Light-based Regeneration Niches: Evidence from 21 Dipterocarp Species using Size-specific RGRs

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ABSTRACT

A continuing challenge in tropical ecology is to explain the coexistence of large numbers of rain forest tree species. One possible coexistence mechanism is partitioning of the highly variable and dynamic forest light environment, in which species that grow better in one light treatment grow worse in another. To test whether species respond differently to the light environment, we estimated growth rates of 21 Dipterocarpaceae species from Malaysian Borneo grown in shade houses for 2 yr in three light treatments (0.3%, 3%, and 18% full sunlight). We made regular measurements of height, diameter, and aboveground biomass, enabling us to calculate growth rates for each response. We estimated size-specific growth rates using nonlinear mixed-effects models, as average relative growth rate was strongly size dependent. For all species, the greatest diameter growth rate was achieved in 18 percent full sunlight, whereas for five of the twenty-one species, the greatest height growth rate was achieved in three percent full sunlight. We investigated correlations among growth rates in different light treatments, but no negative correlations were found, indicating that species growing well in one light treatment did not grow poorly in the others. There were substantial crossovers, however, in species ranks among the three light treatments, indicating that there was no single growth rate hierarchy common to all light treatments. The lack of a single consistent growth hierarchy across light treatments indicates that heterogeneity in the forest light environment could contribute to the maintenance of the diversity of Dipterocarpaceae found in lowland Bornean rain forests via light-based regeneration niches.

Key words: Dipterocarpaceae; light; nonlinear growth; Sabah; saplings; SGR; size-specific RGR; tropical lowland forest.

IN THE FORESTS OF MALAYSIAN BORNEO, 270 species of Dipterocarpaceae dominate the canopy (Ashton 1982). This high diversity is a key feature of tropical forests throughout the world and continues to puzzle ecologists (Ghazoul & Sheil 2010). Although some favor neutral explanations (Hubbell 2001), niche-based explanations of diversity maintenance depend on differences among species in the way they respond to the environment (Tilman & Pacala 1993, Chesson 2000). In particular, a great deal of attention in tropical forests has focused on species partition variability in the light environment (Brokaw & Busing 2000, Chase & Leibold 2003, Ghazoul & Sheil 2010). Light is the resource that most strongly limits plant growth in tropical rain forest understoreys (Grubb 1998), and light availability is highly variable and dynamic because of the opening and closing of canopy gaps (Denslow 1987, Canham *et al.* 1990, Denslow *et al.* 1990). Light partitioning could theoretically occur if each species grows or performs best in a particular light environment (Latham 1992), and owing to the importance of canopy gaps in creating light heterogeneity, this hypothesis is often referred to as gap-size niche partitioning (Brown & Jennings 1998). There is also evidence, however, that niche partitioning may occur in low-light

environments in the absence of canopy gaps (Montgomery & Chazdon 2002).

The role of light partitioning in maintaining diversity in forest communities continues to cause debate. Some authors argue that rank reversals in performance among light treatments rarely occur (Kitajima & Bolker 2003), whereas others argue the opposite (Sack & Grubb 2001, 2003; Baltzer & Thomas 2007). One possible reason for the discrepancies among studies is that they differ in the length of time for which seedlings are monitored; the study duration affects the outcome because it takes time for differences in growth rate to overcome differences in initial size (Sack & Grubb 2001, 2003).

Brown and Whitmore (1992) studied the growth of naturally occurring seedlings of three dipterocarp species (*Hopea nervosa, Shorea johorensis,* and *Parashorea malaanonan*) for a period of 40 mo after creating artificial canopy gaps of different sizes. The authors concluded that there was no evidence to support the light-partitioning hypothesis because *H. nervosa* was the tallest species in all gaps at the end of the monitoring period. This was surprising, given that *H. nervosa* is a slow-growing sub-canopy species, but the authors also noted that *H. nervosa* was the tallest species at the time of gap creation. Whitmore and Brown (1996) measured the seedlings for an additional 3 yr, after which *S. johorensis*, the 'light-demanding' emergent species, had surpassed *H. nervosa* to become the tallest

seedlings in all but the smallest gaps. This illustrates the need to account for differences in initial size when predicting long-term growth from shorter experiments.

Many studies that measure the performance of different species across a light gradient take place in shade houses, rather than in the forest itself, and the most commonly used measure of performance is growth rate, rather than absolute height. Growth rate is nearly always approximated using average relative growth rate (RGR) calculated from two time points. RGR is thought to account for differences in initial size, as the most commonly used formula includes initial size: $RGR = \log(Size_{final}) - \log(Size_{initial})/$ time. As instantaneous RGR almost universally decreases with increasing plant size (MacFarlane & Kobe 2006, Metcalf *et al.* 2006, Rees *et al.* 2010), RGR would, however, only remain constant with size if plants could sustain exponential growth. In fact, RGR typically declines with size because of self-shading by the leaf canopy, increased allocation to structural components, declines in Leaf Area Ratio (due to declines in both Specific Leaf Area and Leaf Mass Fraction), and reduced nutrient availability particularly when plants are grown in pots (Metcalf *et al.* 2006, Turnbull *et al.* 2008). As RGR is almost always a function of plant size, high values of RGR can occur either because plants are simply smaller or because they truly grow faster at a given size (Turnbull *et al.* 2008). The inability of conventional RGR to distinguish between these possibilities is outlined in Fig. 1. Although it is always possible to calculate conventional RGR (Causton 1977), the values will invariably be biased by the difference in plant size to a greater or lesser degree. Thus, a size-specific measure of growth rate is essential, because it is the growth rate at a given size that is more relevant to the outcome of competition in the long term. Although the limitations of conventional RGR have been known and well understood since the 1970s, the problems are rarely recognized and addressed (Evans 1972; Hunt 1982, 1990; Poorter & Pothmann 1992).

In this study, we investigated niche partitioning for light using repeated measures from 21 species of Dipterocarpaceae saplings grown for 2 yr in controlled light conditions. We fitted growth curves using nonlinear mixed-effects models and derived size-specific height, diameter, and aboveground biomass growth rates (SGR) for each species in 0.3 percent, 3 percent, and 18 percent light. We tested the following hypotheses: (1) Do rank crossovers in growth rates occur among different light environments? and, (2) do height, diameter, and aboveground biomass growth rates respond differently to the light environment?

MATERIALS AND METHODS

STUDY SITE.—Shade houses were built at the Sabah Biodiversity Experiment in the Malua forest reserve (5°5′ 20″ N, 117°38′ 32″ E) in Danum Valley Conservation Area, Sabah, Malaysian Borneo. The climate at Danum Valley is aseasonal, but subject to occasional drought; on average it receives 2829 mm of rain every year with a mean annual temperature of 26.8°C (Clarke & Walsh 2006).
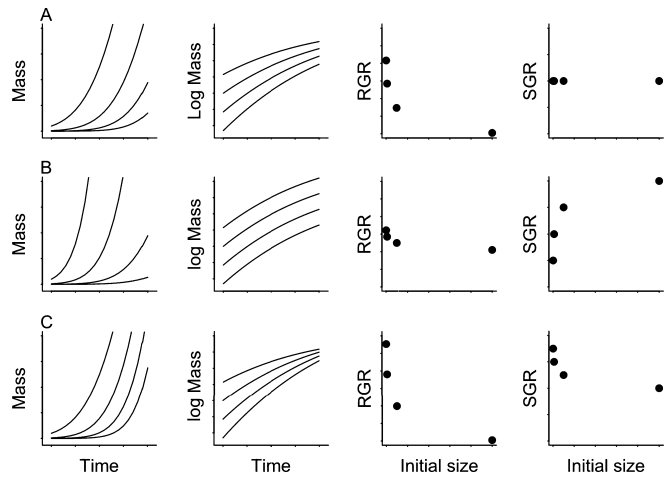

FIGURE 1. The confounding effects of initial size on the measurement of growth rates. We present three different possible scenarios of the relationships between growth rate and initial plant size. In each case, growth is modeled as a Gompertz function where instantaneous RGR slows with increasing size (although the effect will occur with any similar function). For each scenario, we present mass against time (column 1); log mass against time (column 2); average RGR for each 'plant' against initial size (column 3); and the size independent instantaneous growth rate (SGR) from the Gompertz function against initial size (column 4). In (A), we have made the parameters of the function (the 'true' growth rate) identical for all species, but conventional average RGR measurements (third panel) show that species with smaller initial size have a higher growth rate when assessed with this measure. The size-corrected measure, SGR, reveals that they are all on the same growth curve with no physiologic differences (right hand panel). The differences in RGR arise as species start growing from different initial sizes (note that differences in initial size here are so small to be seen, but nevertheless cause RGR to have a negative relationship with initial size in all three cases). In (B), the larger-seeded species have higher size-corrected growth rates and SGR, whereas in (C), the small-seeded species have higher size-corrected growth rates. Notice that conventional average RGR measures are insensitive to these differences and produce negative relationships in all three cases.

EXPERIMENTAL DESIGN.—Fifteen shade houses (5 × 6 × 5 m), separated into five blocks, were constructed to apply three different light treatments in a controlled environment. Each light treatment was replicated five times in a blocked split-plot design with shade houses nested within block. Each block of three light treatments was positioned along a north–south line to minimize shading. To prevent waterlogging and to minimize attacks from smaller herbivores, such as snails, the shade houses were raised 0.5 m from the ground, and the seedlings were supported using wire mesh. Wire mesh was also attached around the sides of the shade houses to protect the seedlings from larger herbivores, such as deer and elephants. Shade cloth with a shading of 70 percent was used to create three different shade treatments, designed to mimic conditions in the shaded forest understorey, small tree-fall gaps, and large tree-fall gaps. The light availability and quality was measured for 2 d in each shade house—adding up to a total of 30 d of light measurements—using PAR sensors, red:far-red

sensors and data loggers (Skye Systems), and referenced using an unobstructed direct sunlight sensor. The data loggers were set to make light measurements every 30 sec and record averages every 30 min. The values of quantity of light for the three shading treatments resulted in $0.3 \pm 0.024\%$ (dark forest understorey), $3 \pm 0.073\%$ (a small tree-fall gap), and $18 \pm 0.23\%$ (a large tree-fall gap) of full daylight (mean $\pm$ SEMs, $n = 730$). The red:far-red ratio was not significantly different among light treatments ($F_{2,8} = 2.45$, $P < 0.15$). The estimates for red:far-red ratio were, 1.41 (95% CI: 1.18–1.64) for the shade environment; 1.16 (95% CI: 0.94–1.38) for the middle light environment; and 1.14 (95% CI: 0.92–1.35) for the high light environment. For comparison, values reported in the primary forest in this area are 0.3 for an understorey, 0.57 for partial shade, and 0.65 for a gap (Barker et al. 1997).

SEEDLINGS.—The species used in this study were all 3-yr old—the most recently available planting material from the last mast fruiting. The 21 species used in this study were: *Dipterocarpus conformis* Slooten, *Dryobalanops lanceolata* Burck, *Hopea sangal* Korth, *H. nervosa* King., *P. malaanonan* (Blanco) Merr., *Parashorea tomentella* (Symington) Meijer, *Shorea ovalis* (Korth.) Blume, *Shorea leprosula* Miq., *Shorea macroptera* Dyer, *Shorea parvifolia* Dyer, *Shorea beccariana* Burck, *Shorea macrophylla* (de Vriese) P.S. Ashton, *Shorea argentifolia* Symington, *Shorea faguetiana* F. Heim, *Shorea gibbosa* Brandis, *S. johorensis* Foxw., *Shorea superba* (Symington), *Shorea parvistipulata* F. Heim, *Shorea guiso* (Blanco) Blume, and *Shorea fallax* Meijer. Nomenclature follows Newman (2010). Due to misidentification, the number of *H. nervosa* seedlings used was double that of the others.

Seedlings were bought from Infrapro FACE nursery where all species are grown in forest topsoil (homogenized using a soil shredder; see Saner et al. 2011) in 7×23 cm black polyethylene bags with the exception of *S. macrophylla,* which was grown in 10×23 cm bags due to its considerably larger seed size. The forest topsoil was collected in the same forest habitat where all the species occur. In the nursery, all seedlings were watered daily and kept under two layers of 70 percent shade-cloth—equivalent to our mid light environment—measured at 3 percent light. In March 2004, the seedlings were transplanted into dried, shredded, unfertilized topsoil in 20×30 cm black polyethylene bags. To reduce transplantation shock, seedlings were allowed to acclimate under two layers of 70 percent shade-cloth for 4 mo. In July 2004, two individuals of each species were randomly placed in each of the 15 shade houses. To reduce the effects of nutrient deficiency, 2.5 g of controlled release fertilizer ('Agroblen', The Scotts Company, Scotts Australia, Baulkham Hills, NSW, Australia; NPK + Mg + Ca + Fe, 17:8:9:3:2:0.05) was applied at the beginning of the experiment. The seedlings were left to acclimate for 6 wk before the first measurements were taken. Seedlings were watered daily, and relocated every 3 mo within each shade house to minimize positioning effects.

To assess initial size (day 0) for each seedling, we counted the number of leaves, the diameter at the base of the stem, and the height to the apex of the stem. The same measurements were repeated on days 65, 220, 442, and 643. In addition to these non-destructive measurements, we destructively harvested one-half of the seedlings on day 220 and the rest at the end of the experiment (day 643). Harvested seedlings were separated into leaves and aboveground woody biomass, and both biomass fractions were dried in an oven at 80°C for approximately 8 d. A small subset of seedlings was weighed repeatedly to insure that the biomass was completely dry (Chave 2005). Thus, for each seedling, we had one direct measure of aboveground biomass and either three or five non-destructive measures of size. To estimate the aboveground biomass on dates prior to harvesting, regressions were established between the non-destructive measures and harvested aboveground biomass (see below, Estimating aboveground biomass). To estimate initial aboveground biomass (prior to any time spent in the light treatments), an average of 20 additional seedlings of each species (range: 11–40) were destructively harvested, after we had measured their height, diameter, and number of leaves.

ESTIMATING ABOVEGROUND BIOMASS.—To estimate both the initial aboveground biomass of each seedling and the subsequent aboveground biomass on other measurement dates, we established regression relationships for each of the species. A separate linear model was fitted for each mass fraction (leaves and woody biomass) of each species. The final models, which explained 95 percent of the variation in the data, were:

$$\ln(mass) = a + b * \ln(diameter) + c * (height) + d * (number\ of\ leaves) \tag{1}$$

The two mass fractions were estimated separately and then summed. Separate regression equations were made for each of the main harvests. The details of the regressions used to predict biomass are described in the Supplementary Material.

FITTING GROWTH CURVES.—We modeled growth as a power law (reviewed in Enquist et al. 1999, West et al. 1999, Coomes 2006, Muller-Landau et al. 2006, Landsberg & Sands 2011), where the absolute growth rate is given by,

$$\frac{dM}{dt} = \alpha M^\beta \tag{2}$$

where α is a growth coefficient, β is the scaling exponent, and M is plant mass or size. When growth is linear, $\beta = 0$, and hence, growth is not dependent on current mass. When growth is exponential, $\beta = 1$, and there is no slowing of instantaneous RGR with increasing mass or size. Finally, for $0 < \beta < 1$, growth is allometric, and instantaneous RGR declines with increasing size or mass. Equation 2 has the following analytical solution when growth is not exponential and $\beta \neq 1$:

$$M = \left(M_0^{1-\beta} + \alpha(1-\beta)t \right)^{1/(1-\beta)} \tag{3}$$

where M_0 is the initial mass (more details of the derivation are provided in Appendix S1). Note that, equation 2 has a change of

form of the solution when $\beta = 1$, Mackenzie (2005), and this can cause problems in model fitting, when the true value of β is close to one, but this situation did not arise in this study. Equation 3 can be fitted to height, diameter, or biomass data by estimating M_0, α, and β (Muller-Landau *et al.* 2006, Russo *et al.* 2007, Hautier *et al.* 2010, Paine *et al.* 2011). We carried out separate analyses for diameter, height, and aboveground biomass. To compare growth rates among species at a common mass or size, we extracted the parameters from the respective fitted models and calculated a size-specific relative growth rate (SGR) as:

$$SGR = \alpha M_c^{(\beta-1)} \tag{4}$$

where M_c is a common reference mass or size. As species shared a single value of the scaling exponent β within each analysis (see Results), differences among species and light in SGR for height, diameter, or aboveground biomass are solely due to differences in the growth coefficient, α, and relative rankings do not depend on the choice of the reference mass or size. Note that SGR is still a RGR and therefore, has the same units as conventional RGR; the difference is only in the method of calculation, in that SGR is instantaneous RGR at a given common size, whereas conventional RGR calculations are averages over the growth interval and implicitly assume that growth is log-linear (as it is calculated on the log biomass scale). We always calculated SGR at the mean size of the middle harvest, as this was where the greatest number of seedlings were measured, where there was the greatest overlap in sizes, and where biomass was directly measured and thus most accurate. For diameter, this size was 8.5 mm, for height 88.5 cm, and for biomass 23.4 g.

The analyses were carried out in R 2.10.1 (R Development Core Team 2010) using nonlinear mixed-effects models in version 3.1-89 of the *nlme* package. The models were parameterized with the substantial dataset of around 2520 measurements (21 species × three light treatments replicated in five blocks with two seedlings of each species with either three or five measurements through time). We followed the detailed advice provided in Pinheiro and Bates (2000) for model fitting and simplification. Seedling identity was fitted as a random effect, so that the full model includes an effect of seedling identity on all three parameters. Further simplification of the random effects was attempted, but not possible, *i.e.,* all three parameters were allowed to vary between individuals. We identified the most parsimonious model (fitted using maximum likelihood) based on minimizing AIC. Species and light treatment were treated as fixed effects. We fitted light treatment as both a continuous variable and as a factor with three levels, but models with light treatment as a factor were always preferred (as judged by the AIC). In the most parsimonious model, M_0 varied with species, and α varied with species, light and the species-by-light interaction, whereas there was a common value of β for all species and light treatments. To reduce heteroscedasticity, variance was modeled as a power function of size. The variance was also allowed to vary among species and light treatments. Variance

modeling was implemented using the *varConsPower* and *varIdent* functions with the *weights* argument of *nlme*. All parameter estimates were taken from the final models fitted using restricted maximum likelihood. Mixed-effects models do not report a traditional R^2, and therefore pseudo-R^2 was calculated using the squared correlation of fitted values and the observed values (Bates 2009).

RESULTS

DIAMETER GROWTH.—The diameter growth model explained a large amount of the variation with a pseudo-R^2 of 0.93. The growth coefficient, α, varied significantly among light treatments (Fig. 2; $F_{2,1840} = 868.9$, $P < 0.0001$) and among species (Fig. 2; $F_{20,1840} = 11.1$, $P < 0.0001$). In contrast with height growth (see below), diameter growth was greatest in the high light treatment for all species, although the species-by-light interaction was still significant (Fig. 2; $F_{40,1840} = 2.4$, $P < 0.0001$). The common scaling exponent, β, for all species and light treatments was estimated at 0.20 (95% CI: 0.09–0.30).

HEIGHT GROWTH.—The height growth model explained a large amount of the variation with a pseudo-R^2 of 0.95. The growth coefficient, α, varied significantly among light treatments (Fig. S1; $F_{2,1838} = 754.8$, $P < 0.0001$) and among species (Fig. S1; $F_{20,1838} = 24.1$, $P < 0.0001$), with the highest values for *H. sangal*, *Shorea superba*, and *Dryobalanops beccarii* in both the high- and mid-light treatments. Species, however, did not respond to light in the same way (Fig. S1; species-by-light interaction: $F_{40,1838} = 4.2$, $P < 0.0001$). Thirteen species had their highest mean SGR in the high light, whereas for three species, (*Shorea beccariana*, *S. Faguetiana*, and *S. leprosula*) mean growth rates were very similar in the mid- and the high-light treatments. Finally, five species (*S. argentifolia*, *S. fallax*, *P. malaanonan*, *P. tomentella* and *S. ovalis*) exhibited the fastest height growth in the mid-light treatment. The common scaling exponent, β, was estimated across all species and light treatments, as 0.51 (95% CI: 0.40–0.62).

ABOVEGROUND BIOMASS GROWTH.—The aboveground biomass growth model had a pseudo-R^2 of 0.93. As with height and diameter growth, the aboveground biomass growth coefficient, α, varied significantly among light treatments (Fig. S2; $F_{2,1836} = 1390.6$, $P < 0.0001$) and among species (Fig. S2; $F_{20,1836} = 16.2$, $P < 0.0001$). Species, however, did not respond to light in the same way (Fig. S2; species-by-light interaction: $F_{40,1836} = 5.2$, $P < 0.0001$). Seventeen species had the highest aboveground biomass growth coefficient; α in the high light treatment, whereas *S. argentifolia* and *S. ovalis* had very similar aboveground biomass growth rates in the high- and mid-light treatments. Finally, *P. malaanonan* and *S. parvifolia* had a higher aboveground biomass growth coefficient, α, in the mid light than in the high light. The common scaling exponent, β, was estimated across all species and light treatments, as 0.57 (95% CI: 0.53–0.60). Linear contrasts were applied to the final
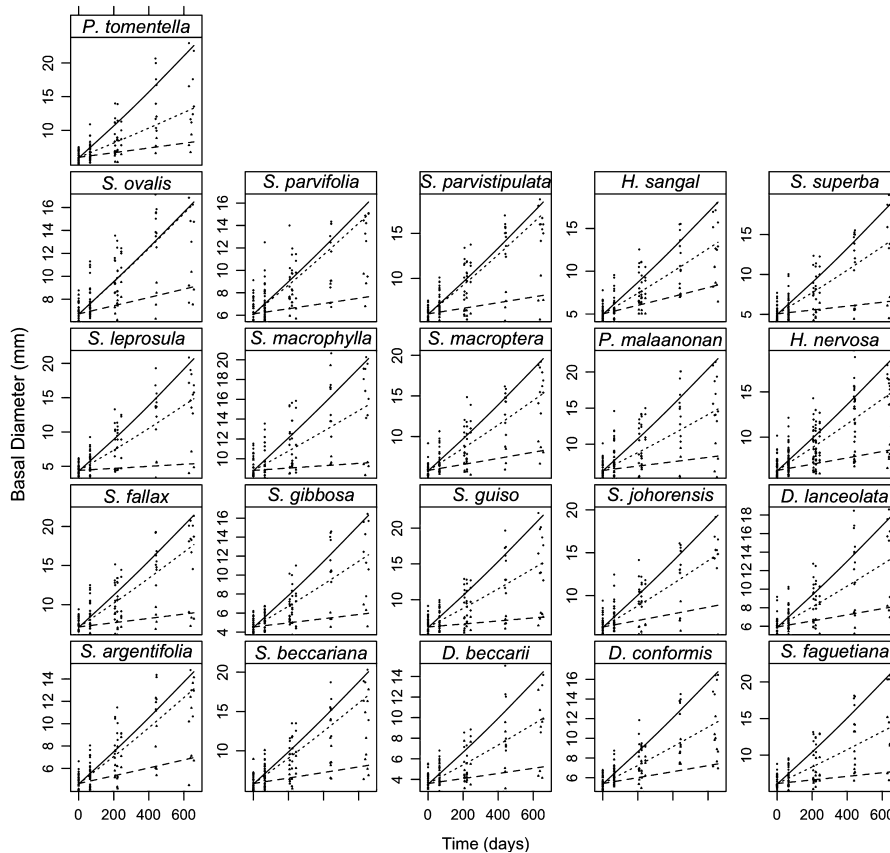
FIGURE 2. Diameter against time growth trajectories for each of the 21 species in the experiment. Solid lines represent the fitted values for the high-light treatment; the dotted line is for the mid-light treatment; and the dashed line is for the low-light treatment. Points are the observed values.

models (for each growth metric) by combining the mid- and high-light environment into one factor. In each case, the model with three light levels was considerably better in terms of AIC, indicating a significant difference between the mid- and high-light treatments. All of the parameter estimates, and confidence intervals on the parameter estimates for each of the models are available in the Supplementary Material, Table S1.

CORRELATIONS AMONG LIGHT TREATMENTS.—Correlations among SGR values in different light treatments were either positive or non-significant—there were no negative trade-offs between growth in different light environments (Fig. 3). There was a strong positive correlation between height SGR in the high- and the mid-light treatments (Fig. 3, center panel; $\rho = 0.65$, df = 19, $P < 0.0013$), although there was no significant correlation between height growth in the high- and low-light treatments. There were no significant correlations among diameter or aboveground biomass SGRs for any light treatments.

As expected, given the paucity of significant positive correlations above, there were a substantial number of crossovers in diameter SGR ranks among the three light treatments (Fig. 4). Accordingly, species ranks were only positively correlated for height SGR in the high- versus mid-light treatments (Spearman

rank correlation coefficient = 0.52, $N = 21$, $P < 0.0180$). All other rank correlations were non-significant, and are supplied in table S2.

These changes in rank performance in SGR are shown by the significant species-by-light interactions in the growth models (see above in results; Fig. 2; Figs. S1 and S2). For example, H. sangal is consistently one of the highest ranked species in aboveground biomass SGR, whereas S. parvistipulata changes from rank 9 in the low light, to rank 2 in the mid light to rank 14 in the high light. In contrast, D. conformis changes from rank 2 in the low light, to rank 20 in the mid light to rank 7 in the high light. Changes in rank for height SGR (Fig. S3) and aboveground biomass SGR (Fig. S4) are broadly similar to those for diameter SGR (Fig. 4).

DISCUSSION

The partitioning of the light environment by tropical trees is thought to be one of the most important niche axes for species coexistence in tropical forests (Denslow 1987, Kobe 1999, Clark et al. 2003, Dent & Burslem 2009). We grew 21 species of Dipterocarpaceae under controlled conditions to test whether growth hierarchies changed along the light gradient. Our three light conditions corresponded to those typically found under the

Height:
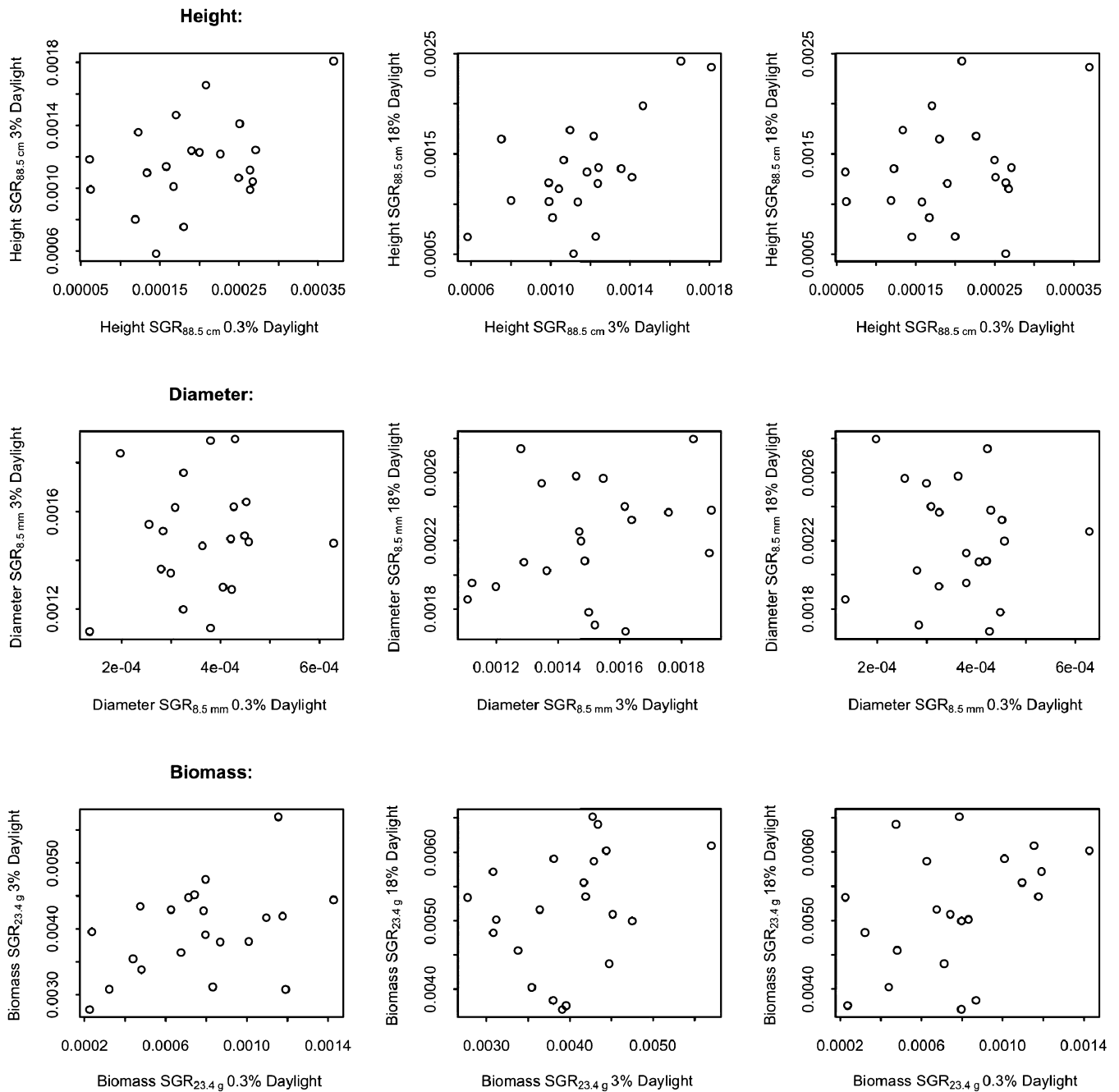

Diameter:

Biomass:

FIGURE 3. SGR calculated with height (first row), diameter (second row), and aboveground biomass (third row) measurements. The panels on the left show the mean SGR in the mid light against the mean SGR in the low light for each species. The center panels are for the mean SGR in the high light against the mean SGR in the mid light. The right hand side panels show mean SGR in the high light against the mean SGR in the low light.

closed canopy and in small and large gaps. We fitted growth curves to multiple measurements using nonlinear mixed-effects models and estimated diameter, height, and aboveground biomass size-specific growth rates (SGRs). Our key finding was a significant interaction between species and light treatment leading to changes in the hierarchy of the estimated mean growth rates among different light treatments (Fig. 4, Table S2). Of the nine potential correlations among species' growth rates (three growth rate measures in three light treatments), only one was significant: a positive correlation between height SGR in high and mid light. Thus, despite the species-by-light interaction, we found no evidence for negative correlations between growth rates in one light treatment and growth rates in another; that is, the species that grew fastest in high light generally were not the slowest growing in low light. Therefore, our results do not support a trade-off between growth under brighter and shadier
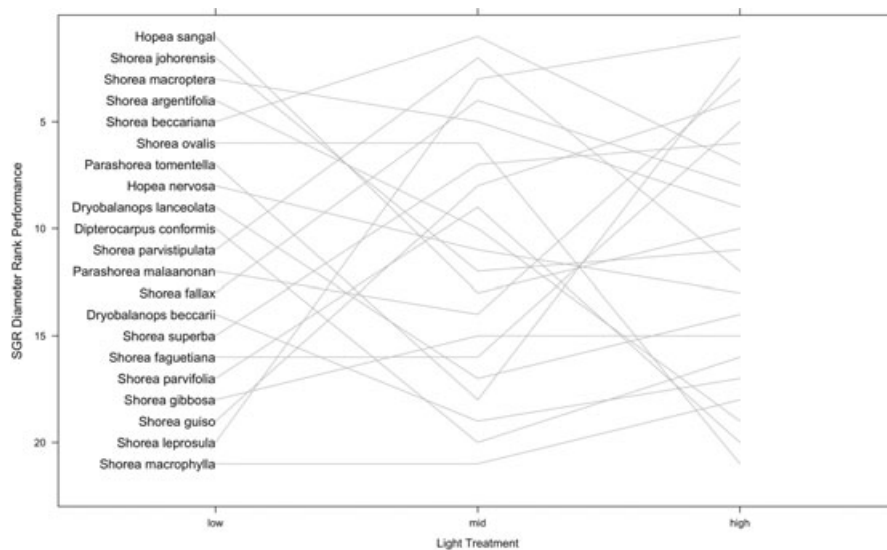
FIGURE 4. Rank performance in diameter SGR, and the crossovers in rank performance from low, to mid to high light. *Hopea sangal*, had the fastest diameter SGR in the low-light treatment.

conditions. A large number of species, however, showed strong rank reversals in estimated mean growth rates (Fig. 4, Table S2). Thus, while our results do not support a negative relationship between growth in the high light and growth in the shade, they suggest some degree of specialization on different light conditions.

Sack and Grubb (2001) reviewed seven studies that compared the RGR of woody seedlings in both high and low irradiance. Four of these studies found a positive correlation between growth in low and high light, two showed no pattern, and only one study showed a negative, but non-significant relationship. The study showing a negative trend included both pioneer and shade-tolerant species (Agyeman *et al.* 1999), whereas all our species were shade tolerant (Swaine & Whitmore 1988). Additional studies were subsequently added by Sack and Grubb (2003), strengthening this analysis.

While previous studies using groups of shade-tolerant tropical trees species e.g., Bloor and Grubb (2003), have found a strong positive correlation between mass-based RGR in high (10%) light and low (0.8%) light, we, in contrast, did not find such strong positive correlations. We believe that this difference may be due to our use of size-specific growth rates, whereas studies that use conventional RGR confound the general slowing of relative growth as size increases, with any species-specific differences seen at a common size. Our study is also unusual in that seedlings were grown for almost 2 yr, whereas many studies of growth in controlled conditions are of shorter duration (Poorter 1999, Saner *et al.* 2011). As outlined in our introduction, differences in initial size are more likely to dominate the results when plants are monitored for shorter periods (Sack & Grubb 2003). Our lack of a general positive relationship between growth rates among different light treatments (Fig. 3) leads to a large number of individual crossovers, or changes in rank performance among

the estimated mean growth rates of different species, some of which are quite dramatic (Fig. 4, Figs. S3 and S4). In contrast to Bloor and Grubb (2003), a small number of species had the highest aboveground biomass growth rates in the intermediate light treatment, which resulted in a larger number of crossovers in our dataset. This means that it is overly simplistic—at least within this group of shade-tolerant species—to label species as either fast or slow growing.

All but four species had higher aboveground biomass growth rates in 18 percent light compared with 3 percent light, although the predictions for these four species were very similar between the two light environments (Fig. S4). The aboveground biomass data are a combination of direct aboveground biomass measurements from two destructive harvests and estimations of aboveground biomass from diameter and height measurements taken at other times, which will add extra noise to these data. However, aboveground biomass growth rates are important, because diameter and height are essentially measures of wood volume and may trade-off against wood density (Chambers *et al.* 2004). Hence, we might potentially expect to see much less variation in aboveground biomass growth rates compared with variation in height and biomass growth rates, but this was not the case. All species had higher basal diameter growth rates in the high-light treatment compared with the mid light (Fig. 2), whereas there were five species that had considerably higher height growth rates in 3 percent light compared with 18 percent light (Fig. S1). The greater height growth in the intermediate light treatment could be seen as an allometric response to light limitation, and hence, this effect was less pronounced for aboveground biomass growth rates. The overall correlation, however, between height SGR in the high- and mid-light treatments was positive (Fig. 3, middle top row), indicating that broadly, species are more consistent in their height growth rates. In general, we find the

same trend for diameter, height, and biomass growth—there was always a species and light interaction. The strength of the interaction was weaker for the biomass data, and this is thought to be largely due to the extra error resulting from allometric regressions. The strength of the interaction was strongest for the height growth, and while this may in part be driven by artificial red:far-red in our shade houses, Poorter (1999) also found a strong selection on height growth in low light for some species.

Although tropical ecologists have a long tradition of carrying out growth rate experiments and making comparisons among species, most of these studies use conventional RGR, often based on measurements made at two time points (Poorter 1999, 2001; Eichhorn *et al.* 2010). As this methodology implicitly assumes linear growth between the log-transformed size data across the time interval, it is only appropriate when comparing species that exhibit exponential (or log-linear) growth (Swanborough & Westoby 1996, Wright & Westoby 1999, Angert *et al.* 2007). Herein, we estimated the parameters of a more general power-law growth formulation, and it is clear that when considering height, diameter, or aboveground biomass growth rates, the scaling exponent is considerably less than one (see equation 2). In contrast to the predictions of the scaling models of West, Brown, and Enquist, the scaling exponent for the aboveground biomass growth rates was significantly lower than their expected value of 0.75, ranging from 0.2 to 0.57 (West *et al.* 1997, 1999). When the scaling exponent is < 1, RGR is strongly size dependent, and small individuals will generally grow faster than large ones, thus biasing comparisons when species differ in their initial sizes (Fig. 1). To correct for differences in initial size among species and to evaluate the intrinsic growth ability of each species in different light environments, we fitted growth curves to multiple measurements. This has rarely been carried out for tree seedlings, not only because of the additional computational and statistical complexity but also because of the extra data required. For example, the estimation of aboveground biomass growth rates requires destructively harvesting many seedlings resulting in intensive data collection and fieldwork. We consider that this extra effort to remove the confounding effect of the general slowing of growth with increasing size will allow clearer ecologic conclusions to be drawn about species differences at a given size. For example, it has recently been shown that species rankings along growth and survival trade-offs can change substantially depending on the size of the individuals examined (Kunstler *et al.* 2009). In addition, Turnbull *et al.* (2008) also show that failing to correct for difference in size leads to erroneous ecologic conclusions.

Although there is considerable advantage to this analysis of comparing growth rates at a constant size, there are nevertheless caveats. The red:far-red ratios were slightly higher than reported in the primary forest in this area (Barker *et al.* 1997, Scholes *et al.* 1997). Red:far-red ratios affect internode extension and consequently height and may contribute to the stronger species–light interaction for the height growth measure. In addition, the analysis in this study does not enable us to incorporate changes in light environment through time. There are potential carryover effects, for example, some individuals were beginning to become pot-bound, as our seedlings were not newly germinated and had been in another nursery. It is not possible through this study to investigate these changes in light or carryover affects. Although our method is an improvement on standard RGR for predicting into the future, the crossovers that we found could still change with time. We do not have belowground biomass data for this dataset, and so our biomass growth data may not tell the whole story.

The debate over the role of light heterogeneity in the maintenance of forest-tree diversity continues (Sack & Grubb 2001, 2003; Kitajima & Bolker 2003; Baltzer & Thomas 2007). Some have suggested—as we have examined here—that species might specialize on a particular light treatment with different species exhibiting different optima, whereas others have emphasized the importance of a generalized trade-off between growth and survival under all light treatments (Kitajima 1994, Kitajima & Bolker 2003). Our results suggest that no single growth hierarchy exists across all light treatments, a result supporting Baltzer and Thomas (2007), who found substantial crossovers in growth rates across a light gradient in a study with Bornean tropical tress. In our study, almost all seedlings survived, and hence, we could not directly test for a growth versus survival trade-off with this dataset. In the light of new methods to derive and compare growth and survival rates at common sizes, the debate about the role of light heterogeneity and growth versus survival trade-offs can be more carefully addressed with long-term field datasets.

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SUPPORTING INFORMATION

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

TABLE S1. *Parameter estimates and confidence intervals from each of the three models.*

TABLE S2. *Spearman's rank correlation rho and P-values for each growth metric for all combinations of light treatments.*

FIGURE S1. Height against time growth trajectories for each of the 21 species.

FIGURE S2. Aboveground biomass against time growth trajectories for each of the 21 species.

FIGURE S3. Rank performance in height SGR, and the crossovers in rank performance from low, to mid to high light.

FIGURE S4. Rank performance in aboveground biomass SGR, and the crossovers in rank performance from low, to mid to high light.

APPENDIX S1. Solving the ordinary differential equation.

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