

Functional traits shape ontogenetic growth trajectories of rain forest tree species

Bruno Hérault^{1*}, Bénédicte Bachelot², Lourens Poorter³, Vivien Rossi⁴, Frans Bongers³, Jérôme Chave⁵, C. E. Timothy Paine², Fabien Wagner¹ and Christopher Baraloto^{6,7}

¹Université des Antilles et de la Guyane, UMR “Ecologie des Forêts de Guyane”, 97387 Kourou Cedex, France;

²AgroParisTech, UMR “Ecologie des Forêts de Guyane”, 97387 Kourou Cedex, France; ³Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands; ⁴CIRAD, UMR “Ecologie des Forêts de Guyane”, 97387 Kourou Cedex, France; ⁵CNRS, Laboratoire Evolution et Diversité Biologique, 31062 Toulouse, France; ⁶INRA, UMR “Ecologie des Forêts de Guyane”, 97387 Kourou Cedex, France; and ⁷Department of Biology, University of Florida, Gainesville, FL 32611, USA

Summary

1. Functional traits are posited to explain interspecific differences in performance, but these relationships are difficult to describe for long-lived organisms such as trees, which exhibit strong ontogenetic changes in demographic rates. Here, we use a size-dependent model of tree growth to test the extent to which of 17 functional traits related to leaf and stem economics, adult stature and seed size predict the ontogenetic trajectory of tree growth.

2. We used a Bayesian modelling framework to parameterize and contrast three size-dependent diameter growth models using 16 years of census data from 5524 individuals of 50 rain forest tree species: a size-dependent model, a size-dependent model with species-specific parameters and a size-dependent model based on functional traits.

3. Most species showed clear hump-shaped ontogenetic growth trajectories and, across species, maximum growth rate varied nearly tenfold, from 0.58 to 5.51 mm year⁻¹. Most species attained their maximum growth at 60% of their maximum size, whereas the magnitude of ontogenetic changes in growth rate varied widely among species.

4. The Trait-Model provided the best compromise between explained variance and model parsimony and needed considerably fewer parameters than the model with species terms.

5. Stem economics and adult stature largely explained interspecific differences in growth strategy. Maximum absolute diameter growth rates increased with increasing adult stature and leaf $\delta^{13}\text{C}$ and decreased with increasing wood density. Species with light wood had the greatest potential to modulate their growth, resulting in hump-shaped ontogenetic growth curves. Seed size and leaf economics, generally thought to be of paramount importance for plant performance, had no significant relationships with the growth parameters.

6. *Synthesis.* Our modelling approach offers a promising way to link demographic parameters to their functional determinants and hence to predict growth trajectories in species-rich communities with little parameter inflation, bridging the gap between functional ecology and population demography.

Key-words: Bayesian modelling, functional traits, growth modelling, leaf economics, leaf–height–seed strategy, plant development and life-history traits, plant strategy, stem economics, tropical rain forest

Introduction

An important objective in plant community ecology is to understand how functional traits determine species perfor-

mance and species sorting across environmental gradients (Grime *et al.* 1997; Diaz *et al.* 2004). Several key traits, summarized in the leaf–height–seed strategy scheme, have been proposed to be universally important for plant performance and to represent important strategy axes (Westoby 1998; Westoby *et al.* 2002). Maximum height

*Correspondence author. E-mail: bruno.herault@ecofog.gf

determines the position of adult plants in the vertical profile of the vegetation, and hence their access to light (Hirose & Werger 1987). Specific leaf area (leaf area divided by leaf mass; SLA) indicates the leaf efficiency for light capture per unit biomass invested (Poorter *et al.* 2009). Seed mass, although not directly related to adult plant performance, is an important indicator of the life-history strategy of species, with fast-growing pioneer species tending to have small seeds (Moles *et al.* 2004). In addition, wood density is emerging as a core plant functional trait for woody species, because it is related to stem construction costs, plant architecture and stability and stem hydraulic conductance (King *et al.* 2006; Chave *et al.* 2009; Anten & Schieving 2010; Markesteijn *et al.* 2011) and hence photosynthetic carbon gain (Santiago *et al.* 2004). Recent evidence shows wood density and other stem traits to vary independently of the leaf economics spectrum (Baraloto *et al.* 2010b), suggesting the existence of at least four trait-defined axes of plant strategies (leaf–height–seed–stem).

Studies investigating one or two of these trait axes have confirmed some of the predicted relationships between traits and the absolute growth rate of woody plants. (i) Tree seedling growth tends to increase with increasing SLA and decreasing seed size (Kitajima 1994; Baraloto, Forget & Goldberg 2005; Poorter & Bongers 2006). (ii) Adult tree diameter growth increases with increasing adult stature and decreasing wood density (Poorter *et al.* 2008). Nevertheless, relatively few plant traits have been included in large comparative trait–rate studies, because many physiological traits are difficult to measure and less readily available in large data bases. Moreover, trait–growth rate relationships are considerably weaker for larger-sized trees compared with seedlings (Wright *et al.* 2010). This suggests either that sheer plant size swamps more subtle trait variation across species, or that different processes, i.e. different functional traits, become important in different phases during ontogeny. For example, SLA is an important driver of interspecific variation in seedling growth because it determines to a large extent the total leaf area (Poorter 1999). In contrast, SLA is weakly or not related to the growth of larger-sized trees (Poorter *et al.* 2008), possibly because total tree leaf area is more determined by the number of active meristems than by variation in SLA (Sterck & Bongers 2001).

An ontogenetic perspective is needed to fully understand how functional traits affect plant growth. The aforementioned studies are limited in the sense that they generally focus on one particular ontogenetic stage (mostly seedlings), or that they ignore intraspecific variation in performance by calculating species' average growth rates over a wide range of statures. Two alternative mechanistic approaches address these limitations explicitly by including resource allocation trade-offs into models of plant growth (Sterck, Poorter & Schieving 2006; Enquist, West & Brown 2009). In these examples, the considerable size-dependent variation in plant performance is incorpo-

rated directly into the model by using allometric scaling coefficients (Enquist, West & Brown 2009) or by whole-plant scaling of changes in leaf traits (Sterck, Poorter & Schieving 2006). However, these models have been difficult to calibrate, and their assumptions have been challenged (Russo, Wiser & Coomes 2007; Russo *et al.* 2008; Coomes & Allen 2009). Thus, developing a general trait-based model for the growth of trees remains an important research goal. Achieving this goal is particularly urgent in highly diverse forests, where the scarcity of the many rare species precludes the parameterization of species-specific growth models, thus impeding our ability to scale from individual growth to community dynamics.

Here, we present an alternative approach, predicting demographic rates from functional traits, and include ontogenetic variation in plant performance. We use as a starting point the growth model of Canham, LePage & Coates (2004), because it best predicts our data (see Materials and methods and Appendix S1 in Supporting Information), is mathematically tractable and has flexible model parameters that are ecologically meaningful (Fig. 1). The growth trajectory depends on G_{max} (the maximum growth rate), on D_{opt} (the diameter at maximum growth) and on K (the kurtosis of growth), which represents the shape of the ontogenetic variation in growth rate. In this study, we analyse size-dependent stem growth of 50 tropical tree species, using a 16-year census data set comprising 5524 trees.

Using a Bayesian modelling framework, we first compared the relative performance of three models parameterized at different integration levels: (i) a d.b.h.-Model where the individual growth is solely dependent on the individual d.b.h. (diameter at 1.3 m height); (ii) a Species-Model where each growth model parameter is species-specific; and (iii) a Trait-Model where the three

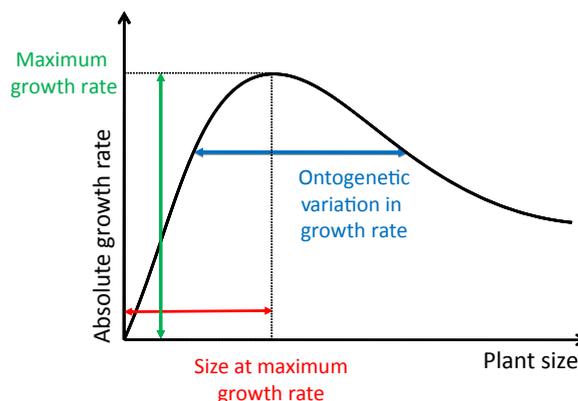


Fig. 1. A general model for adult growth trajectories of trees illustrating the parameters D_{opt} (size at maximum growth rate), K (ontogenetic variation in growth rate) and G_{max} (maximum growth rate). Note that the size at maximum growth rate may (i) be close to zero (monotonic decrease in absolute growth rate through ontogeny after this point), (ii) be equal to maximum plant size (monotonic increase) or (iii) have intermediate values leading to variable hump-shaped growth curves.

growth model parameters (G_{\max} , D_{opt} and K) are constrained to be linear combinations of functional trait values of species. We hypothesized that the Trait-Model would provide the best compromise between explained variance and model parsimony. In parameterizing the Trait-Model, we also hypothesized that (i) maximum growth rate (G_{\max}) would be positively related to trait values indicative of efficient resource acquisition (for example, high SLA and leaf nutrient concentrations), and low construction costs such as low wood density, (ii) stem diameter at optimal growth (D_{opt}) would be positively related to adult stature (maximum height and diameter) and (iii) K , which is inversely related to the peakedness of the growth curve, would depend on wood density as species with less dense wood have the best potential to accelerate their diameter growth because of low construction costs.

Materials and methods

STUDY SITE

The study was conducted at the Paracou experimental site (5°18' N, 52°55' W), a lowland tropical rain forest near Sinnamary, French Guiana. The site receives nearly two-thirds of the annual 3041 mm of precipitation between mid-March and mid-June, and < 50 mm month⁻¹ in September and October (Wagner *et al.* 2011). The most common soils in Paracou are shallow and ferralitic, limited in depth by a more or less transformed loamy saprolite. Some very thick ferralitic soils with free vertical drainage are primarily encountered on the highest residual summits of the area (approximately 40 m a.s.l.). The forest is typical of Guianan rain forests (Ter Steege *et al.* 2006; Rutishauser *et al.* 2010). More than 550 woody species attaining 2 cm d.b.h. have been described at the site, with an average of 142 species of trees ≥10 cm d.b.h. per hectare. The dominant families at the site include Fabaceae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae.

DATA COLLECTION

The study made use of two data sets. First, a total of six square 6.25-ha parcels were established in 1991 for a complete annual inventory of all trees > 10 cm d.b.h. Annual inventories of mortality, recruitment and diameter growth were conducted until 1995 and every 2 years thereafter. Here, we use data until the most recent inventory in 2007, i.e. 16 years of data. Diameter at breast height was calculated from circumference measures made to a precision of 0.5 cm. For trunks without buttresses, measurements were made at 1.3 m above the soil surface. The point of measurement was marked using permanent paint. We examined growth for 5524 trees of the 50 species (see Appendix S2) having at least 13 recorded individuals, with at least three individuals sampled for each tercile of the species d.b.h. range to ensure complete growth trajectories above 10 cm d.b.h. were included. We excluded individuals with buttresses because we were unsure about the height of the initial points of measurement for these trees. Mean annual absolute growth rates (AGR) were calculated from complete forest inventories conducted in 1991 and 2007 (Wagner *et al.* 2010).

Second, information on 17 key functional traits (related to leaf economics, stem economics and life history) for larger trees (> 10 cm

d.b.h.) of the focal species was extracted from a large data base of traits of French Guianan tree species. Details of sample collection and trait measurement are available in the study by Baraloto *et al.* (2010a,b) for the 12 leaf and stem economics traits and in the study by Herault *et al.* (2010) for the 5 life-history traits. Note that we used the 95th percentile diameters as estimates of d.b.h.max to minimize the weight of outliers (see King, Davies & Noor 2006). These traits represent complementary axes of tree ecological strategies in tropical forests (Table 1) and have been proposed to be important for tree performance through ontogeny (Westoby 1998; Weiher *et al.* 1999; Poorter *et al.* 2008). Leaf K and P contents and bark thickness were log-transformed owing to strong data heteroscedasticity. Missing trait values (3.5%) were estimated using multiple imputation with chained equations, as implemented in the mice package of R (van Buuren *et al.* 2006). Unobserved values were estimated through predictive mean matching using all other trait data as predictors, rather than assigning trait mean values as is estimated under other imputation procedures (details in Baraloto *et al.* 2010b).

GROWTH MODELS

We used as a starting point the mathematical models of ontogenetic growth trajectories that have been studied for a long time mainly by temperate foresters. Although many different modelling approaches exist, Zeide (1993) underlined the strengths of a general framework that is now used by many growth modellers. In his framework, the growth trajectory is generally adjusted by a sigmoid curve that can be biologically interpreted and that depends on tree size (d.b.h., height or biomass). In a preliminary study, we compared the predictive power of six of these models (Gompertz, Korf, Logistic, Weibull (in Zeide 1993), Canham, LePage & Coates (2004) and a power function) and retained the Canham growth model because (i) it had the lowest AIC (Akaike Information Criterion) for 19 out of our 50 species and (ii) it has mathematically tractable and ecologically meaningful parameters (Appendix S1). The model can be written as

$$\log(\text{AGR}_{is} + 1) = \text{Max}_s \times \exp\left(-\frac{1}{2} \times \left(\log\left(\frac{\text{DBH}_{is}}{D_{\text{opt}_s}/K_s}\right)\right)^2\right) + \varepsilon_{is} \quad \text{eqn 1}$$

with ε_{is} the error term of individual tree i from species s , which was assumed to follow a centred normal distribution with variance σ_s^2 . AGR_{is} is the observed absolute growth rate of individual tree i from species s (mm year⁻¹), D_{opt_s} is the diameter at optimum growth, K_s is the kurtosis of the growth model, i.e. the ontogenetic variation in growth rate, and Max_s is the maximum value of $\log(\text{AGR} + 1)$ (Fig. 1). Note that we modelled the logarithm of growth instead of growth itself because our data showed a strong heteroscedasticity. As the variance of the growth increases with increasing d.b.h., log-transforming allowed us to use a multiplicative error term ε . However, this led to a unitless Max_s . For clarity in the text, we hereafter use G_{\max_s} , a back-transformed Max_s as ($G_{\max_s} = \exp(\text{Max}_s) - 1$), to provide explicit values of maximum absolute growth rate. Note that when transforming back something modelled on the log-scale to the arithmetic scale, one needs to apply a correction factor. This is because the exponential of the error distribution centred on 0 is not centred on 1 because of the long exponential tail. To take this into account, a simulated error term was added to each log-scale model prediction before transforming back to the arithmetic scale.

Table 1. Functional traits used in the study, role in tree functional strategy (see Baraloto *et al.* 2010b) and their bivariate correlations with parameters Dopt (size at maximum growth rate), *K* (ontogenetic variation in growth rate) and Max (maximum growth rate) of the species-specific diameter growth model ($n = 50$)

	Units	Role	Dopt _s	K _s	Max _s
Leaf economics					
Foliar δ ¹³ C composition (δ ¹³ C) ^a	‰	Resource capture	0.13	0.13	0.10
Foliar C:N (C/N) ^a	cg g ⁻¹	Resource capture and defence	0.17	0.07	0.08
Foliar Km (K) ^a	mg g ⁻¹	Resource capture	0.08	-0.21	0.08
Foliar Nm (N) ^a	cg g ⁻¹	Resource capture	-0.18	-0.02	-0.12
Foliar Pm (P) ^a	mg g ⁻¹	Resource capture	-0.10	-0.06	0.00
Leaf tissue density (LTD) ^a	g cm ⁻³	Resource capture and defence	-0.01	-0.10	-0.14
Laminar total chlorophyll (chlorophyll) ^a	µg mm ⁻²	Resource capture	0.06	0.00	0.18
Laminar toughness (toughness) ^a	N	Defence	-0.09	0.10	-0.24
Specific leaf area (SLA) ^a	cm ² g ⁻¹	Resource capture and defence	-0.14	0.04	-0.05
Life history					
Forest layer (Layer) ^b	Understorey, canopy or emergent	Architecture	2.90	0.22	2.08
Maximum height (Height) ^a	m	Architecture and structure	0.19	0.08	-0.11
Maximum diameter (d.b.h.max) ^a	mm	Architecture and structure	0.66***	0.14	0.46***
Seed mass ^a	g	Reproductive investment	-0.04	-0.15	0.11
Stem and branch orientation ^b	Orthotropic or plagiotropic	Architecture	0.00	0.71	0.07
Stem economics					
Trunk bark thickness (Bark) ^a	mm	Defence	0.54***	0.00	0.29*
Trunk wood moisture content (Wood moisture) ^a	%	Transport and structure	0.16	-0.28	0.40**
Trunk xylem density (Wood density) ^a	g cm ⁻³	Transport, structure and defence	-0.11	0.43***	-0.45***

^aquantitative traits, Pearson's product-moment correlation coefficients.

^bqualitative traits, Kruskal–Wallis test chi-squared statistics.

Using a Bayesian modelling framework (see Appendix S3), we parameterized three models working at three integration levels. In the d.b.h.-Model, an individual's growth is dependent only on its d.b.h. At a given d.b.h., all individuals have the same growth rate, regardless of species. This model can be considered as the null model. In the Species-Model, the growth model parameters are species-specific, meaning that each species has its own growth trajectory. In the Trait-Model, the growth model parameters are constrained to be linear combinations of functional trait variables. The Trait-Model was built following a two-step procedure because of numerical constraints of variable selection in Bayesian models. First, for Max, Dopt and *K*, we built a linear model where the significant functional traits among the 17 were selected by the Bayesian information criterion (BIC, Schwarz 1978) using the R package glmulti (Calcagno 2011). We used this package (i) to find the best variable linear combination that contains the maximum information to link functional traits and Species-Model parameters according to the BIC criterion and (ii) to reduce the multicollinearity problem by eliminating some variables that were highly correlated each other. We used BIC, instead of the classically used AIC, to avoid over-parameterization as this criterion is consistent and parsimonious for model selection with respect to large data sets (Burnham & Anderson 2004). Next, the selected functional traits were incorporated into a single Trait-Model (see Appendix S3 for fur-

ther details), where we generalized the case of the Species-Model assuming that the three parameters Max, Dopt and *K* can be expressed as linear functions of trait values (TG, TD and TK, respectively) for all individuals $i = 1, \dots, n$: $\text{Max}_i = g_0 + g_1 \times \text{TG}_i^1 + \dots + g_p \times \text{TG}_i^p$, $\text{Dopt}_i = d_0 + d_1 \times \text{TD}_i^1 + \dots + d_q \times \text{TD}_i^q$, and $K_i = k_0 + k_1 \times \text{TK}_i^1 + \dots + k_r \times \text{TK}_i^r$. This leads to the following Trait-Model:

$$\begin{aligned} \log(\text{AGR}_i + 1) &= (g_0 + g_1 \times \text{TG}_i^1 + \dots + g_p \times \text{TG}_i^p) \\ &\times \exp\left(-\frac{1}{2} \times \left(\frac{\log\left(\frac{\text{DBH}_i}{d_0 + d_1 \times \text{TD}_i^1 + \dots + d_q \times \text{TD}_i^q}\right)}{k_0 + k_1 \times \text{TK}_i^1 + \dots + k_r \times \text{TK}_i^r}\right)^2\right) + \varepsilon_i \end{aligned} \quad \text{eqn 2}$$

[Correction added after online publication 30 August 2011: the values g_q in equation 2 was corrected to d_q here and in the sentence referring to the equation above] The relative performance of the three competing models was assessed with the BICM (Bayesian Information Criterion Monte Carlo), a posterior simulation-based analogue of the BIC (Raftery *et al.* 2007). The predictive power of the three growth models was quantified through

Table 2. Relative performance of the three growth models

	Log (Likelihood)	N parameters	BICM ^a	RMSEP ^b (mm year ⁻¹)
Trait-Model	-2945	7	5943	0.51
Species-Model	-2307	200	6042	0.43
d.b.h.-Model	-3413	4	6857	0.57

Note that according to the BICM performance criterion, the Trait-Model was retained as the best compromise between variance explained and parameter inflation. The Species-Model was the best in terms of explained variance (highest log (likelihood)) but was less parsimonious. The d.b.h.-Model performed poorly despite its extreme parameter parsimony.

^aPosterior simulation-based analogues of the Bayesian information criterion.

^bRoot mean squared error of predictions.

the root mean squared error of prediction (RMSEP). All analyses were performed using the R project software (<http://cran.r-project.org>).

Results

COMPARING THE THREE GROWTH MODELS

The d.b.h.-Model performed poorly (BICM 6857, Table 2), despite its extreme parameter parsimony (four parameters). We first focus on the Species-Model, which was the best in terms of explained variance (0.43

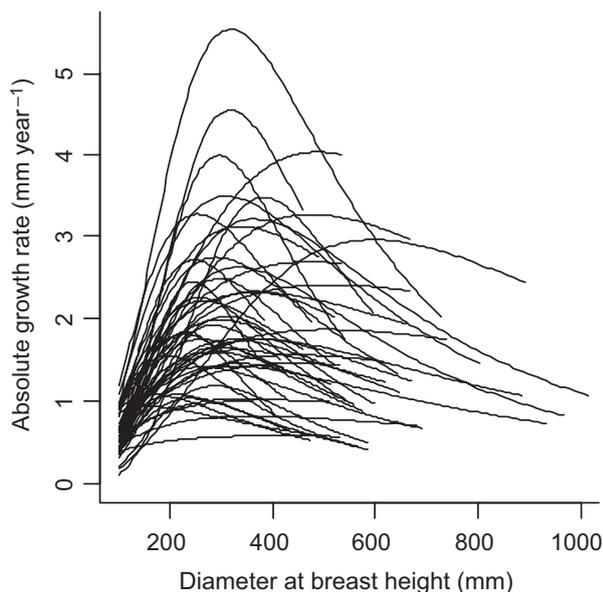


Fig. 2. Diversity of the adult growth trajectories among 50 neotropical trees of French Guiana. Note the continuous variation of the growth curve shapes and parameters (size at maximum growth rate: D_{opt} , ontogenetic variation in growth rate: K , maximum growth rate: G_{max}) of the Species-Model, suggesting that it should be possible to construct continuous trait-based models without having to collapse the great numbers of tropical tree species into a small set of functional groups.

mm year⁻¹ in RMSEP), but which added 196 parameters, resulting in a BICM of 6042. We then present the Trait-Model, which was retained by BICM (5943) as the best performing model, i.e. the best compromise between variance explained and parameter inflation (Table 2).

SPECIES-MODEL AND SIZE-DEPENDENT GROWTH

Most species showed strong size dependency in growth rates, with a peak at intermediate stem diameters (Fig. 2, Appendix S2). D_{opt} , the size at which growth rates are greatest, varied from 157 mm for the understorey species *Chaetocarpus schomburgkianus* (Euphorbiaceae) to 596 mm for the canopy species *Sextonia rubra* (Lauraceae) and averaged 331 mm across species. G_{max} averaged 2.04 mm year⁻¹ and varied from 0.58 mm year⁻¹ for *Bocoa prouacensis* (Fabaceae) to 5.51 mm year⁻¹ for *Symphonia globulifera* (Clusiaceae). Kurtosis (K) varied from 0.55 (corresponding to a spike in absolute growth rate, *Licania laxiflora* (Chrysobalanaceae)) to 1.71 (flat growth curve, *Bocoa prouacensis*) and averaged 0.94.

TRAIT-BASED GROWTH MODELS OF TROPICAL TREES

The selection procedure of the Trait-Model led to a single model (Table 3) combining four functional traits (d.b.h.max, Wood Density, Height and $\delta^{13}C$). Diameter at maximum growth (D_{opt}) was significantly and positively correlated with a single trait, the maximum tree size (d.b.h.max, $R^2 = 0.43$). K increased with wood density ($R^2 = 0.19$), meaning that species with denser wood less modulate their growth (i.e. they have flatter growth curves). Maximum growth rate was explained by four functional traits ($R^2 = 0.45$), increasing with increasing d.b.h.max and decreasing with maximum height, wood density and $\delta^{13}C$. All in all, the Species-Model and the Trait-Model growth curves matched each other closely (Fig. 3, Appendix S4). As the most common species have more individuals, and thus have greater weight in the inference of the Trait-Model, one may expect relatively poor predictions to be made for rare species. We do not, however, observe such a system-

Table 3. Estimated parameters of the Trait-Model, D_{opt} (size at maximum growth rate), K (ontogenetic variation in growth rate) and Max (maximum growth rate)

Predictors	Estimates	95% credibility intervals
D_{opt}		
d.b.h.max	0.60	[0.57; 0.63]
K		
Wood density	1.28	[1.20; 1.37]
Max		
d.b.h.max	1.5×10^{-3}	$[1.4 \times 10^{-3}; 1.6 \times 10^{-3}]$
Wood density	-1.00	[-1.10; -0.90]
Height	-1.2×10^{-2}	$[-1.4 \times 10^{-2}; -1.0 \times 10^{-2}]$
$\delta^{13}C$	-4.9×10^{-2}	$[-5.3 \times 10^{-2}; -4.5 \times 10^{-2}]$

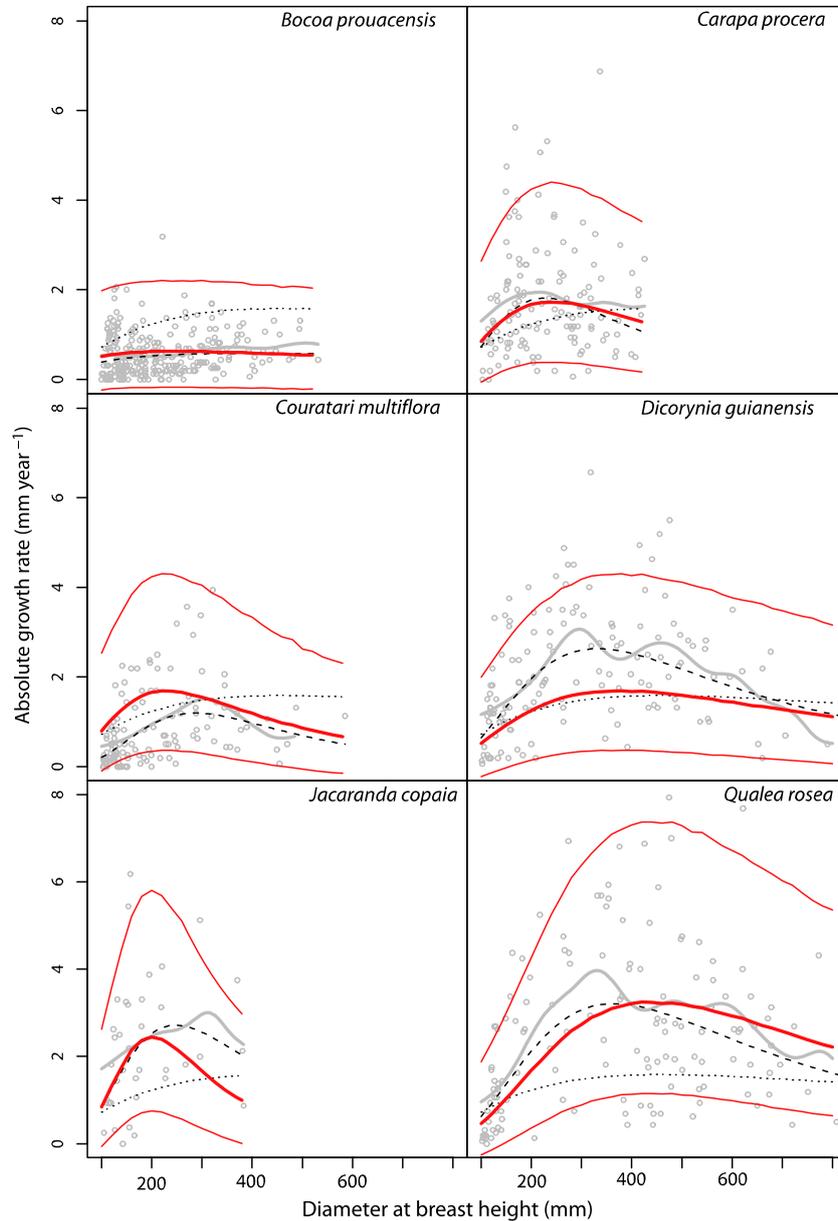


Fig. 3. Modelled adult growth trajectories of six neotropical tree species. Observed absolute diameter growth rates plotted against the observed tree diameters at breast height (light grey line). The curves indicate the predictions of the Species-Model (black dashed line), the d.b.h.-Model (black dotted line) and the Trait-Model (thick red line with 95% credibility intervals shown thinner; lines appear dark grey in print).

atic degradation of the quality of predictions in the 50 studied species (Fig. 4).

Discussion

In this study, we modelled size-dependent growth of tropical tree species and found that by using a few traits mainly related to plant size and stem economics, we could successfully predict growth trajectories of 50 rain forest tree species. This suggests that our Trait-Model approach could be used to predict tree growth in highly diverse tropical forests for which growth data may be lacking, but functional trait data are available.

SIZE-DEPENDENT TREE GROWTH

Most species showed size-dependent growth, with maximal growth rates attained at intermediate sizes (Fig. 2). Growth may increase rapidly with tree size because taller trees have better access to light and a larger photosynthetic area (Sterck *et al.* 2003). Upon attaining the canopy, many species may spread their crown to further enhance light capture and maximize growth (Poorter, Bongers & Bongers 2006). At even larger diameters, growth rates can decrease because constant biomass investment leads to less overall diameter increment. In addition, four other mechanisms may contribute to the decline in growth rate at larger

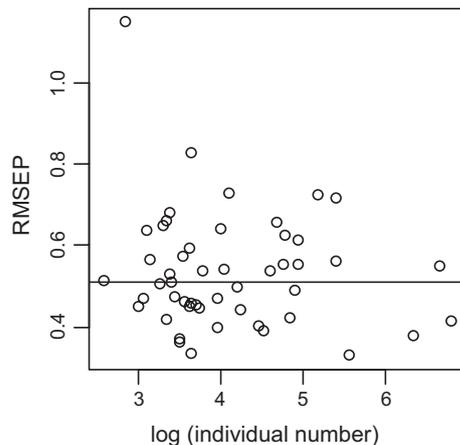


Fig. 4. Quality of the Trait-Model predictions versus species commonness. The Trait-Model inference may be strongly influenced by the species relative abundances. To test whether there is a systematic bias towards good predictions for common species and relatively poor predictions for rare species, we plotted the Trait-Model root mean squared error of predictions (RMSEP) against the logarithm of the species frequency. Note that the global RMSEP was found to be 0.51 (horizontal line). We showed that there was no direct relationship between RMSEP and species commonness ($R^2 < 0.001$, $P = 0.30$).

sizes: (i) the respiration load of roots and stems becomes too high (Ryan & Yoder 1997); (ii) hydraulic pathways become too long, leading to water stress and stomatal closure (Koch *et al.* 2004); (iii) resources are reallocated to reproduction (Thomas 1996); or (iv) trees begin to senesce. Only one species (*Bocoa prouacensis*, Appendix S2) had D_{opt} equivalent to $d.b.h._{max}$. Thus, the hump-backed growth–diameter relationships appear pervasive among the majority of these species. This argues against the use of simplistic monotonic power–law relationships for modelling the relationship between diameter growth and tree size (Muller-Landau *et al.* 2006; Coomes & Allen 2009; Enquist, West & Brown 2009). Such a power–law relationship applies when all species are pooled (as in the $d.b.h._{Model}$), but it may mask the trait-based species-level patterns that shape it. In our data set, the community-level power-law-type relationship is clearly the result of overlapping species-specific hump-shaped growth curves, in which species attaining larger sizes tend to have faster growth (Fig. 2).

The root mean squared error of prediction of the Species-Model was $0.43 \text{ mm year}^{-1}$, relative to mean growth rate of $1.52 \text{ mm year}^{-1}$. Such a relatively low error level is remarkable, given that we modelled only the growth trajectory, with no consideration of tree-to-tree variation in resource availability, density dependence, genetics, abiotic factors or tree vigour (Kariuki *et al.* 2006).

FUNCTIONAL TRAITS AS PREDICTORS OF SIZE-DEPENDENT GROWTH

This is one of the first studies to relate the parameters of a tree growth trajectory model to functional traits, provid-

ing an important extension to previous studies focussing on species mean or on upper-quantile growth rates (Poorter *et al.* 2008; Wright *et al.* 2010). The parameter D_{opt} represents the tree diameter at which a species realizes its greatest annual growth increment. This parameter was well predicted by a single functional trait, the maximum size ($d.b.h._{max}$) of the species, with larger species realizing their maximum growth at larger sizes. Interestingly, we found that most species attain their maximum growth at 60% of their maximum size (Table 3). Two alternative mechanisms may explain this pattern. First, it may reflect differences in $d.b.h._{height}$ allocation such that for all species, 60% $d.b.h._{max}$ represents the point at which its crown reaches the canopy ($>25 \text{ m}$). Alternatively, the stage for optimal growth rates may be driven by internal shifts in allocation, affecting the balance between photosynthesizing and respiring tissue, or the balance between vegetative growth and reproduction (Thomas 1996).

The parameter K indicates the kurtosis of the growth curve, i.e. the ontogenetic variation in growth rate. It is important to note that in our growth model, K is inversely linked to the ‘peakedness’ of the size-dependent growth curve. As hypothesized, wood density was a reasonable predictor of K , but a large proportion of variance in K remained unexplained (Fig. 5). Among the three parameters of the growth models, we believe that K may be the most dependent on extrinsic factors. For example, a sudden increase in irradiance because of a new canopy gap would lead to a sudden growth and therefore to a small K , whereas the same tree located in the understorey may exhibit a slow growth and therefore a high K . This may explain why functional traits alone cannot accurately predict K . Nevertheless, the value of K did increase with wood density. This finding is consistent with a positive correlation between wood density and shade tolerance (Poorter *et al.* 2010). Species with light wood and associated low volumetric construction costs may have the best potential to accelerate their growth at intermediate sizes when they attain the forest canopy, resulting in a hump-shaped trajectory. On the contrary, heavy-wooded species with constrained construction potential, such as *Bocoa prouacensis*, generally exhibit a platykurtic behaviour, highlighting their slow, but relatively constant, growth pattern even once they attain the canopy (Herault *et al.* 2010).

Maximum absolute growth rate (Max) varied widely among species and was well predicted by a suite of four functional traits (Fig. 5). Maximum growth increased strongly with $d.b.h._{max}$ (Table 2). Species that attain large sizes may realize faster growth rates simply because they intercept more light because of their taller stems and larger crowns. In contrast, the maximum growth was negatively related to maximum tree height. This counterintuitive result may be explained because, for a given $d.b.h._{max}$, species that attain great heights invest in rapid vertical growth rather than diameter increment. Species with higher wood density had lower maximum growth in line

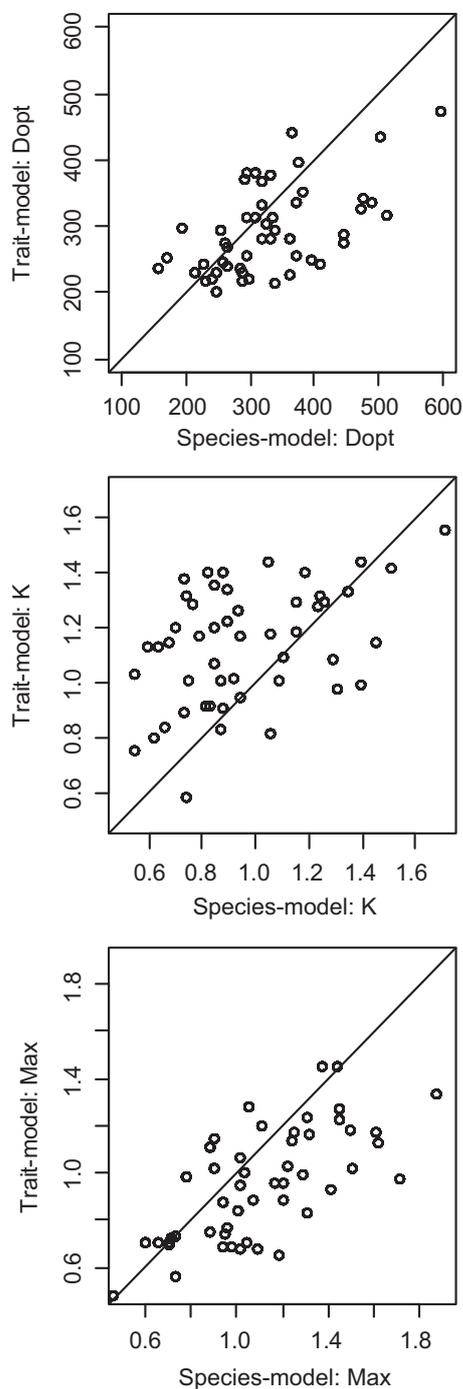


Fig. 5. Comparison of the parameters of the Species- and Trait-growth Models. Trait-Model estimates of Dopt (size at maximum growth rate), K (ontogenetic variation in growth rate) and Max (maximum growth rate) plotted against the observed Species-Model parameters. The identity line indicates that the Trait-Model slightly under-predicted Dopt and Max, while slightly over-predicted K . Note that the Dopt and K parameters of the Trait-Model are, respectively, equal to $0.60 \cdot \text{d.b.h.} \cdot \text{max}$ and $1.28 \cdot \text{wood density}$, highlighting the direct relationships between these two functional traits and the Dopt and K of the Species-Model.

with predictions (Poorter *et al.* 2008). A low wood density not only implies cheap volumetric construction cost, facilitating rapid expansion in tree diameter and height, but

also tends to be associated with a high hydraulic capacity and hence large photosynthetic carbon gain (Santiago *et al.* 2004; Markesteijn *et al.* 2011). The negative relationship between $\delta^{13}\text{C}$ and maximum growth is consistent with other studies finding low isotope estimations of water use efficiency for faster-growing or heliophilic species, reflecting their tendency to higher photosynthetic capacity per stomatal conductance (Bonal *et al.* 2000).

Surprisingly, leaf traits had very little effect on tree growth. Positive relationships between SLA and tree growth have often been found for small seedlings growing under standardized conditions, but this relationship is weak or absent for large trees growing in the field (Poorter *et al.* 2008; Wright *et al.* 2010), consistent with our results. Contrasting explanatory power for adult tree growth of traits describing leaf and stem economics strengthens the argument that stem and leaf tissues offer different axes of plant strategies (Baraloto *et al.* 2010b).

Conclusions

We used a trait data base that is unprecedented in terms of scale and detail for tropical rain forest trees in concert with long-term growth data for a large number of tropical tree species, but we found that relatively few functional traits predicted plant growth. Only two of the four axes in the proposed leaf–height–seed–stem scheme appear to substantially contribute to the growth dynamics of the 50 studied species. Adult stature (diameter, height) represents an important strategy axis of variation in tall, closed-canopy tropical forests where there is strong asymmetric competition for light (Kohyama *et al.* 2001). An important additional trait is wood density, which is at the nexus of many different plant functions (Chave *et al.* 2009), and which is thought to be important for both plant growth and survival. Leaf traits are less important; however, based on the leaf economics spectrum, we had expected a larger role for nutrient concentrations in predicting photosynthetic capacity and carbon gain (Wright *et al.* 2004). Seed size is a poor predictor of adult growth rates, although it might be very important for the regeneration strategy (Moles *et al.* 2004; Baraloto, Goldberg & Bonal 2005).

Our approach offers a promising way to model individual growth; the explicit link between functional traits and growth parameters may bridge the gap between individual-based and community-level models with little parameter inflation. This is a necessary step towards the development of global community trait-based models with no requirement to collapse the great numbers of tree species into a small set of functional groups.

Acknowledgements

A grant from the ANR to C.B. and J.C. supported the BRIDGE project. This manuscript is also part of the CLIMFOR project (FRB grant to B.H.). We thank all participants of the project BRIDGE who participated

in field and laboratory collection and treatment of specimens. Field research was facilitated by the Guyafor permanent plot network in French Guiana which is managed by CIRAD (Centre de coopération Internationale en Recherche Agronomique pour le Développement) and ONF (Office National des Forêts). Basic annual funding and stipends were provided by CIRAD, the institution of Paracou. This study has been possible thanks to the important field work realized at Paracou by many people of CIRAD; L. Schmitt, P. Pétronelli, D. Max, O. N'Gwete, Mo. Baisie, Mi. Baisie, K. Ficadici, A. Etienne, F. Kwasié, K. Martinus, P. Naisso and R. Santé. We thank David Coomes and two anonymous referees for useful comments on previous drafts of the manuscript.

References

- Anten, N.P.R. & Schieving, F. (2010) The role of wood mass density and mechanical constraints in the economy of tree architecture. *American Naturalist*, **175**, 250–260.
- Baraloto, C., Forget, P.M. & Goldberg, D.E. (2005) Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology*, **93**, 1156–1166.
- Baraloto, C., Goldberg, D.E. & Bonal, D. (2005) Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology*, **86**, 2461–2472.
- Baraloto, C., Paine, C.E.T., Patino, S., Bonal, D., Herault, B. & Chave, J. (2010a) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, **24**, 208–216.
- Baraloto, C., Paine, C.E.T., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.M., Herault, B., Patino, S., Roggy, J.C. & Chave, J. (2010b) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338–1347.
- Bonal, D., Sabatier, D., Montpied, P., Treméaux, D. & Guehl, J.M. (2000) Interspecific variability of delta C-13 among trees in rainforests of French Guiana: functional groups and canopy integration. *Oecologia*, **124**, 454–468.
- Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods Research*, **33**, 261.
- van Buuren, S., Brand, J.P.L., Groothuis-Oudshoorn, C.G.M. & Rubin, D.B. (2006) Fully conditional imputation in multivariate imputation. *Journal of Statistical Computation and Simulation*, **76**, 1049–1064.
- Calcagno, V. (2011) *GLM model selection and multimodel inference made easy*. <http://cran.r-project.org/web/packages/glmulti/glmulti.pdf>.
- Canham, C., LePage, P. & Coates, K. (2004) A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research*, **34**, 778–787.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Coomes, D.A. & Allen, R.B. (2009) Testing the metabolic scaling theory of tree growth. *Journal of Ecology*, **97**, 1369–1373.
- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
- Enquist, B.J., West, G.B. & Brown, J.H. (2009) Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 7046–7051.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H. *et al.* (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.
- Herault, B., Ouallet, J., Blanc, L., Wagner, F. & Baraloto, C. (2010) Growth responses of neotropical trees to logging gaps. *Journal of Applied Ecology*, **47**, 821–831.
- Hirose, T. & Werger, M. (1987) Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia*, **72**, 520–526.
- Kariuki, M., Rolfe, M., Smith, R.G.B., Vanclay, J.K. & Kooyman, R.M. (2006) Diameter growth performance varies with species functional-group and habitat characteristics in subtropical rainforests. *Forest Ecology and Management*, **225**, 1–14.
- King, D.A., Davies, S.J. & Noor, N.S.M. (2006) Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *Forest Ecology and Management*, **223**, 152–158.
- King, D.A., Davies, S.J., Tan, S. & Noor, N.S.M. (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, **94**, 670–680.
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**, 419–428.
- Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. *Nature*, **428**, 851–854.
- Kohyama, T., Suzuki, E., Partomihardjo, T. & Yamada, T. (2001) Dynamic steady state of patch-mosaic tree size structure of a mixed dipterocarp forest regulated by local crowding. *Ecological Research*, **16**, 85–98.
- Markesteyn, L., Poorter, L., Bongers, F., Paz, H. & Sack, L. (2011) Hydraulics and life-history of tropical dry forest tree species: coordination of species drought- and shade-tolerance. *New Phytologist*, **191**, 480–495.
- Moles, A.T., Falster, D.S., Leishman, M.R. & Westoby, M. (2004) Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology*, **92**, 384–396.
- Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavejchewin, S. *et al.* (2006) Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters*, **9**, 575–588.
- Poorter, L. (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology*, **13**, 396–410.
- Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, **87**, 1733–1743.
- Poorter, L., Bongers, L. & Bongers, F. (2006) Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology*, **87**, 1289–1301.
- Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriquez, G. *et al.* (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, **89**, 1908–1920.
- Poorter, H., Niinemets, U., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.
- Poorter, L., McDonald, I., Alarcon, A., Fichtler, E., Licona, J.C., Pena-Claros, M., Sterck, F., Villegas, Z. & Sass-Klaassen, U. (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*, **185**, 481–492.
- Raftery, A., Newton, M., Satagopan, J. & Krivitsky, P. (2007) Estimating the integrated likelihood via posterior simulation using the harmonic mean identity. In *Bayesian statistics* (eds J. Bernardo, M. Bayarri, J. Berger, A. Dawid, D. Heckerman, A. Smith & M. West), pp. 1–45. Oxford university Press, Oxford.
- Russo, S.E., Wiser, S.K. & Coomes, D.A. (2007) Growth-size scaling relationships of woody plant species differ from predictions of the Metabolic Ecology Model. *Ecology Letters*, **10**, 889–901.
- Russo, S.E., Brown, P., Tan, S. & Davies, S.J. (2008) Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology*, **96**, 192–203.
- Rutishauser, E., Wagner, F., Herault, B., Nicolini, E.A. & Blanc, L. (2010) Contrasting above-ground biomass balance in a Neotropical rain forest. *Journal of Vegetation Science*, **21**, 672–682.
- Ryan, M. & Yoder, B. (1997) Hydraulic limits to tree height and tree growth. *BioScience*, **47**, 235–242.
- Santiago, L.S., Goldstein, G., Meinzer, F.C., Fisher, J.B., Machado, K., Woodruff, D. & Jones, T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia*, **140**, 543–550.
- Schwarz, G.E. (1978) Estimating the dimension of a model. *Annals of Statistics*, **6**, 461–464.
- Sterck, F.J. & Bongers, F. (2001) Crown development in tropical rain forest trees: patterns with tree height and light availability. *Journal of Ecology*, **89**, 1–13.
- Sterck, F.J., Poorter, L. & Schieving, F. (2006) Leaf traits determine the growth-survival trade-off across rain forest tree species. *American Naturalist*, **167**, 758–765.
- Sterck, F.J., Bongers, F., Durrant, H.J., Martinez-Ramos, M. & De Kroon, H. (2003) Module responses in a tropical forest tree analyzed with a matrix model. *Ecology*, **84**, 2751–2761.
- Ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.F., Prevoist, M.F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vasquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444–447.
- Thomas, S.C. (1996) Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *Oikos*, **76**, 145–154.

- Wagner, F., Rutishauser, E., Blanc, L. & Hérault, B. (2010) Effects of plot size and census interval on descriptors of forest structure and dynamics. *Biotropica*, **42**, 664–671.
- Wagner, F., Hérault, B., Stahl, C., Bonal, D. & Rossi, V. (2011) Modeling water availability for trees in tropical forests. *Agricultural and Forest Meteorology*, **151**, 1202–1213.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, **10**, 609–620.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. et al. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright, S., Kitajima, K., Kraft, N., Reich, P., Wright, I.J., Bunker, D. et al. (2010) Functional traits and the growth-mortality tradeoff in tropical trees. *Ecology*, **91**, 3664–3674.
- Zeide, B. (1993) Analysis of growth equations. *Forest Science*, **39**, 594–616.

Received 16 February 2011; accepted 27 July 2011
Handling Editor: David Coomes

Supporting Information

Additional Supporting Information may be found in the online version of this article. [Correction added after online publication 1 September 2011: the supporting information was replaced to correct mistakes in the data.]

Appendix S1. Relative performance of six commonly-used growth models used to predict the growth performance of 5524 individual trees from 50 neotropical species.

Appendix S2. List of the 50 neotropical tree species used for growth modelling: values of the parameters of the Species-Model and values of the functional traits used selected for inclusion in the Trait-Model.

Appendix S3. Detailed MCMC algorithms used to calibrate the growth models.

Appendix S4. Modelled adult growth trajectories of 50 neotropical trees.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.