

## Size-dependent changes in light requirements of tropical trees: weak light–growth relationships in seven Caribbean rainforest species preclude testing a general hypothesis

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In tropical forests light is presumed to be the most important limiting resource for trees below the forest canopy, and interspecific variation in shade tolerance an important driver of tree community composition. It has been hypothesized that tree light requirements may increase with tree size, but to date no study has explicitly quantified ontogenetic changes in light requirements for tropical trees. Here we make use of a field measure of whole-plant light compensation point (WPLCP) to quantify size-related shifts in light requirements of seven Dominican rainforest tree species, at two distinct size categories: saplings and pole-size juveniles. Although our dataset was large (representing 429 trees remeasured over a 13-month period), relative tree growth rate was only weakly related to estimated light levels ( $r^2 = 0\text{--}0.36$ ) across all species/size groups, and WPLCP could thus only be estimated for saplings of three species, and juveniles of one species. Both sapling and juvenile WPLCPs were significant for only one species, where we observed a size-dependent decrease in light requirements, a result contradicting our hypothesis. However, generalizations possible from our dataset are limited, as WPLCP could not be accurately determined within species/size groups, and did not match *a priori* qualitative shade-tolerance rankings. Overall, our data neither confirm nor deny a hypothesized ontogenetic increase in light requirements of tropical trees. We suggest that the highly dynamic canopies of Dominican rainforests due to strong, persistent winds on the island make estimates of understory light levels using hemispherical photography unreliable: a limitation that is likely present, though less pronounced, in many forest ecosystems.

### Introduction

Interspecific differences in shade tolerance of trees have long been identified as an important axis of biological variation in forest ecosystems, particularly in highly diverse, structurally

complex tropical rainforests (Swaine & Whitmore 1988, Wright 2002). Partitioning of light resources by species in forest understories or gaps, underpins a realized performance trade-off between high-light growth and low-light mortality that ultimately contributes to the maintenance

of tree species diversity (Grubb 1977, Hubbell & Foster 1992, Kobe *et al.* 1995, Kobe 1999, Walters & Reich 2000a, 2000b, Lin *et al.* 2002, Gravel *et al.* 2010, Wright *et al.* 2010). Furthermore, variation in shade tolerance has been identified as an important factor structuring tropical tree communities, even when other mechanisms of coexistence such as negative density-dependent mortality are present (Janzen 1970, Connell 1971, Comita & Hubbell 2009).

Ecologists have begun to develop a comprehensive mechanistic understanding of the morphological, physiological, biomechanical, and reproductive traits that mediate a species' shade tolerance (Baltzer & Thomas 2007a, 2007b, Valadares & Niinemets 2008). However, important uncertainties regarding the causes and consequences of variation in shade tolerance exist, due to the fact that relatively few studies have examined species light requirements beyond the regeneration niche (Grubb 1977, Poorter *et al.* 2005). Shade tolerance is most often regarded as a static trait that remains invariant during the course of tree development (Pacala *et al.* 1996, Messier *et al.* 1999). But ecologists and forest managers have long recognized the occurrence of size-dependent changes in tree light requirements (Baker 1949, Givnish 1988), and studies have highlighted the potential importance of size-dependent changes in light requirements for forest management (Messier *et al.* 1999, Claveau *et al.* 2005) and simulation modeling (Kunstler *et al.* 2009).

Currently, the most direct evidence of size-dependent changes in light requirements stems from observational studies examining light habitats occupied by trees, sampled across a range of sizes (Clark & Clark 1992, Poorter *et al.* 2005, Lusk *et al.* 2008). For example, in a study of 47 West African rainforest species, Poorter *et al.* (2005) found that in all but two species, there is a positive relationship between tree height and light habitat occupied. This study suggests a possible trend of increasing light requirements occurring with increasing tree size: results and interpretations shared with similar studies of five Costa Rican rainforest species (Clark & Clark 1992), and 13 temperate rainforest species in New Zealand (Lusk *et al.* 2008). Given the vertical gradient in light levels through the

canopy, the positive relationship between tree height and light levels provides at best indirect information on possible ontogenetic changes in tree light requirements. However these observational studies have also found rank shifts among species in light habitat preferences among tree species (Clark & Clark 1992, Poorter *et al.* 2005, Lusk *et al.* 2008). This suggests that the degree of size-dependent increases in light requirements differ among species, possibly as a result of interspecific variation in size-dependent changes in biomass allocation (Lusk 2004, Cheng *et al.* 2005, Claveau *et al.* 2005), crown architecture (Cao 2001, Claveau *et al.* 2002, Delagrangue *et al.* 2004), leaf phenology (Seiwa 1999b, a, Augspurger & Bartlett 2003), leaf lifespan (Lusk *et al.* 2008), and/or leaf-level physiology (Givnish 1988, Rijkers *et al.* 2000, Thomas & Winner 2002, Niinemets 2006).

It has also been suggested that ontogenetic changes in light requirements vary systematically across functional groups. For example, Lusk *et al.* (2008) hypothesized that early-successional pioneer species should be more ontogenetically variable in terms of light requirements (showing more pronounced increases in light requirements) as compared with mid- or late-successional species. This was expected because pioneers show steep declines in leaf area ratio as they increase in size (Lusk 2004, Lusk *et al.* 2008) and therefore steep size-dependent declines in their ratio of assimilative: respiratory tissues (Givnish 1988). However to date this hypothesis have only received qualitative support from observational data (Lusk *et al.* 2008).

In the present study we sought to quantify size-dependent changes in light requirements of seven Caribbean rainforest tree species, at two developmental stages: (1) saplings, and (2) pole-sized juvenile trees. We used whole-plant light compensation point (WPLCP) as a measure of species' light requirements (Moad 1992, Baltzer & Thomas 2007a, 2007b). Proper estimates of WPLCP, measured in mols of photosynthetically active radiation (400–700 nm; PAR)  $\text{m}^{-2} \text{day}^{-1}$ , are contingent on a strong positive relationship between light availability and tree growth, a pattern commonly reported in tropical forest saplings (e.g., King 1991, Poorter 2001, Kurokawa *et al.* 2004, Makana & Thomas 2005, Baltzer

& Thomas 2007a). Generally, WPLCP corresponds to the  $x$  intercept of the growth–light relationship, or the light level corresponding to zero growth (Moad 1992, Makana & Thomas 2005, Baltzer & Thomas 2007a, 2007b). In this method, biologically meaningful WPLCP values are estimated only if there is a negative  $y$  intercept/positive  $x$  intercept, in the light–growth relationship.

We hypothesized that within species, WPLCP would increase from sapling to pole-size trees. We also hypothesized that early successional species would show stronger size-dependent increases in light requirements as compared with mid- or late-successional species. In testing these hypotheses, our study sought to be the first to (1) quantify absolute size-dependent increases in WPLCP in tropical trees, and (2) compare the rate of increase in WPLCP across functional shade-tolerance groups.

## Methods

### Study site and species

Our study was conducted in Dominica, West Indies (15°30'N, 61°30'E), at two sites: Springfield Field Station (“SFS”: 15°35'N, 61°37'E) and Morne Trois Pitons National Park (“MTP”: 15°21'N, 61°21'E). SFS is a ~50-year-old secondary forest regenerating on a former citrus plantation, and is characterized by a relatively low forest canopy (~20 m) dominated by native pioneer species such as *Cordia sul-*

*cata* (Boraginaceae) and *Cecropia schreberiana* (Cecropiaceae). Forests at SFS receive ~3000 mm of rainfall annually, distributed seasonally with a wet period occurring between July and October, and a less wet period from November through June (Nicolson *et al.* 1991, Smith *et al.* 2009). Forests in MTP are classified as “rainforests” (Hodge 1943, Nicolson *et al.* 1991), receiving an average annual rainfall of ~4400 mm, also distributed seasonally. The rainforest canopy in MTP reaches ~30–40 m, and is dominated primarily by *Dacryodes excelsa* (Burseraceae) and both *Sloanea caribaea* and *S. dentata* (Elaeocarpaceae; Lack 1991, Nicolson *et al.* 1991). The primary disturbance in MTP and SFS forests is strong winds associated with Atlantic hurricanes, most recently Hurricane David in 1979 and Hurricane Dean in 2007.

### Tree growth measurements

We selected 24–44 individuals of seven native forest tree species, in each of two distinct size classes: saplings (50–150 cm height ( $H$ ) at initial measurement), and juvenile trees (1–6 cm diameter ( $D$ ) at 1.3 m above ground level at the time of initial measurement;  $n = 429$  trees in total, Table 1). Species were chosen to provide adequate abundances for sampling and span a range of qualitative shade-tolerance groups (Table 1). Additionally, we included only species that did not show pronounced lateral branching below our juvenile size threshold. The size distinction of saplings ensured that sampled stems were no

**Table 1.** Species habit, qualitative shade tolerance and sample sizes for seven Dominican rainforest tree species.

Species	Shade tolerance	Habit	$n$ (saplings)	$n$ (juveniles)
<i>Amanoa caribaea</i> (Euphorbiaceae)	very tolerant	tree to 25 m <sup>a</sup>	44	39
<i>Cordia reticulata</i> (Boraginaceae)	mid-tolerant	tree 8–10 m <sup>b</sup>	27	25
<i>Cordia sulcata</i> (Boraginaceae)	pioneer	tree to 15 m <sup>b</sup>	30	24
<i>Dacryodes excelsa</i> (Burseraceae)	mid-tolerant	tree to 30 m <sup>a</sup>	28	34
<i>Licania ternatensis</i> (Chrysobalanaceae)	very tolerant	tree to 35 m <sup>b</sup>	28	36
<i>Miconia mirabilis</i> (Melastomataceae)	pioneer	tree to 15 m <sup>b</sup>	29	26
<i>Sterculia caribaea</i> (Sterculiaceae)	mid-tolerant	tree to 20 m <sup>a</sup>	33	26

<sup>a</sup> Tree habit (i.e. species  $H$ ) estimated as the mean  $H$  measured for the six largest trees by  $D$  (following Wright *et al.* 2010), in three 0.25 ha forest inventory plots in MTP (K. Ickes & S. J. Dewalt unpubl. data).

<sup>b</sup> Tree habit taken from Nicolson *et al.* (1991).

longer reliant on seed reserves for growth, while the size threshold for juvenile stems ensured sampled individuals had not reached reproductive maturity (confirmed visually on each sample tree by A. R. Martin and E. R. Stedman). For all individuals in our sample, we only measured trees that were healthy in appearance, with no signs of mechanical damage (i.e. broken appendages, stem scars, forking), or other abiotic stress (i.e. epicormic branching, chlorotic leaves).

All stems were initially measured in April 2007, and remeasured in May 2008. For saplings, we measured  $H$  from stem base to the tip of the apical branch, and  $D$  at 2–5 cm above-ground. For pole-size stems  $D$  was measured at 1.3 m aboveground, and  $H$  was measured from soil to the tip of the apical branch using a laser rangefinder (Laser Technology Inc., Colorado, USA). To ensure consistency in point of measurement, the initial point of measurement was marked with non-toxic paint. Additionally, on 17 August 2007, Hurricane Dean crossed over Dominica inflicting damage to forest canopies in some areas. Thus any stems exhibiting signs of mechanical damage, were in close proximity ( $\leq 5$  m) to large tree-falls, or judged to have been killed by random branch falls, were excluded from our dataset.

To calculate relative growth rates (RGR), we used  $D^2 \times H$  as a non-destructive proxy for tree biomass (Kohyama 1991, Kurokawa *et al.* 2004, Baltzer & Thomas 2007a). RGR of biomass ( $RGR_{\text{biomass}}$ ) was then calculated as:

$$RGR_{\text{biomass}} = \frac{[\ln(D_2^2 \times H_2) - \ln(D_1^2 \times H_1)] / (t_2 - t_1)}{\quad} \quad (1)$$

where  $D_1$  and  $D_2$  are stem diameter at the beginning ( $t_1$ ) and the end ( $t_2$ ) of the census interval, respectively, and  $H_1$  and  $H_2$  are tree height at the beginning and the end of the census interval, respectively.

## Light environments

Tree light environments were characterized with hemispherical photography using a Nikon Coolpix 1200 fitted with an FC-E8 fisheye converter (Nikon, Tokyo, Japan). For stems  $\leq 1.5$  m

$H$ , photos were taken directly above saplings using an extendable tripod. For stems  $> 1.5$  m  $H$ , photos were taken by mounting the camera onto a telescoping pole, fitted with a self-leveling gimble equipped with an electronic north finder (Regent Instruments Inc., Quebec, Canada). All photos were taken within five days of the initial growth measurement, in early morning, dusk, or on overcast days to minimize light scatter. For each image, the optimal camera exposure was set manually following Zhang *et al.* (2005). To analyze images, true color hemiphotos were first automatically converted into binary images using Sidelook v1.1 software (Nobis 2005, Nobis & Hunziker 2005), and light calculations (measured as photosynthetic photon flux density (PPFD) in mol PAR  $\text{m}^{-2} \text{day}^{-1}$ ) were then performed on binary images with WinScanopy 2003 software (Regent Instruments Inc., Quebec, Canada). For analysis, above-canopy diffuse radiation was estimated as 46% of direct radiation (Alados *et al.* 2002).

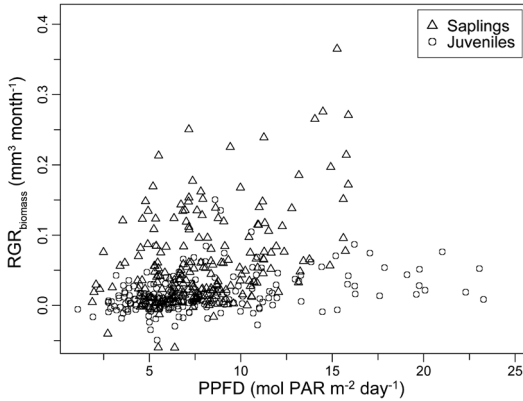
To address alterations to local light environments caused by Hurricane Dean, a second hemiphoto was taken above each stem at the time of the second growth measurement. A weighted average was then calculated to quantify PPFD over the entire measurement period, such that:

$$\text{PPFD} = \frac{[(t_{\text{pre}} \times \text{PPFD}_1) + (t_{\text{post}} \times \text{PPFD}_2)]}{\times (t_2 - t_1)} \quad (2)$$

where  $\text{PPFD}_1$  and  $\text{PPFD}_2$  represent the light incident on a tree pre- and post-Hurricane Dean, respectively,  $t_{\text{pre}}$  represents the time interval between the first growth measurement and the passing of Hurricane Dean, and  $t_{\text{post}}$  represents the time interval between Hurricane Dean and the second growth measurement.

## WPLCP estimation

For WPLCP estimation, we first pooled all data ( $n = 429$  observations) and observed a highly heteroscedastic or fan-shaped PPFD– $RGR_{\text{biomass}}$  relationship (Fig. 1). To account for heteroscedasticity and possible site effects, we used the entire pooled dataset to model  $RGR_{\text{biomass}}$  as a function of PPFD using



**Fig. 1.** Relationship between PPFD and  $RGR_{biomass}$  for saplings ( $n = 219$ ) and juvenile stems ( $n = 210$ ) from seven Dominican rainforest tree species.

linear mixed-effects models, with variance proportional to mean PPFD in the lme4 package in R v. 2.9.2 (Pinheiro & Bates 2000, R Development Core Team 2009). In the pooled data, the full model was of the form:

$$RGR_{biomass} = \beta_0 + \beta_1 L + \beta_2 Sp + \beta_3 Sz + \beta_4 Sp \times Sz + \beta_5 L \times Sp \times Sz + \mu Si + \varepsilon \quad (3)$$

where  $\beta_0$  is the intercept,  $\beta_1$ ,  $\beta_2$ , and  $\beta_3$ , are model coefficients for the continuous variable light ( $L$ ), and the categorical variables species ( $Sp$ ) and size ( $Sz$ ), respectively, and  $\beta_4$  and  $\beta_5$  are the coefficients for the interaction terms (Table 2). Lastly,  $\mu Si$  represents a random site effect, and  $\varepsilon$  is the error that is proportional to mean PPFD.

In the pooled analysis, the most parsimonious model was the reduced model that did not include a species, size or either interaction terms (“Reduced” model in Table 2). Additionally, we found the variance component associated with  $Si$  was negligible (Table 2). Thus, because our AIC-selected model did not account for several of our parameters of interest (i.e. species, size, or interspecific differences in slope of the PPFD– $RGR_{biomass}$  relationships), we analyzed the data in 14 species/size groups individually. Within each species/size group, we then first used linear regression with a 2nd order polynomial term to test for nonlinearity in  $RGR_{biomass}$ –PPFD relationships. For all 14 tests, 2nd order polynomial regression parameters were not significant ( $p \geq 0.06$ ) indicating non-linear models were not appropriate for our data. We therefore used censored linear regression with variance proportional to mean PPFD, to examine  $RGR_{biomass}$  as a function of PPFD. For each group, WPLCP was estimated as the  $x$  intercept of the PPFD– $RGR_{biomass}$  relationship, and 95% confidence intervals around WPLCP were calculated based on the error associate with the  $y$  intercept for each censored regression.

## Results

### Light–growth relationships

In our data, we found that  $RGR_{biomass}$  for Dominican trees was poorly predicted by PPFD, with only five species/size groups showing signifi-

**Table 2.** Generalized linear mixed-effects model estimating  $RGR_{biomass}$  as a function of light ( $L$ ), species ( $Sp$ ), tree size as a categorical variable (i.e. sapling vs. juveniles,  $Sz$ ), and interaction terms, for the pooled dataset ( $n = 429$ ). In all models, site effects ( $Si$ ) were included as a random effect, and error was proportional to mean PPFD.

Model	Fixed effects					Random effect		Model evaluation		
	$L$	$Sp$	$Sz$	$Sp \times Sz$	$L \times Sp \times Sz$	$Si$	Variance	AIC	Log–Lik. ratio	$\Delta AIC$
Reduced	x					x	0	8.343	–0.1717	
1	x	x				x	< 0.00001	20.28	–0.1385	11.94
2	x	x	x			x	0	22.22	–0.1099	13.88
3	x	x	x	x		x	< 0.00001	34.19	–0.0928	25.85
Full	x	x	x	x	x	x	0	60.16	–0.0811	51.82

cant PPFD–RGR<sub>biomass</sub> relationships (Table 3 and Fig. 2). We found that in saplings, RGR<sub>biomass</sub> was only significantly predicted by PPFD for *A. caribaea*, *C. sulcata*, *M. mirabilis* and *S. caribaea* (Table 3, Figs. 2C, F, G and 3A). For juvenile stems, *S. caribaea* was the only species where RGR<sub>biomass</sub> was significantly predicted by PPFD (Table 3 and Fig. 2G). Of these five species/size groupings, RGR<sub>biomass</sub> of *M. mirabilis* saplings was most closely correlated with light availability, with PPFD predicting 36.2% of the variation in observed RGR<sub>biomass</sub> (Table 3 and Fig. 2G). However, for the additional four species/size groups,  $\leq 17.5\%$  of variation in RGR<sub>biomass</sub> was predicted by PPFD. Yet for the additional nine species/size groups where PPFD was not significantly related to RGR<sub>biomass</sub>,  $\leq 2.4\%$  of the variation in RGR<sub>biomass</sub> (0.44% on average), was explained by PPFD (Table 3). Light–growth relationships did not change when using either direct or indirect light independently (data not shown).

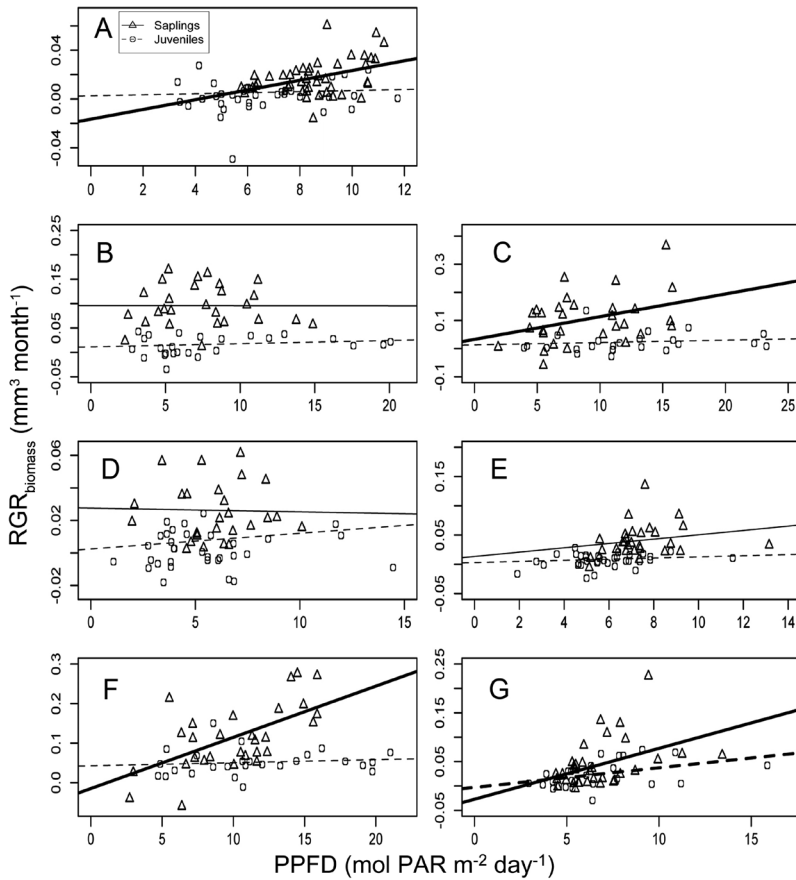
## WPLCP estimates

Overall, we only attained biologically meaningful WPLCP estimates at both the sapling (WPLCP<sub>sap</sub>) and juvenile size classes for *S. caribaea* (Table 3), and were thus only able to calculate size-dependent changes in light requirements for one species. In *S. caribaea*, WPLCP decreased from 2.6 mol PAR m<sup>-2</sup> day<sup>-1</sup> in saplings, to 0.72 mol PAR m<sup>-2</sup> day<sup>-1</sup> in juveniles (Table 3 and Fig. 2G), a result counter to our prediction. However, due to weak PPFD–RGR<sub>biomass</sub> relationships ( $r^2 = 0.159$  and 0.176 for *S. caribaea* saplings and juveniles, respectively), the estimates of WPLCP showed very low precision. Upper and lower 95% confidence intervals for *S. caribaea* juveniles ranged from not biologically meaningful (i.e. a positive y intercept) to 6.93 mol PAR m<sup>-2</sup> day<sup>-1</sup>, while WPLCP<sub>sap</sub> ranged from 0.64 to 4.56 mol PAR m<sup>-2</sup> day<sup>-1</sup> (Table 3).

In addition to *S. caribaea*, we attained estimates for sapling light requirements in *A. cari-*

**Table 3.** Linear model fits from a censored regression procedure predicting RGR<sub>biomass</sub> as a function of light availability (PPFD), for seven Dominican rainforest tree species at two size classes. Significant PPFD–RGR<sub>biomass</sub> relationships are set in boldface. Whole-plant light compensation point (WPLCP) estimates are calculated as the x intercept from the PPFD–RGR<sub>biomass</sub> relationship for each species/size group, and are in units of mol PAR m<sup>-2</sup> day<sup>-1</sup>. Non-biologically meaningful WPLCP estimates (i.e. positive y intercepts) are represented by “n.a.”

Species	Size	Intercept ( $\pm$ SE)	Slope ( $\pm$ SE)	$r^2$	$p$	WPLCP (95% CI range)
<i>A. caribaea</i>	juvenile	0.002 (0.004)	0.0004 (0.001)	0	0.429	n.a.
	sapling	<b>-0.017 (0.012)</b>	<b>0.004 (0.001)</b>	<b>0.155</b>	<b>0.0047</b>	<b>4.15</b> (n.a.–9.87)
<i>C. reticulata</i>	juvenile	0.011 (0.006)	0.0007 (0.001)	0.008	0.286	n.a.
	sapling	0.096 (0.021)	-0.00003 (0.003)	0	0.993	n.a.
<i>C. sulcata</i>	juvenile	0.013 (0.017)	0.0008 (0.001)	0	0.51	n.a.
	sapling	<b>0.033 (0.037)</b>	<b>0.0081 (0.004)</b>	<b>0.109</b>	<b>0.042</b>	n.a.
<i>D. excelsa</i>	juvenile	0.002 (0.006)	0.001 (0.001)	0.002	0.308	n.a.
	sapling	0.028 (0.013)	-0.0002 (0.002)	0	0.912	n.a.
<i>L. ternatensis</i>	juvenile	0.003 (0.004)	0.001 (0.001)	0.024	0.183	n.a.
	sapling	0.013 (0.026)	0.0037 (0.003)	0.009	0.277	n.a.
<i>M. mirabilis</i>	juvenile	0.043 (0.016)	0.0008 (0.001)	0	0.55	n.a.
	sapling	<b>-0.015 (0.034)</b>	<b>0.013 (0.003)</b>	<b>0.362</b>	<b>0.0003</b>	<b>1.14</b> (n.a.–6.28)
<i>S. caribaea</i>	juvenile	<b>-0.003 (0.012)</b>	<b>0.004 (0.002)</b>	<b>0.176</b>	<b>0.019</b>	<b>0.72</b> (n.a.–6.39)
	sapling	<b>-0.027 (0.01)</b>	<b>0.0104 (0.004)</b>	<b>0.159</b>	<b>0.0124</b>	<b>2.60</b> (0.64–4.56)



**Fig. 2.** Light (PPFD) to growth ( $RGR_{biomass}$ ) relationships for (A) *Amanoa caribaea*, (B) *Cordia reticulata*, (C) *Cordia sulcata*, (D) *Dacryodes excelsa*, (E) *Licania ternatensis*, (F) *Miconia mirabilis*, and (G) *Sloanea caribaea*. Relationships are presented for the sapling and juvenile size classes, and thick lines represent significant (at  $p < 0.05$ ) relationships between PPFD and  $RGR_{biomass}$ .

*baea* and *M. mirabilis*, where  $WPLCP_{sap}$  was estimated as 4.15 and 1.14  $mol PAR m^{-2} day^{-1}$ . Yet again due to poor PPFD– $RGR_{biomass}$  relationships, the 95% confidence intervals for  $WPLCP_{sap}$  were very wide: from not biologically meaningful to 9.87  $mol PAR m^{-2} day^{-1}$  in *A. caribaea*, and from not biologically meaningful to 6.28  $mol PAR m^{-2} day^{-1}$  in *M. mirabilis*. In one case, a significant PPFD– $RGR_{biomass}$  relationship did not result in a meaningful  $WPLCP_{sap}$  estimate: in saplings of *C. sulcata*, PPFD significantly predicted  $RGR_{biomass}$  ( $r^2 = 0.109, p = 0.042$ ), yet the y intercept was positive.

When considering  $WPLCP_{sap}$  alone, observed species' light requirements did not match with *a priori* shade-tolerance classifications. For example, the highest observed  $WPLCP_{sap}$  was found for *A. caribaea*, which is one of the most shade-tolerant species in our dataset. Conversely, qualitative classifications and the literature (Lack 1991) suggest that *M. mirabilis* is one of most

light-demanding species in our dataset, however  $WPLCP_{sap}$  for *M. mirabilis* was very low at 1.14  $mol PAR m^{-2} day^{-1}$ . In fact when compared with existing estimates from other studies (Baltzer & Thomas 2007a), the  $WPLCP_{sap}$  of *M. mirabilis* estimated here would make *M. mirabilis* one of the most shade-tolerant species pantropically.

## Discussion

The main salient result of our study was that any test of hypotheses concerning light requirements was limited by exceptionally poor growth–light relationships in the dataset. In our study, we were only able to quantify size-dependent shifts in light requirements of one Dominican rainforest tree species, with our analyses suggesting a size-dependent decrease in light requirements in *S. caribaea*. This result directly contradicts our hypothesis, and that of other authors (Waring

1987, Givnish 1988, Clark & Clark 1992, Poorter *et al.* 2005, Lusk *et al.* 2008).

### Light and tree growth in tropical forests

Pantropically, published studies have reported strong increases in RGR as a function of light (e.g., Poorter 2001, Kurokawa *et al.* 2004, Makana & Thomas 2005, Baltzer & Thomas 2007a). While growth responses of tropical trees to increased light may differ in shape between linear (Makana & Thomas 2005, Baltzer & Thomas 2007a) or curvilinear responses (Poorter 1999, 2001), PPFD alone commonly explains up to 80% of within-species variation in RGR. For example, Makana and Thomas (2005) found PPFD explained 27%–81% of the variation in relative  $H$  growth in six Central African timber species, while Baltzer and Thomas (2007a) found PPFD explained 19%–79% of the variation in  $RGR_{\text{biomass}}$  in 20 Malaysian rainforest tree species. Additionally, Poorter (2001) found direct radiation alone explained 28%–90% of the variation in RGR. In our study however, PPFD was significantly related to  $RGR_{\text{biomass}}$  in only five species/size groups. Within this small subset, *M. mirabilis* saplings were the only group where PPFD explained > 20% of the variation in  $RGR_{\text{biomass}}$ , and with this exception, PPFD explained ~5% of  $RGR_{\text{biomass}}$  variation on average: well below values in prior published studies.

In tropical trees, non-significant light–growth relationships, though relatively uncommon in the literature, are not without precedent. Light was unrelated to sapling growth in four of 24 Malaysian studied by Baltzer and Thomas (2007a) and in one of six Amazonian species studied by Poorter (2001). In the four Malaysian species studied by Baltzer and Thomas (2007a), PPFD only explained 6%–20% of the variation in  $RGR_{\text{biomass}}$ : values comparable to four of the species/size groups studied here. Specifically, in our study PPFD explained between 10.1%–17.6% of the variation in  $RGR_{\text{biomass}}$  for *C. sulcata* and *A. caribaea* saplings, and both saplings and juveniles of *S. caribaea* (Table 3 and Fig. 2A, C, G).

With respect to unpublished data, we speculate that other studies have attained results

similar to ours, observing non-significant light–growth relationships in trees. We are immediately aware of one study where PPFD was significantly related ( $p \leq 0.05$ ) to relative  $H$  growth in only 10 of 20 Chinese temperate species (Saprunoff 2005), and PPFD explained only 18.3% of the variation in relative  $H$  growth on average (range 7.5%–39.4%). The study by Saprunoff (2005) also estimated positive WPLCP values for 18 species, all of which were < 1 mol PAR m<sup>-2</sup> day<sup>-1</sup>. These results lead to weak differentiation between WPLCP estimates for functionally distinct species. For example, in shade-intolerant pioneer species such as *Populus davidiana* and shade-tolerant species such as *Acer mono* (He *et al.* 2002), WPLCP was estimated as 0.3085 and 0.4113 mol PAR m<sup>-2</sup> day<sup>-1</sup>, respectively.

We are also aware of one study from the tropical rainforests on Barro Colorado Island, Panama, where light levels were positively related to tree growth in 21 species, yet species-specific variation in the light–growth relationship (i.e. the slope of the PPFD–growth relationship) was not detectable (H. Muller-Landau unpubl. data). Beyond the data from Saprunoff (2005) and H. Muller-Landau (unpubl. data), thoroughly evaluating the robustness of our non-significant results remains difficult due to publication biases, or the file-drawer effect (Jennions *et al.* 2004, Kotze *et al.* 2004).

### Possible causes of weak light–growth relationships

The present study directly replicated methods that have been successfully used to quantify light requirements of tropical trees at other sites, had similar or greater sample sizes, comparable census intervals, and indeed used the same equipment as prior studies (Makana & Thomas 2005, Baltzer & Thomas 2007a). It is thus very unlikely that the lack of significant results is due to faulty field methods, equipment, or analytical methods.

One possible reason for our non-significant relationships is that our methods may not be sensitive to a decoupling of growth rates from light levels, due to resource storage in trees.

Specifically, assimilated C may be deposited as non-structural carbohydrates (NSCs) that can be mobilized for future growth during periods of stress and disturbance (Chapin *et al.* 1990, Poorter & Kitajima 2007); NSC storage may also be especially pronounced in forests subject to frequent disturbance. Studies from temperate and tropical forests have found NSC concentrations are positively correlated with understory survival rates, and that shade-tolerant species have higher NSC concentrations than less shade-tolerant species (Kobe 1997, Poorter & Kitajima 2007). One interpretation of this trend is that shade-tolerant species would show growth that is more likely to be independent of incident light levels. Or as it pertains to our methods, resource storage should make light–growth relationships in shade-tolerant species more “noisy”. But this was not the case. The WPLCP values we obtained were found in tolerant (*A. caribaea*), mid-tolerant (*S. caribaea*) and early successional species (*M. mirabilis*, Tables 1 and 3), indicating that resource storage is not systematically obscuring light–growth relationships in our study species. Also both Baltzer and Thomas (2007a) and Makana and Thomas (2005) did not correct for resource storage, but still accurately estimated WPLCP over a range of shade-tolerance classifications within comparable census intervals. Therefore prior research indicates our methods should be capable of estimating WPLCP, despite inter- and intraspecific variation in NSC storage.

We suggest that the most likely reason for our poor observed  $RGR_{\text{biomass}}$ –PPFD relationships is a failure to accurately estimate light levels using hemispherical photographs due to extremely windy conditions on Dominica. For the year 2007, Smith *et al.* (2009) reported annual average wind speeds of  $9.5 \text{ m s}^{-1}$  at SFS and higher elevations of MTP: winds that rank between 5–6 on the Beaufort scale. These strong winds result in frequent motion of tree branches in the crowns of canopy and sub-canopy trees, leading to highly variable understory light regimes over short time scales. At other sites, short-duration ( $\leq 10$  minutes) bursts of direct light, or sunflecks, can reach up to  $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and may contribute between ~30%–60% of total daily PPFD in forest understories (Pearcy 1990, Chazdon & Pearcy 1991, Leakey *et al.* 2003).

Hemispherical photo analysis has been assumed capable of estimating PPFD from sunflecks in tropical forest understories (Leakey *et al.* 2003). However, hemispherical photos may not be accurately capturing sunfleck contributions when forest canopies are especially dynamic. For instance, in the lowland forests of Danum Valley, Borneo, canopy wind speeds rarely exceed  $2.5 \text{ m s}^{-1}$  (Collier *et al.* 2010), yet sunfleck duration and intensity in Danum remains very variable across longer (12-day) intervals (Leakey *et al.* 2003). In Dominica, despite careful field and analytical methods, high winds likely lead to inaccuracies in estimating long-term understory light levels, and may preclude accurately quantifying PPFD–RGR relationships in these forests. More broadly, we suspect that hemiphoto analysis may drastically underestimate local PPFD in any system where the canopy is highly dynamic on short time scales.

Another possible reason for our poor observed  $RGR_{\text{biomass}}$ –PPFD relationships, is that intraspecific variation in RGR may predominantly be a function of unmeasured tree-specific characteristics. Poorter (2001) found that in saplings of five Bolivian rainforest species, initial leaf area is a strong predictor of height growth independent of light availability, and in two species, explained more of the variation in growth than either direct or indirect light availability. However, in our study, although initial leaf area was not measured, it could be included as a likely significant covariate in  $RGR_{\text{biomass}}$ –PPFD analysis. Another characteristic that may explain some of the variation in  $RGR_{\text{biomass}}$  is light quality, however light quality has generally been found to be of minor consequence in comparison to light quantity (Turnbull 1991, Kitajima 1994), and studies have still observed strong PPFD– $RGR_{\text{biomass}}$  relationships despite excluding light quality correction (Baltzer & Thomas 2007b).

## Conclusions

Overall, our lack of strong PPFD– $RGR_{\text{biomass}}$  relationships precluded us from robustly addressing critical questions in forest ecology and tree biology: do absolute light requirements

of trees increase through ontogeny, and if so, which guilds of species experience the largest increases? Although existing literature allows for strong hypotheses to be developed with regards to these questions, explicitly addressing them with quantitative methods is essential. Our study made use of well-established field and analytical methods. While they failed to produce significant results, we suggest the methods presented here form a strong basis for future research, but with important precautionary considerations. Most notably, there may be important limitations to the use of hemispherical photography to accurately quantify light in tropical forests subject to high winds or with otherwise highly dynamic canopies.

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