest species of different plant functional types (PFTs) differ in their gas exchange properties (Kitajima 1994; Slot *et al.* 2013), hydraulic properties (e.g. Markesteijn *et al.* 2011) and allocation strategies (Kitajima 1994; Markesteijn and Poorter 2009) – trait differences that reflect their respective strategies on the so called ‘fast-slow’ growth continuum (Wright *et al.* 2004). Early-successional, light-demanding species have traits associated with rapid resource acquisition and growth, such as high rates of photosynthesis and respiration, high hydraulic conductivity in stems and leaves, and rapid initial height growth, whereas late-successional, shade-tolerant species have more conservative resource use, with greater investment into defence and tissue longevity at the cost of lower growth rates (Wright *et al.* 2010). Given these systematic trait differences and the differences in environmental conditions of the niches occupied by species of different PFTs (Bazzaz and Pickett 1980) it is likely that PFTs also differ in their temperature sensitivity. In the above-mentioned Costa Rican study the early-successional *Z. longifolia* had a significantly higher estimated high-temperature CO₂ compensation point than the late-successional *D. oleifera* (Vargas and Cordero 2013), but apart from that estimated difference, tropical PFT differences in the temperature sensitivity of photosynthesis are currently unknown.

In the study presented here, we measured net photosynthesis and respiration in seedlings of three common tropical forest tree species between 20 and 55°C and determined the effect of photorespiration on the temperature-response characteristics. We studied two early-successional species, *Ficus insipida* Willd. (Moraceae) and *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Malvaceae), and one late-successional species, *Calophyllum longifolium* Willd. (Calophyllaceae). Experiments under controlled-environment conditions often serve to parameterise ecosystem and earth-system models, as controlled-environment conditions are superior at isolating environmental influences of interest. To assess the comparability of such laboratory-based measurements of seedlings with observations on trees in the field we also studied how net CO₂ exchange rates in upper-canopy leaves of *F. insipida* changed as leaf-temperatures changed during the diurnal cycle. We further monitored *F. insipida* leaf temperature in the field using two different methods of thermocouple attachment to test which method reproduced

most closely the true leaf temperature, as predictions for physiological temperature dependence in the field hinge upon accurate leaf temperature data.

Materials and methods

Plant material

Seeds of *Ficus insipida* Willd., *Calophyllum longifolium* Willd. and *Ochroma pyramidale* (Cav. ex Lam.) Urb. were collected in the vicinity of Panama City, Republic of Panama (8.9833°N, 79.5167°W) and germinated in trays with potting soil (Miracle-Gro, Stern’s Miracle-Gro Products, Port Washington, NY, USA). When seedlings had two true leaves they were transferred into individual 2.8 L pots (Tall One Treepot, Stuewe and Sons, Tangent, OR, USA) with potting soil, and maintained well-watered at ambient irradiance and temperature in Panama City.

Gas-exchange measurements in the laboratory

After 2 months, when the plants had on average 10 leaves, measurements were made on attached leaves ($n = 4–6$; one leaf per plant) in a temperature-controlled gas-exchange cuvette (GWK-3M; Walz GmbH, Eiffeltrich, Germany) attached to an Li-6252 infrared gas analyser (Li-Cor, Lincoln, NE, USA). Leaves were sealed in the chamber at the petiole, enabling measurements of entire leaves. Rapid internal air-mixing eliminated boundary layer resistance. The photosynthetic photon flux density (PPFD) at leaf level was set to the prior-determined saturating level of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, provided by a red-blue LED grow panel (SS-GU300w, Sunshine Systems, Wheeling, IL, USA) placed ~30 cm above the cuvette. The CO₂ concentration of the air entering the chamber was set to slightly over 400 $\mu\text{mol mol}^{-1}$, such that photosynthesis never depleted cuvette CO₂ concentrations to below 365 $\mu\text{mol mol}^{-1}$. Leaf temperature was monitored abaxially with an OS36T infrared thermocouple (Omega, Stamford, CT, USA). Non-photorespiratory conditions of 2% O₂ were created by mixing air entering the cuvette with nitrogen gas at a ratio of 1 to 9.5. The air mixture was then passed through soda lime before pure CO₂ was added to generate the desired CO₂ concentration.

Plants were taken to the laboratory 2 h after sunrise to ensure that photosynthesis was induced. Leaf gas exchange was first measured at an air temperature of 25°C. Usually a minimum of 20 min elapsed before CO₂ fluxes, leaf temperature and the dew point temperatures of air leaving the cuvette stabilised. After lowering the temperature to 20°C and recording constant gas-exchange rates, the leaves were again measured at 25°C; data were discarded if CO₂ uptake rates did not return to those obtained earlier. We used this protocol to obtain as wide a temperature range as possible, while ensuring that the first, suboptimal temperature did not negatively affect responses at higher temperatures. Air temperature was increased in steps of 5°C up to 55°C (*C. longifolium*) or 60°C (other species). Rates of dark respiration (R_{dark}) were measured between 20 and 55°C on a separate set of leaves following the same protocol, except that respiration measurements were made in the early morning hours on plants that were darkened before sunrise.

Dew point temperatures of the air entering and exiting the cuvette were measured with two MTSMK1 dew point

mirrors (Walz GmbH). These measurements, combined with leaf temperature data, enabled us to calculate rates of transpiration (E), stomatal conductance (g_s), and intercellular CO₂ concentrations (C_i) using von Caemmerer and Farquhar (1981) equations.

Gas-exchange measurements in the field

Photosynthesis was measured on upper-canopy leaves of a ~35 m tall *F. insipida* tree in Parque Natural Metropolitano, a 256 ha reserve of 80–120-year-old semi-deciduous moist tropical forest in Panama City, Republic of Panama. Mean annual temperature at the site is 26.3°C, and annual rainfall averages 1740 mm, most of which falls during the rainy season (May–December). Repeated access to leaves was possible with a 42 m tall construction crane. In the early dry season (January 2013), six fully-expanded, sun-exposed leaves in the upper canopy were tagged and then measured 11 times between 0800 hours and ~solar noon with an Li-6400 infrared gas analyser (Li-Cor) at 400 μmol mol⁻¹ CO₂, under ambient irradiance and temperature.

Diel patterns of *F. insipida* leaf temperature were monitored with fine-wire copper-constantan thermocouples attached to the abaxial side of six leaves of the same *F. insipida* tree and values were recorded on a CR1000 datalogger (Campbell Scientific, Logan, UT, USA) every minute. Two thermocouples were attached to each leaf; the tip of one was attached with porous tape (Transpore 3M, Neuss, Germany), the other was held in place with a custom-made lightweight plastic clip (see Fig. S1, available as Supplementary Material to this paper). The thermocouples did not affect the leaf angles. Porous tape is commonly used to attach thermocouples, but we were interested to see how the tape would affect the dynamic changes in leaf temperature under ambient, upper-canopy conditions and how thus-recorded leaf temperatures would compare to those recorded with thermocouples clipped onto the leaves, and with values recorded with infrared thermometry (MiniTemp MT6, Raytek, Santa Cruz, CA, USA).

Respiration rates were measured between 0600 and 1100 hours on a different set of 13 leaves from the same tree that were pre-darkened with aluminium foil since the preceding sunset. Each leaf was measured once, using changes in ambient temperature to generate a gradient in leaf temperatures at which respiration was measured, enabling us to construct a species-level temperature-response curve (see Slot *et al.* 2013).

Curve fitting of temperature response of leaf gas exchange

Net photosynthetic CO₂ exchange was plotted against measured leaf temperature (T_{leaf}) and second-order polynomial curves were fitted following Cunningham and Read (2002) as:

$$\text{photosynthesis} = b \times (T_{\text{leaf}} - T_{\text{min}}) \times \left(1 - e^{c \times (T_{\text{leaf}} - T_{\text{max}})}\right), \quad (1)$$

where T_{min} and T_{max} are the (theoretical) low- and high-temperature CO₂ compensation points, and b and c are constants. All four variables were estimated using a non-linear solver function in Microsoft Excel 2010 (Microsoft Corporation, Redmond, WA, USA), minimising the sums of the squared deviation of measured values from the fitted model. The temperature optimum of net photosynthesis (T_{opt}) was calculated for each leaf by solving for T_{leaf} when setting the first derivative of Eqn 1 to zero. A_{opt} , the assimilation rate at T_{opt} was calculated by setting T_{leaf} to T_{opt} in Eqn 1.

Statistical analyses

Differences in physiological traits across species were assessed with analyses of variance. Comparisons between physiological traits of *F. insipida* measured *in situ* and in the laboratory were made using two-tailed *t*-tests. All analyses were performed in R ver. 3.1.0 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Photosynthesis: species differences and photorespiration

The short-term temperature-response of net photosynthesis could be approximated with a second-order polynomial curve for all leaves ($r^2 > 0.95$ for all curves, and no systematic over- or under-estimations). The optimum temperature of photosynthesis (T_{opt}) as calculated from the fitted photosynthesis-temperature response curves, differed significantly among species ($P < 0.05$), with the early-successional species *F. insipida* showing the highest values, and the late-successional species *C. longifolium* showing the lowest values (Table 1; Fig. 1). The rates of photosynthesis at the optimum temperature (A_{opt}) were higher in the two early-successional species *F. insipida* and *O. pyramidale* than in *C. longifolium* (Table 1).

Under non-photorespiratory conditions (i.e. O₂ concentration of 2%), both T_{opt} ($P = 0.006$) and A_{opt} ($P = 0.002$) values were significantly higher than under ambient oxygen conditions.

Table 1. Means ± s.e. of the optimum temperature of net photosynthesis (T_{opt}) and the rate of net photosynthesis at T_{opt} (A_{opt}) of seedling leaves of three tropical tree species measured at 21% and 2% oxygen concentration (O₂), and dark respiration rate at 25°C (R_{25}) measured at 21% O₂. Also shown are the rate of photorespiration (R_{photo}) at 30°C, and R_{photo} as a proportion of net photosynthesis (A_{net}) at 2% oxygen concentration

Species	O ₂ (%)	<i>n</i>	T_{opt} (°C)	A_{opt} (μmol m ⁻² s ⁻¹)	R_{25} (μmol m ⁻² s ⁻¹)	R_{photo} at 30°C (μmol m ⁻² s ⁻¹)	$R_{\text{photo}}/A_{\text{net}}$ at 2% O ₂ at 30°C																				
<i>Calophyllum longifolium</i>	21	4	26.6 ± 0.8	5.5 ± 0.7	0.54 ± 0.07	2.6 ± 0.9	0.30 ± 0.08																				
	2	4	28.9 ± 0.4	7.9 ± 1.2				<i>Ficus insipida</i>	21	4	29.2 ± 0.5	13.7 ± 1.3	0.73 ± 0.05	5.2 ± 0.4	0.27 ± 0.01	2	4	30.4 ± 0.2	18.6 ± 1.4	<i>Ochroma pyramidale</i>	21	6	27.8 ± 0.6	12.4 ± 0.7	0.75 ± 0.04	3.6 ± 0.6	0.22 ± 0.02
<i>Ficus insipida</i>	21	4	29.2 ± 0.5	13.7 ± 1.3	0.73 ± 0.05	5.2 ± 0.4	0.27 ± 0.01																				
	2	4	30.4 ± 0.2	18.6 ± 1.4				<i>Ochroma pyramidale</i>	21	6	27.8 ± 0.6	12.4 ± 0.7	0.75 ± 0.04	3.6 ± 0.6	0.22 ± 0.02	2	6	29.3 ± 0.7	14.6 ± 0.9								
<i>Ochroma pyramidale</i>	21	6	27.8 ± 0.6	12.4 ± 0.7	0.75 ± 0.04	3.6 ± 0.6	0.22 ± 0.02																				
	2	6	29.3 ± 0.7	14.6 ± 0.9																							

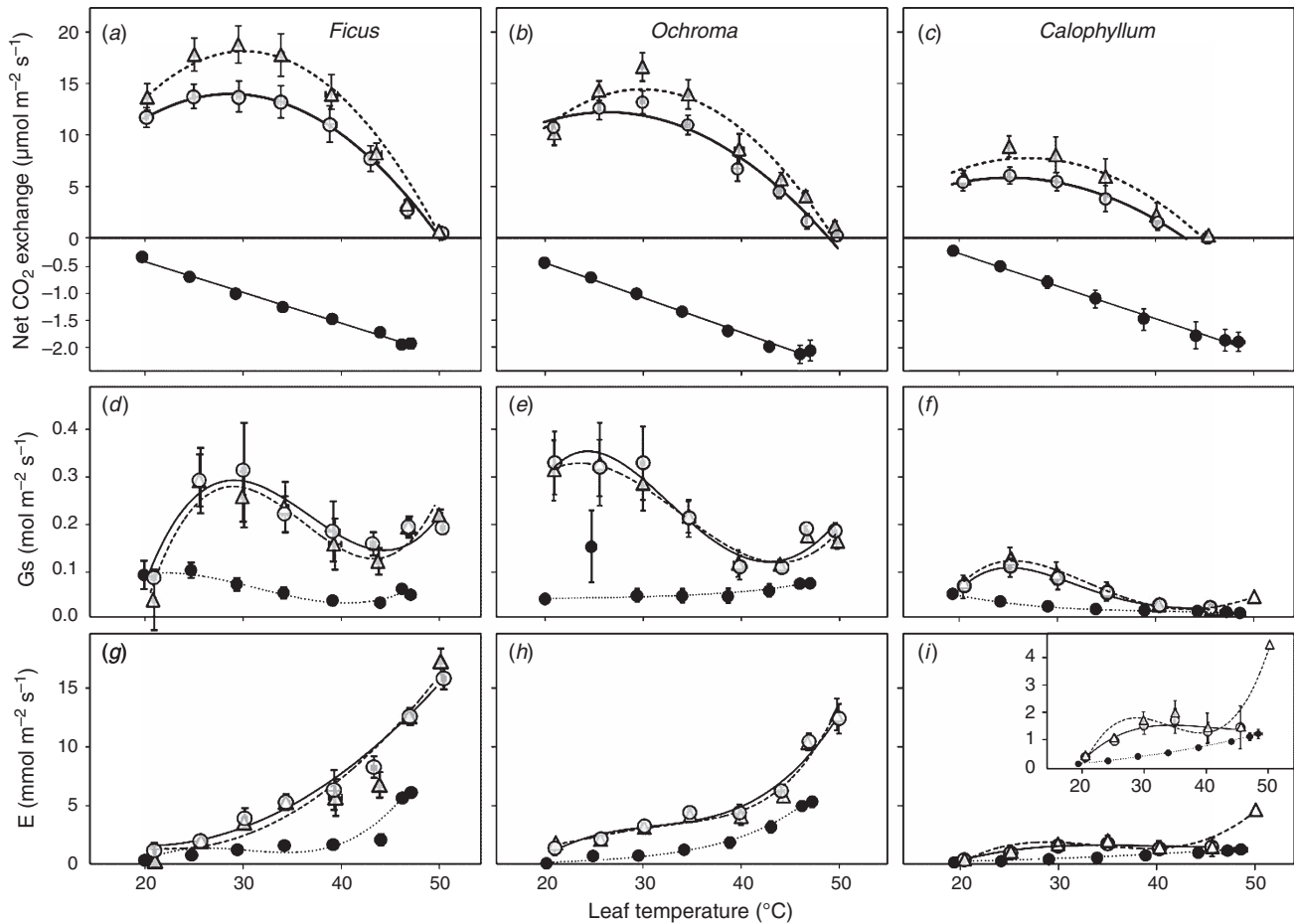


Fig. 1. Temperature responses of net CO₂ exchange (a–c), stomatal conductance (g_s) (d–f), and transpiration (E) (g–i) of *Ficus insipida*, *Ochroma pyramidale*, and *Calophyllum longifolium* seedlings (mean \pm s.e.; $n=4-6$) measured in the laboratory. Measurements were made at 21% (open circles, solid lines) and ~2% oxygen (triangles, dashed lines) and a photosynthetic photon flux density of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Closed circles represent measurements in the dark at ambient (21%) oxygen concentration. Net photosynthesis data were fitted with 2nd order polynomials (see text for full explanation); respiration data are fitted with linear lines, and g_s and E data with 2nd or 3rd order polynomials.

As was the case under ambient O₂, at low O₂ T_{opt} was highest in *F. insipida* and lowest in *C. longifolium* (Table 1). A_{opt} was also highest in *F. insipida* and lowest in *C. longifolium* at low O₂ (Table 1). In all three species rates of photorespiration peaked around 30°C, near T_{opt} of net photosynthesis. The highest rates of photorespiration were recorded in *F. insipida*, whereas *C. longifolium* had the lowest values (Table 1). In contrast, photorespiration as a proportion of photosynthesis at 2% O₂ and 30°C was highest in *C. longifolium*, lowest in *O. pyramidale*, with intermediate values in *F. insipida* (Table 1). Photorespiration as a proportion of photosynthesis at 2% O₂ gradually increased with rising temperature before increasing steeply above 40°C (*Calophyllum*) to 45°C (*Ficus* and *Ochroma*), reaching maximum values ranging from 0.49 ± 0.28 in *F. insipida* to 0.91 ± 0.32 in *C. longifolium*. At this point net photosynthesis rates and absolute rates of photorespiration were approaching zero.

Regardless of the O₂ concentration, stomatal conductance (g_s) largely exhibited similar optimum curves as net photosynthesis with values increasing up to a T_{leaf} of ~30°C

before gradually dropping as temperature further increased (Fig. 1). At very high T_{leaf} (>45°C), however, stomata reopened and g_s strongly increased again. This pattern was consistent across species, although the absolute values of g_s at any given temperature differed greatly among species, with *C. longifolium* maintaining the lowest g_s values at all temperatures (Fig. 1). Despite similar temperature optima of photosynthesis and g_s , net photosynthesis only correlated strongly with g_s in *C. longifolium* leaves (Fig. 2). Transpiration (E) also steeply increased above 45°C, but in contrast to g_s , E increased monotonically as temperature increased (with the exception of a slight depression at 40°C in *C. longifolium* – see inset in Fig. 1i). Stomatal opening at high T_{leaf} occurred despite high vapour pressure deficit under these conditions, consistent for all species and both O₂ concentrations (Fig. 2). As a result of the low rates of net photosynthesis and the high stomatal conductance C_i (intercellular CO₂ concentration) equalled C_a (CO₂ concentration of the air) at high temperatures, i.e. $C_a - C_i$ values approached zero (see Fig. S2).

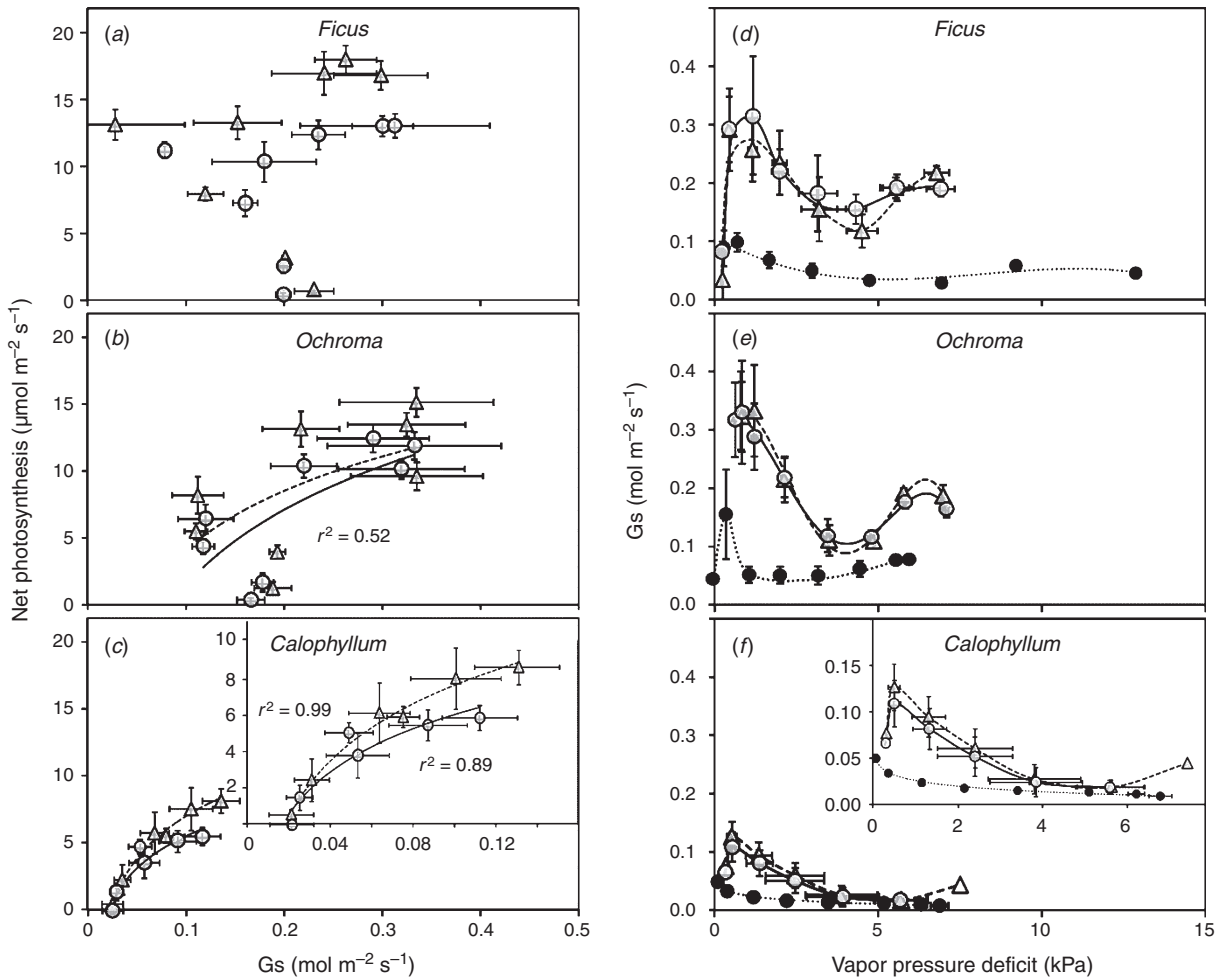


Fig. 2. Relationships between seedling stomatal conductance (g_s) and net photosynthesis (a–c), and between g_s and leaf-to-air vapour pressure deficit (VPD) (d–f) (mean \pm s.e.; $n = 4–6$) for leaves measured between 20 and 50°C. Measurements were made in the laboratory at 21% (circles) and ~2% oxygen (triangles) at a photosynthetic photon flux density of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Net photosynthesis correlated linearly with $\log_{10}(g_s)$ in *Calophyllum longifolium* measured at ambient (solid line) and at low oxygen concentration (dashed line). In *Ochroma pyramidale* the correlation was marginally significant at low oxygen. Closed circles in d–f represent measurements in the dark at ambient (21%) oxygen concentration.

Dark respiration

Respiration rates increased with increasing leaf temperature, but as is clear from Fig. 1, this increase was not exponential. Even in the part of the curve before 45°C, which appeared to be a thermal optimum, the data were best fitted with a linear or quadratic curve. The slopes of linear respiration-temperature response fits did not differ significantly among species, but respiration at a set temperature of 25°C (R_{25}) was significantly lower in *C. longifolium* leaves than in leaves of *O. pyramidale* and *F. insipida*. Although less pronounced, during respiration measurements g_s and E followed similar patterns as those during photosynthesis measurements (Fig. 1), including increased g_s at the highest temperatures in *O. pyramidale* and *F. insipida*.

Field versus laboratory

Photosynthetic temperature responses in the field were assessed by studying CO_2 exchange during the early part of a bright day

as leaf temperatures rose concomitantly with increases in PPFD (Fig. 3a–c). In parallel with rising leaf temperatures the leaf-to-air vapour pressure deficit also increased (Fig. 3d). All of these environmental variables correlated strongly and positively with each other ($r^2 > 0.9$, $P < 0.01$ for all correlations) (Fig. S3) and net photosynthesis correlated strongly and negatively with each factor ($r^2 > 0.9$, $P < 0.01$ for all correlations) (Fig. 4a–c). As each of these environmental variables increased, net photosynthesis decreased in very strong correlation ($r^2 > 0.99$, $P < 0.01$) with decreasing g_s (Fig. 4d).

Compared with laboratory-studied leaves of seedlings, field-measured upper-canopy leaves of *F. insipida* had marginally significantly higher T_{opt} values ($P = 0.06$) at $32.4 \pm 0.9^\circ\text{C}$ (mean \pm s.e.) and significantly higher mean A_{opt} of $22.9 \pm 0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($P < 0.001$). However, the high-temperature CO_2 compensation point was significantly higher in laboratory-measured than in field-measured leaves ($P < 0.01$), by $\sim 5^\circ\text{C}$ (Fig. 5a). In contrast to the observations in the laboratory, g_s did not increase at high temperatures in the field, but

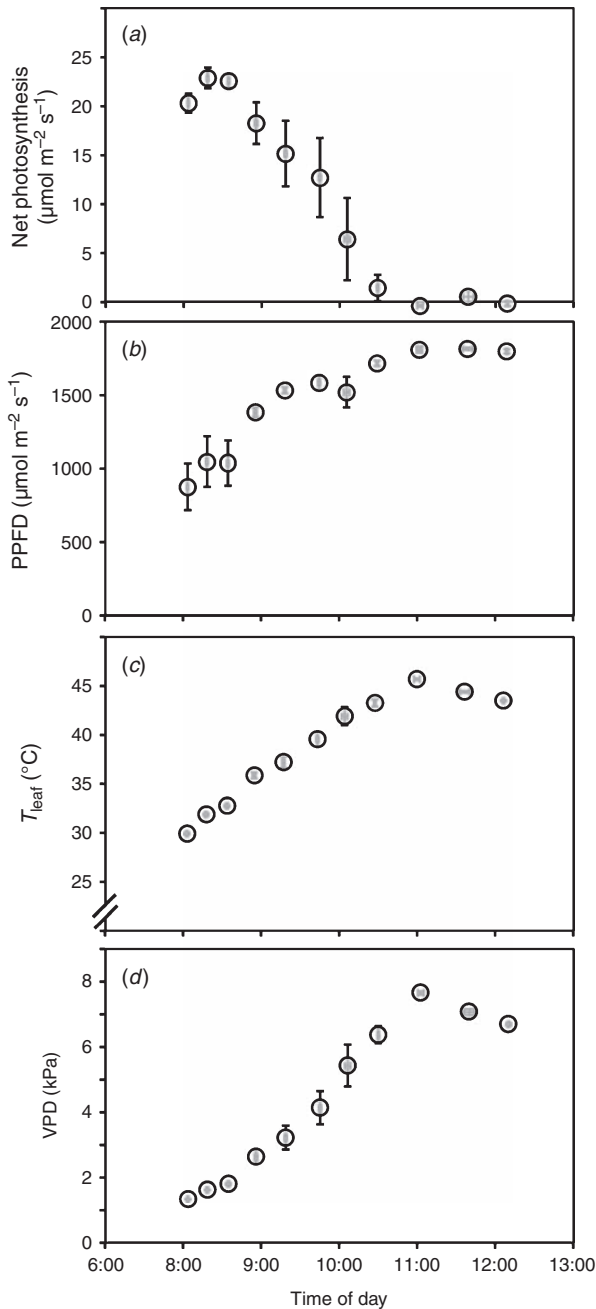


Fig. 3. Changes in net photosynthesis (a), photosynthetic photon flux density (PPFD) at leaf level (b), leaf temperature (T_{leaf}) (c), and leaf-to-air vapour pressure deficit (VPD) (d) over time in *Ficus insipida* measured in the field on 15 January 2013.

approached zero before T_{leaf} reached 45°C (Fig. 5b). Dark respiration was higher in the field than in the laboratory (R_{25} of 1.4 ± 0.1 vs $0.74 \pm 0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$). The temperature sensitivity of respiration was also higher in the field (Fig. 5c), as the mean linear slope of laboratory-measured respiration versus temperature was significantly lower than the slope of the field-measured respiration versus temperature (*t*-test, $P < 0.05$). Leaf mass per area was significantly higher in the field than in the laboratory (132.4 ± 4.9 vs $41.3 \pm 2.3 \text{ g m}^{-2}$).

The temperature range over which net photosynthesis in the field was positive corresponded with the frequency distribution of daytime (0600 to 1800 hours) leaf temperatures recorded in the same period. T_{opt} of net photosynthesis was marginally higher than the most frequently recorded temperatures, both those measured with thermocouples taped to leaves and those clipped onto leaves. About 40% of recorded leaf temperatures were greater than T_{opt} (Fig. 6), and on days with high PPFD T_{leaf} exceeded T_{opt} for much of the day (Fig. S1).

Leaf temperatures

Leaf temperatures measured with thermocouples clipped onto target leaves differed considerably from the values recorded from thermocouples taped to the same leaves, with thermocouples clipped onto the leaves recording daytime values that were on average 0.56°C lower than thermocouples taped to the same leaves. Although this daily mean difference is modest, in full sunlight ($>1750 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) clipped-on thermocouples recorded values that were on average 1.6°C (0.60 – 2.5°C , 10th and 90th percentiles respectively) lower than taped thermocouples, and differences in temperature between the two methods within individual leaves occasionally exceeded 7°C at any one time. Taped thermocouples occasionally recorded values $>48^{\circ}\text{C}$ (Fig. S4). At night the clipped-on thermocouples recorded on average 0.14°C (0.06 – 0.22°C , 10th and 90th percentiles) higher values than taped thermocouples. Comparison of the two methods with measurements of abaxial leaf temperature with a hand-held infrared thermometer over a $\sim 25^{\circ}\text{C}$ temperature range indicated that at high temperatures the thermocouples clipped onto the leaves record significantly lower values than both the taped thermocouples and the infrared thermometer.

Discussion

There is uncertainty about the fate of tropical forests in a warming world, as little is known about the thermal optima and maxima of tropical forest tree performance. Leaves of tropical forest trees frequently experience very high temperatures during the day with negative consequences to their capacity to take up carbon in photosynthesis. Indeed, at full solar radiation net photosynthesis may approach zero because of stomatal closure associated with high leaf temperatures, in what is called midday depression (e.g. Zotz *et al.* 1995; Pons and Welschen 2003; Cernusak *et al.* 2013). Here we have shown that tropical tree species differ significantly in their optimum temperature of photosynthesis and in their high-temperature CO_2 compensation points. We also show that laboratory-derived physiological parameters describing the temperature response of seedlings do not necessarily translate well to the more complex conditions of trees in the field. We will first discuss the species difference and its significance for understanding the effects of climate warming on tropical forests, then we will discuss the differences between *in situ* and laboratory-based measurements. Finally, we will discuss some issues associated with monitoring of leaf temperature in the field.

Species-specific temperature sensitivity of photosynthesis

Our observations confirm the sensitivity of lowland tropical forest species to high temperature (Doughty and Goulden

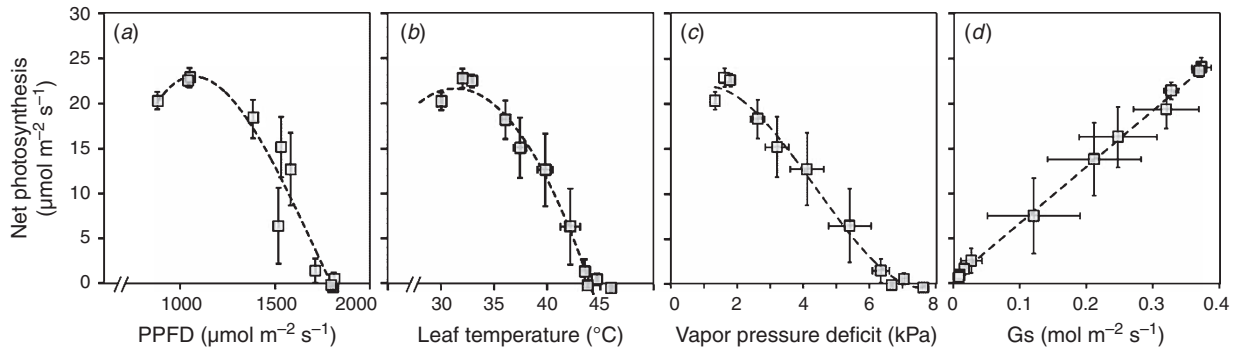


Fig. 4. Correlations between net photosynthesis and photosynthetic photon flux density (PPFD) (a), leaf temperature (b), leaf-to-air vapour pressure deficit (c), and stomatal conductance (g_s) of *Ficus insipida* leaves in the field (mean \pm s.e.; $n = 6$), measured 11 times between 0800 and 1230 hours on 15 January 2013.

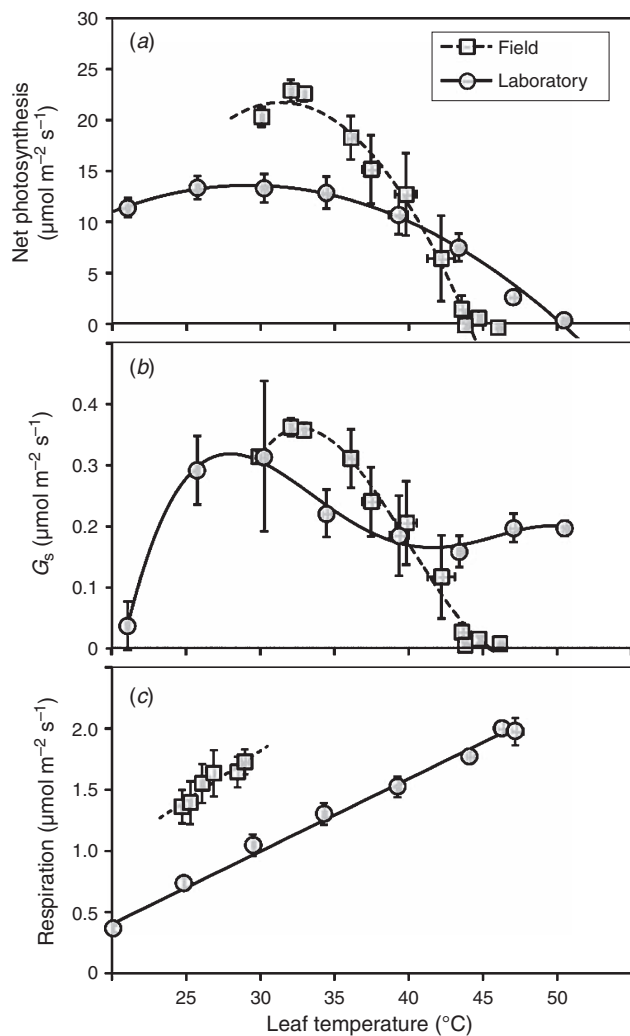


Fig. 5. Mean rates (\pm s.e.) of net photosynthesis (a), stomatal conductance (g_s) (b), and dark respiration (c) in relation to leaf temperature for *Ficus insipida* leaves measured in the laboratory ($n = 4$) and in the field ($n = 6$). Net photosynthesis and g_s data are fitted with 2nd and 3rd order polynomial curves, respectively. Respiration data are presented with a linear fit.

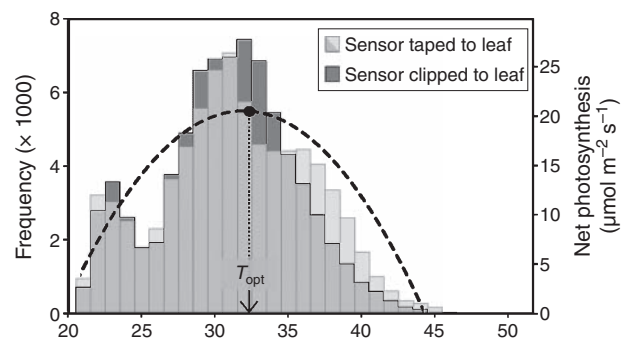


Fig. 6. Frequency distribution of 1 min mean leaf temperatures recorded with thermocouple wires either taped or clipped onto the abaxial side of six *Ficus insipida* leaves in the field. Overlaid is the curve describing the temperature response of net photosynthesis according to Eqn 1, as shown in Fig. 5a, indicating the optimum leaf temperature for net photosynthesis (T_{opt}) of $\sim 32.4^\circ\text{C}$.

2008; Doughty 2011; Vargas and Cordero 2013; Krause *et al.* 2015). With net photosynthesis peaking close to mean ambient temperatures, plants frequently operate under super-optimal temperatures. The decrease in photosynthesis rates above T_{opt} is in part due to increased photorespiration, as evidenced by the shift in T_{opt} towards higher temperatures, and higher photosynthesis rates at high temperatures under non-photorespiratory conditions in all three study species. However, although the proportional importance of photorespiration in determining net photosynthesis at 21% O_2 increased with rising temperature, photosynthesis at both 21 and 2% O_2 decreased above 30–35°C. Stomatal conductance only exhibits strong control over net photosynthesis in *C. longifolium* (Fig. 2), suggesting that much of the decrease in net photosynthesis at temperatures exceeding T_{opt} in the early-successional species *F. insipida* and *O. pyramidale* were neither caused by photorespiration, nor by stomatal restrictions on CO_2 diffusion.

Mitochondrial respiration in the light also increases with temperature (e.g. Way *et al.* 2015) and this affects the temperature response of net photosynthesis. Lin *et al.* (2012) did a sensitivity analysis to evaluate which factor had the

greatest effect on the position of T_{opt} ; stomatal behaviour, mitochondrial respiration, or photosynthetic biochemistry, for example, photorespiration, high-temperature inactivation of Rubisco (Crafts-Brandner and Salvucci 2000; Salvucci and Crafts-Brandner 2004; Sage *et al.* 2008), or electron transport (Wise *et al.* 2004). They found that each component could have an equally large effect. However, due to the technical challenge of parallel measurements of net photosynthesis and mitochondrial respiration in the light – especially when exploring temperature ranges with potentially irreversible effects on photosynthesis – the effect of respiration in the light on temperature responses of net photosynthesis is poorly documented. Nevertheless, respiration in the light (and species differences therein) is a likely candidate explanation for T_{opt} and the decrease in net photosynthesis above T_{opt} , with biochemical restrictions further contributing at very high temperatures (Crafts-Brandner and Salvucci 2000; Wise *et al.* 2004; Sage and Kubien 2007; Sage *et al.* 2008).

The higher rates of net photosynthesis of early-successional species compared with the late-successional species (see also Krause *et al.* 2015) are consistent with the ecological strategy of high metabolic activity, rapid growth, and shorter leaf life spans in early successional species (Wright *et al.* 2004). Higher T_{opt} values and higher carbon compensation points for the early-successional species likely reflect the microclimatic conditions of their regeneration niche. Early-successional species germinate and grow under high sun exposure whereas late-successional species germinate and grow in the shaded forest understory. Given the strong relationship between irradiance and leaf temperature (Doughty and Goulден 2008), early-successional seedlings experience, on average, higher *in situ* tissue temperatures than late-successional seedlings in their respective habitats. Juveniles of tropical pioneer trees have significantly higher hydraulic conductivity than shade tolerant species (Markesteijn *et al.* 2011), and may thus be able to maintain physiological activity under higher VPD during high temperature exposure than late-successional species, as suggested by much less negative midday water potentials found in pioneers compared with shade tolerant species in the field (Markesteijn *et al.* 2011). If T_{opt} and T_{max} values reported here indeed reflect adaptations to the species' regeneration niche, climate warming will move all species closer to their thermal thresholds. An important but as yet unanswered question is whether early and late-successional species differ in their capacity to acclimate to warming. *C. longifolium* showed a distinct increase in T_{opt} when grown at high temperature regimes, but at the cost of reduced A_{opt} (Slot and Winter 2016), whereas no such reduction in A_{opt} was found in early-successional species (Slot and Winter, Unpublished results). To date no study has systematically evaluated differences in photosynthetic acclimation traits across plant functional types of tropical forest trees.

Dark respiration did not increase exponentially with increasing temperature, in contrast to the general assumption. Whereas it may be difficult to assess the exact functional shape of the temperature response curve over a narrow temperature range, we measured respiration over a $\sim 30^\circ\text{C}$ range, enough to distinguish among functional forms. Although the relationship is commonly observed to be exponential, Hüve *et al.* (2012) showed considerable variation in the shape of the response

curves across three temperate herbs measured over a $\sim 25^\circ\text{C}$ range, and a recent study with *Oryza sativa* (rice) reported distinctly linear responses over a $\sim 14^\circ\text{C}$ range (Peraudeau *et al.* 2015). A model using an exponential relationship when a linear fit better describes the actual response overestimates respiration rates at high temperatures, especially when the reference temperature is static in the analysis (Vanderwel *et al.* 2015). Future research will need to assess how widely distributed the non-exponential temperature responses of dark respiration rates are among tropical species.

Can we apply laboratory-obtained physiological parameters to tropical forests?

Temperature response curves of net photosynthesis were distinctly different between seedlings studied in the laboratory and sun-exposed canopy leaves in the field (Fig. 5). Despite lower T_{opt} laboratory-measured seedlings had significantly higher high-temperature CO_2 compensation points. In the field, the increase in leaf temperature coincides with increases in irradiance and VPD. Stomata tend to close when the VPD exceeds a threshold that is specific to the unique conditions of the leaf in question. Temperature affects VPD, but can also affect hydraulic conductance and supply of water to the mesophyll (e.g. Ionenko *et al.* 2010; von Caemmerer and Evans 2015), thereby affecting the leaf water status and the sensitivity of stomata to VPD. It has been suggested that irradiance may have a direct effect on hydraulic conductance (possibly through changes of aquaporin synthesis), and thus cause stomatal closure (Tyree *et al.* 2005) during the 'midday depression.' Delivery of water to transpiring leaves of tall trees is a greater challenge than delivery of water to seedling leaves, and this may in part explain why, in the super-optimal temperature range, stomatal conductance of leaves in the field decreased at lower temperatures than in the laboratory, and consequently, that seedlings maintained positive net photosynthesis rates at higher temperatures.

The distinction between laboratory-based measurements and field observations is critical. Isolating one environmental factor – in this case, temperature – to study its effect on a physiological response of the plant is valuable for our understanding of the mechanisms by which plants respond to the environmental stimulus of interest, although even in the laboratory, maintaining stable VPD is difficult at elevated temperatures. Under natural conditions the plant's observed behaviour represents the integrated responses to multiple factors, including VPD and irradiance. Moreover, compared with seedlings canopy trees have different leaf structure (e.g. higher LMA as reported here), and carbohydrate dynamics (e.g. Baber *et al.* 2014). This complicates translating laboratory-based studies to processes occurring in the forest. Nonetheless, any laboratory-based measurement used for model parameterisation is likely done on small plants, even if the model is used to simulate forest processes. A model parameterised on our laboratory-based measurements, which show increases in stomatal conductance at very high temperatures and low stomatal control over net photosynthesis, would likely yield erroneous predictions for processes in the field, where stomatal conductance remained low in the high temperature range.

Despite the importance of T_{opt} and A_{opt} , these parameters are not generally used in ecosystem- and dynamic global vegetation models. Instead, parameters from the Farquhar/von Caemmerer/Berry biochemical model of photosynthesis (Farquhar *et al.* 1980; von Caemmerer and Farquhar 1981) are more commonly used; the maximum rate of RuBP carboxylation (V_{cmax}) and the maximum rate of RuBP regeneration (J_{max}). The modelled temperature dependence of these parameters (Bernacchi *et al.* 2001, 2003), parameterised using *Nicotiana tabacum* L. can successfully simulate temperature response curves of net photosynthesis, and thus T_{opt} and A_{opt} . The *N. tabacum* plants used to parameterise the models of Bernacchi *et al.* (2001, 2003) were grown and measured under highly controlled conditions, as were the *Citrus limon* (L.) Osbeck and *Populus euphratica* Oliv. plants used for model validation. At high temperatures in the laboratory we found that C_i approached C_a values; under such conditions net photosynthesis is unlikely to be limited by RuBP carboxylation, and V_{cmax} should increase. Indeed, V_{cmax} increases exponentially with temperature in Bernacchi *et al.* (2001). However, measurements on tropical tree species often show deviation from this exponential rise, with a significant drop in V_{cmax} at high temperatures (Kositsup *et al.* 2009; Vårhammer *et al.* 2015), which coincides with stomatal closure (Kositsup *et al.* 2009). This suggests that the difference between laboratory- and field-derived measurements of gas exchange at high temperature may be common in tropical vegetation, and that laboratory-obtained measurements should be used with caution when aiming to inform models that are used to predict carbon fluxes in tropical forests.

Leaf temperature monitoring in the field

The two methods for leaf temperature monitoring we used (taping fine-wire thermocouples to leaves or clipping them onto leaves) yielded different values. Covering the part of the leaf that is being monitored with glue or tape could potentially affect the capacity of that part of the leaf to be cooled by transpiration. However, the largest difference between the two methods occurred at high temperatures when under field conditions stomata were closed, essentially eliminating transpirational cooling. Such high temperatures occur when direct sunlight heats leaves above ambient temperatures (compare e.g. 15 January (sunny) and 17 January (cloudy) in Fig. S1). Consistent with Krause *et al.* (2010), we found that leaf temperatures occasionally reached values of $\geq 48^\circ\text{C}$ under conditions of full solar radiation (Fig. S4). The fact that under these conditions taped thermocouples record values much closer to those recorded with infrared thermometry suggests that the thermocouples clipped onto the leaves at least partly measured air temperatures, thereby underestimating maximum leaf temperatures (see also Mott and Peak 2011). We therefore argue that using porous tape that does not completely suppress leaf transpiration would be the recommended method of thermocouple attachment, especially in wind-exposed canopy leaves, and when the aim is to evaluate maximum temperatures leaves experience in the field.

Conclusions

We have shown that species belonging to different plant functional types show different photosynthetic temperature

response characteristics. Future research on a larger number of species will have to assess whether functional types also differ in their thermal plasticity and their capacity to acclimate to climate warming. Laboratory-based measurements show some fundamentally different temperature response patterns with respect to high-temperature stomatal conductance behaviour and, possibly related to this, the measured high-temperature CO_2 compensation point. Temperature response traits used for model parameterisations should therefore be verified in the field if the model aims to make predictions about natural vegetation.

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