

Functional traits explain light and size response of growth rates in tropical tree species

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Abstract. Relationships between functional traits and average or potential demographic rates have provided insight into the functional constraints and trade-offs underlying life-history strategies of tropical tree species. We have extended this framework by decomposing growth rates of ~130 000 trees of 171 Neotropical tree species into intrinsic growth and the response of growth to light and size. We related these growth characteristics to multiple functional traits (wood density, adult stature, seed mass, leaf traits) in a hierarchical Bayesian model that accounted for measurement error and intraspecific variability of functional traits. Wood density was the most important trait determining all three growth characteristics. Intrinsic growth rates were additionally strongly related to adult stature, while all traits contributed to light response. Our analysis yielded a predictive model that allows estimation of growth characteristics for rare species on the basis of a few easily measurable morphological traits.

Key words: *adult stature; Barro Colorado Island; leaf area; leaf nutrient concentration; life-history theory; maximum height; Panama; plasticity; seed mass; shade tolerance; wood density.*

INTRODUCTION

Life-history strategies of tropical tree species describe how plants allocate resources to different organs and how these allocation “decisions” translate into a species’ ability to compete for resources and finally to grow, survive, reproduce, and disperse (e.g., Westoby et al. 2002). Allocation strategies are reflected by anatomical and morphological plant traits, e.g., light vs. dense wood, small vs. big seeds, or small vs. tall adult stature. To understand the functional constraints and trade-offs underlying different life-history strategies, it is essential to gain insight into the relationships between traits and demographic rates. Recent studies have mainly focused on establishing relationships between traits and average demographic rates (Poorter et al. 2008) or field-based proxies of potential demographic rates (Wright et al. 2010). However, an equally important aspect of life-history variation is the degree to which species are able to adjust their performance to temporal changes in resource availability or during ontogeny (Valladares and Niinemets 2008) (see Plate 1). Do morphological traits explain the sensitivity of growth with respect to light and size?

A suite of functional traits is considered key among forest trees. Maximum height, leaf area, seed mass, leaf mass per area, and wood density have been proposed as independent plant strategy axes representing fundamental aspects of tree anatomy and physiology: tree size, leaf size, seed size, leaf economics, and wood economics,

respectively (e.g., Weiher et al. 1999, Westoby et al. 2002, Wright et al. 2004, Chave et al. 2009, Baraloto et al. 2010, Muller-Landau 2010). Each of these reflect trade-offs related to competition for resources, persistence under resource shortage (e.g., shade tolerance), dispersal, and/or resistance to pests or mechanical damage. Although significant relationships between maximum height and seed mass as well as between leaf area and wood density have been reported, relationships are typically weak, exhibit considerable residual variation, or only appear when contrasting life-forms (e.g., woody and herbaceous) are pooled (Wright et al. 2007).

The few studies that have analyzed the impact of several of these traits on growth rates of tropical tree species found that growth decreased with wood density and, to a lesser extent, seed mass or volume, but increased with maximum height. Leaf traits were at best weakly related to growth (Poorter et al. 2008, Wright et al. 2010). These results were consistent between large trees (≥ 10 cm diameter at breast height [dbh]) and saplings (1–5 cm dbh) and independent of whether average relative growth rate (RGR) or the 95th percentile of RGR were analyzed. Using average RGR to represent a species’ growth strategy and indication of shade tolerance, however, introduces several problems.

First, RGR declines as plants grow (Hunt 1982). For species with different size ranges, comparative analyses based on average RGR at least partly confound growth and size and, thus, may lead to erroneous conclusions (e.g., Turnbull et al. 2008, Paine et al. 2012). Consequently, a recent study explicitly modeling ontogenetic growth curves reached slightly different conclusions. Growth characteristics, such as maximum growth and

Manuscript received 17 April 2012; revised 13 June 2012; accepted 14 June 2012. Corresponding Editor: R. T. Corlett.

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the shape of the growth curve, were to a large degree explained by wood density and maximum height, whereas relationships with seed and leaf traits disappeared (Héroult et al. 2011).

Second, growth rates respond to local resource availability, and species' average growth rates may reflect their differential distribution with respect to resource availability (Clark and Clark 1999). As an example, pioneer species may have higher average growth rates because they occur primarily in gaps where they receive high light or because they have a high intrinsic growth potential or both. Therefore, we propose that intrinsic growth rates of different species should be compared at the same size and light availability (cf. Rüger et al. 2011a). Moreover, estimating the light and size dependence of growth at the species level opens up the possibility of assessing how the response of growth rates to resource availability and tree size relates to functional traits in tree species following different life-history strategies.

We hypothesize that species with light wood, small seeds, and/or leaf traits indicative of a high priority on resource exploitation (e.g., low leaf mass per area, high leaf nutrient content) should grow faster and possess a higher capacity to adjust their growth rates to changing light conditions because these traits are commonly associated with a syndrome of low shade tolerance (Grime 1994, Poorter and Rose 2005, Valladares and Niinemets 2008). We also expect that taller species respond more strongly to light because they potentially experience increasing light levels as they grow to the canopy, while small-statured species may remain in the shaded understory for their whole life cycle. The response of growth to tree size has been shown to be significantly related to wood density and maximum height (Héroult et al. 2011), but we lack clear hypotheses on whether and in which direction leaf or seed traits might affect the response of growth to size.

To assess the relationships between growth characteristics and functional traits, we applied a two-level hierarchical Bayesian model, where individual growth is a function of light and size, whereas species-level parameters, i.e., "intrinsic" growth rates, light, and size dependence of growth, are related to the functional traits of a species. Hierarchical models include rare species by combining probability models for growth variation within species and among species (Clark 2005). The Bayesian approach allows incorporating intraspecific variation in functional traits and negative growth observations by correctly modeling measurement error (Clark et al. 2007, Rüger et al. 2011a). The integration of various sources of uncertainty represents a major methodological improvement in the analysis of ecological data.

In summary, our aim was to predict size- and light-standardized growth rates as well as the response of growth to light and size from functional traits across 171 tree species occurring at Barro Colorado Island (BCI), Panama. To our knowledge, this was the first time that

the sensitivity of tree performance to resource availability has been related to functional traits across a diverse tree community. Forest census data from the 50-ha plot at BCI provided information on the spatial location, size, and diameter growth of individual trees. Yearly canopy census data that recorded vegetation density in six height layers were used as a proxy of light availability for each individual tree (Rüger et al. 2011b), and an extensive trait data base gave access to functional traits of the species (Wright et al. 2010).

METHODS

Growth and trait data

We analyzed data from the tropical moist forest on BCI, Panama (9°9' N, 79°51' W). In the 50-ha Forest Dynamics Plot, all free-standing woody stems ≥ 1 cm diameter at breast height (dbh) were mapped, identified to species and measured in 1981–1983, 1985, and every 5 years thereafter (Condit 1998; data *available online*).⁴ Here we used the census intervals from 1985–1990 and 1990–1995 because these were the only intervals with consistent canopy census data. We discarded cases where a tree survived but its stem was measured at a different height, or where one stem broke so a resprouted stem of the same tree was measured. Due to their lack of secondary growth, we excluded palm species. Because dbh values were rounded down to the nearest 5 mm for all stems < 55 mm in 1985 but not in 1990, it was necessary to round 1990 dbh values below 55 mm down as well before calculating growth rates. Rounding down may bias growth estimates of small stems, but Condit et al. (1993) showed that the bias is minimal. We estimated the level of shading for each tree from a three-dimensional canopy census conducted annually from 1983 to 1996, except for 1994. We converted this measure of shading to an estimate of light availability by comparing the distribution of shade estimates to a published distribution of irradiance (Wirth et al. 2001, Rüger et al. 2011b). To avoid edge effects of the light availability calculation, we excluded all individuals within 20 m of plot edges.

As species-level predictors of growth characteristics, we used wood density (WD, g/cm^3), maximum height (H_{max} , m), leaf area (LA, cm^2), and seed mass (SM, g). Additionally, we explored two variables related to the leaf economics spectrum (Wright et al. 2004): leaf mass per area (LMA, g/m^2) and leaf nutrient content (NP, no units). NP was calculated as the first axis of a PCA between leaf nitrogen and leaf phosphorus concentrations and represents a combined measure of the two tightly correlated leaf nutrients. Our aim was to restrict the species-level predictors to a set of nearly independent traits. Therefore, we compared models including just one of the two representatives of the leaf economics spectrum (LMA or NP).

Traits were measured as described in Wright et al. (2010). Wood density was estimated as an area-weighted average

⁴ <http://ctfs.arnarb.harvard.edu/webatlas/datasets/bci/>

of wood specific gravity across wood cores. When wood density was not available, we used wood density from Chave et al. (2009). Maximum height equaled the mean height of the six trees with largest dbh in the 50-ha plot and a nearby 38.4-ha plot (King et al. 2006). LMA, leaf area, and leaf nutrient concentrations were measured on shade leaves only receiving indirect light. The leaves were taken from the tallest foliage of six of the smallest individuals of each species in the 50-ha plot. For eight pioneer species lacking shade leaves, we used leaf traits measured on sun-exposed leaves of the six smallest individuals instead. Seed mass refers to endosperm and embryo. For 26 species, seed mass was unavailable and we used diaspore dry mass from Daws et al. (2005). SM and LA distributions were highly right-skewed and we used log-transformed values.

Traits were measured on several individuals per species and intraspecific trait variation was included as a fixed prior in the model: $\mathcal{N}(\text{mean}, \text{SD})$. For species lacking a reported standard deviation, we used the average standard deviation for the same trait across the other species. For leaf N and leaf P, no information on uncertainty was available, and we estimated SD of NP as 10% of the trait value. To test the impact of accounting for this uncertainty in predictor variables, we compared models accounting for intraspecific trait variation with models assuming fixed (mean) trait values.

To control for phylogenetic relatedness between species, we included the first two axes of a principal coordinate analysis (PCoA; Gower 1966) on phylogenetic distances calculated from a bar code phylogeny for the BCI 50-ha plot (PH₁, PH₂; Diniz-Filho et al. 1998, Kress et al. 2009). By including coarse phylogenetic relatedness among the species, we controlled for similarity of growth characteristics between closely related species that is not captured by the functional traits (e.g., due to secondary compounds).

Hierarchical Bayesian model

We fit a two-level hierarchical model in which individual tree growth was a species-specific function of light availability and initial dbh, and species-level parameters were predicted by the functional traits (Gelman and Hill 2007). At the core of the model is the functional relationship predicting the absolute dbh growth rate (mm/yr) of individual i of species j ($\text{pred}_{i,j}$) as a power function (linear log-log relationship) of light availability and initial dbh

$$\log(\text{pred}_{i,j}) = a_j + b_j \times \log(\text{light}_{i,j}) + c_j \times \log(\text{dbh}_{i,j}) \quad (1)$$

where parameters a_j , b_j , and c_j describe the intrinsic growth rate and the light and size response of growth of species j , respectively (Rüger et al. 2011a). In contrast to recent studies on larger trees (dbh ≥ 10 cm) that fit unimodal relationships between absolute dbh growth and dbh (e.g., Hérault et al. 2011), we only allowed monotonic increases or decreases of growth with dbh. In previous studies, we found that only a small proportion of BCI species showed a unimodal response of growth to dbh (Rüger et al. 2011a, Rüger and Condit 2012). Moreover, our data set includes many rare

species. As species become rarer, it gets increasingly difficult to fit complex models, and in our case the more complex models predicted artificially low or high growth rates at large dbh in some species (Rüger et al. 2011a, Paine et al. 2012).

Process error, i.e., variation of growth at a given light availability and dbh was modeled using a lognormal distribution:

$$\text{true}_{i,j} \sim \text{Lnorm}(\text{pred}_{i,j}, \sigma_{p,j}) \quad (2)$$

where $\text{true}_{i,j}$ is the estimated true growth rate of tree i . The process error ($\sigma_{p,j}$) was estimated for each species. Using a lognormal distribution, the process error automatically scales with predicted growth. The process error ($\sigma_{p,j}$) was assumed to vary lognormally across the community with hyperparameters μ_h and σ_h . Uniform, non-informative priors for both parameters were

$$\mu_h, \sigma_h \sim U(0.001, 100). \quad (3)$$

Data entered our model as the observed annual dbh growth of individual i ($\text{obs}_{i,j}$, mm/yr) and were assumed to be subject to measurement error. We used remeasurement data to fit dbh measurement error assuming there are two types of error: routine error caused by a slightly different placement of the calipers or tape measure, and large error caused by missing a decimal place or recording a number with the wrong tree. We fit the error as the sum of two normal distributions (Chave et al. 2004, Rüger et al. 2011a). Thus,

$$\begin{aligned} \text{obs}_{i,j} \sim & (1-f) \times \mathcal{N}(\text{true}_{i,j}, \text{SD}_1 / \text{int}_i) \\ & + f \times \mathcal{N}(\text{true}_{i,j}, \text{SD}_2 / \text{int}_i) \end{aligned} \quad (4)$$

with standard deviation SD_1 describing the size-dependent error component and standard deviation SD_2 the size-independent error component affecting $f = 2.7\%$ of the observations (Rüger et al. 2011a). Standard deviations have to be adjusted to the time period elapsed between the two dbh measurements of the tree (int_i) from which the annual growth rate has been calculated.

Functional traits were used as linear species-level predictors of a_j , b_j , and c_j . Thus,

$$\begin{aligned} a_j \sim & \mathcal{N}(\alpha_0 + \alpha_1 \times \text{WD}_j + \alpha_2 \times H_{\text{max},j} + \alpha_3 \times \text{SM}_j + \alpha_4 \\ & \times \text{LA}_j + \alpha_5 \times \text{LE}_j + \alpha_6 \times \text{PH}_{1,j} + \alpha_7 \times \text{PH}_{2,j}, \sigma_a) \end{aligned} \quad (5)$$

$$\begin{aligned} b_j \sim & \mathcal{N}(\beta_0 + \beta_1 \times \text{WD}_j + \beta_2 \times H_{\text{max},j} + \beta_3 \times \text{SM}_j + \beta_4 \\ & \times \text{LA}_j + \beta_5 \times \text{LE}_j + \beta_6 \times \text{PH}_{1,j} + \beta_7 \times \text{PH}_{2,j}, \sigma_b) \end{aligned} \quad (6)$$

$$\begin{aligned} c_j \sim & \mathcal{N}(\gamma_0 + \gamma_1 \times \text{WD}_j + \gamma_2 \times H_{\text{max},j} + \gamma_3 \times \text{SM}_j + \gamma_4 \\ & \times \text{LA}_j + \gamma_5 \times \text{LE}_j + \gamma_6 \times \text{PH}_{1,j} + \gamma_7 \times \text{PH}_{2,j}, \sigma_c) \end{aligned} \quad (7)$$

where LE is the predictor that represents the leaf economics spectrum, i.e., LMA or NP.

Visual inspection revealed that the relationship between $H_{\max,j}$ and a_j differed for small and large trees. Therefore, we fit separate regression lines for small ($H_{\max,j} < 25$ m) and tall-statured ($H_{\max,j} \geq 25$ m) trees

$$\alpha_2 \begin{cases} \alpha_{2,\text{small}} & \text{if } H_{\max,j} < 25 \text{ m} \\ \alpha_{2,\text{large}} & \text{if } H_{\max,j} \geq 25 \text{ m.} \end{cases} \quad (8)$$

The deviance information criterion (DIC) of the model with two separate regression lines was smaller than the DIC of the model with an overall regression ($\Delta\text{DIC} = 60$) indicating a substantially better fit.

The standard deviations σ_a , σ_b , and σ_c measure the between-species variation. As we did not have prior knowledge, we used non-informative priors for these hyperparameters:

$$\alpha_{0-7}, \beta_{0-7}, \gamma_{0-7} \sim \mathcal{N}(0, 100) \quad (9)$$

$$\sigma_a, \sigma_b, \sigma_c \sim U(0, 2). \quad (10)$$

Posterior distributions of the model parameters were obtained using a Markov chain Monte Carlo (MCMC) method (Gelman et al. 2004). To speed up the convergence, we weakened the within-chain correlation of a with b and c by centering the light and dbh data on $\overline{\text{light}} = 0.05$ and $\overline{\text{dbh}} = 50$ mm:

$$\log(\text{pred}_{i,j}) = a_j + b_j \times (\log(\text{light}_{i,j}) - \log(\overline{\text{light}})) \\ + c_j \times (\log(\text{dbh}_{i,j}) - \log(\overline{\text{dbh}})). \quad (11)$$

Thus, a_j represents the log of predicted annual growth of a tree with 5 cm dbh that receives 5% light and enables a comparison of intrinsic growth rate at fixed light and size. We chose 5 cm as the size for comparison because many understory treelets do not reach much larger sizes; and 5% light is a common light level for trees with a dbh of 5 cm. For an in-depth exploration of the growth model, see R uger et al. (2011a). We monitored convergence by running two chains with different initial values and used Gelman and Rubin's convergence diagnostics (implemented in the coda package in R) and a value of 1.1 to detect convergence (Gelman et al. 2004). Convergence required 100 to 3700 iterations. We used a burn-in period of 5000 iterations and an additional 10 000 iterations were used for analysis. All analyses were carried out using R version 2.11.1 (R Development Core Team 2010). The R code of the model is provided in the Supplement.

Analysis of results

From the posterior distributions we computed the mean and credible intervals (CI) of all species-specific parameters and the hyperparameters. The significance of traits as predictors of species-specific growth parameters was assessed by a 90% CI, 95% CI, 99% CI, or 99.9% CI

that did not include zero. The goodness-of-fit of the species-level predictions of growth characteristics from traits was assessed by a measure of explained variance (r^2) and the root mean square error of prediction (RMSEP). Explained variance r^2 was calculated as

$$r^2 = 1 - \frac{E(\text{Var}(\varepsilon = p_{\text{pred}} - p))}{E(\text{Var}(p))} \quad (12)$$

where p_{pred} is the species-specific parameter p (a , b , or c) predicted from the traits, i.e., the predicted position of the species on the regression line at a given time step, and p the "true" value of the parameter for the species at that time step (Gelman and Hill 2007).

We simulated growth trajectories for four hypothetical species. The four species correspond to combinations of WD and H_{\max} that represent 10th and 90th percentiles of WD and H_{\max} : a tall species with light wood ($H_{\max} = 34.6$ m, $\text{WD} = 0.39$ g/cm³), a small species with light wood ($H_{\max} = 7.7$ m, $\text{WD} = 0.39$ g/cm³), a tall species with dense wood ($H_{\max} = 34.6$ m, $\text{WD} = 0.73$ g/cm³), and a small species with dense wood ($H_{\max} = 7.7$ m, $\text{WD} = 0.73$ g/cm³). We predicted the growth characteristics for these trait combinations (assuming the other traits were equal to the average across species) and simulated dbh trajectories for low and high light using the 10th and 90th percentile of light at a given dbh, respectively. We limited this analysis to 10 cm dbh for small species ($H_{\max} = 7.7$ m) because they rarely get much bigger and to 30 cm dbh for tall species ($H_{\max} = 34.6$ m) because our analysis is dominated by smaller trees and for larger trees parameter estimates are increasingly uncertain.

To compare these same hypothetical species in terms of biomass growth, we calculated their biomass increment per year and unit height (i.e., for a 1 cm thick wood disk) from their predicted annual dbh growth (dbh.growth):

$$\text{biomass.growth} = \text{WD} \times ((\text{dbh} + \text{dbh.growth})^2 - \text{dbh}^2). \quad (13)$$

RESULTS

Complete trait data were available for 169 species with 129 774 individuals in the first and 171 species with 130 550 individuals in second census interval. Species-level correlations between mean trait values were consistently low ($r < 0.28$), but often significant (Table 1). The model including NP as a predictor performed slightly better in terms of r^2 and RMSEP than the model including LMA. Otherwise, results were qualitatively very similar. Therefore, we report results for models including LMA in the Supplemental Material (Appendix A). Coefficients of the species-level regressions are given in Appendix B.

Growth rates at standardized conditions (5% light, 5 cm dbh) significantly decreased with WD and increased

TABLE 1. Pearson correlation coefficients for pairwise relationships between key functional traits and variables describing phylogenetic relatedness.

Variable	H_{\max}	SM	NP	LA	PH ₁	PH ₂
WD	-0.13	0.17*	-0.16*	-0.28***	-0.12	0.17*
H_{\max}		0.12	0.27***	0.23**	0.36***	0.01
SM			-0.12	0.13	0.14	0.05
NP				0.18*	0.07	-0.03
LA					0.27***	-0.04

Notes: Abbreviations are wood density (WD), maximum height (H_{\max}), seed mass (SM), leaf nutrient content (NP), leaf area (LA), and the first and second axis of a principal coordinate analysis of a bar code phylogeny (PH₁, PH₂). NP is the first axis of a principal component analysis between leaf tissue nitrogen and phosphorus concentrations. LA and SM are log-transformed.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

with H_{\max} for trees reaching $H_{\max} < 25$ m (Table 2, Fig. 1). For trees with $H_{\max} \geq 25$ m, there was no significant relationship between intrinsic growth rates and H_{\max} . Light response (b) significantly decreased with WD and SM, and increased with H_{\max} . The size response (c) changed from being negative ($c < 0$) at low WD to being positive ($c > 0$) at high WD, on average. In the first census interval, the size response was also significantly positively correlated with H_{\max} . In the first census interval, LA was significantly positively related to light response and negatively to size response, while in the second census interval the same was true for NP. Among the growth parameters, light response was best explained by functional traits ($r^2 = 0.49$ – 0.54 , Table 2). When we did not account for intraspecific variation in traits, r^2 increased by up to 10 percentage points and credible intervals for the relationships of traits with model parameters got narrower leading to slightly stronger significance of relationships (Appendix A). When we did not account for phylogenetic relatedness among species, r^2 decreased by up to 5 percentage points, although the first phylogenetic axis was only marginally significantly related to the light response in the first census interval (Appendix A).

Light response was positively correlated with intrinsic growth rates ($r = 0.61$) and negatively with size response ($r = -0.38$). Size response and intrinsic growth rates were only weakly correlated ($r = -0.17$). Species with high

intrinsic growth rates and high sensitivity to light were less abundant than species with the opposite characteristics (Fig. 2). We identified several species with uncommon parameter combinations (Fig. 2). The most conspicuous one was *Alseis blackiana*, which had the slowest intrinsic growth but responded strongly and positively to both light and size. *Cordia bicolor* had an intermediate intrinsic growth rate but the strongest response of growth to light and the fourth most negative response to size (Fig. 2). *Zanthoxylum belizense* grew fastest at standardized conditions, responded positively to light and negatively to size (Fig. 2).

Tall species (34.6 m) with low WD (0.39 g/cm^3) always grew fastest and grew from one to 30 cm dbh within 60 years under high light conditions (Fig. 3). Small-statured species with high WD grew slowly and required more than 150 years to grow from one to 10 cm dbh under low light conditions (Fig. 3). Surprisingly, biomass growth up to a dbh of 20 cm was identical for light-wooded and dense-wooded species that reach the same H_{\max} (Fig. 4). For larger trees, biomass growth began to diverge and dense-wooded species produced more biomass than light-wooded species.

DISCUSSION

Modeling growth as a function of light availability and tree size allowed us to decompose growth rates of tropical tree species into the intrinsic growth rate at

TABLE 2. Coefficients of determination of the species-level regressions between key functional traits and parameters of the individual-level growth model.

Growth parameters	Independent variables (species' traits)						r^2	RMSEP
	WD	H_{\max}	SM	LA	NP	PH		
1985–1990								
Intrinsic growth, a	-10.1%***	15.7%***	-2.2%*				0.35	0.51
Light response, b	-12.1%***	4.8%*	-7.2%***	2.5%*		4.5%†	0.54	0.16
Size response, c	11.7%***	8.2%**		-6.7%***			0.30	0.26
1990–1995								
Intrinsic growth, a	-15.4%***	12.9%***					0.37	0.51
Light response, b	-5.1%***	3.3%***	-5.5%***		5.2%**		0.49	0.18
Size response, c	7.9%***		0.6%†		-0.4%†		0.21	0.29

Notes: Entries express the proportion of variance (r^2) that each trait explains in addition to all other traits (difference in r^2 between the full model and the model excluding the focal trait). Variance r^2 is a measure of explained variance taking into account the uncertainty in a , b , and c (Eq. 12). RMSEP is the root mean square error of prediction. Significant entries are preceded by the sign of the relationship if negative. Empty cells occur where the relationship was not significant.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † $P < 0.1$.

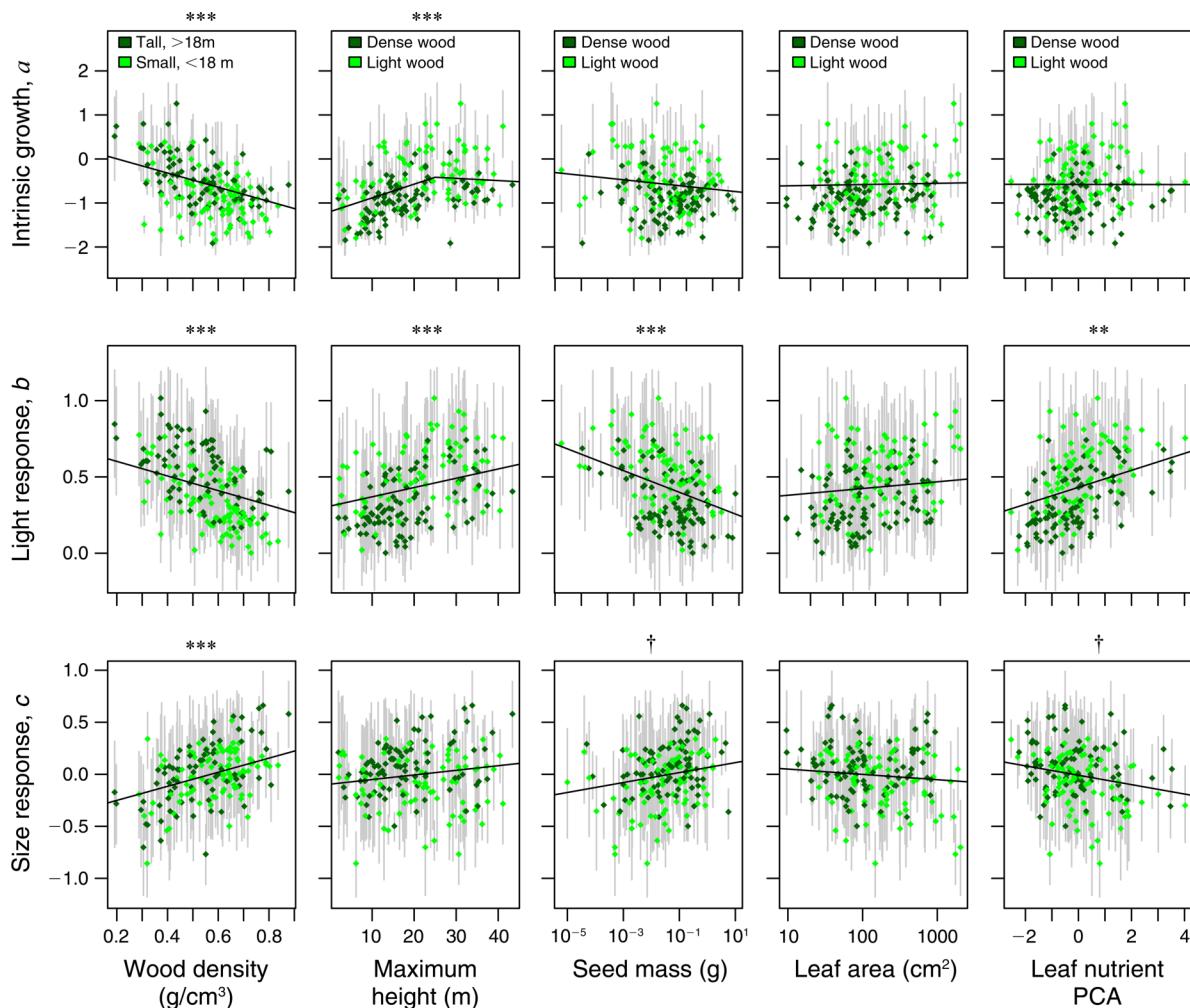


FIG. 1. Relationships between functional traits and species-level growth characteristics. Means (points) and 95% credible intervals (lines) of the species-specific parameters of the growth model for 171 tree species in the census interval 1990–1995 at BCI, Panama. The intercepts of the regression lines are calculated for average values of the other traits. Significance of predictors is indicated by asterisks and daggers.

** $P < 0.01$; *** $P < 0.001$; † $P < 0.1$.

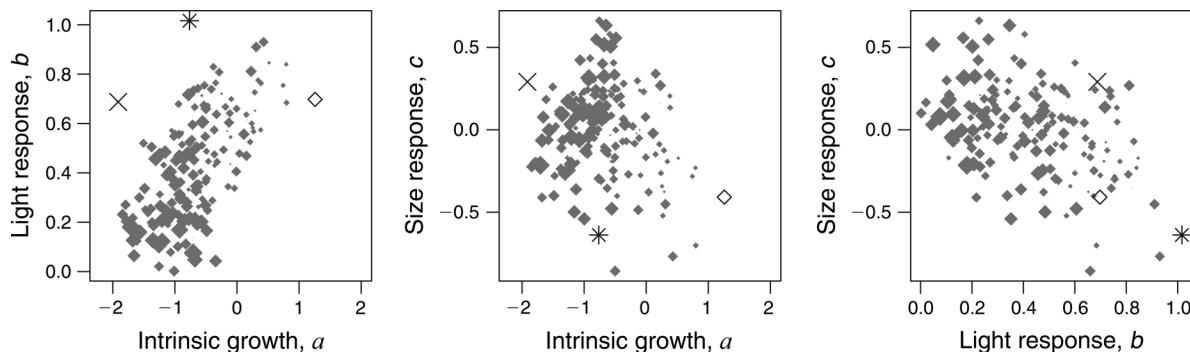


FIG. 2. Pairwise plots of the species-specific parameters of the growth model. The size of the dots is proportional to log abundance of the species. Correlation coefficients are: $a-b$, $r = 0.61$; $a-c$, $r = -0.17$; $b-c$, $r = -0.38$. Three species with uncommon parameter combinations are identified with symbols: ×, *Alseis blackiana*; stars (*), *Cordia bicolor*; open diamonds (◇), *Zanthoxylum belizense*.

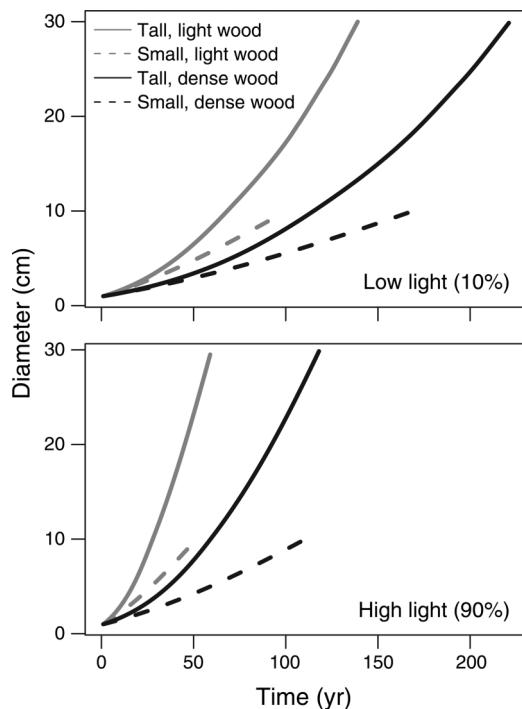


FIG. 3. Diameter trajectories under low and high light for four hypothetical species. The four species correspond to combinations of wood density (WD) and maximum height (H_{\max}) that represent 10th and 90th percentiles: a tall species with light wood ($H_{\max} = 34.6$ m, $WD = 0.39$ g/cm³), a small species with light wood ($H_{\max} = 7.7$ m, $WD = 0.39$ g/cm³), a tall species with dense wood ($H_{\max} = 34.6$ m, $WD = 0.73$ g/cm³), and a small species with dense wood ($H_{\max} = 7.7$ m, $WD = 0.73$ g/cm³). Light conditions represent the 10th (low) and 90th (high) percentile of light at a given dbh, respectively.

standardized conditions and the response of growth to light and size. Relating these growth characteristics to multiple functional traits in a hierarchical Bayesian model permitted a more mechanistic understanding of trait–rate relationships than previous studies while at the same time accounting for several sources of uncertainty including measurement error in growth rates and intraspecific trait variability. Our three key findings were that (1) all traits (wood density, adult stature, seed mass, leaf nutrient content) contributed independently to light response, (2) intrinsic growth rates were mostly determined by wood density and adult stature, and (3) size response was less well predicted by functional traits with the exception of wood density.

Relationships between functional traits and growth characteristics

Wood density has already been identified as a key trait determining average or potential growth rates (Muller-Landau 2004, Poorter et al. 2008, Chave et al. 2009, Wright et al. 2010, Hérault et al. 2011) and the size response of growth (Hérault et al. 2011). However, we could additionally show that wood density is also an important predictor of the ability of a species to respond

to temporal changes in light availability. Species with low wood density grew fast, were able to respond to periods of higher light availability and showed declining growth rates at larger sizes. In contrast, species with dense wood grew slowly, were less able to exploit temporally favorable growth conditions but sustained increasingly faster diameter growth at larger sizes. These findings are in line with the common view that species with low wood density prioritize short-term gains over long-term benefits. These characteristics might result from a trade-off between low construction cost (for given strength) in low-density wood vs. low maintenance cost through reduced stem respiration in stems with dense wood as suggested by Larjavaara and Muller-Landau (2010). Whether more mechanistic wood traits (e.g., vessel diameter or hydraulic conductivity) would be even better predictors of tree growth than wood density, remains highly controversial and may depend on the level of water stress the trees experience (Poorter et al. 2010, Fan et al. 2012).

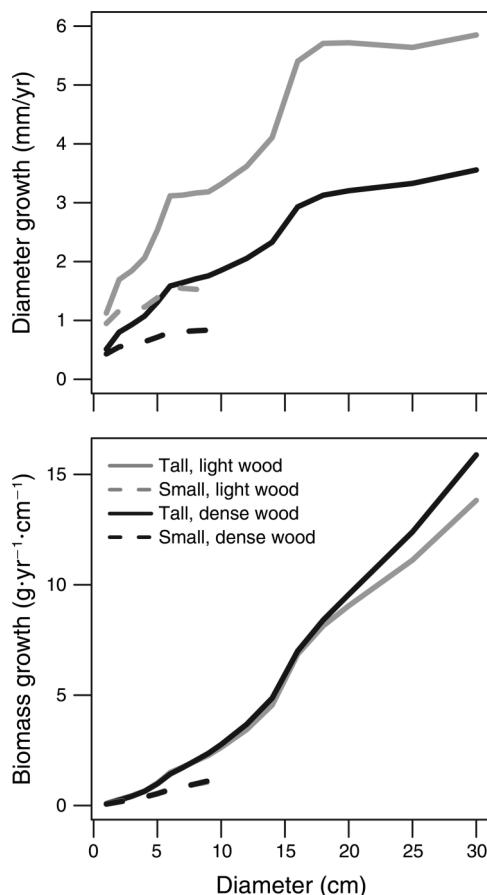


FIG. 4. Diameter and biomass growth of four hypothetical species. The four species correspond to combinations of wood density and maximum height that represent 10th and 90th percentiles (see legend of Fig. 3). Growth was calculated for median light availability for each 1-cm dbh class.



PLATE 1. Tree-fall gap on Barro Colorado Island (BCI), Panama. Tree species differ in their ability to exploit temporal increases in light availability. Photo credit: Christian Ziegler.

Maximum height was the second most important determinant of growth characteristics and was especially strongly related to intrinsic growth rates. Tall species grew faster than small-statured species (e.g., Thomas 1996, Poorter et al. 2008). However, within the species that potentially emerge over the main forest canopy ($H_{\max} > 25$ m), there was no relationship between maximum height and intrinsic growth rate. This might explain why $RGR-H_{\max}$ relationships in Wright et al. (2010) became insignificant when tree species with $H_{\max} < 20$ m were excluded. Tall species also responded more strongly to higher light. This may be because they eventually reach the canopy and gain access to sunlight while small-statured species may remain in the shaded understory for their whole life cycle.

Seed mass was unrelated to intrinsic growth rates, but was negatively correlated with the response of growth to light. Similarly, in an earlier study, seed mass was significantly correlated with growth rates of the fastest growing saplings (95th percentile of RGR), which presumably grow under more favorable conditions (Wright et al. 2010). Seed mass is unlikely to directly affect growth of plants ≥ 1 cm dbh, but the negative association between seed mass and light response in a model including several traits confirms that seed mass is indeed an independent component of a syndrome of traits related to the light sensitivity of a species (Poorter and Rose 2005). Species with small seeds survive less well in deep shade than species with large seeds (Grime and Jeffrey 1965) but have larger dispersal distances

(Muller-Landau et al. 2008) and a greater chance of being deposited in gaps where they can take advantage of the high light.

Leaf traits (LMA, leaf nutrient content, and leaf area) were not related to intrinsic growth rates. This is in line with findings of previous studies (Poorter et al. 2008, Wright et al. 2010, Hérault et al. 2011). Neither the association of high leaf nutrient content (or low LMA) with higher photosynthetic capacity per unit leaf mass (Wright et al. 2004, Poorter and Bongers 2006), nor with higher susceptibility to herbivory (e.g., Coley 1983) seem to affect intrinsic growth rates. Likewise, traits related to leaf toughness (e.g., cellulose content, lamina density, and thickness) were not related to growth rates in 197 shade-tolerant species at BCI, possibly because the higher cost of constructing tough leaves is compensated by their longer life span (Westbrook et al. 2011).

Although high photosynthetic capacity is expected to allow for a flexible response to temporal changes in resource availability (Grime 1994), only leaf nutrient content, and not LMA, contributed significantly to higher light response (see Appendix A). This stronger relationship of leaf nutrient content with light sensitivity may be due to its lower correlation with the other traits in the multivariate analysis as compared to LMA. Alternatively, leaf nutrient content may be more mechanistically linked to plant metabolism and growth than LMA, which incorporates tissue density and tissue thickness (Westbrook et al. 2011).

However, the relationships between leaf traits (nutrient content, leaf area) and growth characteristics were inconsistent between the two census intervals. This may be due to relatively large correlations between leaf traits and other traits. In contrast to conclusions from bivariate analyses (Poorter and Bongers 2006), in multivariate analyses including wood density and maximum height as predictors of tree growth, leaf traits appear to be only weak predictors of growth characteristics (Wright et al. 2010). Thus, using leaf traits, especially LMA (or its inverse, SLA) to describe a plant's growth strategy is not justified, at least for tropical tree species.

Comparing models that did or did not account for intraspecific variation in traits revealed that r^2 was larger and relationships were slightly more significant when trait uncertainty was ignored. This indicates that studies ignoring intraspecific trait variation tend to overestimate the predictive power of relationships.

The continuum of growth strategies

Low sensitivity of growth with respect to light is part of a syndrome of life-history characteristics related to conservative resource use, including slow intrinsic growth rates and high shade tolerance (Strauss-Debenedetti and Bazzaz 1991, Valladares and Niinemets 2008). This syndrome characterizes the majority of tree species in the 50-ha plot and the most abundant species. Among these are many understory trees with dense wood and well-defended leaves to withstand the numerous disadvantages of being small (Kitajima 1994), such as being shaded, being hit by falling trees or branches (Romero and Bolker 2008) and being exposed to high levels of herbivory or pathogen attack (Coley and Barone 1996, Gilbert and Reynolds 2005).

At the other extreme are species with high intrinsic growth potential, high sensitivity of growth to light, and a tendency to grow slower at larger size. These species tend to be rarer and include many pioneer species, among them canopy and emergent long-lived pioneers (e.g., *Apeiba membranacea*, *Cavanillesia platanifolia*, *Ceiba pentandra*, *Jacaranda copaia*, *Spondias mombin*) and short-lived medium-sized pioneer species (*Cecropia* spp., *Cordia alliodora*, *Miconia argentea*, *Ochroma pyramidale*, *Pourouma bicolor*, *Trema micrantha*, *Zanthoxylum* spp.). Although these coarse syndromes describe general growth strategies, interspecific variation is large. For example, species with average intrinsic growth rates covered nearly the full range of light sensitivity.

There are also exceptions. The most conspicuous exception was *Alseis blackiana*, a tall species ($H_{\max} = 29$ m) with dense wood (0.58 g/cm^3), which would be expected to have an intermediate intrinsic growth rate and light sensitivity. However, *Alseis* is an unusual species as it has slow growth in the shade but is highly sensitive to light and size. This finding extends conclusions from the early life-history to the sapling

and adult stage. *Alseis* seedlings showed characteristics of pioneers (higher seed germination in gaps and strong plastic response to light) as well as of shade-tolerant species (high persistence of established seedlings in understory) and was classified by Dalling et al. (2001) as a shade-persistent pioneer tree.

Interestingly, biomass production was nearly constant for species differing widely in wood density. This means that trees of similar adult stature sequester similar amounts of carbon, independent of whether the carbon is allocated to a large volume of light wood or a small volume of dense wood. Thus, knowing a species' maximum height theoretically allows the calculation of its average biomass growth. This again shows that tree species take an allocation "decision" prioritizing either short-term gains through faster growth of light-wooded stems at the cost of increased maintenance expenditures and mortality vs. long-term carbon gain and survival by growing slower but investing in well-defended stems of high wood density that are less costly to maintain in the long run (Kraft et al. 2010, Larjavaara and Muller-Landau 2010). This result also extends the finding of constant productivity independent of average wood density at the stand scale (Baker et al. 2009, Falster et al. 2011) to the scale of individual trees.

CONCLUSIONS

Decomposing tree growth into intrinsic growth rates and the response of growth to light and size yielded a predictive model that allows estimation of growth characteristics for rare species on the basis of a few easily measurable morphological traits. This may be especially useful given the high proportion of rare species in the tropics. Established relationships between traits and demographic rates may also facilitate the trait-based parameterization of dynamic forest simulation models (Purves and Pacala 2008, Valladares and Niinemets 2008). However, the relationships established here for BCI might not hold across sites with different climate and soils. For example, in less dynamic forests in French Guiana, fast-growing species responded less to variation in resource availability than did slow-growing species (Hérault et al. 2010).

Future research should also integrate trait-rate studies focusing on the response to resource availability of all demographic processes, i.e., growth, mortality, and recruitment, to identify fundamental trade-offs and evolutionary constraints of life-histories of tropical tree species (Wright et al. 2003, 2010). Such analyses would provide a more complete picture of tropical tree demographics allowing for multidimensional ordination of species in life-history space (e.g., Dalling et al. 2001). Another line of research worth further attention is the identification of the mechanisms underlying the patterns of trait-rate and trait-plasticity relationships explored here. To this end, mechanistic models of tree growth explicitly representing metabolism and allocation should

be applied (e.g., Ogle and Pacala 2009, Falster et al. 2011, Sterck et al. 2011).

ACKNOWLEDGMENTS

We thank Jens Doleschal and the Center for Information Services and High Performance Computing, Technische Universität Dresden, for the parallelization of the R code and provision of computing resources. We also thank Karin Nadrowski and Gerald van den Boogaart for statistical advice, John Kress for providing the phylogenetic tree, and Bruno Hérault and Timothy Paine for helpful comments. N. Rüger was funded by research grants from Deutsche Forschungsgemeinschaft DFG (RU 1536/2-1) and the Center for Tropical Forest Science (CTFS). The BCI plot has been made possible through the support of the U.S. National Science Foundation (most recently, grant no. 0948585 to S. P. Hubbell), the John D. and Catherine D. McArthur Foundation, and the Smithsonian Tropical Research Institute. Functional trait data were funded by the F. H. Levinson Fund. We thank the dozens of field assistants and botanists who have collected data in the BCI plot over the past 30 years.

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SUPPLEMENTAL MATERIAL

Appendix A

Significance of functional traits in alternative models excluding phylogenetic information, intraspecific variability of functional traits, or replacing leaf nutrient content with LMA (*Ecological Archives* E093-244-A1).

Appendix B

Coefficients of the species-level regressions between functional traits and growth parameters as well as residuals of the final growth model (*Ecological Archives* E093-244-A2).

Supplement

R code of the hierarchical Bayesian model (*Ecological Archives* E093-244-S1).

Ecological Archives --A1

Nadja Rüger, Christian Wirth, S. Joseph Wright, and Richard Condit. 2012.
Functional traits explain light and size response of growth rates in tropical tree species. *Ecology* 93:2626–2636. <http://dx.doi.org/10.1890/12-0622.1>

APPENDIX A. Significance of functional traits in alternative models excluding phylogenetic information, intraspecific variability of functional traits, or replacing leaf nutrient content with LMA.

Note: In Tables A1–A3 and A5–A8 the direction of all significant relationships (positive or negative) is the same as in Table 2 of the main manuscript.

Significance of predictors in alternative models excluding phylogenetic information and/or intraspecific variability of functional traits

TABLE A1. Significance of predictors, proportion of explained variance (R^2), and root mean square error of prediction (RMSEP) of the model with phylogenetic information but without intraspecific variability of functional traits (**PH noSD**).

Growth parameters		Independent variables (species' traits)						R^2	RMSEP
		WD	H _{max}	SM	LA	NP	PH		
1985–1990	Intrinsic growth (<i>a</i>)	***	***/-	*				0.35	0.52
	Light response (<i>b</i>)	***	***	***	***			0.61	0.14
	Size response (<i>c</i>)	***	***		***			0.38	0.25
1990–1995	Intrinsic growth (<i>a</i>)	***	***/-					0.37	0.51
	Light response (<i>b</i>)	***	***	***		**		0.59	0.17
	Size response (<i>c</i>)	***				.		0.28	0.28

TABLE A2. Significance of predictors, proportion of explained variance (R^2), and root mean square error of prediction (RMSEP) of the model with intraspecific variability of functional traits but without phylogenetic information (**noPH SD**).

Growth parameters		Independent variables (species' traits)						R^2	RMSEP
		WD	H _{max}	SM	LA	NP			
1985–1990	Intrinsic growth (<i>a</i>)	***	***/-	.				0.35	0.52
	Light response (<i>b</i>)	***	***	**	*			0.49	0.16
	Size response (<i>c</i>)	***	*		***			0.29	0.26
1990–1995	Intrinsic growth (<i>a</i>)	***	***/-					0.35	0.51
	Light response (<i>b</i>)	***	***	***		***		0.51	0.18
	Size response (<i>c</i>)	***		.		.		0.22	0.28

TABLE A3. Significance of predictors, proportion of explained variance (R^2), and root mean square error of prediction (RMSEP) of the model with-out intraspecific variability of functional traits and phylogenetic information (**noPH noSD**).

Growth parameters		Independent variables (species' traits)						R^2	RMSEP
		WD	H _{max}	SM	LA	N/P			
1985–1990	Intrinsic growth (<i>a</i>)	***	***/-	.				0.35	0.52
	Light response (<i>b</i>)	***	***	**	***			0.60	0.14
	Size response (<i>c</i>)	***	**		***			0.39	0.25
1990–1995	Intrinsic growth (<i>a</i>)	***	***/-					0.36	0.51
	Light response (<i>b</i>)	***	***	***		**		0.61	0.16
	Size response (<i>c</i>)	***				.		0.25	0.28

Significance of predictors in models including leaf mass per area (LMA) as a predictor instead of leaf nutrient content (NP)

TABLE A4. Pearson correlation coefficients between LMA and other functional traits. LA and SM were log transformed.

	WD	H _{max}	SM	LA	PH ₁	PH ₂	NP
LMA	0.15*	-0.09	0.11	-0.004	0.16*	0.15*	-0.56***

TABLE A5. Significance of predictors, proportion of explained variance (R^2), and root mean square error of prediction (RMSEP) of the model with phylogenetic information and intraspecific variability of functional traits (**PH SD**).

Growth parameters		Independent variables (species' traits)						R^2	RMSEP
		WD	H _{max}	SM	LA	LMA	PH		
1985–1990	Intrinsic growth (<i>a</i>)	***	***/-	*				0.36	0.52
	Light response (<i>b</i>)	***	*	**			*	0.51	0.16
	Size response (<i>c</i>)	***	**		***			0.30	0.26
1990–1995	Intrinsic growth (<i>a</i>)	***	***/-					0.38	0.51
	Light response (<i>b</i>)	**	**	***				0.43	0.19
	Size response (<i>c</i>)	***		*				0.19	0.29

TABLE A6. Significance of predictors, proportion of explained variance (R^2), and root mean square error of prediction (RMSEP) of the model with phylogenetic information but without intraspecific variability of

functional traits (**PH noSD**).

Growth parameters		Independent variables (species' traits)						R^2	RMSEP
		WD	H _{max}	SM	LA	LMA	PH		
1985–1990	Intrinsic growth (<i>a</i>)	***	***/-	*				0.37	0.52
	Light response (<i>b</i>)	***	**	**	***	*		0.63	0.14
	Size response (<i>c</i>)	***	***		***			0.40	0.25
1990–1995	Intrinsic growth (<i>a</i>)	***	***/-			.		0.41	0.50
	Light response (<i>b</i>)	***	**	**		.		0.54	0.17
	Size response (<i>c</i>)	***						0.24	0.28

TABLE A7. Significance of predictors, proportion of explained variance (R^2), and root mean square error of prediction (RMSEP) of the model with intraspecific variability of functional traits but without phylogenetic information (**noPH SD**).

Growth parameters		Independent variables (species' traits)						R^2	RMSEP
		WD	H _{max}	SM	LA	LMA			
1985–1990	Intrinsic growth (<i>a</i>)	***	***/-	*				0.36	0.52
	Light response (<i>b</i>)	***	**	**	**			0.49	0.16
	Size response (<i>c</i>)	***	**		***			0.29	0.26
1990–1995	Intrinsic growth (<i>a</i>)	***	***/-			.		0.38	0.51
	Light response (<i>b</i>)	***	***	**				0.45	0.19
	Size response (<i>c</i>)	***		.				0.19	0.29

TABLE A8. Significance of predictors, proportion of explained variance (R^2), and root mean square error of prediction (RMSEP) of the model without intraspecific variability of functional traits and phylogenetic information (**noPH noSD**).

Growth parameters		Independent variables (species' traits)						R^2	RMSEP
		WD	H _{max}	SM	LA	LMA			
1985–1990	Intrinsic growth (<i>a</i>)	***	***/-	*				0.37	0.52
	Light response (<i>b</i>)	***	**	**	**	*		0.60	0.14
	Size response (<i>c</i>)	***	***		***			0.39	0.24
1990–1995	Intrinsic growth (<i>a</i>)	***	***/-			.		0.40	0.50
	Light response (<i>b</i>)	***	***	***	.			0.54	0.16
	Size response (<i>c</i>)	***		.	.			0.24	0.28

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Ecological Archives --A2

Nadja Rüger, Christian Wirth, S. Joseph Wright, and Richard Condit. 2012. Functional traits explain light and size response of growth rates in tropical tree species. *Ecology* 93:2626–2636. <http://dx.doi.org/10.1890/12-0622.1>

APPENDIX B. Coefficients of the species-level regressions between functional traits and growth parameters as well as residuals of the final growth model.

TABLE B1. Coefficients of the species-level regressions between key functional traits and parameters of the individual-level growth model (a , b , c). Significant coefficients are highlighted in bold.

Growth parameters		Independent variables (Species' traits)						PH ₁	PH ₂
		Intercept	WD	H _{max}	SM	LA	NP		
1985–1990	Intrinsic growth (a)	0.347	-1.323	small 0.035 large -0.005	-0.045	0.012	0.002	0.001	0.001
	Light response (b)	0.408	-0.544	0.005	-0.030	0.032	0.022	0.001	0
	Size response (c)	-0.197	0.640	0.008	0.006	-0.072	-0.018	-0.001	0
1990–1995	Intrinsic growth (a)	0.315	-1.613	small 0.031 large -0.005	-0.031	0.012	-0.001	0.001	0.001
	Light response (b)	0.370	-0.479	0.006	-0.033	0.019	0.056	0.001	0
	Size response (c)	-0.296	0.677	0.004	0.021	-0.022	-0.045	0	0

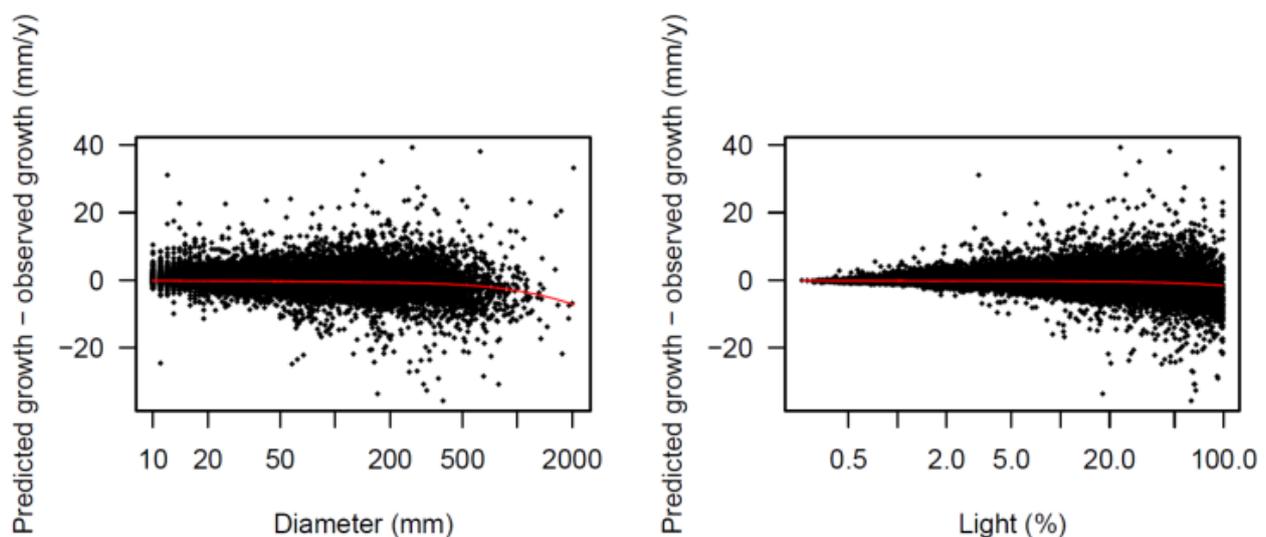


FIG. B1. Residuals of the final growth model (1990–1995). Note that the increase of growth error with growth, and hence light, is accounted for (see Eq. 2 of the main manuscript).

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