Elevated night-time temperatures increase growth in seedlings of two tropical pioneer tree species

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Summary

- Increased night-time temperatures, through their influence on dark respiration, have been implicated as a reason behind decreasing growth rates in tropical trees in the face of contemporary climate change.
- Seedlings of two neo-tropical tree species (*Ficus insipida* and *Ochroma pyramidale*) were grown in controlled-environment chambers at a constant daytime temperature (33°C) and a range of increasing night-time temperatures (22, 25, 28, 31°C) for between 39 d and 54 d. Temperature regimes were selected to represent a realistic baseline condition for lowland Panama, and a rise in night-time temperatures far in excess of those predicted for Central America in the coming decades. Experiments were complemented by an outdoor open-top chamber study in which night-time temperatures were elevated by 2.4°C above ambient.
- Increasing night-time temperatures resulted in > 2-fold increase in biomass accumulation in growth-chamber studies despite an increase in leaf-level dark respiration. Similar trends were seen in open-top chambers, in which elevated night-time temperatures resulted in stimulation of growth.
- These findings challenge simplistic considerations of photosynthesis-directed growth, highlighting the role of temperature-dependent night-time processes, including respiration and leaf development as drivers of plant performance in the tropics.

Introduction

Contemporary global warming has been accompanied by the narrowing of the diel (24 h) temperature range by the asymmetric rise in night-time and daytime temperatures (Kukla & Karl, 1993; Easterling *et al.*, 1997). The complex interaction of changing atmospheric chemistry, water-vapor feedback, and cloud behavior is difficult to predict (Dai *et al.*, 1997; Lobell *et al.*, 2007), yet it is likely that the emergence of novel temperature regimes in the tropics (Diffenbaugh & Scherer, 2011) will include the continued asymmetric rise of night-time temperatures (IPCC, 2007), with potentially profound implications upon plant growth in an already compromised ecosystem (Wright, 2010).

Several recent meta-analysis of plant responses to increasing temperature (Lin *et al.*, 2010; Way & Oren, 2010) have highlighted how tropical species may be particularly vulnerable to increases in both daytime and night-time temperatures. In temperate and boreal systems productivity is often limited by seasonal minima, and an increase in temperature may be associated with the extension of the growing season or a shift towards a temperature optimum for growth. By contrast, humid tropical (lowland) systems with their relatively stable climatic envelope (Wright *et al.*, 2009) are presumed to operate at, or close to their thermal optimum (Janzen, 1967; Ghalambor *et al.*, 2006) and

may possess only limited tolerance to increasing temperatures (Colwell *et al.*, 2008; Laurance *et al.*, 2011; Corlett, 2012).

Dark respiration (R_d) (i.e. non-photorespiratory mitochondrial respiration) provides cells with metabolic precursors, usable energy (i.e. ATP), and reducing equivalents (e.g. NADH) (Ryan, 1991; Amthor, 2000). As in all organisms, R_d of tropical trees is known to rise in response to short-term increases in temperature (Cavaleri *et al.*, 2008) and, as such, the elevated respiratory-carbon loss at higher growth temperatures has been invoked in the explanation of empirical (Clark *et al.*, 2003, 2010; Loescher *et al.*, 2003; Larjavaara & Muller-Landau, 2012) and predicted (Cox *et al.*, 2000; Cowling & Shin, 2006) decreases in productivity of tropical forests with changing climate. However, this interpretation precludes long-term acclimatization of R_d (Atkin & Tjoelker, 2003; Atkin *et al.*, 2005) and is predicated upon carbon-source dynamics, the net balance between photosynthesis (*A*) and R_d determining plant growth. This framework does not address potential changes in carbon use efficiency (Hansen *et al.*, 2009) or phenological development (Wolfe-Bellin *et al.*, 2006), the highly dynamic nature of thermal responses seen in R_d (Atkin *et al.*, 2005), or how plant metabolic rates may be sink rather than source mediated (Körner, 2003; Sala *et al.*, 2012). Indeed, if we assume growth to be regulated within a simplistic source-centric framework increased R_d in response to temperature would need to reflect a substantive increase in maintenance costs (e.g.

increased turn-over of cellular components, or energy requirements to maintain ion gradients; Penning de Vries, 1975) or an increase in wastage (e.g. futile cycling or decoupling of the mitochondrial electron transport chain from oxidative phosphorylation; Amthor, 2000).

Previous studies on seedlings of tropical tree species have demonstrated that growth can be maintained at day/night temperatures in excess of those in the current home range of the species (Cunningham & Read, 2003) through, among other things, acclimatization of R_d in response to changes in mean growth temperature (A. W. Cheesman & K. Winter, unpublished). Yet, fundamental questions still exist as to how changes in night-time temperature and a reduction in diel temperature range may affect tropical forests. Although we recognize that the rise of night-time temperatures and reduction of temperature range in the tropics will have profound implications beyond the direct impact of temperature on plant physiological processes, including alteration of precipitation patterns (Kitoh & Arakawa, 2005) and nutrient cycling (Salinas *et al.*, 2011), our aim was to elucidate the direct effects of night-time warming upon biomass accumulation and plant development. We examined growth in two neotropical pioneer tree species using both indoor controlled-environment growth-chambers, and outdoor open-top chambers. In linking results from highly-controlled growth chambers with those derived from outdoor studies under more natural conditions, including variation in diel temperature and natural sunlight, we demonstrate profound positive effects of elevated nocturnal temperatures on biomass accumulation.

Materials and Methods

Plant material

We studied the effects of increasing night-time temperature on two fast-growing tropical pioneer tree species, *Ficus insipida* Wild. (Moraceae) and *Ochroma pyramidale* Cav. ex Lam.Urb. (Bombacaceae). Both species, found naturally throughout the lowland tropical Americas, are known to be shade intolerant only able to regenerate in natural clearings or anthropogenically disturbed landscapes (Phillips, 1990; Dalling *et al.*, 1998). Seeds, collected from trees growing at 0–50 m above mean sea level within forests surrounding Panama City were set out in seed-tray flats and germinated in a ventilated screen-house (70% natural sunlight) at the Santa Cruz Experimental Field Facility, Smithsonian Tropical Research Institute, Gamboa, Panama. After emergence of cotyledons at least three seedlings were transplanted to experimental pots, and seedlings established before thinning and initiation of heat treatments.

Controlled–environment growth chambers

We employed four GC15 plant growth chambers (EGC, Chagrin Falls, OH, USA) housed at the Tupper Center of the Smithsonian Tropical Research Institute in Panama City. Seedlings were established in 1.75 l pots (TP-49 Treepot; Stuewe & Sons, Tangent, OR, USA) containing a nonsterilized mix of native topsoil and

20% (by volume) vermiculite used to improve soil structure. Six individuals were harvested for determination of initial biomass (averaging 6 mg dry mass in *F. insipida* and 39 mg in *O. pyramidale*) while a further 10 seedlings of each species were assigned to each of the four chambers. All chambers were maintained with a 12 h light period (Philips TL841 fluorescent bulbs, 500 µmol photosynthetically active radiation (PAR) $m^{-2} s^{-1}$ at pot height), and regulated air temperatures (T_{air}). T_{air} during the light period was set to 33°C and dark period temperatures randomly assigned as either 22, 25, 28 or 31°C. Transition of T_{air} between the light and dark set-points was completed within 10 min. The chamber treatment of 33°C/22°C represents a realistic mean daily temperature (27.5°C) and diel temperature range (11°C) for lowland Panama, while the 9°C rise in night-time temperatures exceeds even the most pessimistic scenarios for central America (IPCC, 2007). Plants were watered every day and rotated within each chamber every 3 d to standardize illumination. Final harvest and determination of biomass accumulation–allocation occurred after either 38 d in *O. pyramidale* or 54 d in *F. insipida*, with time-periods chosen to standardize for difference in absolute growth rates between species. Stem height was measured to apical meristem, and plants separated into leaf-lamina, stem + petioles, and roots. Leaf area was determined using a Li-3100 leaf area meter (Li-Cor, Lincoln, NE, USA) and roots were separated from soil by hand sorting, dry sieving and washing. All samples were dried to constant mass at 70°C, weighed, and stored under ambient laboratory conditions until further analysis. Biomass and leaf area data were used to calculate mean relative growth rates (RGR $g g^{-1} d^{-1}$), leaf mass per area (LMA, $g m^{-2}$), leaf area ratio (LAR, $cm^2 g^{-1}$) and shoot to root mass ratio (S : R $g g^{-1}$).

In the days before final harvest, leaf-level gas exchange was measured on the youngest fully-developed leaf using a Li-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA) under both night-time and daytime growth conditions. Cuvette temperature (T_{cuv}) of the Li-6400 was set to that of the specific growth chamber, and reference [CO_2] regulated at c. 400 µl l^{-1}. Dark respiration was determined during the last 5 h of the 12-h dark period. Net CO_2 uptake rates (A_{500}) were measured between the second and sixth hours of the light period using a red/blue LED light source (500 µmol $m^{-2} s^{-1}$). For a subset of both *F. insipida* (five individuals per chamber) and *O. pyramidale* (four individuals per chamber) a more complete photosynthetic characterization was carried out; including light response curves (PAR = 1300, 1000, 500, 250, 100, 50 µmol $m^{-2} s^{-1}$) and A–C_i curves (C_a = 400, 250, 50, 500, 750, 1000, 1250 µmol $CO_2 mol^{-1}$ air). During A–C_i curves T_{cuv} was 33°C and PAR saturating at 1000 µmol $m^{-2} s^{-1}$.

Open top chambers

Six open-top chambers were installed at the Santa Cruz Experimental Field Facility (Fig. 1; see the Supporting Information, Fig. S1). Chambers consisted of a hexagonal steel frame (volume of 2.55 m^3) with lower chamber walls of reflective insulation and an upper portion (87 cm) of clear film gauge-50 Tefzel ETFE
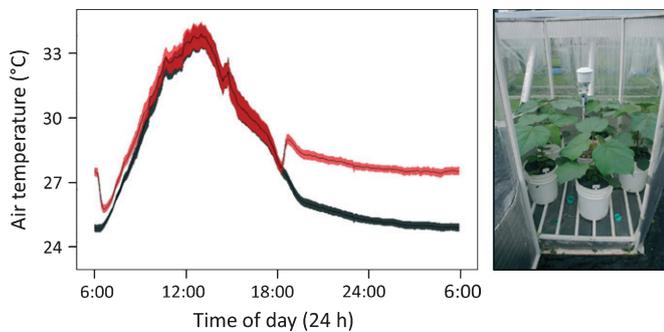
Fig. 1 Diel temperature regimes of open-top chambers maintained at the Santa Cruz Experimental Field Facility in Gamboa, Panama, used to investigate the effects of elevated night-time warming on *Ochroma pyramidale*. Lines represent arithmetic mean of three chambers averaged over the course of the experiment ± 1 SE

film (CS Hyde Company Inc., Lake Villa, IL, USA). Ventilation was provided by six independent fans (TD-150; Soler &Palau, Jacksonville, FL, USA) drawing ambient air from a shaded position and delivering to a polyethylene distribution plenum in the lower portion of each chamber. Airflow in three of the chambers was heated from 18:00 h to 06:00 h by 2×400 W inline electrical resistance heaters (cat. no 20055K112; McMaster-Carr, Los Angeles, CA, USA) per chamber. The use of inline heating ensured that heated air was well mixed before delivery to the chamber. Temperatures within each chamber were monitored via T-type (copper-constantan) thermocouples within standard radiation shielding linked to a CR1000 data logger (Campbell Scientific, Logan, UT, USA). T_{air} during the hours of daylight showed little difference between treatments (Fig. 1) with temperatures at midday averaging *c.* 3°C above those recorded at a nearby (< 10 m) meteorological station (Fig. S1). The PAR at the site averaged a daily maximum of 1200 μmol m^{-2} s^{-1} over the course of the experiment, with some cloudless days recording levels up to 2000 μmol m^{-2} s^{-1}. Air vapor pressure deficit, calculated outside the chambers, averaged a daily high of 1.5 kPa but did climb to 3 kPa on certain days (Fig. S1). During the night the use of in-line heating provided a robust method of tracking ambient temperature +2.4°C over the course of the experiment (Fig 1).

Five seedlings of *O. pyramidale* were established in 30 19-l plastic buckets containing the same fertile soil mix as in previous experiments. Seedlings were transplanted to buckets and grown for *c.* 3 wk under a transparent rain-out shelter before seedlings were thinned to a single individual per pot (mean plant total dry mass = 1.2 g) and randomly assigned to a chamber. After a further 10 d of nonheated equilibration plants were again randomized between the chambers and the warming treatment in three of the chambers was initialized. Warming treatment continued for 33 d before determination of leaf-level gas flux measurements and biomass accumulation/allocation as in previous experiments, with additional stem cross-section area determined at the root-shoot interface using image-J (www.rsb.info.nih.gov/ij) analysis of scaled photographs. Pots received ambient rainfall, with additional daily watering, as required, to maintain soils at close to field capacity.

Statistics

Given practical limitations on the number of environmental chambers available, and to avoid potentially confounding issues of pseudoreplication, data were analysed at the level of the chamber within species. Biomass accumulation/allocation was analysed using the chamber mean of 10 replicate plants, with simple linear regression employed to determine potential relationships between night-time temperature and response parameter. Further analysis of derived variables LMA and LAR were also carried out using linear regression of chamber means. Leaf-level gas fluxes A_{500} (rate of CO_2 uptake at 500 μmol PAR m^{-2} s^{-1}) and R_d of plants measured at growth conditions were initially analysed by linear regression against night-time temperature. The apparent Q_{10} of R_d was determined by linearization of the exponential relationship between mean leaf temperature and R_d across treatments, while light response and A–C_i curve fitting was carried out using tools developed by Kevin P. Tu (www.landflux.org) following Thornley & Johnson (1990) and Ethier & Livingston (2004), respectively. Biomass allocation (total biomass, shoot height, shoot : root ratio, leaf area, LAR), morphological characteristics (LMA, stem cross-section), and physiological performance A_{sat} (net CO_2 uptake at saturating light intensity – 1500 μmol PAR m^{-2} s^{-1}), leaf-level R_d of plants from the open-top chamber experiment were first averaged within chambers ($n = 5$) and then compared between treatments ($n = 3$) using simple *t*-test. All statistical tests were carried out using R (R Development Core Team, 2012) with reported values representing mean ± 1 SD unless otherwise stated.

Results

Controlled-environment growth chambers

Both *F. insipida* and *O. pyramidale* (0.95) showed a substantial, and significant, increase in total biomass with increasing night-time temperatures (Fig. 2), from a mean of 0.85 ± 0.26
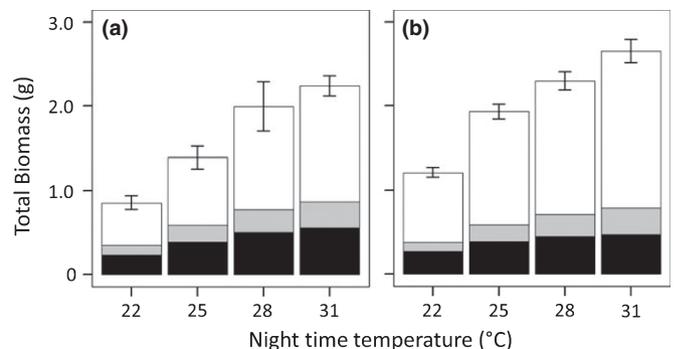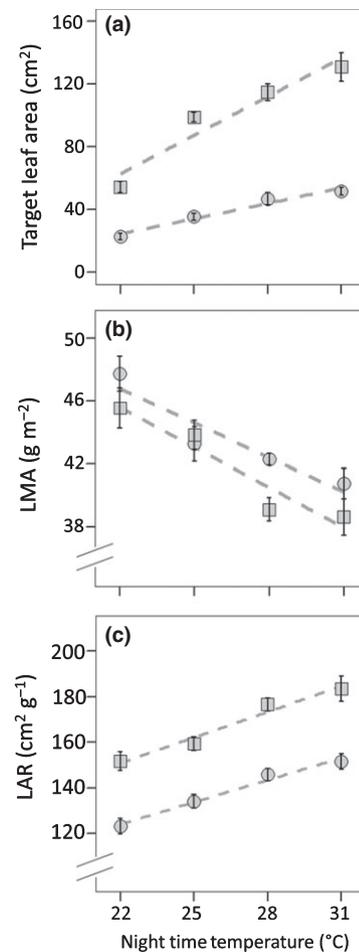

Fig. 2 Total biomass accumulation and allocation patterns in seedlings of two neotropical tree species grown in controlled-environment chambers at a standard daytime temperature (33°C) and a range of night-time temperatures. (a) *Ficus insipida*; (b) *Ochroma pyramidale*. Open bars, leaf; tinted bars, stem; closed bars, root. Bars represent chamber means ($n = 10$) with error bars representing ± 1 SE of total biomass.

to 2.24 ± 0.39 g in *F. insipida* ($F_{1,2} = 72.21$, $R^2 = 0.96$, $P < 0.05$) and from 1.21 ± 0.18 to 2.65 ± 0.45 g in *O. pyramidale* ($F_{1,2} = 56.03$, $R^2 = P < 0.05$). The rate of increase in total biomass with increasing night-time temperature was similar in both species (equal to 0.16 g °C^{-1}). This increase in biomass represented an increase in mean RGR from 0.091 ± 0.005 to 0.109 ± 0.003 g g^{-1} d^{-1} in *F. insipida* and from 0.090 ± 0.004 to 0.110 ± 0.005 g g^{-1} d^{-1} in *O. pyramidale* (Table S1).

Associated with the substantial change in total biomass and relative growth rate, there was pronounced change in biomass allocation (Fig. 2a,b, Table S1). In both *F. insipida* and *O. pyramidale* the proportion of seedlings found as shoot biomass (i.e. leaf + stem + petiole) increased, from 72.8 ± 2.6 to $75.4 \pm 1.8\%$, and from 77.8 ± 2.2 to $82.3 \pm 2.1\%$ of total biomass respectively, although only in *O. pyramidale* was this shown to be a significant increase in chamber means ($F_{1,2} = 29.78$, $R^2 = 0.91$, $P < 0.05$). The leaf area of the latest fully developed leaf targeted for gas flux measurements more than doubled in *F. insipida* and *O. pyramidale*, from 23 ± 6 to 51 ± 8 cm^2 in *F. insipida*, and from 54 ± 11 to 131 ± 28 cm^2 in *O. pyramidale* as night-time temperature rose from 22 to 31°C (Fig. 3a). Associated with this increase in individual leaf area was either a marginally significant ($F_{1,2} = 16.2$, $R^2 = 0.84$, $P = 0.056$) decrease in LMA of *F. insipida*, from 48 ± 3.5 to 41 ± 3.1 g m^{-2}, or a significant ($F_{1,2} = 21.5$, $R^2 = 0.87$, $P < 0.05$) reduction in LMA of *O. pyramidale*, from 46 ± 4.1 to 39 ± 3.7 g m^{-2}. Leaf area ratio showed a significant increase in both *F. insipida* ($F_{1,2} = 106$, $R^2 = 0.97$, $P < 0.01$) and *O. pyramidale* ($F_{1,2} = 61$, $R^2 = 0.95$, $P < 0.05$) with increasing nighttime temperatures, from 123 ± 11 to 152 ± 11 cm^2 g^{-1} in *F. insipida*, and from 152 ± 13 to 183 ± 17 cm^2 g^{-1} in *O. pyramidale*, respectively (Fig. 3c).

Analysis of leaf-level gas flux showed no monotonic change in A_{500} at 33°C across treatments (Fig. 4), with rates averaging 12.4 ± 0.6 and 15.1 ± 0.6 µmol m^{-2} s^{-1} in all treatments of *F. insipida* and *O. pyramidale*, respectively. In *F. insipida* R_d measured at night-time growth temperatures increased significantly ($F_{1,2} = 49.1$, $R^2 = 0.94$, $\beta = 0.092$, $P < 0.05$) from 1.02 ± 0.10 to 1.82 ± 0.21 µmol m^{-2} s^{-1} across the four treatments. By contrast, the increase in R_d in *O. pyramidale* from a chamber mean of 1.17 ± 0.15 to 1.46 ± 0.13 µmol m^{-2} s^{-1} was found to be nonsignificant ($F_{1,2} = 4.1$, $R^2 = 0.5$, $\beta = 0.027$, $P = 0.182$). The 'apparent Q_{10}' of R_d determined across plants developed under, and measured at increasing night-time temperatures was found to be 1.95 in *F. insipida*, but only 1.22 in *O. pyramidale*. There was no significant difference in the light response curves of photosynthetic CO_2 uptake in either species across the four temperature treatments, with A_{sat} rates averaging 17.2 ± 0.9 and 20.0 ± 0.8 µmol m^{-2} s^{-1}, and light compensation point averaging 28 ± 3.3 and 26 ± 2.5 µmol PAR m^{-2} s^{-1} in *F. insipida* and *O. pyramidale*, respectively (Table S2). Analysis of A–C_i curves revealed no significant difference in either J_{max} or V_{cmax}, averaging 154 ± 5.7 µmol m^{-2} s^{-1} and 93 ± 6.4 µmol CO_2 m^{-2}s^{-1} or 158 ± 2.7 µmol m^{-2} s^{-1} and 96 ± 2.8 µmol CO_2 m^{-2}s^{-1} across all treatments in *F. insipida* and *O. pyramidale*, respectively (Table S2).

Fig. 3 Growth parameters of seedlings of two neotropical tree species (circles, *Ficus insipida*; squares, *Ochroma pyramidale*) grown in controlled-environment chambers at a standard daytime temperature (33°C) and a range of night-time temperatures. (a) Area of latest fully developed leaf, (b) leaf mass per area of seedlings, (c) leaf area ratio of seedlings. Symbols represent treatment mean ($n = 10$) ± 1 SE.

Open-top chambers

Total biomass accumulation showed a significant ($t_{(4)} = 3.09$, $P < 0.05$) increase under elevated night-time temperatures, averaging 28.9 ± 0.9 and 32.7 ± 1.9 g in control and elevated night-time chambers respectively (Fig. 5). This increase in total biomass was attributed to a significant increase in both leaf ($t_{(4)} = 4.44$, $P < 0.05$) and stem + petiole ($t_{(4)} = 2.95$, $P < 0.05$) biomass of plants grown under elevated night-time temperature, with root mass showing no substantial change (Fig. 5). This resulted in a significant ($t_{(4)} = 2.88$, $P < 0.05$) difference in the shoot to root ratio between treatments, averaging 2.8 ± 0.08 and 3.3 ± 0.28 in control and elevated nighttime temperature chambers, respectively (Table 1). Associated with increased leaf mass under elevated temperatures was a significant ($t_{(4)} = 3.16$, $P < 0.05$) increase in total leaf area (0.41 ± 0.03 to 0.47 ± 0.02 m^2), but unlike the growth chamber study there was no significant decrease in LMA or increase in LAR (Table 1). Leaf-level gas flux rates in leaves developed under chamber conditions
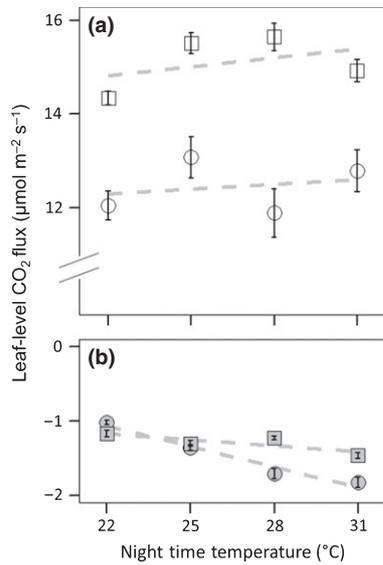
Fig. 4 Leaf-level gas flux measurements of two neotropical tree species (circles, *Ficus insipida*; squares, *Ochroma pyramidale*) grown in controlled-environment chambers at a standard daytime temperature (33°C) and a range of night-time temperatures. (a) Net photosynthetic CO_2 uptake at 33°C; (b) dark respiration measured at the temperature at which seedlings were cultivated. Symbols represent treatment mean ($n = 10$) $\pm$ 1 SE.

Table 1 Growth and morphological characteristics of *Ochroma pyramidale* grown in open-top chambers under control or elevated night-time (+2.4 °C) temperatures

	Control	Elevated	Significance
Whole plant			
Total biomass (g)	28.9 ± 0.9	32.7 ± 1.9	< 0.05
Shoot to root ratio	2.8 ± 0.1	3.3 ± 0.3	< 0.05
Leaf area (m^2)	0.41 ± 0.03	0.47 ± 0.02	< 0.05
Stem height (cm)	39.5 ± 1.9	43.5 ± 2.4	< 0.1
Leaf area ratio (cm^2 g^{-1})	141 ± 6.0	145 ± 3.1	ns
Stem cross section $\times 10^4$ (m^2)	1.56 ± 0.15	1.75 ± 0.12	ns
Target leaf			
Leaf mass per area (g m^{-2})	39.1 ± 1.7	39.3 ± 0.9	ns
A_{sat} (µmol CO_2 m^{-2} s^{-1})	27.5 ± 1.09	27.3 ± 2.61	ns
Transpiration – light (mmol H$_2$O m^{-2} s^{-1})	4.7 ± 0.15	4.8 ± 0.25	ns
Transpiration – dark (mmol H$_2$O m^{-2} s^{-1})	0.38 ± 0.22	0.35 ± 0.15	ns
$R_{d(25)}$ µmol CO_2 m^{-2} s^{-1}	0.77 ± 0.09	0.76 ± 0.04	ns

Values represent arithmetic mean of chamber means ($n = 3$) $\pm$ 1 SD. ns, not significant.

showed no difference between treatments when measured at a common temperature; A_{sat} averaged 27.4 ± 1.8 µmol m^{-2} s^{-1} at a temperature of 33°C, while $R_{d(25)}$ averaged 0.76 ± 0.04 µmol m^{-2} s^{-1} across all six chambers. Similarly, both daytime and night-time transpiration rates showed no significant difference between treatments, averaging 4.7 ± 0.2 and 0.36 ± 0.4 mmol H$_2$O m^{-2} s^{-1}, respectively, across all chambers (Table 1).
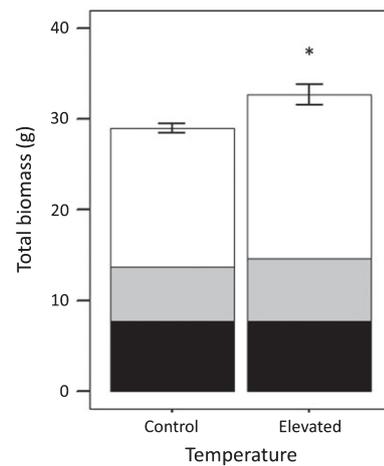
Discussion

Contrary to the notion of adverse effects of increasing night-time temperatures on tropical tree performance (Clark *et al.*, 2003, 2010), our results demonstrate that under well-watered conditions elevated night-time temperature promotes growth in seedlings of two neotropical pioneer tree species. In the experiments that employed controlled-environment chambers growth was positively affected in both species, even at 31°C, far in excess of night-time temperatures currently seen in lowland Panama (Fig. 2). Results from naturally lit open-top chambers were consistent with this finding, showing an increase in biomass of *O. pyramidale* in response to moderate night-time warming (Fig. 5).

In the indoor study, a positive growth response was paralleled by pronounced changes in leaf morphology (Fig. 3), with an expansion of leaf area driving both a decrease in LMA and an increase in LAR. Leaf morphology may be particularly sensitive to elevated night-time temperatures given that the biophysical basis of expansive growth (Pantin *et al.*, 2012) often causes leaf expansion to peak during the night (Schurr *et al.*, 2000; Pantin *et al.*, 2011). In addition, and although leaf physiognomy

Fig. 5 Biomass accumulation–allocation in *Ochroma pyramidale* grown in open-top chambers under either control or elevated (+2.4°C) night-time temperatures. Open bars, leaf; tinted bars, stem; closed bars, root. Bars represent arithmetic mean of chamber means ($n = 3$) with error bars representing $\pm$ 1 SE of total biomass. Asterisk denotes significant difference ($t_{(4)} = 3.09$, $P < 0.05$) in total biomass.

(Royer *et al.*, 2009) and LMA (Cordell *et al.*, 1998; Poorter *et al.*, 2009) are known to vary in response to climatic conditions, differences in leaf morphology may represent an indirect effect mediated through enhanced phenological development, that is, the speeding up of plant development, under higher night-time temperatures. In the open-top chamber study, with substantially greater final biomass than in the growth-chamber study, there was no difference in LMA observed as a result of night-time warming: LMA values (*c.* 39 g m^{-2}) were similar to those seen at high night-time temperatures in the growth chamber study (Fig. 3b).

Leaf-level R_d measured as part of the growth-chamber study showed a general increase with temperature, but to a level

generally below that predicted by instantaneous Q_{10} measurements (Cavaleri *et al.*, 2008). Although the apparent Q_{10} of *F. insipida* was 2, it was only 1.2 in *O. pyramidale*, suggesting significant acclimatization of R_d. Indeed, both species have previously been shown to demonstrate pronounced thermal acclimatization of R_d in response to mean growth temperature (A. W. Cheesman & K. Winter, unpublished) and our results highlight the need to consider long-term acclimatization of R_d in tropical trees (Atkin & Tjoelker, 2003).

We saw no increase in photosynthetic carbon gain per unit leaf area as a result of altered sink strength (indicated by higher R_d) at higher night-time temperatures (Turnbull *et al.*, 2004). Yet, there was clearly a pronounced increase in biomass accumulation. Increasing LAR and decreasing LMA could both account for an increase in C gain per unit biomass. Similarly, changes in R_d of non-photosynthetic tissues (Saveyn *et al.*, 2008), or a change in carbon-use efficiency (Hansen *et al.*, 2009), could contribute to increased growth under higher night-time temperatures.

The results of the open-top chamber study were consistent with those seen in controlled-environment chambers with the one species tested, *O. pyramidale*, showing a significant difference in total biomass after only 1 month of elevated (+2.4°C) night-time temperatures. We had expected to find a difference in leaf-level R_d when measured at a common temperature (25°C) as a result of Type II acclimatization (Atkin & Tjoelker, 2003), but instead saw no significant difference in either $R_{d(25)}$ or $A_{sat(33)}$. This finding does not preclude changes in total night-time R_d and suggests a need for a characterization of diel gas fluxes as part of further acclimation studies.

In the agronomic literature the influence of elevated night-time temperature on phenological development has long been recognized (Grace, 1988). Despite increased respiration rates, elevated night-time temperatures have been shown to result in no change, or indeed an increase, of total biomass accumulation in crop plants such as rice (Ziska & Manalo, 1996; Cheng *et al.*, 2009), sorghum and sunflower (Manunta & Kirkham, 1996) as well as tobacco (Camus & Went, 1952) and cotton (Königer & Winter, 1993). However, many researchers have considered this finding as secondary to the noted catastrophic loss of yield resulting from the temperature sensitivity of flower development (Nielsen & Hall, 1985) and seed maturation (Seddigh *et al.*, 1989; Peng *et al.*, 2004; Prasad *et al.*, 2006). Studies in more natural systems have also seen impacts on plant phenological development. For example, the large herbaceous perennial, *Phytolacca americana* (Phytolaccaceae) demonstrated no difference in biomass accumulation but achieved flower set faster as a result of night-time temperatures increasing from 20°C to 24°C (Wolfe-Bellin *et al.*, 2006). More recently, studies in temperate North America have demonstrated that elevated night-time temperatures in urban environments increase growth rates in seedlings of red oak, *Quercus rubra* (Searle *et al.*, 2012).

There is a growing consensus on the need to re-examine the dynamic interplay between respiration and plant growth in a changing environment (Atkin *et al.*, 2010). The general paradigm of plant respiration, as codified in Amthor's (2000) reassessment of the literature following McCree (1974), distances itself from previous models, which distinguished between growth and maintenance respiration. Instead, it considers individual processes requiring support from respiration (e.g. maintenance of ion gradients, nitrate reduction–assimilation, cell division, phloem loading, etc.) and how these processes vary in response to both ontogenic and environmental change. The general paradigm model moves away from considering R_d merely leading to the loss of carbon that would otherwise be used for growth. It provides a means of understanding the dynamic nature of R_d in response to environmental factors (Atkin *et al.*, 2007; Slot *et al.*, 2008) and highlights the need to gain a better understanding of the temperature response of component processes (Ryan, 2010). Our results, which demonstrate increased growth at elevated night-time temperatures, emphasize the role of temperature-dependent night-time processes as drivers of plant performance in the tropics while affirming the productive role of plant respiration.

We do not currently know the degree to which our results, obtained with seedlings of two pioneer species, can be extended to mature trees; physiological processes uniquely associated with adult trees (i.e. secondary woody thickening, extensive hydraulic structures, and reproductive effort) may be particularly vulnerable to increasing night-time temperatures. Nonetheless, it is apparent that elevated night-time temperatures can markedly stimulate growth of tropical tree species at the critical seedling stage. Further work is required, especially on later life stages, to better assess the implications of our findings as they pertain to the structure and functioning of tropical forests in the face of ongoing climate change.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online
version of this article.

Fig. S1 Overview of open-top chambers used in study.

Table S1 Growth characteristics of tropical tree seedlings grown
in controlled-environment chambers

Table S2 Photosynthetic characteristics of tropical tree seedlings
grown in controlled-environment chambers

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