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Thermal acclimation of leaf respiration of tropical trees and lianas: response to experimental canopy warming, and consequences for tropical forest carbon balance

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Abstract

Climate warming is expected to increase respiration rates of tropical forest trees and lianas, which may negatively affect the carbon balance of tropical forests. Thermal acclimation could mitigate the expected respiration increase, but the thermal acclimation potential of tropical forests remains largely unknown. In a tropical forest in Panama, we experimentally increased nighttime temperatures of upper canopy leaves of three tree and two liana species by on average 3 °C for 1 week, and quantified temperature responses of leaf dark respiration. Respiration at 25 °C (R_{25}) decreased with increasing leaf temperature, but acclimation did not result in perfect homeostasis of respiration across temperatures. In contrast, Q_{10} of treatment and control leaves exhibited similarly high values (range 2.5–3.0) without evidence of acclimation. The decrease in R_{25} was not caused by respiratory substrate depletion, as warming did not reduce leaf carbohydrate concentration. To evaluate the wider implications of our experimental results, we simulated the carbon cycle of tropical latitudes (24°S–24°N) from 2000 to 2100 using a dynamic global vegetation model (LM3VN) modified to account for acclimation. Acclimation reduced the degree to which respiration increases with climate warming in the model relative to a no-acclimation scenario, leading to 21% greater increase in net primary productivity and 18% greater increase in biomass carbon storage over the 21st century. We conclude that leaf respiration of tropical forest plants can acclimate to nighttime warming, thereby reducing the magnitude of the positive feedback between climate change and the carbon cycle.

Keywords: carbon flux, climate change, DGVM, experimental leaf warming, global warming, NPP, Panama, respiration, tropical forest

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Introduction

Contemporary tropical forests exist in a narrow temperature range (Janzen, 1967; Wright *et al.*, 2009), close to what may be a high temperature threshold (Doughty & Goulden, 2008). Models predict unprecedented warming in the tropics over this century (Diffenbaugh & Scherer, 2011), which will push the majority of tropical forests into a climate envelope currently not occupied by closed-canopy forests (Wright *et al.*, 2009). Tropical forests are currently considered to be an important sink for atmospheric carbon (Phillips *et al.*, 1998; Baker *et al.*, 2004; Lewis *et al.*, 2009), but how they will respond to climate warming is uncertain, as illustrated by the large discrepancy in predictions among dynamic global vegetation models (DGVMs) and Earth system models (Friedlingstein *et al.*, 2006; Ahlström *et al.*, 2012).

The physiological responses of vegetation to temperature and CO_2 are the largest sources of uncertainty in such dynamic models (Arneth *et al.*, 2012; Booth *et al.*, 2012; Cernusak *et al.*, 2013; Huntingford *et al.*, 2013). Model outputs vary partly because the models are highly sensitive to parameters describing the temperature response of leaf carbon exchange (Ziehn *et al.*, 2011; Booth *et al.*, 2012) and thermal acclimation of photosynthesis and respiration of vegetation is addressed in some models but not others (Smith & Dukes, 2013). The current lack of empirical data on thermal acclimation of tropical forest vegetation, particularly upper canopy leaves that account for a large fraction of photosynthesis and leaf respiration, is an obstacle to evaluating and improving models and reducing model uncertainty (Booth *et al.*, 2012). Studies with arctic, boreal, temperate, and alpine plants have shown that respiration of many species acclimates to changes in

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ambient temperature (e.g., Billings *et al*., 1971; Larigauderie & Körner, 1995; Arnone & Körner, 1997; Tjoelker *et al*., 1999a,b, 2008, 2009; Atkin *et al*., 2000; Bolstad *et al*., 2003; Lee *et al*., 2005; Bruhn *et al*., 2007; Ow *et al*., 2010). Because tropical forests experience minimal seasonal temperature changes (Wright *et al*., 2009), it has been speculated that the capacity to acclimate to elevated temperature may have been lost (Janzen, 1967; Cunningham & Read, 2002).

Leaf dark respiration (nonphotorespiratory mitochondrial respiration) is highly sensitive to changes in temperature, with most published estimates indicating roughly a doubling with a 10 °C rise in temperature (i.e., $Q_{10} = 2.0$) (e.g., Amthor, 1984). Photosynthesis also increases with temperature, but peaks at a lower temperature than respiration (Hüve *et al*., 2011). Consequently, without physiological acclimation, further temperature rise in tropical forests may reduce photosynthesis while increasing respiration, which may reduce NPP and the size of the potential carbon sink of tropical forests. Respiration is essential to growth and survival of plants, as it provides the energy and carbon skeletons for biosynthesis (Penning de Vries, 1975). However, the increase in respiration with temperature is primarily attributable to increased demand for cellular maintenance (Amthor, 1984; Ryan, 1991), and is not necessarily associated with increased growth. Respiration associated with growth is believed to be only indirectly affected by warming; it increases with warming only when growth itself is stimulated by rising temperature (Frantz *et al*., 2004). In tropical species, however, warming generally results in a decrease in growth (see meta-analyses by Lin *et al*., 2010; Way & Oren, 2010; but see Cheesman & Winter, 2013). This suggests that unless respiration can sufficiently acclimate to warmer temperatures, carbon available for growth, and the potential of tropical forests to store carbon, may diminish under a warmer future climate.

Acclimation of respiration to elevated temperature is characterized by a decreased rate at the new temperature compared to nonacclimated plants (Atkin & Tjoelker, 2003; Atkin *et al*., 2005;. See Fig. 1). When acclimation also decreases Q_{10} this is referred to as Type I acclimation; in case of Type II acclimation, only respiration at a set temperature decreases while Q_{10} does not change (Atkin & Tjoelker, 2003). Net photosynthesis of tropical trees and lianas has been shown to decrease with warming by a few degrees above current ambient temperatures (Doughty, 2011), suggesting limited capacity for physiological acclimation of tropical species. To what extent respiration in tropical tree and liana species can acclimate to elevated nighttime temperatures is currently unknown.

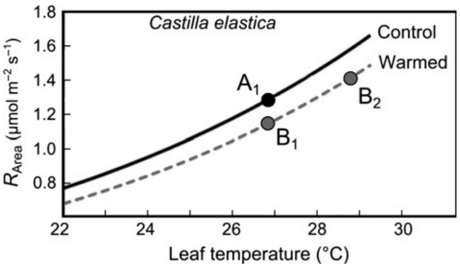

Fig. 1 Example of thermal acclimation of respiration using data for experimentally warmed and control leaves of *Castilla elastica*. Warmed leaves exhibit downregulation of respiration at a set temperature ($A_1 > B_1$). Acclimation is not completely homeostatic, because acclimated leaves respire more at their average nighttime temperature (28.8 °C) than control leaves at their average nighttime temperature (26.6 °C) ($A_1 < B_2$).

The main objective of our study was to experimentally determine whether dark respiration of fully expanded upper-canopy leaves in a tropical forest can acclimate to elevated nighttime temperature. We focused on nighttime temperature because of the importance of nighttime temperature for tropical forest growth (Clark *et al*., 2010, 2013) and because global warming continues to be more pronounced at night than during the day (IPCC, 2007). We further asked whether along with changes in respiration, warming results in changes in other leaf functional traits. Such parallel changes could provide insights on the mechanisms underlying the acclimation process. For example, several studies on temperate and boreal tree species have suggested an important role of leaf nitrogen and carbohydrates in thermal acclimation of respiration (Lee *et al*., 2005; Tjoelker *et al*., 2008, 2009). Interspecific variation in how easily measured leaf traits respond to warming could also point to potentially valuable correlates or predictors of thermal acclimation of respiration. To address these objectives we developed a unique protocol to experimentally warm branch segments (including leaves) of trees and lianas in the upper canopy of a semideciduous tropical forest in Panama, making use of a 42-m tall construction crane that enables access to the metabolically most active upper-canopy leaves. We quantified how average nighttime leaf temperature during 6–8 days of experimental warming affected leaf dark respiration at 25 °C and the short-term temperature response of respiration (Q_{10}). Our main hypothesis was that tropical canopy leaves acclimate to nighttime warming by downregulating respiration rates at a set temperature of 25 °C, or by downregulating Q_{10}.

Our second main objective was to scale up our experimental results to estimate the consequences of leaf respiratory acclimation for the tropics-wide carbon-cycle using a dynamic global vegetation model, LM3VN (Shevliakova *et al.*, 2009; Gerber *et al.*, 2010). We hypothesized that physiological acclimation by leaves would substantially reduce the warming-induced increase in respiration fluxes from tropical forests over the 21st century. Our overall goal, therefore, was to quantify acclimation potential of dark respiration of upper canopy leaves in tropical forests and evaluate its implications for the net carbon-balance of the tropical forest biome.

Materials and methods

Study site and species selection

The study was conducted in Parque Natural Metropolitano (PNM, 8°59′N, 79°33′W, 100 m a.s.l.), a seasonally dry tropical forest near the Pacific coast of Panama, near Panama City, between June and October 2012. Annual rainfall at the site averages 1740 mm, most of which falls during the rainy season from May through December. Annual mean nighttime temperature at PNM between 1995 and 2012 was 24.5°C (range 23.3–26.1 °C). The 256-hectare protected area consists of 80–150 year old secondary forest with tree heights up to 40 m. A 42-m tall construction crane with a 51-m long jib enabled access to canopy leaves.

We selected three tree species (*Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels; *Luehea seemannii* Triana & Planch.; *Castilla elastica* var. *costaricana* (Liebm.) CC. Berg) and two liana species (*Bonamia trichantha* Hallier f.; *Stigmaphyllon lindenianum* A. Juss.) from the upper forest canopy. Henceforth the species will be referred to by their genus name only. Together these species contribute >25% of the total canopy area.

In situ warming protocol

Nighttime warming of upper-canopy terminal shoots (or individual leaves on them) was achieved by infrared reflective frames fitted with flexible heat rope (Big Apple Herpetological, Inc., New York, NY, USA), positioned 5–10 cm below the target leaves (Fig. 2). The design was adjusted to the architecture of the species; it was flat for most species with horizontal leaf display, but cone-shaped for *Anacardium* to account for this species' whorled leaf arrangement on vertically oriented terminal branches. Identical frames without heat rope were fit on control shoots. The heat rope temperature was controlled by a thermostat, which triggered warming when nighttime air temperature dropped below 25 °C. The treatments were given for 1 week; although exact duration of the experiment varied from 6 to 8 days due to logistical constraints, treatment duration did not affect the measured traits. This method resulted in an increase in mean nighttime leaf temperature during the experimental period of 1–7 °C compared to the control leaves. In total, 154 fully developed, mature leaves were included in the experiment, of which 67 were successfully warmed (average warming over experimental period >1 °C, and no warming >10 °C at any time) and 87 were used as controls. To assess the repeatability and consistency of the results, we set up warming and control frames twice in *Anacardium* and *Luehea*. These repeated experiments were done on different branches and several weeks apart. Temperatures of warmed and control leaves were monitored with type T copper-constantan thermocouple wires attached to the abaxial side of the leaf, and recorded at 5-min intervals with a Campbell 21X datalogger (Campbell Scientific, Logan, UT, USA).

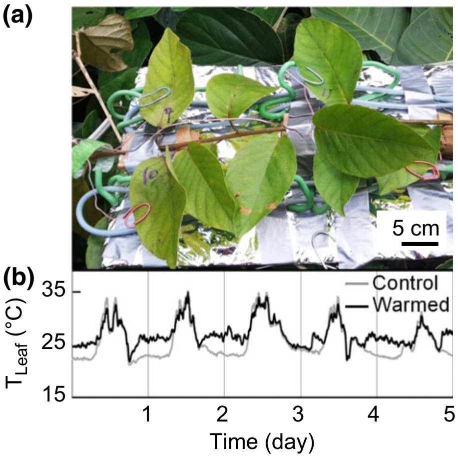

Fig. 2 A warming frame fit to *Bonamia trichantha* (a), and the average temperatures of control and warmed leaves for 5 days (12–17 October 2012) of the 6-day experiment with this species (b). Natural leaf angles were maintained as much as possible. Leaves were prevented from touching the heating rope by fitting rubber-coated twist-tie frames between the leaf and the heating rope.

Dark respiration measurements

At the end of the treatment, twigs were collected predawn at ~06:00 hours, immediately recut under water, and brought back to the laboratory in darkness for measurements. Dark respiration was measured on whole leaves at 2–5 (mode = 3) temperature points between 20 and 32 °C with a Walz gas exchange cuvette (GWK 3M; Walz Mess- und Regeltechnik, Eiffeltrich, Germany) connected to a LI-6252 infrared gas analyzer (Licor, Lincoln, NE, USA). For more details on the gas exchange system, see Holtum & Winter (2003). Petioles were cut under water and sealed in a 5 ml glass vial with parafilm to prevent dehydration during measurement. All leaves were measured within 10 h of collection. No trend in respiration rates with time since collection was detected within this period.

For each leaf that was measured at 3 or more temperatures a least-square regression line was fit to the $\log_{10}$-transformed leaf respiration rate (R) vs. leaf temperature (T_{Leaf}) data according to:

$$\log_{10}(R) = a + bT_{\text{Leaf}} \tag{1}$$

The data fit to this equation was strong for all leaves ($r^2 > 0.92$). Q_{10} values were calculated from these equations as:

$$Q_{10} = 10^{10b} \tag{2}$$

When R was measured at only two temperatures, Q_{10} was calculated as:

$$Q_{10} = \left(\frac{R_{T2}}{R_{T1}}\right)^{\left(\frac{10}{(T_2 - T_1)}\right)} \tag{3}$$

where T_1 and T_2 are the lower and higher measurement temperature, respectively.

R values of all leaves were converted to respiration rate at 25 °C (R_{25}) as:

$$R_{25} = \frac{R_T}{Q_{10}^{(T-25)/10}} \tag{4}$$

For each leaf R_{25} was calculated for all temperature points and averaged to get a single R_{25} to use in our analyses. The temperature response of R may deviate from a simple exponential curve, so to test the robustness of our data to alternative functional forms of the temperature response we also calculated R_{25} from a simple Arrhenius function, and from a modified Arrhenius function (described in Lloyd & Taylor, 1994). Analyses of leaf temperature effects on R_{25} calculated with these three different methods yielded identical results (Data S1). In the remainder we therefore only report R_{25} values calculated according to Eqn. 4.

Functional trait data

Leaf area was measured with a LI-3000 leaf area meter (Licor) and leaf mass per unit area (LMA) was calculated as leaf blade mass after drying for >96 h at 60 °C, divided by leaf area. Tissue N concentration was determined with an elemental analyzer (Costech Analytical, Los Angeles, CA, USA). Concentrations of nonstructural carbohydrates (simple sugars and starch) were determined following Dubois *et al.* (1956) with modifications. Briefly, simple sugars (monosaccharides) were extracted in 80% (v/v) ethanol from 10 to 15 mg ground samples by shaking followed by two 2-h incubations. The supernatant from each sample was collected in a volumetric flask and brought up to 10 ml. Starch was hydrolyzed to glucose from the pellet in 1.1% hydrochloric acid at 100 °C. Glucose concentrations were determined colorimetrically with the phenol-sulfuric acid method.

We measured light-saturated photosynthetic capacity (A_{sat}) after seven nights of warming in one warming experiment of *Anacardium* (16 leaves) and one *Luehea* experiment (12 leaves). A_{sat} was measured *in situ* on intact leaves at ambient temperature (range 29–31 °C) and saturating irradiance of 2000 μmol photons m^{-2} s^{-1} with a LI-6400 (Licor). The CO_2 concentration during measurements was maintained at 400 ppm using the built-in CO_2 regulator, and relative humidity was kept between 65% and 85%. All photosynthesis measurements were taken before 09:00 hours to avoid mid-day stomatal closure, which can occur as early as 10:00 hours (Zotz *et al.*, 1995).

Data analysis

To assess acclimation we compared R_{25} and Q_{10} values of control and warmed leaves, determined the statistical relationship between R_{25} and average nighttime T_{Leaf} during the treatment, and we calculated acclimation ratios according to the set temperature method ($\text{Acclim}_{\text{SetTemp}}$) and the homeostasis method ($\text{Acclim}_{\text{Homeo}}$). $\text{Acclim}_{\text{SetTemp}}$ was calculated according to Loveys *et al.* (2003) as:

$$\text{Acclim}_{\text{SetTemp}} = \frac{R_{25}\text{Control}}{R_{25}\text{Warmed}} \tag{5}$$

If acclimation has taken place $\text{Acclim}_{\text{SetTemp}}$ values are >1.0. To determine to what extent acclimation approached complete homeostasis of respiration across temperatures we used the homeostasis method (Loveys *et al.*, 2003):

$$\text{Acclim}_{\text{Homeo}} = \frac{R_{\text{Control}} \text{ at } T_{\text{Control}}}{R_{\text{Warmed}} \text{ at } T_{\text{Warm}}} \tag{6}$$

where T_{Warm} and T_{Control} are the mean nighttime leaf temperatures experienced by warmed and control leaves respectively. When acclimation is completely homeostatic, $\text{Acclim}_{\text{Homeo}}$ is 1.0; values less than 1.0 indicate that acclimation of the warmed leaf is not completely homeostatic. Acclimation ratios provide a conceptually simple way to assess acclimation. However, acclimation ratios fail to account for the considerable variation in temperature within both warmed and control leaves in our experiments. We therefore also assessed acclimation by regressing R_{25} against the average nighttime leaf temperature over the week preceding the R_{25} measurement, where a steeper "acclimation slope" represents greater acclimation. Acclimation slopes and ratios were calculated by species, and by experiment within species for the two *Anacardium* and *Luehea* experiments.

Treatment and species effects on Q_{10}, R_{25}, and other leaf traits were analyzed with analysis of covariance (ANCOVA), where average nighttime leaf temperature during the experimental period was a continuous predictor. Interaction effects between temperature and species identity were included in the ANCOVA models to assess whether the effect of temperature on the response variables differed among species. All statistical analyses were performed in R version 2.14.1 (R Development Core Team, 2011).

Scaling up to the global tropics using a dynamic global vegetation model

We used the LM3VN dynamic global vegetation model to evaluate the consequences of our empirical results for the global tropical carbon cycle. LM3VN was designed as a component of the Geophysical Fluid Dynamics Laboratory (GFDL) Earth system models. The model simulates land-atmosphere exchanges of energy, carbon, and water; vegetation dynamics (including evergreen and deciduous tropical trees); and coupled carbon and nitrogen cycles. A single plant functional type is allowed to occupy a grid cell, which for the tropical area is a C4 grassland or a forest. Deciduousness depends on water availability and occurs when water availability drops below a critical threshold. The transition from grassland to forest occurs if biomass exceeds 2.5 kg m^{-2}. We modified LM3VN to account for our new Q_{10} estimates for tropical leaf respiration, and we included a new formulation for thermal acclimation of leaf respiration. Acclimation was parameterized such that R_{25} was adjusted based on average leaf temperature of the preceding 7 days:

$$\frac{d\overline{T_{\mathrm{Leaf}}}}{dt} = k\left(T_{\mathrm{Leaf}} - \overline{T_{\mathrm{Leaf}}}\right) \tag{7}$$

$$R_{25} = R_{\mathrm{Control}}\left(1 - r\overline{T_{\mathrm{Leaf}}}\right) \tag{8}$$

where $\overline{T_{\mathrm{Leaf}}}$ is the temperature to which the leaves are acclimated, T_{Leaf} the leaf temperature (calculated half-hourly in LM3VN), R_{Control} is the unacclimated R_{25} calculated as a fixed proportion of V_{Cmax} (maximum rate of Rubisco carboxylation) in LM3VN (Moorcroft *et al.*, 2001; Shevliakova *et al.*, 2009), r is a parameter that denotes relative acclimation per unit temperature change set to be the mean acclimation slope obtained from the field experiment, and k the adjustment rate ($k = 0.143$ day^{-1}). To be congruent with the empirical study, we modified the temperature dependence of respiration in LM3VN from an Arrhenius-type equation to a Q_{10} function. We quantified effects of acclimation as the model results from $r > 0$ (acclimation) vs. $r = 0$ (no acclimation). To simulate the tropical carbon cycle (24°S to 24°N latitude) over the 21st century, we forced LM3VN with climate output from the GFDL CM2.1 model (Delworth *et al.*, 2006) as simulated for the Intergovernmental Panel on Climatic change (IPCC) A2 emissions scenario (a high emissions scenario). We combined modeled changes in temperature and precipitation with reanalysis data (Sheffield *et al.*, 2006) by calculating the monthly low frequency changes of CM2.1 climates (17-year running average) and adding to a 17-year (1950–1967) recurring interannual cycle. This procedure preserves the climatology, and the daily, seasonal, and interannual climate cycles while accounting for long-term changes. Levels of CO_2 were prescribed with historical values until 2008 and then as predicted from the Bern-CC (Joos *et al.*, 2001) output under the A2 IPCC emission scenario. Nitrogen deposition was based on static spatial fields as estimated for the years 1850, 1993, and 2050 (Dentener, 2006) which we interpolated linearly over time to obtain temporal trends of annual deposition.

Using a simple scaling approach we also estimated the change in nocturnal leaf respiratory carbon flux at the stand level at our study site with 4 °C nighttime warming, both with and without acclimation of respiration (Data S2). Qualitative consistency in the predictions of the biome-level and stand-level models would confirm that the results for the global tropics are driven by acclimation and not by other model assumptions of LM3VN.

Results

Warming effect on respiration

The average increase in nighttime leaf temperature achieved by the warming frames ranged across species from of 1.8–3.4 °C (Table 1). Average nighttime leaf temperature had a significant effect on R_{25} (ANCOVA, $P = 0.001$; Data S1). R_{25} decreased with nighttime temperature for all five species ($P = 0.03$ for the null hypothesis that positive and negative slopes are equally likely; $P = 0.008$ if each of the seven experiments is considered an independent trial) (Fig. 3a–i). However, when species were analyzed separately, the slope of R_{25} vs. temperature was significant for only one species (*Anacardium*). Species identity and the interaction between leaf temperature and species identity were not significant ($P = 0.55$, and $P = 0.70$, respectively), nor was the duration of the experimental warming ($P = 0.76$). Leaf nitrogen content (N) per unit leaf area increased significantly with nighttime temperature (see details below), so that R_{25}/N yielded stronger relationships with temperature than R_{25} (Fig. 3f–j). Across species, R_{25} decreased by an average of 3.0%, or 0.027 μmol CO_2 m^{-2} s^{-1} per degree of warming (Fig. 4), and R_{25}/N decreased by 4.2% per degree of warming (not shown).

$\mathrm{Acclim}_{\mathrm{SetTemp}}$ values calculated with R_{25} were >1.0 in all seven experiments and were very similar among species, with values ranging from 1.04 to 1.14 (Table 1). $R_{25\ \mathrm{Warmed}}$ was significantly lower than $R_{25\ \mathrm{Control}}$ when all leaves were combined ($P < 0.01$), but at the species level $R_{25\ \mathrm{Warmed}}$ was significantly lower than $R_{25\ \mathrm{Control}}$ for only two of five species (*Castilla* and *Stigmaphyllon*; Table 1). $\mathrm{Acclim}_{\mathrm{SetTemp}}$ values for R_{25}/N were a little higher, with an overall mean of 1.17. Acclimation did not result in complete homeostasis of respiration; respiration of warmed leaves measured at their average nighttime temperature was higher than respiration of control leaves measured at the average control nighttime temperature ($\mathrm{Acclim}_{\mathrm{Homeo}}$ ratios between 0.73 and 0.94; Table 1). Even for *Castilla*, which exhibited the steepest decline in R_{25} with nighttime temperature (Fig. 3), respiration rates of warmed leaves at their average nighttime T_{Leaf} of 28.8 °C were 10% higher than respiration rates of control leaves at their average nighttime T_{Leaf} of 26.8 °C (Fig. 1).

Q_{10} values ranged from 2.5 to 3.0 but were not significantly different among species ($P = 0.45$) and there was no trend in Q_{10} values with average nighttime T_{Leaf} ($P = 0.98$). A reduction in R_{25} values but no change in Q_{10} suggests that these tropical leaves exhibited Type II acclimation in response to nighttime warming.

Warming effects on other leaf traits

Nighttime leaf warming resulted in a significant increase in nitrogen per unit area (N_{Area}; +1.9% per °C relative to the mean of the control leaves; $P = 0.002$), simple sugars per unit area ($\mathrm{Sugar}_{\mathrm{Area}}$; +2.0% per °C;

Table 1 Tree and liana species used in this study, their average leaf temperature, and respiration (*R*) traits of control and warmed leaves. R_{25} is the mean *R* at 25°C, R_{25}/N is the R_{25} per unit leaf nitrogen, and Q_{10} is the temperature sensitivity of *R*. The 'set temperature' and 'homeostasis' acclimation ratios ($\mathrm{Acclim}_{\mathrm{SetTemp}}$, $\mathrm{Acclim}_{\mathrm{Homeo}}$), and the acclimation slopes ($\mathrm{Acclim}_{\mathrm{Slope}}$) for R_{25} and R_{25}/N are shown, where the slope represents the change in R_{25} or R_{25}/N per °C (Δ flux °C^{-1}). For *Anacardium* and *Luehea*, results from two replicate experiments are shown. Different letters indicate significant ($P < 0.05$) differences between control and treatment. Significant acclimation slopes ($P < 0.05$) are shown in bold

				T_{Leaf}	R_{25}	R_{25}/N		$\mathrm{Acclim}_{\mathrm{SetTemp}}$		$\mathrm{Acclim}_{\mathrm{Homeo}}$		$\mathrm{Acclim}_{\mathrm{Slope}}$ (Δ flux °C^{-1})	
Species	Growth form		Treatment	°C	µmol m^{-2} s^{-1}	nmol (mg N)$^{-1}$ s^{-1}	Q_{10}	R_{25}	R_{25}/N	R_{25}	R_{25}/N	R_{25}	R_{25}/N
Anacardium excelsum	Tree	1	Control	24.7^a	0.91	44	2.3	1.13	1.09	0.83	0.80	**−0.047**	**−2.0**
			Warmed	28.0^b	0.81	40	2.6						
		2	Control	23.8^a	0.75	40	2.6	1.12	1.08	0.84	0.82	**−0.027**	**−1.1**
			Warmed	27.0^b	0.67	37	2.4						
Castilla elastica	Tree		Control	26.8^a	1.06^a	48^a	2.9	1.14	1.15	0.94	0.95	−0.062	**−3.2**
			Warmed	28.6^b	0.94^b	42^b	3.0						
Luehea seemannii	Tree	1	Control	24.4^a	0.94	50^a	2.7	1.04	1.14	0.84	0.92	−0.029	−2.1
			Warmed	26.6^b	0.90	44^b	2.6						
		2	Control	24.7^a	0.99	45	2.5	1.14	1.24	0.82	0.89	−0.015	**−1.8**
			Warmed	28.1^b	0.88	36	2.7						
Bonamia trichantra	Liana		Control	24.0^a	0.73	59^a	3.0	1.05	1.21	0.73	0.84	−0.008	**−2.7**
			Warmed	27.4^b	0.69	48^b	2.9						
Stigmaphyllon lindenianum	Liana		Control	24.5^a	1.03^a	53^a	2.8	1.14	1.27	0.91	1.00	−0.021	−2.6
			Warmed	26.6^b	0.91^b	42^b	3.0						

$P = 0.019$), and simple-sugar to starch ratio (SS ratio; 2.9% per °C; $P = 0.008$). LMA, and concentrations of N and simple sugars per unit mass increased marginally significantly with warming, whereas total nonstructural carbohydrate (TNC) was not affected by warming. Photosynthetic capacity (A_{sat}) was not affected by nighttime warming in either *Anacardium* or *Luehea* (*t*-test of control vs. warming $P > 0.05$; no correlation with nighttime temperature at the leaf level).

Across-species correlates of acclimation

We explored whether the small differences among species in the *degree* of acclimation correlated with leaf traits that are associated with plant metabolism, using trait means of control leaves to characterize the species. The acclimation slopes (from regressing R_{25} on mean nighttime T_{Leaf} over the preceding week) correlated with species means of SS ratio ($P = 0.050$; $r^2 = 0.77$; Fig. 5). Small differences among species in average nighttime T_{Leaf} of warmed leaves during the experimental period also had a marginally significant effect ($P = 0.10$) on acclimation: *Castilla* had the highest mean nighttime temperature and the strongest acclimation, whereas *Stigmaphyllon* had the lowest mean nighttime temperature and the second smallest acclimation (after *Bonamia*; Fig. 5). Acclimation slopes did not correlate significantly with leaf N content, LMA or species means of R_{25} (data not shown).

Consequences of acclimation for the tropical forest carbon cycle

Accounting for acclimation when subjecting LM3VN to the A2 climate scenario reduced 21st century leaf respiration relative to a no-acclimation scenario (Fig. 6, Data S3). The model-prediction of the increase in leaf respiration per unit leaf area over the 21st century is 35% lower with acclimation than without acclimation. Furthermore, acclimation enabled growth and the maintenance of a larger standing biomass, such that modeled annual respiration integrated across the tropical forest biome was approximately the same in the acclimation and the non-acclimation scenario (Table 2). Acclimation resulted in an increase in NPP across the tropics by the end of this century that was 1.2 Pg carbon yr^{-1} (or 21% higher) compared to the no-acclimation scenario, allowing for an 18% more carbon storage (47 vs. 40 Pg) in tropical biomass over the course of the 21st century (Table 2). Respiration per unit leaf area increased compared to current fluxes, by 14% and 21%, with and without acclimation respectively (Table 2). Flux calculations at the stand level at our study site similarly predicted a large decrease in the warming-induced rise in respiration over the 21st century (Data S2). The estimates from LM3VN are lower than for our stand-level estimates, partly due to a mere 2 °C warming in the canopy of tropical forests. In the LM3VN model, evaporative cooling from a larger LAI did offset some of the 3 °C warming in the free

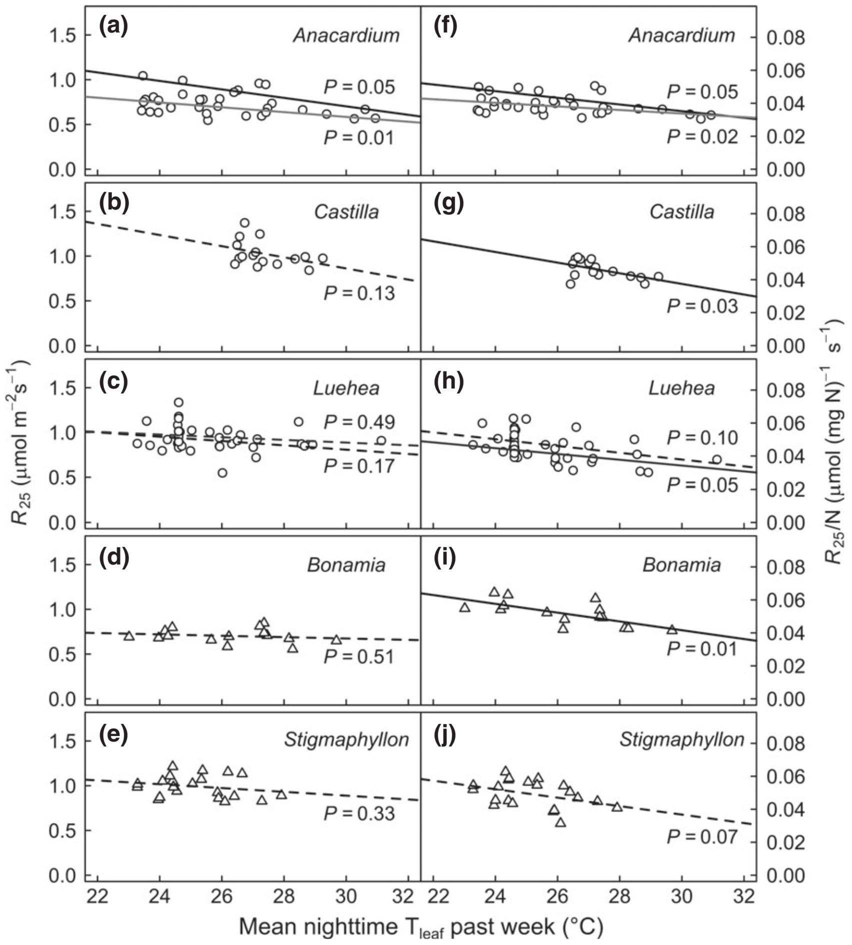

Fig. 3 Leaf dark respiration at 25 °C (R_{25}) per unit leaf area (a–e) and per unit leaf nitrogen (f–j) in relation to the average nighttime temperature these leaves experienced in the preceding 6–8 days. Warmed and control leaves are combined in these graphs. Circles and triangles represent tree and liana species respectively. For *Anacardium* and *Luehea*, separate lines (gray and black) are shown for each of two replicate experiments. The slopes of these lines represent the 'acclimation slopes' referred to in the main text. Dashed lines are not significant at $P = 0.05$.

atmosphere (see also Bonan, 2008; Ban-Weiss *et al.*, 2011). Assuming acclimation of respiration and its positive effect on the carbon balance in hotter environment enabled tropical forests to persist in some grid cells that turned to savanna/grassland in the no-acclimation scenario.

Discussion

Consistent acclimation of respiration to elevated nighttime temperature

Leaf respiration acclimated to *in situ* nighttime warming of fully developed tree and liana leaves in the upper canopy of a tropical forest. Acclimation is indicated by the significant negative correlation between nighttime temperature and R_{25}, and by the $\text{Acclim}_{\text{SetTemp}}$ values >1.0 in all seven experiments on five species. Respiration rate per unit leaf nitrogen showed acclimation even more strongly. Our observations on tropical forest leaves concur with studies of arctic, boreal, and temperate species showing that thermal acclimation of respiration of pre-existing leaves can occur within a few days (Billings *et al.*, 1971; Atkin *et al.*, 2000; Bolstad *et al.*, 2003; Lee *et al.*, 2005), without apparent transient effects of temperature shock (Bolstad *et al.*, 2003). Acclimation of leaves developed at a new temperature tends to be greater than acclimation of pre-existing leaves (Loveys *et al.*, 2003; Armstrong *et al.*, 2006). As nights gradually warm over the 21st century, canopy respiration is likely to be downregulated to a greater degree than what we observed for pre-existing leaves because of turnover of leaves and individuals. The results we present here should thus be seen as conservative estimates of the effects of acclimation on respiratory carbon fluxes with climate warming.

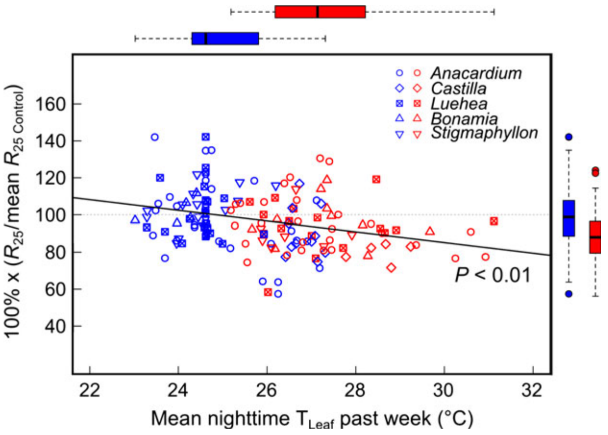

Fig. 4 Respiration at 25 °C (R_{25}) in relation to the average nighttime leaf temperature during the experiment, standardized as the percentage of the mean R_{25} of control leaves of the same species (blue). Horizontal box plots indicate the mean, median, and range of warmed (red) and control (blue) leaves across species. Vertical box plots show the mean, median and range of standardized R_{25} values of warmed and control leaves.

Correlates of acclimation

Carbohydrate concentrations were not lower in warmed leaves than in control leaves, nor did they decrease as average nighttime leaf temperature increased. Thus, the observed acclimatory downregulation was not a result of a greater degree of substrate limitation at the end of the night. Fully developed leaves lack the capacity to import carbohydrates from other sources within the plant (Turgeon, 2006) and are thus independent of carbohydrates that are exported from other leaves in the experiment. Interestingly, however, expressed per unit leaf area, the concentration of simple sugars, the primary substrate of respiration, increased with temperature, as did the simple-sugar to starch ratio. The increase of sugar content was unlikely due to stimulation of photosynthesis in response to night-time warming such as reported by Turnbull *et al.* (2002), as A_{sat}, measured before 09:00 hours, was not affected by warming. Warming can also reduce carbohydrate export from leaves (Jiao & Grodzinski, 1996), e.g., when sieve plate pores become blocked by callose (McNairn & Currier, 1968). A decrease in carbohydrate export could explain the increase in $\mathrm{Sugar}_{\mathrm{Area}}$ and the marginally significant increase in sugar concentration per unit mass.

The absence of a positive correlation between R_{25} and sugar content suggests that R_{25} of these leaves was not substrate limited. Nor is it likely that there were treatment differences in demand for respiratory products through changes in sink strength away from the source leaves, as branches with warmed and control leaves always had comparable numbers of young leaves (that were not warmed themselves, and thus experienced no treatment-related change in sink strength). Most likely, the decrease in R_{25} with temperature resulted from a change in respiratory capacity, associated with changes in concentrations or relative amounts of mitochondrial enzymes (Atkin *et al.*, 2005). Type II acclimation (i.e., a decrease in the elevation of the temperature response curve of respiration, without a change in Q_{10}) is indeed associated with a reduced respiratory capacity (Atkin *et al.*, 2005). The observed increases in leaf N concentration (on both area and mass bases) with temperature might be associated with shifts in relative amounts of enzymes that differ in N content (Atkin *et al.*, 2005).

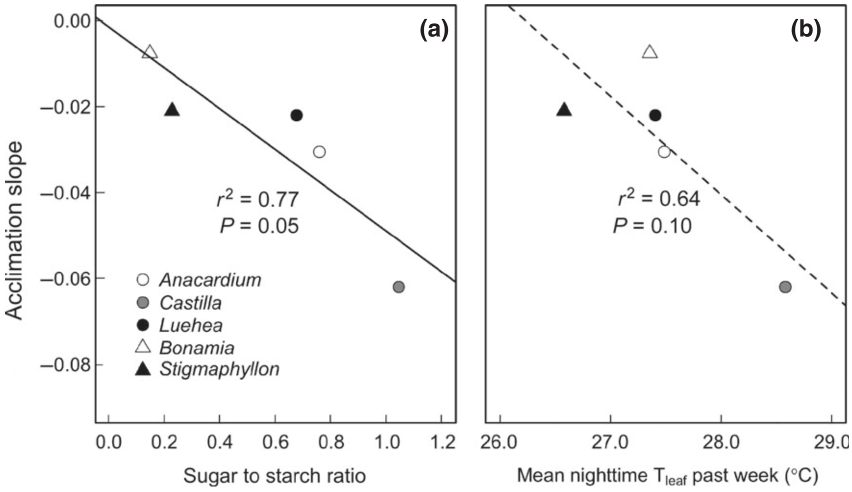

Fig. 5 Correlations between the mean acclimation slope of the five study species and (a) simple-sugar to starch ratio, and (b) mean nighttime leaf temperature of warmed leaves. The acclimation slope is the slope of R_{25} plotted against the mean nighttime leaf temperature of preceding 6–8 days (Fig. 3; more negative indicates stronger acclimation).

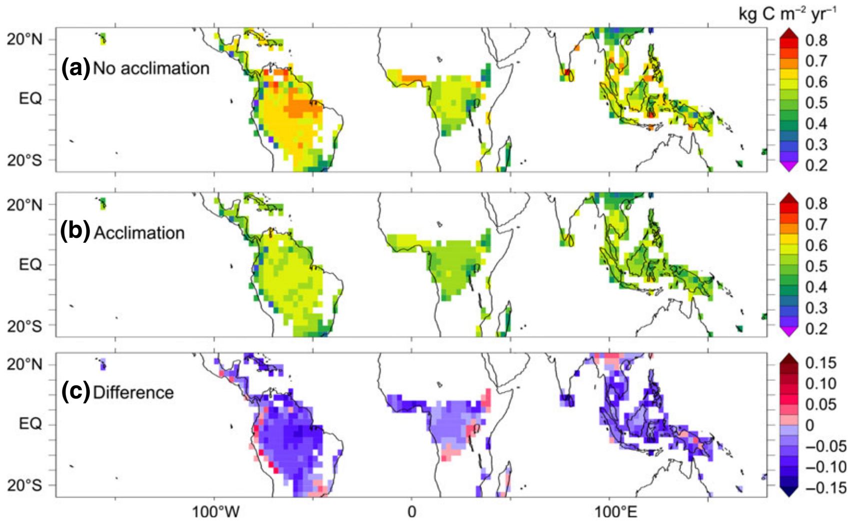

Fig. 6 Maps of leaf respiration rates per unit leaf area averaged over the years 2080–2099 simulated from the LM3VN dynamic global vegetation model forced with a climate projection derived from the IPCC AR4 A2 emissions scenario, without accounting for thermal acclimation of respiration (a), with acclimation derived from the experimental results in the present study (b), and the difference between the two scenarios (c). All grid cells are shown where tropical forests are predicted to occur in LM3VN.

Table 2 Results of simulations with the LM3VN dynamic global vegetation model of tropical forest traits at the end of the 20th century and the end of the 21st century with and without accounting for thermal acclimation of respiration

	Time period	No acclimation	With acclimation	% Difference
Leaf respiration (g C m^{-2} leaf yr^{-1})	1980–2000	459	453	−1
	2080–2100	556	516	−7
	Change	97	63	−35
Leaf respiration (Pg C yr^{-1})	1980–2000	46.1	47.2	2
	2080–2100	70	70	0
	Change	23.9	22.8	−5
Net Primary Productivity (Pg C yr^{-1})	1980–2000	17.8	18.4	3
	2080–2100	23.4	25.2	8
	Change	5.6	6.8	21
Live biomass (Pg C)	1980–2000	229	234	2
	2080–2100	269	281	4
	Change	40	47	18
LAI (m^2 m^{-2})	1980–2000	4.4	4.4	0
	2080–2100	5.6	5.7	2
	Change	1.2	1.3	8
Leaf temperature (°C)	1980–2000	25	25	0
	2080–2100	27	27	0
	Change	2	2	0
Area* (×1000 km^2)	1980–2000	24 240	25 000	3
	2080–2100	23 750	24 680	3
	Change	−490	−320	35

*Area where tropical forest is predicted in 1980–2100 and 2080–2100.

Acclimation in both trees and lianas

There was no evidence that trees and lianas differed in their acclimatory capacity. Doughty (2011) found that A_{sat} of canopy tree leaves was more negatively affected by *in situ* warming than A_{sat} of liana leaves, suggesting lianas had a greater capacity for acclimation, but a mechanistic explanation for this observation was not identified. Boreal conifer tree species acclimate more completely than co-occurring deciduous broadleaved species (Tjoelker *et al.*, 1999a,b), but studies of temperate species have not found systematic differences in acclimation capacity among different plant functional types (Campbell *et al.*, 2007), or between inherently slow and fast growing species (Loveys *et al.*, 2003). An assessment of thermal acclimation of a larger number of tropical trees and lianas will be necessary to verify our result of comparable acclimation capacity across trees and lianas, and to test for differences among plant functional types (e.g., early- vs. late-successional trees).

Across species, greater acclimation was observed with higher sugar to starch ratio in leaves. On the other hand, leaf nitrogen or TNC concentrations did not show any relationship with acclimation potential, similar to Loveys *et al.* (2003) working on nine herbaceous species. Compared to tree leaves, the liana leaves in our experiment had significantly lower concentrations of simple sugars and lower sugar to starch ratios (Fig. 5a). However, the across-species correlation between sugar to starch ratio and acclimation slope was not solely driven by lianas.

Consequences of acclimation for predicted respiratory carbon fluxes from tropical forests

When incorporated in a global land model, acclimation of respiration reduced the warming-induced increase in respiratory carbon release from tropical forests by the end of the 21st century, enabling 21% greater increase in NPP and 7 Pg additional carbon storage in live biomass. Simulations with the JULES model by Atkin *et al.* (2008) also predicted that acclimation reduces warming-induced increase of respiration in the tropics, although at the global scale their simulations showed negligible influence of acclimation because acclimation in cooler climates resulted in an increase in respiration compared to the nonacclimation simulation. Our analysis restricted to the tropics indicated that the acclimation potential of tropical trees can significantly mitigate warming-induced respiration at the biome level. Calculations of respiratory carbon fluxes from the canopy of our study forest with a simple scaling model showed qualitatively similar results, confirming that our conclusions about the effect of acclimation on respiratory carbon fluxes over the 21st century are robust to different model assumptions. Interestingly, the modest acclimation we employed in the DGVM resulted in some grid cells being maintained as closed-canopy forest at end-of-century climate that would have otherwise been converted to low-productivity savanna/grassland with lower capacity for carbon storage in live biomass. Without acclimation the carbon balance in these grid cells dropped below a threshold level that the model requires to maintain closed canopy forest. In these few grid cells respiration increased compared to the no-acclimation scenario because more live biomass was maintained.

Significance for modeling

It has long been recognized that thermal acclimation should be considered in global vegetation models (King *et al.*, 2006). Many DGVMs and ecosystem models, however, still do not address acclimation even though they may incorporate temperature-dependence of Q_{10} (see for reviews of such models Wythers *et al.*, 2005; Smith & Dukes, 2013). The magnitude of the effect of a modest amount of thermal acclimation on estimated tropical carbon fluxes that we report further stresses the importance of developing temperature-dependent respiration algorithms for global models that address temperature effects at multiple time scales. The equation describing the temperature-dependent Q_{10} across species and biomes (Tjoelker *et al.*, 2001; Atkin & Tjoelker, 2003) underestimates Q_{10} values in tropical climates; e.g., for a measurement temperature of 26 °C a Q_{10} of 2.0 is predicted (Atkin & Tjoelker, 2003). In the current study, Q_{10} values ranged from 2.5 to 3.0 for measurements around 26 °C (measurement interval 20–32 °C). We recently determined Q_{10} values of upper-canopy leaves of 28 tree and liana species at PNM, a seasonally dry tropical forest (Slot *et al.*, 2014), and of 20 tree species from Parque San Lorenzo, an old-growth evergreen rainforest on the Atlantic side of Panama (M. Slot *et al.*, unpublished dataset), and across these 48 species Q_{10} values around measurement temperature of 26 °C averaged 2.5. This confirms that Q_{10} values >2.0 are not uncommon in tropical forests (see also Slot *et al.*, 2013 and references therein). Warming did not reduce Q_{10}, so even when leaves acclimate, their short-term sensitivity to temperature remains high. These results suggest that a temperature-dependent Q_{10} alone is not sufficient to estimate temperature-dependent respiration fluxes at a global scale. It will be important to increase our understanding about global patterns in respiration in relation to temperature, both in the short-term (cf Q_{10} values), and over timescales of acclimation, to further improve our ability to reliably simulate the global carbon cycle.

Concluding remarks

In situ warming of upper-canopy leaves demonstrated that mature (fully developed) leaves of tropical trees and lianas can acclimate to elevated nighttime temperatures in 6–8 days by downregulating R_{25} independent of availability of respiratory substrate. Because leaves newly developed at elevated temperature are likely to acclimate to a greater degree than pre-existing leaves as we used here, our estimates of the potential impact of acclimation are conservative. Nevertheless, implementation of these acclimation responses into simulations of pan-tropical leaf respiration under end-of-century temperatures reveals the potential of acclimation to reduce the potential positive feedback between climate warming and the carbon cycle.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Test of the robustness of our main results against alternative formulations of the functional form of the temperature response of respiration.
Data S2. Simple scaling of foliar acclimation to the stand level, and simulation of the effect of elevated temperature on the respiratory carbon flux of a tropical forest canopy in Panama under current (1995–2011) temperatures and under elevated nighttime temperatures.
Data S3. Maps of leaf respiration rates per unit ground area averaged over the years 2080–2099 simulated from the LM3VN dynamic global vegetation model forced with a climate projection derived from the IPCC AR4 A2 emissions scenario. Maps are shown for simulated respiration rates without accounting for thermal acclimation (a), accounting for acclimation derived from the experimental results in the present study (b), and the difference between the two scenarios (c). All grid cells are shown where tropical forests are predicted to occur in LM3VN.