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High tolerance of tropical sapling growth and gas exchange to moderate warming

Martijn Slot [iD] | Klaus Winter

Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama

Correspondence
Martijn Slot
Email: martijnslot78@gmail.com

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Abstract

1. The effects of global warming on tropical forest growth and carbon storage are uncertain. While observations on canopy trees indicate negative correlations between temperature and growth, some seedling studies suggest the opposite. These contrasting results may reflect ontogenetic differences in temperature responses, or differences between the performance of potted plants under controlled conditions and plants under more variable conditions in the field.

2. To try to bridge the gap between highly controlled experiments on small seedlings and field observations on canopy trees we conducted two sets of outdoor experiments on saplings up to 2.5 m tall; one set to study the effects of night warming, and another set on the effects of day warming. To test the hypothesis that night warming would reduce growth in tropical saplings through stimulation of respiration, we grew the early-successional species *Ochroma pyramidale* in large 380-L soil containers under ambient night-time temperature and ambient +4.5°C. To test the hypothesis that day warming would reduce growth by reducing photosynthesis we compared plants in multi-species and single-species mesocosms rooted in the ground under ambient and passively warmed daytime conditions. In all experiments we monitored growth and measured foliar physiology and plant biomass allocation.

3. Neither night warming nor day warming significantly affected biomass accumulation and allocation. Height growth increased with night warming in *O. pyramidale*, but decreased with day warming in late-successional species. Night warming resulted in acclimation of dark respiration. Day warming resulted in acclimation of photosynthesis in early-successional species, but warming decreased photosynthesis in late-successional tree species.

4. The seedling-to-sapling transition is a critical stage in the life of trees. We found no evidence that in this juvenile growth phase moderate increases in mean temperature reduce the performance of tropical trees, although increases in peak daytime temperature may negatively impact photosynthesis, especially in late-successional species.

KEYWORDS
climate change, global warming, mesocosms, photosynthesis, plant functional traits, respiration, saplings, thermal acclimation, tropical forest

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1 | INTRODUCTION

Global warming may have dramatic consequences for the mitigating effect that tropical forests have on atmospheric and climate change (Malhi et al., 2009). Tropical forests are an important sink for atmospheric carbon (Lewis et al., 2009; Pan et al., 2011), but appear to be close to a high-temperature threshold (Doughty & Goulden, 2008). Recent decreases in growth rate of mature tropical forests suggest a slowdown in their carbon sink potential in response to a changing climate (Brienen et al., 2015). Furthermore, studies based on inter-annual observations consistently indicate that tropical tree growth is reduced in years with above-average temperatures (Clark, Clark, & Oberbauer, 2010, 2013; Clark, Piper, Keeling, & Clark, 2003; Dong et al., 2012; Feeley, Wright, Supardi, Kassim, & Davies, 2007; Vlam, Baker, Bunyavejchewin, & Zuidema, 2014). The physiological mechanisms underlying these responses have not been investigated.

Negative effects of elevated day temperatures (Doughty & Goulden, 2008; Vlam et al., 2014) likely reflect the reduction in photosynthetic capacity following exposure to high temperature extremes (Doughty, 2011) or reductions in net photosynthesis rates due to increased leaf-to-air vapour pressure deficit at higher temperatures (Slot & Winter, 2017a; Tan et al., 2017). Studies that report night temperature as a correlate of growth of tropical canopy trees (Clark et al., 2003, 2010, 2013; Dong et al., 2012; Feeley et al., 2007; Vlam et al., 2014) or of net carbon exchange (Anderegg et al., 2015) generally suggest temperature-stimulated CO_2 loss from respiration as a putative mechanism for the observed growth reduction. However, there is increasing evidence that leaf respiration of tropical trees can acclimate to elevated night-time temperature, thereby reducing respiratory carbon loss with rising temperatures (Slot & Kitajima, 2015; Slot, Rey-Sánchez, Gerber, et al., 2014). Furthermore, such a simple, carbon-centric view would ignore the fact that respiration is a productive process fuelling cellular activity. Even when acclimation is incomplete (i.e. at their respective ambient temperatures respiration is higher in warmed plants than in controls), this does not necessarily translate to growth reduction. Cheesman and Winter (2013a) found that tropical seedlings that were warmed above ambient temperatures at night had both elevated leaf respiration, and significantly higher growth rates than control plants. Clearly, more experimental work is needed to address these apparently conflicting results for seedlings and canopy trees.

Because of the inherently different time-scales of studies that correlate canopy tree growth with annual temperatures, and experimental studies with small seedlings, reconciling their sometimes opposing results is a challenge. The discrepancies may reflect true ontogenetic differences in temperature sensitivity, for example related to differences in biomass distribution and leaf display (Poorter et al., 2015), or to differences in carbon source vs. carbon sink control over growth (Körner, 2003). However, they may also simply reflect the difference between performance of well-watered potted plants maintained under controlled conditions and plants in the field that experience a wide range of sources of potential growth-impacting biotic and abiotic variations.

Here we aimed to bridge the gap between controlled-environment studies on small seedlings and observational studies on canopy trees by focusing on saplings up to 2.5 m tall. Saplings, treelets >30 cm in height that have shed their cotyledons (Kohyama, 1987), may take decades to reach the canopy, during which they will experience gradually rising temperatures that only the best-adjusted individuals will tolerate. In line with common observations on canopy trees, we hypothesized that night warming would reduce growth in tropical saplings and that this reduction would be associated with stimulation of respiration. To test this hypothesis (Hypothesis 1) we grew plants in large soil containers inside tall, naturally lit glass-aluminium chambers, at ambient and elevated night temperature. Warming during the day was hypothesized to reduce sapling growth by reducing photosynthesis (Hypothesis 2). This was tested using passive daytime warming of mixed- and single-species mesocosms of saplings growing directly in the soil. We further hypothesized that soil drought would exacerbate the hypothesized negative effects of warming during the day on growth (Hypothesis 3). We assessed the effects of day and night-time temperature increases on photosynthesis, respiration, growth, biomass allocation, leaf display and foliar carbohydrate dynamics.

2 | MATERIALS AND METHODS

2.1 | Plant material

Seeds of nine widely distributed tropical tree species (Table 1) were collected near Panama City, Republic of Panama and germinated in trays with potting soil (Miracle-Gro®, Stern's Miracle-Gro Products, Port Washington, NY). Of these species, five are early-successional, three late-successional and one—*Clusia pratensis* Seem.—is a light-demanding, slightly leaf-succulent tree species with facultative crassulacean acid metabolism (CAM) (Holtum, Aranda, Virgo, Gehrig, & Winter, 2004) that is typically found in early stages of forest recovery on abandoned pastures and other open habitats (Table 1). After germination seedlings were transferred into individual 2.8 L pots (Tall One Treepot™, Stuewe and Sons, Tangent, Oregon) with potting soil until they were transplanted into the experimental plots, at which point they had at least five true leaves. The treatments were initiated ≥1 week after the plants had been transplanted. At this point, most plants were already 2–8 months old and their growth was no longer dependent on seed reserves. The experiments were conducted at the Smithsonian Tropical Research Institute's Santa Cruz Experimental Field Facility in Gamboa, Republic of Panama.

Past studies linking tree growth reduction to temperature have found effects large enough to suggest that significant treatment effects would be detectable in a single warming experiment. For example Clark et al. (2013) reported a *c.* 20% decrease in stand biomass increment with 0.8°C increase in temperature. Thus, warming by 4–5°C as applied in this study would be expected to translate into very large effect sizes that would be easily-detectable, despite logistical and infrastructural constraints on sample size—i.e. the number of available tall glasshouses and mesocosm enclosures (see Figure S1). Nonetheless, since smaller, perhaps more realistic effect sizes require

TABLE 1 Species used, the families they belong to, their functional type as based on their successional status, and the replicate experiments they were used in (see also Table 2)

			Experiment	
Functional type	Species	Family	Night warming	Day warming
Early successional	*Cecropia insignis* Liebm.	Urticaceae		3
	Ficus insipida Willd.	Moraceae		1, 2, 3, 4
	Luehea seemannii Triana & Planch	Malvaceae		3
	Ochroma pyramidale (Cav. ex Lam.) Urb.	Malvaceae	1, 2, 3	3
	Tabebuia rosea (Bertol.) Bertero ex A.DC.	Bignoniaceae		1, 2
Late successional	*Calophyllum longifolium* Willd.	Clusiaceae		1, 2
	Ormosia macrocalyx Ducke	Leguminosae		1, 2
	Virola surinamensis (Rol. ex Rottb.) Warb.	Myristicaceae		1, 2, 3
[a]	*Clusia pratensis* Seem.	Clusiaceae		3

[a]A leaf-succulent species with facultative CAM photosynthesis that generally grows in sun-exposed areas.

larger sample sizes to be detected with confidence, we repeated the experiments multiple times and analysed treatment effects across the repeated experiments (see below).

2.2 | Night warming experiments

2.2.1 | Growth conditions

Plants were grown in six naturally lit 2.0 × 2.0 × 5.0 m (length, width, height) chambers (Figure S1a). These chambers consist of a 1.5 m high concrete base and a 3.5 m tall glass-aluminium top. Seedlings of *Ochroma pyramidale* (Cav. ex Lam.) Urb. were transferred to individual 1-m tall, *c.* 380-L soil containers filled with a 80%:20% (v/v) mixture of local top soil and river sand The soils at the study site are clay-textured and compact, but have high cation-exchange capacity and are relatively nutrient rich (B. Turner, pers. com). In three of the chambers air was heated during the night (6 p.m. till 6 a.m.) with 1,000 W radiant heaters (King Electrical Manufacturing Co., Seattle, WA, USA) with the aim to elevate temperatures by *c.* 5°C. The other three chambers were maintained at ambient temperature. Fans improved air mixing within all chambers. During the day the chambers' doors were kept open for ventilation, but on sunny days passive warming increased chamber temperatures above ambient air temperatures by a few degrees in both treatments. Air temperature in each chamber was monitored with copper-constantan thermocouple wires placed in ventilated radiation shields at a height of 2 m, and values were logged to a CR10X datalogger (Campbell Scientific, Logan, UT, USA) at 5 min intervals. The plants were watered 3–6 times per week. This experiment was repeated three times (see Table 2).

2.2.2 | Measurements

Plant height was measured on a weekly basis. After about 10 weeks, when the saplings exceeded 150 cm in height, diurnal patterns in net photosynthesis were measured with an LI-6400 portable photosynthesis system (LI-COR BioSciences, Lincoln, NE, USA) at ambient CO_2 concentration (*c.* 390 ppm), temperature, irradiance and relative humidity. Three fully expanded sun-exposed leaves per plant were selected and measured pre-dawn at the ambient temperature of the chamber, and the measured areas were marked. After these dark respiration measurements net photosynthesis rates of the same areas were measured 7–11 times during the day at 45–60 min intervals. At least an hour after sunset dark respiration was measured once more. The highest recorded values in full sunlight (1,200–1,500 μmol m^{-2} s^{-1} quanta) were taken as light-saturated photosynthesis rates (A_{Max}). In the third night-warming experiment R_{Dark} was measured on one detached leaf per plant at four or five different set temperatures in the laboratory in a temperature-controlled gas-exchange cuvette (GWK-3M; Walz GmbH, Eiffeltrich, Germany) attached to other Walz gas exchange equipment and a LI-6252 infrared gas analyser (LI-COR). These measurements were completed within *c.* 4 hr. The slope of the natural log-transformed respiration rates vs. leaf temperature was used to calculate the Q_{10}, the proportional increase in dark respiration per 10°C temperature rise, as $Q_{10} = e^{\wedge (slope \times 10)}$. To enable comparisons across experiments and treatments, respiration rates were standardized to 25°C as $R_{25} = \frac{R_{Dark}}{Q_{10}^{(0.1 \times (T_{Leaf} - 25))}}$, where Q_{10} was set to 2.1—the mean Q_{10} measured in experiment 3—if it was not measured, and T_{Leaf} was the leaf temperature recorded by the leaf thermocouple of the LI-6400 cuvette.

Leaf tissue was sampled for carbohydrate analyses (see below) at the end of the light period and again pre-dawn the following day from the leaves on which gas exchange was measured. At each sample time *c.* 12.5 cm^2 was taken from each of three leaves per plant (five punches of 1.8 cm diameter) and stored in liquid nitrogen; pre-dawn the same leaves were sampled as the evening before. At this time average leaf area of target leaves exceeded 400 cm^2, so removal of 12.5 cm^2 leaf area the preceding evening is unlikely to have affected carbohydrate status in the morning.

When the tallest plant in the experiment attained a height of 2.5–2.75 m, all plants were harvested. Leaf area was measured with an LI-3100 leaf area metre (LI-COR) and leaves, stems and roots were

TABLE 2 Description and dates of the three night warming experiments and the 4 day warming experiments, their conditions (well-watered vs. dry), species used, number of plants per treatment (n), gas exchange parameters collected and leaf water potential (Ψ) and carbohydrate sampling times, and which hypothesis the experiments aimed to address

| Hypothesis	Exp.	Replicate	From	To	Conditions	Species	n	Gas exchange — Photosynthesis	Respiration	Ψ	Carbohydrates
H1	Night warming	1.	28/04/2014	11/07/2014	Watered	Ochroma	3	Diurnal A_{Net} at ambient conditions	p.m. and a.m.		p.m. and a.m.
		2.	22/08/2014	17/11/2014	Watered	Ochroma	3		p.m.		p.m. and a.m.
		3.	05/08/2015	06/11/2015	Watered	Ochroma	3		p.m.		p.m. and a.m.
H2	Day warming	1.	10/05/2013	16/09/2013	Watered	Ficus	3	Diurnal A_{Net} at ambient conditions	p.m. and a.m.		
H3						Tabebuia	3				
						Ormosia	3				
						Calophyllum	3				
						Virola	3				
		2.	12/01/2014	29/04/2014	Dry	Ficus	3	Diurnal A_{Net} at ambient conditions	p.m.	Pre-down	
						Tabebuia	3				
						Ormosia	3				
						Calophyllum	3				
						Virola	3				
		3.	26/09/2014	10/12/2014	Watered	Cecropia	3	A-Ci curves at 32°C (early-successional species)			
						Ochroma	3				
						Ficus	3				
						Luehea	3				
						Virola	3				
						Clusia	3				
		4.	30/01/2015	22/06/2015	Watered	Ficus	15	A-Ci curves at 32°C and 37°C, A_{Max} at 31°C and 36°C	a.m.		
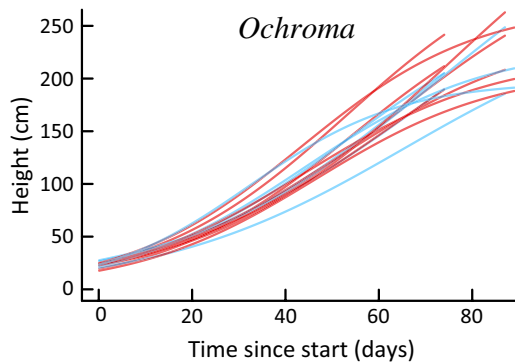
FIGURE 1 Fitted curves of height growth vs. time for *Ochroma pyramidale* plants at ambient (blue) and elevated night-time temperatures (red). Curves from all three experiments are shown, excluding outliers (see text). Three-parameter logistic growth curves were fitted individual tree growth data (>11 weekly height measurements) with r^2 values >0.99 for all plants

dried at 70°C until their mass was stable. Relative growth rate (RGR) and relative height growth rate (RGR_{Height}) were calculated for each sapling. RGR was calculated as

$$RGR = \frac{\ln(Mass_{Final}) - \overline{\ln(Mass_{Initial})}}{\Delta T},$$

where $Mass_{Initial}$ was the initial dry mass determined for three plants harvested on day 1 of the experiments, and ΔT is the duration of the experiment in days. Weekly height measurements were fitted with three-parameter logistic curves, from which mean RGR_{Height} was determined following Paine et al. (2012).

2.2.3 | Carbohydrate analyses

Nonstructural carbohydrates (simple sugars and starch) were determined according to Dubois, Gilles, Hamilton, Rebers, and Smith (1956) with modifications of Slot, Rey-Sánchez, Winter, and Kitajima (2014). Simple sugars were extracted in 80% (v/v) ethanol by shaking overnight at 27°C, followed by centrifugation and two further incubations in 80% ethanol at 30°C for 2 hr each. Supernatants from the three incubations were combined and sugar content was determined colorimetrically at 487 nm via the phenol–sulphuric acid method. Starch was hydrolysed to simple sugars from the pellet in 1.1% hydrochloric acid at 100°C for 45 min. Starch was determined as glucose equivalents using the phenol–sulphuric acid method. Overnight turnover was calculated as the percentage decrease in carbohydrate concentrations between the end of the day and the end of the night relative to the concentration at the end of the day.

2.3 | Day warming experiments

2.3.1 | Growth conditions

We constructed six chambers from 1.8 × 1.8 × 2.5 m (length, width, height) aluminium-tube frames with clear corrugated polycarbonate roofs (Figure S1c). Passive daytime warming was achieved by

wrapping transparent Flex-O-Glass® polycarbonate sheet (Warp Bros, Chicago Inc., IL, USA) around three of the chambers from a height of 15 cm to 2.35 m, leaving 15 cm strips at the bottom and at the top for ventilation. The lower 30 cm of all chambers was fitted with fine-mesh chicken wire to protect the plants from herbivory by locally abundant medium-sized herbivores such as green iguanas (*Iguana iguana* L.) and agoutis (*Dasyprocta punctata* Gray). The chambers were arranged in a line with 2 m spacing, with control and warming chambers alternating. Seedlings (species mixtures or single species; Table 2) were planted directly in the soil in the mesocosms after weeds were manually removed, and plants were watered three to six times per week. Air temperature was monitored at 1.6 m height with CS107 temperature probes (Campbell Scientific) in naturally ventilated radiation shields, and relative humidity was monitored in four chambers (two warmed, two controls) with HMP60-L temperature and relative humidity probes (Campbell Scientific). Soil moisture content in the top 20 cm was monitored with ECH20 soil moisture probes (Decagon Devices Inc., Pullman, WA, USA). All environmental values were logged at 5-min intervals on CR1000 dataloggers (Campbell Scientific).

This experiment was repeated thrice as mixed-species mesocosms with five or six species in each chamber—each represented by one plant—and once as a single-species mesocosm with five *Ficus insipida* Willd. plants per chamber (Table 2). To evaluate hypothesis 3, on the potential interacting effects of warming and drought, we replicated day warming experiment 1 with the same group of species in the dry season, and after seedling establishment we stopped watering the plants until the end of the experiment (see Table 2). The experiment was then repeated again under well-watered conditions, this time with several new species. The new species were selected largely based on the availability of viable seeds at the time of the experiment, while adding more species also enabled us to draw more general conclusions about the effects of daytime warming on tropical sapling growth. Finally, to increase the number of observations at the species level, in the fourth experiment we planted five individuals of the same species (*F. insipida*) in each chamber (Table 2). When grown in full sunlight the late-successional species used in experiments 1–3 do not show signs of photodamage (M. Slot & K. Winter, pers. obs), so although they more commonly experience shaded understorey conditions, there is no indication that the experimental warming was confounded by light stress.

2.3.2 | Measurements

Plant height was measured weekly. After about 4 months (in experiments 1 and 2), when most plants had exceeded 30 cm in height, diurnal patterns in net photosynthesis were measured on all plants with an LI-6400 portable photosynthesis system (LI-COR) on one recently expanded sun-exposed leaf per plant. Measurements were made at ambient CO_2 concentration (c. 390 ppm), temperature, irradiance and relative humidity (RH). In the first experiment dark respiration was measured both pre-dawn and >1 hr after sunset; in later experiments it was only measured either pre-dawn or after sunset (Table 2). Dark respiration rates were standardized to 25°C as described above.

In experiments 3 and 4 we measured light-saturated (1800 μmol quanta $m^{-2} s^{-1}$) net photosynthesis rates at 11 different CO_2 concentrations ranging from 50 to 1800 ppm using the built-in CO_2 mixer of the LI-6400 at a target temperature of *c.* 32°C. These data were used to construct curves of net photosynthesis (*A*) vs. intercellular CO_2 concentration (C_i). Maximum rates of RuBP carboxylation (V_{CMax}, reflecting Rubisco limitation) and RuBP regeneration (J_{Max}, reflecting electron transport limitation) at measurement temperature were calculated according to Farquhar, von Caemmerer, and Berry (1980) using the "PLANTECOPHYS" package (Duursma, 2015) in R version 3.1.3 (R Development Core Team, 2015, R Foundation for Statistical Computing, Vienna, Austria). In experiment 1 and 2 the highest recorded net photosynthesis rate was taken as A_{Max}; in experiments 3 and 4 A_{Max} was determined as the rate of light-saturated photosynthesis at 400 ppm CO_2.

To evaluate the effect of growth temperature on photosynthetic performance at different temperatures, we also measured *A - C_i* curves at 37°C in experiment 4. We further measured light-saturated photosynthesis of five control plants and five warmed plants first at *c.* 32°C (ambient temperature in the control treatment) and then at *c.* 37°C (ambient temperature in the warmed chamber).

At the end of the drought experiment (day warming experiment 2) pre-dawn water potential was determined with a Scholander-type pressure chamber on one leaf per plant in all 30 plants of the experiment (Table 2).

When the tallest plant in each of the experiments had reached a height of 2.0–2.5 m, all plants were harvested. Roots were dug up by hand and washed with water. Leaf area was measured with an LI-3100C leaf area metre (LI-COR) and leaves, stems and roots were dried at 70°C until they reached stable mass. RGR and RGR_{Height} were calculated as before, using the initial dry mass determined for five plants per species harvested on day 1 of each experiment.

2.4 | Statistical analyses

We determined treatment effects for all traits of interest from their effect sizes calculated as Cohen's *d* (Cohen, 1988). Ninety-five-% confidence intervals of Cohen's *d* values were calculated using the "MBESS" package in R (Kelley, 2007). To synthesize warming effects across replicate experiments, standardized mean effect sizes were calculated using random-effects models developed for meta-analyses (Hedges & Vevea, 1998). In this approach effect sizes are weighted by the inverse of experiment-level variance—i.e. higher weight was given to the experiments with small variance—and when calculating variance across experiments differences in variance within the replicate experiments are accounted for. In the calculation of standardized mean effect sizes gas exchange measurements from the night warming experiments were averaged across the three leaves that were measured on each plant. Similarly, data from day warming experiment 4 (in which five *F. insipida* plants were planted in each chamber) were averaged by chamber to avoid issues with pseudoreplication. Treatment effects within experiments (e.g. Tables S1 and S2) were evaluated with two-sided Student's *t*-tests, unless we had

specific hypotheses about the response variables (e.g. night warming effects on R_{25}, RGR, etc.), in which case one-sided *t*-tests were used. All analyses were performed in R version 3.1.3. All plant-level growth, biomass allocation, gas-exchange and carbohydrate data are publicly available (Slot & Winter, 2017c).

In mesocosm (day warming) experiment 4 we found roots from a tall tree *c.* 15 m away in one of the warmed chambers. Soil moisture in the top 20 cm was not reduced—plants were frequently watered—but plant biomass at final harvest was 60% lower in that chamber than in the other chambers, suggesting that below-ground competition affected performance. This chamber was excluded from the analyses. In two night-warming experiments one of the plants was affected by an unidentified pathogen, causing yellowing of leaves and significantly stunting growth. These plants—in both cases from the control treatment—were excluded from the analyses.

3 | RESULTS

3.1 | Night warming

3.1.1 | Growth and biomass allocation

Across experiments, the treatment resulted in average night warming by 4.2°C (range across three experiments: 3.6–4.7°C) with fairly uniform warming across the high-temperature chambers, increasing mean night-time temperature from *c.* 25.9 to *c.* 30.1°C (Figure S1b). This night warming resulted in a moderate increase in height growth of *Ochroma* saplings (Figures 1 and 2). Within about 90 days, warmed plants grew almost 2 m, from 22 ± 5 cm (mean pre-treatment height across experiments ±*SEM*) to 216 ± 9 cm, compared to 201 ± 7 cm for control plants. Biomass accumulation did, however, not differ between treatments, with dry mass increasing from *c.* 13 ± 3 g at the start of the experiments to 1,418 ± 80 g and 1,422 ± 90 g at final harvest in warmed and control plants respectively. Consistent with these observations on absolute growth, there was a positive effect of night warming on RGR_{Height} across experiments, but no effect on biomass RGR (Figure 2).

There was a tendency towards increased allocation of biomass to leaves at the cost of allocation to roots in warmed plants, but this was not significant across experiments (Figure 2). In addition to the apparent increased allocation to leaves in warmed plants, warmed plants increased leaf display; leaf area ratio (LAR; total leaf area divided by total plant dry mass) significantly increased, while leaf mass area (LMA; leaf mass divided by leaf area) decreased with night warming (Figure 2; Table S1).

3.1.2 | Gas exchange

Dark respiration rates of control and warmed plants measured at their respective ambient night temperatures did not differ significantly, indicating that acclimation led to near-homeostatic rates of respiration across temperatures (Figure 3a). Respiration rates at 25°C (R_{25}) were lower in warmed than in control plants across
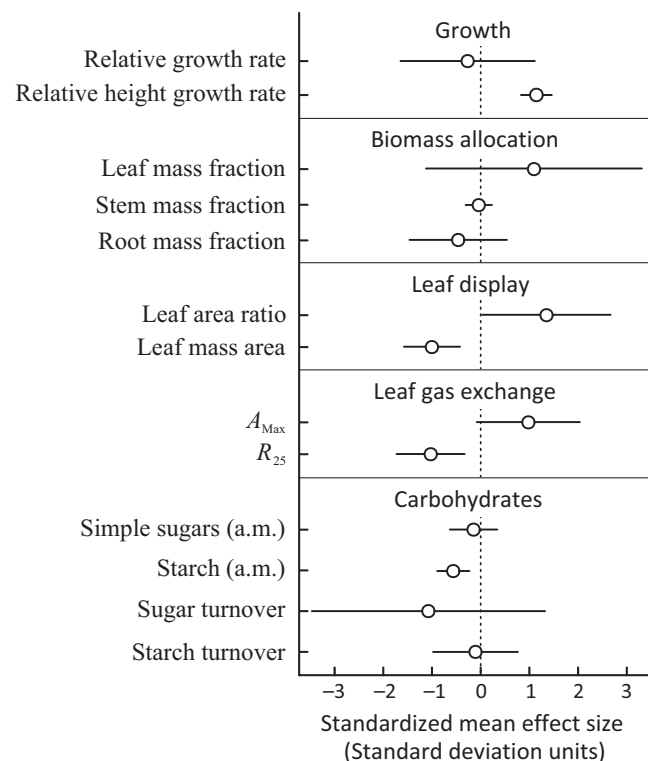
FIGURE 2 Standardized mean effect sizes (and 95% confidence intervals) of three night warming experiments with *Ochroma pyramidale* saplings illustrating the warming effects on growth, biomass allocation, leaf display, leaf gas exchange traits and traits associated with carbohydrate dynamics. When warming reduces a response trait the effect size is negative; when it stimulates a response trait the effect size is positive
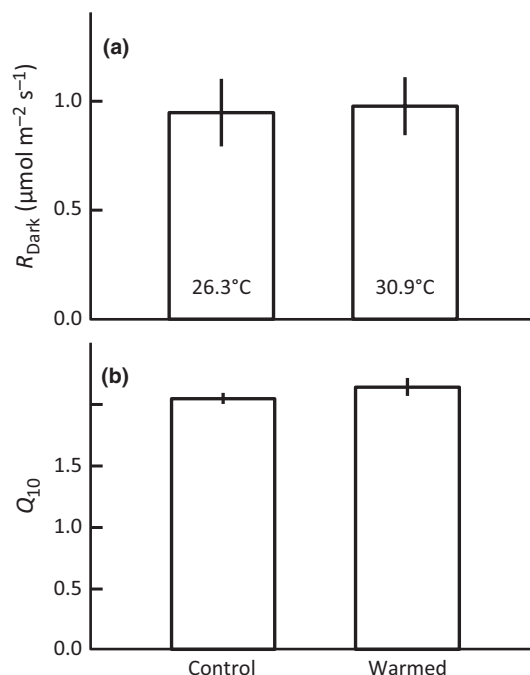

FIGURE 3 Dark respiration rates of warmed and control saplings of *Ochroma pyramidale* measured at their respective night-time temperatures (a) and the temperature sensitivity of dark respiration (Q_{10}) (b) of the same plants

experiments (Figure 2). Acclimation was not associated with a decrease in the short-term temperature sensitivity of dark respiration (Q_{10}) (Figure 3b). Due to considerable intra-treatment variation, down-regulation of R_{25} was only marginally significant ($p < .1$) at the level of the experiment in experiments 1 and 2 (Table S1). Diurnal changes in net photosynthesis were largely driven by changes in irradiance and followed similar patterns in warmed and control leaves (Figure 4). Although in experiment 1 maximum light-saturated rates of net photosynthesis (A_{Max}) tended to be higher in plants warmed at night (Figure 4a), this difference was not significant across experiments (Figure 2).

3.1.3 | Carbohydrates

Total nonstructural carbohydrate concentrations were higher at the end of the day than at the end of the night. Concentrations of simple sugars did not significantly decrease during the night, but starch content was *c.* 27% lower at the end of the night than at the end of the day. This is consistent with daytime accumulation of carbohydrates, temporarily stored as starch, followed by night-time export of photosynthates and respiratory substrate utilization. However, despite lower pre-dawn starch concentrations in warmed plants, the overnight turnover of sugars and starch was not significantly increased in plants experiencing warm nights (Figure 2).
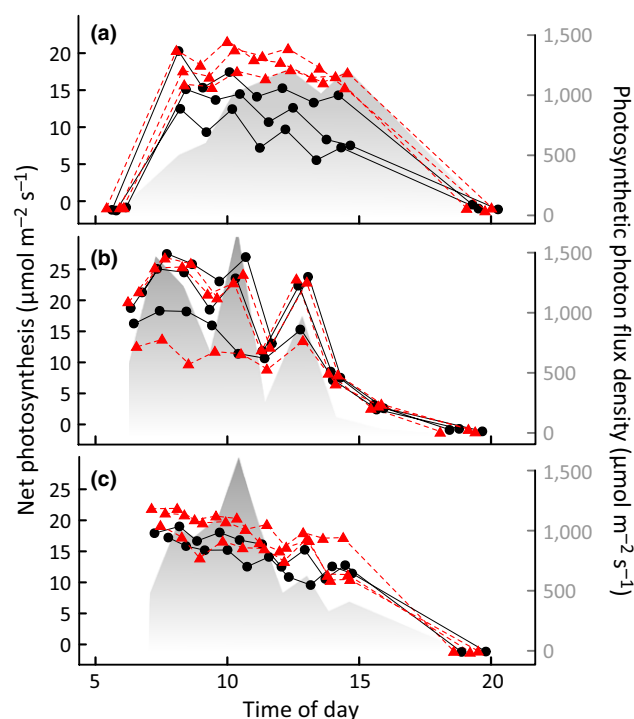

FIGURE 4 Diurnal patterns in net photosynthesis of *Ochroma pyramidale* saplings grown at ambient (black circles, solid black lines) and elevated (red triangles, dashed red lines) night temperatures in three experiments (a–c). Values are means of measurements on three leaves per plant. Grey areas indicate photosynthetic photon flux density recorded at the time of photosynthesis measurements (secondary y axis)

3.2 | Day warming

3.2.1 | Growth and biomass allocation

Passive warming resulted in a moderate increase of 2.6°C (with a range of 2.0–2.8°C across experiments) in mean daytime temperature (6 a.m.–6 p.m.). However, mean daily maximum temperatures increased by 5.4°C (range 4.9–5.9°C), resulting in mean maximum air temperatures of *c.* 38.0°C and frequent occurrence of temperatures >40°C on sunny days, leading to low RH and high vapour pressure deficit (VPD) of the air (Figure S2). Height growth of saplings in outdoor mesocosms was not affected by day warming (Figure 5). Day warming generally did not affect RGR, with the exception of *F. insipida*, for which RGR was slightly reduced (Figure 6a). RGR$_{height}$ was reduced in two late-successional species (Figure 6b), but both exhibited minimal height growth during the 75–129 days of treatment (Figure 5).

Biomass allocation (mass fractions of leaves, stems and roots) (Figure 6c–e) and leaf display traits were minimally affected by warming (Figure 6f,g), and no systematic differences were found among species, or between functional groups (early-successional vs. late-successional species). Only the early-successional *Luehea*—used in a single experiment—showed significant effects, with a strong increase in allocation to roots (Figure 6e), and a strong decrease in LAR in warmed plants (Figure 6f). Otherwise, the absence of treatment effects was consistent across experiments (Table S2). At the end of the experiments, the average mesocosm had accumulated 3.8 m^2 of leaves, and a total dry mass of *c.* 750 g, of which *c.* 25% (*c.* 170 g) was found below-ground in roots.

3.2.2 | Gas exchange

Plants experiencing day warming exhibited similar diurnal patterns of net photosynthesis in experiments 1 and 2, but for several species maximum mid-day values of net photosynthesis were slightly lower in warmed plants than in control plants when measured at their respective ambient temperatures (Figure 7). The species that experienced a significant decrease in A_{Max} at elevated temperature were all late-successional species; standardized mean effect sizes also tended to be negative in early-successional species, but for the early-successional species the decrease in A_{Max} was not significant (Figure 8a). Daytime warming had no effect on dark respiration rates at 25°C (R_{25}) (Figure 8b).

The J_{Max}/V_{CMax} ratio, determined in experiments 3 and 4, was significantly reduced by warming when warmed and control plants were all measured at *c.* 32°C, with the exception of *Cecropia insignis* Liebm. (Figure 8e), indicating increased control over photosynthesis by the maximum rate of electron transport. The decrease in J_{Max}/V_{CMax} resulted from small increases in V_{CMax} and decreases in J_{Max} in warmed plants (Figure 8c,d). Similarly, when measured at their respective growth temperatures, the J_{Max}/V_{CMax} ratio was lower in warmed than in control plants (*t* test, *p* < .001). Light-saturated photosynthesis of warmed and control plants of *F. insipida* in experiment 4 was also reduced at high measurement temperature (*c.* 37°C, with an average leaf-to-air VPD of 2.0 MPa) compared to ambient temperature (*c.* 32°C; VPD *c.* 0.8 MPa) in all plants, but at their respective growth temperatures photosynthesis of control and warmed plants was almost identical (Figure S3).

3.2.3 | Effects of drought on daytime warming

In experiment 2 we stopped watering the mesocosms once the plants were established and the warming treatment was initiated. Because the same species were studied as in experiment 1, experiment 2 could be used to test our third hypothesis and evaluate the interaction between soil moisture deficit and daytime air warming. Volumetric soil water content between 0 and 20 cm depth steadily decreased during 12 weeks in both treatments. Relative humidity of the air (RH) was significantly lower in the warmed mesocosms than in controls (Figure
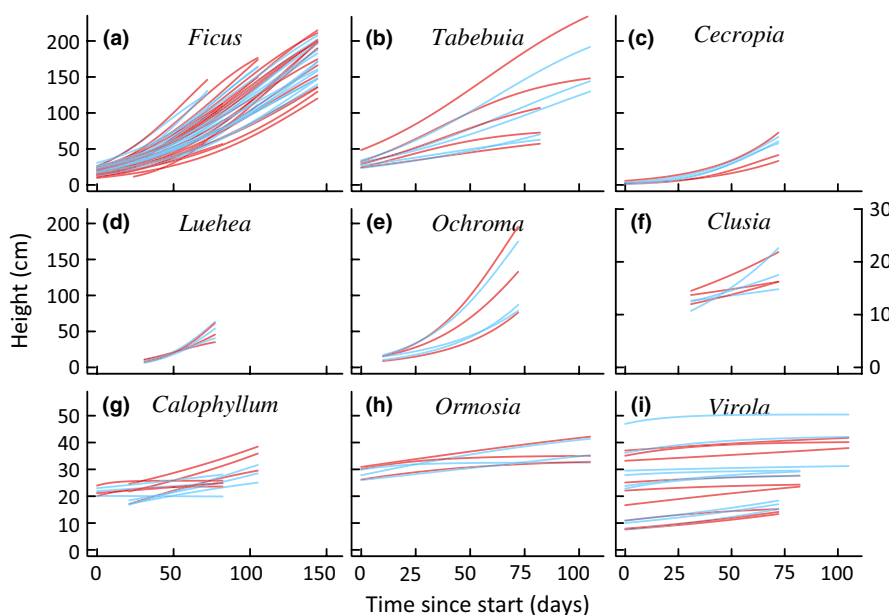

FIGURE 5 Height growth curves for all plants in day warming mesocosm experiments, with curves of plants from control mesocosms in blue and plants from warmed mesocosms in red. Individual plant height growth data (5–10 [exp 1–3] or 20 [exp 4] weekly height measurements) were fitted with three-parameter logistic curves, where r^2 values were on average 0.94 for plants that grew at least 10 cm (range 0.74–1.00). *Clusia* and *Luehea* in experiment 3 were planted 4 weeks after the other species
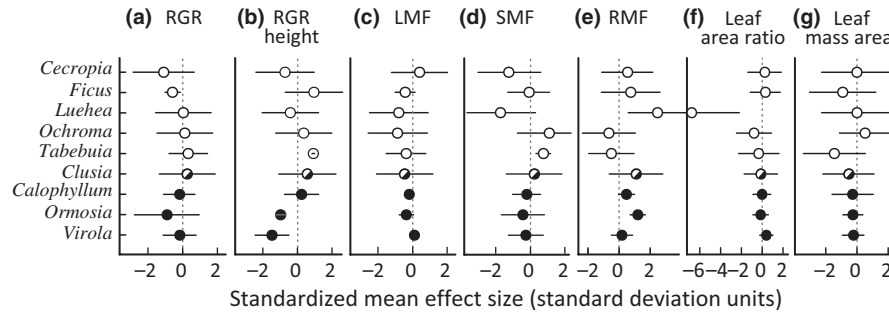
FIGURE 6 Standardized mean effect sizes (and 95% confidence intervals) of one to four mesocosm experiments (depending on species. See Table 1) illustrating the relative effect of day warming on growth (a, b), biomass allocation (c–e) and leaf display traits (f,g) of five early-successional species (open circles), three late-successional species (closed circles) and one intermediate species (partially closed circles). When warming reduces a response trait the effect size is negative; when it stimulates a response trait the effect size is positive
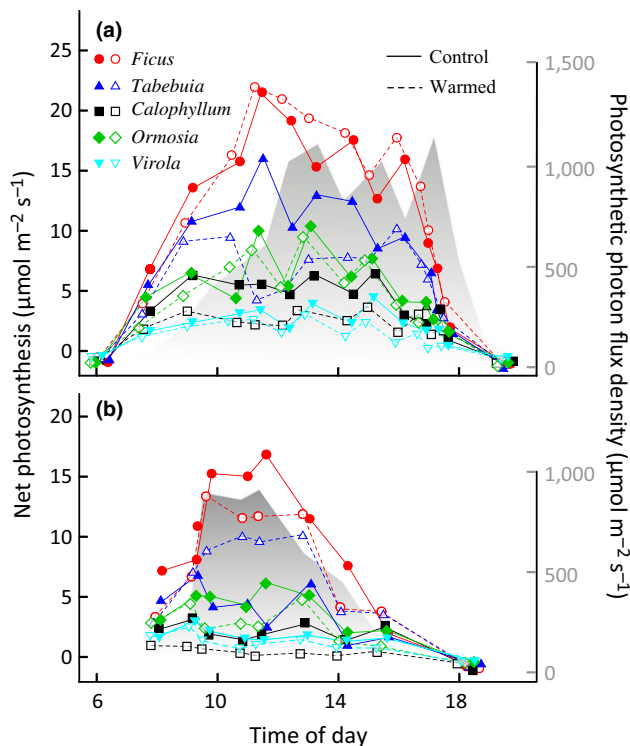

FIGURE 7 Diurnal patterns in net photosynthesis of saplings grown at ambient (solid lines, closed symbols) and elevated (dashed lines, open symbols) day temperatures in experiments 1 (a) and 2 (b). Values are means of measurements on three plants per treatment. Grey areas indicate photosynthetic photon flux density recorded at the time of photosynthesis measurements (secondary y axis)

S2), and minimum RH was lower in the dry season than in the wet season. Nevertheless, experiment 2 did not yield consistently different results than experiment 1 in terms of growth, biomass allocation and physiology traits, and the drought effect did not interact with the warming treatment (no main effect of drought and no significant drought × warming interaction effects in ANOVAs of the combined data from experiments 1 and 2). Experiment 2 was therefore included in the calculation of standardized mean effect sizes used to evaluate warming effects across experiments. In the drought experiment,

pre-dawn water potentials were most negative in the smallest plants—which were the late-successional species—but they were not affected by warming, and the values were less negative than those reported for seedlings in a nearby forest during a strong dry season (Tobin, Lopez, & Kursar, 1999). The most negative values were found in *Virola suri-namensis* (Rol. ex Rottb.) Warb. (−2.0 ± 0.2 MPa in control plants vs. −2.1 ± 0.2 MPa in warmed plants). *Tabebuia rosea* DC. plants had the least negative values (−0.7 ± 0.1 MPa and −0.9 ± 0.1 MPa in control and warmed plants respectively). Despite water potentials low enough to suggest that *Virola* and other late-successional plants may have experienced mild drought stress, RGR was not lower in experiment 2 than in experiment 1. The root mass fraction (root mass as a fraction of total plant mass) was marginally higher in the drought experiment than in the control experiment ($p = .08$), and roots went deeper than in experiment 1 (M. Slot, pers. obs.), suggesting a potential mechanism by which the plants secured access to deeper soil water.

4 | DISCUSSION

We conducted seven experiments in which seedlings of common tropical tree species developed into saplings over a period of several months in soil containers and mesocosms under naturally dynamic environmental conditions, at temperatures comparable to those predicted for the end of the current century. Night temperatures of 4–5°C above the current ambient did not reduce the growth of saplings of *O. pyramidale*, an early-successional tree species, and increasing maximum temperatures during the day by 5–6°C did not decrease growth of a range of early-successional species, while the performance of late-successional species appears more sensitive to increased temperature maxima.

4.1 | Night temperature, respiration and tropical forests

Rising night temperatures have been linked to decreased tropical tree growth (Clark et al., 2003, 2010, 2013; Dong et al., 2012; Feeley et al., 2007; Vlam et al., 2014) and a reduction in the terrestrial carbon sink
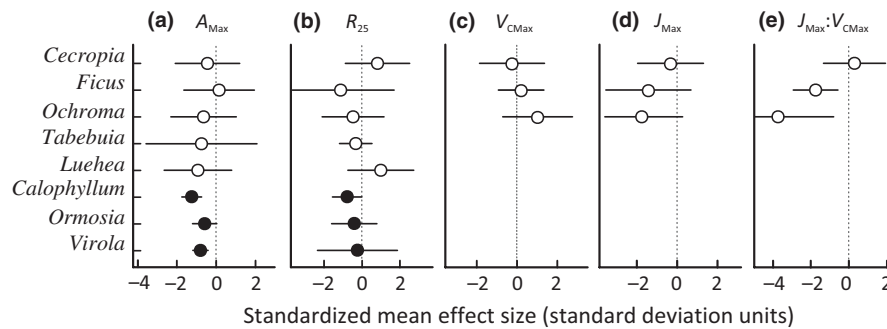
FIGURE 8 Standardized mean effect sizes (and 95% confidence intervals) of one to four mesocosm experiments (depending on species. See Table 1) illustrating the relative effect of day warming on light saturated photosynthesis (A_{Max}; a), dark respiration standardized to 25°C (R_{25}; b), and the maximum rates of RuBP carboxylation (V_{CMax}; c) and RuBP regeneration (J_{Max}; d), and their ratio (e) measured at c. 32°C of five early-successional species (open circles) and three late-successional species (closed circles). When warming reduces a response trait the effect size is negative; when it stimulates a response trait the effect size is positive

(Anderegg et al., 2015). The putative mechanism for the observed night temperature-tree growth correlations is that stimulation of temperature-dependent respiration during warm nights effectively reduces the amount of carbon available for tree growth. Our results do not support this hypothesis. Thermal acclimation resulted in down-regulating of respiration rates in saplings that were warmed at night, which lead to homeostasis of respiration rates across growth temperatures. These results are consistent with previous studies with tropical tree species, both on seedlings (Cheesman & Winter, 2013a, 2013b; Fahey, Winter, Slot, & Kitajima, 2016; Slot & Winter, 2017b) and on leaves of canopy trees (Slot et al., 2014).

Although there is a general tendency towards acclimation of leaf respiration, species differ in the degree to which they acclimate (Cheesman & Winter, 2013a, 2013b; Fahey et al., 2016), and often homeostasis is not achieved (Slot & Kitajima, 2015). It is therefore plausible that temperature-stimulated respiration leads to increased foliar carbohydrate depletion in some tropical species. However, the question is whether that would cause significant growth reductions, as overnight depletion of carbohydrates can stimulate daytime photosynthesis by removing a sugar-regulated feedback inhibition of photosynthesis (e.g. Neales & Incoll, 1968). For example Turnbull, Murthy, and Griffin (2002) showed that as warming stimulated respiration in *Populus deltoides*, pre-dawn foliar carbohydrate concentrations decreased, and the greater this depletion, the stronger the stimulation of photosynthesis during the day.

4.2 | Temperature response of tree growth and plant carbon limitation

The effect of elevated night temperature depends on respiratory acclimation and photosynthetic compensation, but it will also depend on the extent to which plant growth is carbon limited. Growth of tropical trees may not be strongly carbon limited. Rather, it is thought to be limited by sink activity—the use of, or demand for carbohydrates in biosynthesis, energy generation and allocation to symbionts or storage (Körner, 2003, 2009). Support for this hypothesis comes from the observation that tropical forest species maintain relatively high

concentrations of carbohydrates (Würth, Pelaez-Riedl, Wright, & Körner, 2005)—in this study *O. pyramidale* leaves contained c. 11% starch even at the end of the night—and that increasing the carbon source through CO_2 fertilization of tropical canopy leaves mainly leads to an increase in foliar carbohydrate concentration, rather than stimulating growth (Lovelock, Virgo, Popp, & Winter, 1999; Würth, Winter, & Körner, 1998a). In fact, there is evidence that 150 years of gradually rising atmospheric CO_2 concentration has not translated into increased growth of tropical canopy trees (van der Sleen et al., 2015, 2017). However, in the deep shade, where seedlings operate close to their light compensation point, CO_2 fertilization does stimulate growth (Würth, Winter, & Körner, 1998b). Light limitation equates to carbon limitation (low light limits photosynthetic carbon uptake), so the degree of carbon limitation tropical plants experience—and thus the risk of growth reduction with night warming—may depend on the plant's light environment, and therefore change during plant ontogeny.

In our experiments the plants received full, natural irradiance and they neither appeared carbon limited (as suggested by high pre-dawn carbohydrate concentrations and relatively small night-time carbohydrate turnover), nor did they experience increased carbon loss in respiration due to warming. While this explains why we did not find support for the hypothesis that night warming would decrease growth, the fact that warming did not stimulate sapling growth conflicts with previous controlled experiments on tropical tree seedlings, including *O. pyramidale* (Cheesman & Winter, 2013a, 2013b). While huge sample sizes are required to detect small treatment effects, previous studies found very large effect sizes, both the positive temperature effect in seedlings (Cheesman & Winter, 2013a) and the negative effect in canopy trees (e.g. Clark et al., 2013); effect sizes that would have been detected in our thrice-replicated sapling experiment, had they indeed existed. Interestingly, together these results suggest an ontogenetic cross-over in warming effects on tropical trees, with elevated night temperatures stimulating growth in seedlings, not affecting growth of saplings, and reducing growth of canopy trees. The mechanism behind this apparent ontogenetic cross-over is unclear. One possibility is that warming stimulates sink activity more strongly in seedlings than in saplings or canopy trees. Another possibility has to do with ontogenetic changes

in biomass distribution. We measured leaf respiration, because leaves experience the strongest temperature fluctuations and leaf respiration accounts for *c.* 50% of all autotrophic respiration in tropical trees (Malhi, 2012). It is possible that root and stem respiration of tropical species have lower thermal acclimation capacity than leaf respiration, and therefore that any growth stimulation by warming is increasingly countered by increased carbon loss as stem- and root mass fractions increase during ontogeny (Poorter et al., 2015). Clearly, more research into controls over plant growth across ontogeny is needed, and the effect of temperature on these controls needs to be studied.

4.3 | Daytime warming and plant performance

In contrast to our hypothesis, we found that saplings in warmed mesocosms did not suffer systematic reductions in biomass accumulation, despite experiencing daily maximum temperatures 5–6°C above current maxima. Rather, we found signs of thermal acclimation of photosynthesis in early-successional species, and no changes in dark respiration, biomass distribution and leaf display across species. Relative height growth rates in late-successional species were reduced, but total growth was so small in these species (see Figure 5g–i) that ecological interpretation of this result would be premature. For the same reason, however, we cannot rule out the possibility that late-successional species would show growth decline if warming was continued over longer periods. Photosynthesis of late-successional species was reduced in response to elevated day temperatures, possibly as a result of occasionally exceeding thermal threshold temperatures (Doughty, 2011). The optimum temperature for photosynthesis is lower in seedlings of late-successional species than of early-successional species (Slot, Garcia, & Winter, 2016), so episodic high temperatures may affect late-successional species in particular. Slow growth rates of late-successional species also mean that leaves impacted by high-temperature stress are not as readily replaced as in fast-growing species with shorter leaf-lifespans. Late-successional species may thus be at greater risk from rising day temperatures.

4.4 | Plant ontogeny and physiological plasticity to day warming

While in seedlings the optimum and maximum temperature for net photosynthesis is higher in early- than in late-successional species (Slot et al., 2016), in leaves of canopy trees this difference in temperature-response traits disappears (Slot & Winter, 2017a). This change probably reflects adaptation to the common ontogenetic trajectories of early- and late-successional canopy trees; while early-successional species tend to germinate in open areas and maintain high-light exposure—and thus higher tissue temperatures—throughout their development, late-successional canopy species start out as seedlings in the shaded understorey—buffered against high leaf temperatures—but experience high light and high temperature conditions as adults in the canopy (e.g. Poorter, Bongers, Sterck, & Wöll, 2005). At the sapling stage, the predominant light environment is still strongly contrasting between early- and late-successional species (King, 1991).

Adaptation to different environmental conditions would thus result in different thermal tolerances of early- and late-successional species, consistent with observations on seedlings, which is indeed what the results of the current experiments suggest. The large ontogenetic change in environmental conditions associated with the height-light trajectory of late-successional species has led to the hypothesis that late-successional species should have greater physiological plasticity than early-successional species. Testing this for sun-shade plasticity Rozendaal, Hurtado, and Poorter (2006) found some support for this hypothesis. Whether the inherent thermal plasticity also differs systematically between saplings of contrasting ecological groups remains to be seen.

4.5 | Acclimation of photosynthesis

We found a trend towards reduced J_{Max} values in early-successional species grown at elevated day temperatures. This is consistent with a recent analysis along a tropical elevation gradient that showed a negative effect of growth temperature on J_{Max} (Bahar et al., 2017). The resulting reduction in J_{Max}/V_{Cmax} ratio indicates that at high growth temperature electron transport exerted greater control over net photosynthesis than at low temperature. Because the temperature optimum of electron transport-limited photosynthesis tends to be higher than that of Rubisco-limited photosynthesis, a reduction in this ratio following thermal acclimation may lead to an increase in the optimum temperature of net photosynthesis (Hikosaka, Ishikawa, Borjigidai, Muller, & Onoda, 2006). The fact that A_{Max} of warmed *F. insipida* plants measured at elevated temperature was similar to A_{Max} of control plants measured at control temperature, suggests that photosynthesis of these saplings had indeed acclimated, and that the optimum temperature had shifted towards higher values in response to warming, consistent with observations on tropical seedlings (Slot & Winter, 2017b).

4.6 | Tropical forests and future climates

Warming only at night or warming only during the day did not reduce growth of tropical saplings. These results illustrate a significant degree of physiological high-temperature resilience of these tropical species. Nonetheless, to fully understand the potential threats of global warming for tropical forests, we need to account for the multi-faceted nature of atmospheric and climate change. For example rising CO_2 concentrations strongly interact with plant responses to increased temperature and reduced rainfall by reducing photorespiration and improving water use efficiency (Berry & Björkman, 1980; Holtum & Winter, 2010); day and night temperature are increasing at the same time, and their effects are likely to compound one another; and some areas in the tropics will get wetter, while other areas will get drier.

Drought may exacerbate the effects of high temperature on plant performance (e.g. Teskey et al., 2015). Our drought experiment did not allow for a direct test of hypothesis 3 on the interacting effects of water limitation and elevated air temperature because the plants were able

to access sufficient water to sustain growth rates equivalent to those in the well-watered experiments. However, it did present an analogue of future climates with increased leaf-to-air vapour pressure deficit (VPD). Maximum rates of photosynthesis of warmed plants were lower in the dry season than in the wet season for most species (Table S2), as were stomatal conductance values (data not shown). Stomatal conductance already is a key limitation of photosynthesis of tropical trees at high temperatures (Slot & Winter, 2017d; Tan et al., 2017), and the warming-induced rise in VPD will be exacerbated by drought events.

To better understand future processes in tropical forests, experimental research will be instrumental. Seedling experiments under controlled conditions can help identify mechanisms of temperature responses, but field experimentation with saplings and trees offers a more realistic representation of conditions that tropical forests of the future will experience. Experimental warming in the tropics and large-scale mesocosm experiments in which temperature as well as precipitation and [CO_2] are manipulated will therefore be paramount to increasing our understanding of potential feedbacks between the atmosphere and the tropical terrestrial biosphere in a warmer world.

AUTHORS' CONTRIBUTIONS

M.S. and K.W. conceived and designed the experiments; M.S. collected and analysed the data and led the writing of the manuscript. K.W. contributed significantly to the final version of the manuscript.

DATA ACCESSIBILITY

All plant-level growth, biomass allocation and foliar physiology data are archived in the Dryad Digital Repository, https://doi.org/10.5061/dryad.t2q82 (Slot & Winter, 2017c)

ORCID

Martijn Slot (iD) http://orcid.org/0000-0002-5558-1792

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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