ORIGINAL ARTICLE



# Contrasted allometries between stem diameter, crown area, and tree height in five tropical biogeographic areas

Elodie Blanchard<sup>1</sup> · Philippe Birnbaum<sup>1,2</sup> · Thomas Ibanez<sup>1</sup> · Thomas Boutreux<sup>1</sup> · Cécile Antin<sup>3</sup> · Pierre Ploton<sup>3</sup> · Grégoire Vincent<sup>3</sup> · Robin Pouteau<sup>1</sup> · Hervé Vandrot<sup>1</sup> · Vanessa Hequet<sup>4</sup> · Nicolas Barbier<sup>3</sup> · Vincent Droissart<sup>3,5</sup> · Bonaventure Sonké<sup>5</sup> · Nicolas Texier<sup>3,5</sup> · Narcisse Guy Kamdem<sup>5</sup> · Donatien Zebaze<sup>5</sup> · Moses Libalah<sup>5</sup> · Pierre Couteron<sup>3</sup>

Received: 9 September 2015/Accepted: 3 June 2016/Published online: 18 June 2016 © Springer-Verlag Berlin Heidelberg 2016

#### Abstract

*Key message* Across five biogeographic areas, DBH-CA allometry was characterized by inter-site homogeneity and intra-site heterogeneity, whereas the reverse was observed for DBH-H allometry.

Abstract Tree crowns play a central role in stand dynamics. Remotely sensed canopy images have been shown to allow inferring stand structure and biomass which suggests that allometric scaling between stems and crowns may be tight, although insufficiently investigated to date. Here, we report the first broad-scale assessment of stem vs. crown scaling exponents using measurements of bole diameter (DBH), total height (H), and crown area (CA) made on 4148 trees belonging to 538 species in five biogeographic

Communicated by E. Beck.

Elodie Blanchard blanchard@iac.nc

- <sup>1</sup> Institut Agronomique Néo-Calédonien (IAC), Diversité Biologique et Fonctionnelle des Écosystèmes terrestres, Laboratoire de Botanique et d'Écologie Végétale Appliquées, BP A5, 98848 Noumea, New Caledonia
- <sup>2</sup> Centre de Coopération Internationale en Recherche Agronomique Pour le Développement (CIRAD), UMR 51-AMAP, Boulevard de la Lironde, TA A-51/PS2, 34398 Montpellier Cedex 5, France
- <sup>3</sup> Institut de Recherche Pour le Développement (IRD), UMR AMAP, Boulevard de la Lironde, TA A-51/PS2, 34398 Montpellier Cedex 5, France
- <sup>4</sup> Institut de Recherche Pour le Développement (IRD), BP A5, 98848 Nouméa, New Caledonia
- <sup>5</sup> Laboratoire de Botanique Systématique et d'Ecologie, Département des Sciences Biologiques, Ecole Normale Supérieure, Université de Yaoundé I, BP 047, Yaoundé, Cameroon

areas across the wet tropics. Allometries were fitted with power functions using ordinary least-squares regressions on log-transformed data. The inter-site variability and intra-site (sub-canopy vs. canopy trees) variability of the allometries were evaluated by comparing the scaling exponents. Our results indicated that, in contrast to both DBH-H and H-CA allometries, DBH-CA allometry shows no significant inter-site variation. This fairly invariant scaling calls for increased effort in documenting crown sizes as part of tree morphology. Stability in DBH-CA allometry, indeed, suggests that some universal constraints are sufficiently pervasive to restrict the exponent variation to a narrow range. In addition, our results point to inverse changes in the scaling exponent of the DBH-CA vs. DBH-H allometries when shifting from sub-canopy to canopy trees, suggesting a change in carbon allocation when a tree reaches direct light. These results pave the way for further advances in our understanding of niche partitioning in tree species, tropical forest dynamics, and to estimate AGB in tropical forests from remotely sensed images.

**Keywords** Allometry · Tree architecture · Stem size · Ontogeny · Crown light exposure · Rainforest

# Introduction

Forest ecosystems are complex three-dimensional arrangements of individual trees. Most models of forest structure and dynamic still rely on diameters at breast height (DBH) as an easy-to-measure proxy for 3D tree dimensions, such as tree height and crown sizes. In fact, data on tree height (H) and crown dimensions are more difficult to acquire than DBH, especially from very large tropical trees that predominantly contribute to forest

structure (Lindenmayer et al. 2012; Lutz et al. 2013) and to carbon and biomass storage (AGB, Slik et al. 2013; Fauset et al. 2015; Bastin et al. 2015). Data on H are increasingly integrated in forest models (e.g., Kohyama et al. 2003; Feldpausch et al. 2012), notably with the recent use of airborne LiDAR (light detection and ranging) to measure forest height (e.g., Clark et al. 2004; Kennel et al. 2013). In comparison, crown size, shape, and position are seldom used (but see Harja et al. 2012; Bohlman and Pacala 2012; Taubert et al. 2015; Farrior et al. 2016), while it has been shown that they are appropriate variables to predict tree growth and mortality (Moravie et al. 1999; King 2005; Muller-Landau et al. 2006). To improve models in spite of difficulties in data acquisition, authors used tree allometries to estimate tree H and crown dimensions from DBH (e.g., Harja et al. 2012; Bohlman and O'Brien 2006; Antin et al. 2013).

In recent decades, the variability of allometries between tree DBH and H, and its consequences for understanding stand dynamics and forest AGB estimation have raised increasing interest (e.g., Aiba and Kohyama 1996; Thomas 1996; Feldpausch et al. 2011; Banin et al. 2012; Lines et al. 2012; Harja et al. 2012; Thomas et al. 2015). In comparison, the allometries between crown dimensions and either DBH or H have received a very little interest. Most studies focused on the trade-off between investments in H versus crown expansion during ontogeny by comparing species adult stature (King 1996; Henry and Aarssen 1999; Kohyama et al. 2003; Poorter et al. 2003, 2006; Osunkoya et al. 2007; King and Clark 2011). Nevertheless, recent publications highlighted the importance of crown allometries in understanding the structural organization of forest stands and their productivity (Mäkelä and Valentine 2006; Coomes et al. 2012; Attocchi and Skovsgaard 2015; Muller-Landau et al. 2006), the diversification of tree architecture (Olson et al. 2009), niche partitioning in trees within a forest stand (Lines et al. 2012; Antin et al. 2013), and the variations in canopy structure (Bohlman and O'Brien 2006; Bohlman and Pacala 2012; Palace et al. 2015; Farrior et al. 2016). It was also recently demonstrated that including information on crown widths in classical AGB allometric models (i.e., based on DBH, H and wood density, Chave et al. 2005, 2014) greatly improved model fit, particularly in the case of large trees (Goodman et al. 2014; Ploton et al. 2016).

Allometries are of increasing importance in the development of remote sensing surveys of forests to estimate forest AGB at landscape and regional scales. Both tree H and crown sizes have been shown to be good predictors of AGB, and may be measured by remotely sensed information. For instance, AGB was modelled from canopy height data derived from airborne LiDAR (Asner 2009; Saatchi et al. 2011; Baccini et al. 2012; Zolkos et al. 2013; Bouvier et al. 2015) or from assessments of crown size distribution of canopy trees derived from textural analysis of very high spatial resolution (VHR) optical images (Proisy et al. 2007; Barbier et al. 2010; Ploton et al. 2013; Bastin et al. 2014; Singh et al. 2015). However, neither LiDAR nor VHR optical data provide direct data on tree DBH, which is the traditional biomass predictor and the main stand structure variable measured in the field. To be comparable with DBH-based data, remote sensing information needs to be complemented by allometric relationships, which is the missing link to infer DBH-based stand variables from canopy metrics.

Patterns of tree allometries partly reflect the fundamental concepts in plant architecture defined by the balance between plant form and functions (Hallé et al. 1978; Barthélémy and Caraglio 2007). During tree ontogeny, tree growth results from a trade-off between vertical growth of the stem to reach the sunniest layer of the vegetation and horizontal expansion of the crown to maximize light interception. Hence, dense stands promote vertical growth (Montgomery and Chazdon 2001; Osunkoya et al. 2007; Bohlman and Pacala 2012), while increasing light availability and lateral empty space promote horizontal crown expansion. In turn, this expansion is associated with the thickening of the stem base required for mechanical support at the expense of vertical growth (Sterck and Bongers 2001; King 1996; Yamada et al. 2005). Mechanical interactions between trees limit lateral crown extension through branch abrasion of moving canopies, which is illustrated by the so-called "crown shyness gap" in the canopy layer (Jacobs 1955; Putz et al. 1984). Tree strategies for resource allocation and their influence on allometries are, thus, mainly driven by competition for space (Hajek et al. 2015) and light (Banin et al. 2012; Lines et al. 2012), which mainly depend on the position of the crown within the 3D structure of the forest stand.

In parallel, several studies have shown that allocation patterns between tree dimensions can differ among species, according to different species-specific traits, such as the adult stature (Aiba and Kohyama 1996; Kohyama et al. 2003; Bohlman and O'Brien 2006; Iida et al. 2011), wood density (Anten and Schieving 2010; Iida et al. 2012; Thomas et al. 2015), or responses to resource availability (Poorter et al. 2003; Kitajima et al. 2005; Quesada et al. 2012). In allometric equations, the scaling exponent of the power function can also be shaped by the environmental conditions of the stand (e.g., Sterck and Bongers 2001; Osada et al. 2004; Nogueira et al. 2008; Lang et al. 2010; Heineman et al. 2011), the local environment of an individual tree, and by the diversity of tree communities (e.g., Iwasa et al. 1985; King and Maindonald 1999; Poorter et al. 2003; Kitajima et al. 2005).

In reverse to all these sources of variation, some general mechanical growth constraints promote stability in the allometric relationship between DBH and crown size. Indeed, the mechanical constraints exerted by leaves on stems supporting them and the hydraulic constraints suffered by stems that have to supply water to leaves may drive the size and total area of leaves deployed by the stems (Niklas 1992; Westoby et al. 2002; Westoby and Wright 2003). The metabolic theory of ecology (MTE, West et al. 1999; Brown et al. 2004) has generated specific allometric predictions by some of these constraints. The MTE theory is based on the assumption that the metabolic scaling is invariably reflected into the morphological scaling. However, several studies suggest that the MTE fails to predict the observed scaling exponent of the H-DBH allometry (Poorter et al. 2003; Coomes et al. 2003; Bohlman and O'Brien 2006; Muller-Landau et al. 2006), whereas the MTE may better predict the scaling exponent of the crown allometries [i.e., DBH-crown area (CA) allometry] (Antin et al. 2013). Furthermore, the correlation between canopy metrics (computed from remotely sensed data) and stand parameters (measured in the field) supports the hypothesis of a fairly stable allometric relationship between the dimensions of the crown and of the stem (Read et al. 2003; Couteron et al. 2005; Broadbent et al. 2008).

While it has been shown that DBH-H allometry is largely site-dependent in tropical forests (Feldpausch et al. 2011; Banin et al. 2012; Vincent et al. 2012), the variability of DBH-CA allometry across biogeographic areas has, to our knowledge, never been addressed. Is the scaling exponent of the DBH-CA allometry as variable as the scaling exponent of the DBH-H allometry? Does scaling vary between biogeographic contexts or does it depend on the position of the trees in the local stand arrangement? To address these questions, data from five tropical forests located in different biogeographic areas with different climates and disturbance levels were gathered. First, intersite variability and intra-site variability of DBH-CA, DBH-H, and H-CA allometries were compared. A stable scaling exponent between DBH and CA across tropical forests would allow the use of simple crown area parameters to improve AGB allometric models and to predict stand structure variables at large scale from airborne and space borne sensors. Second, allometries of species able to reach the canopy at maturity were analyzed to determine to what extent intra-site variability can be consistently interpreted as a consequence of the "liberation" effect (Cusset 1980), i.e., the full extension of crown when a tree reaches the upper canopy layer. This "liberation" effect should result in a higher allocation of biomass to crown expansion when a tree reaches the canopy layer. Thanks to our multi-site analysis of some sources of variability of the allometries implying the three fundamental dimensions of a tree, we are able to provide guidelines for the future research now needed to better link and model crown and stem dynamics at individual and stand levels.

# Materials and methods

#### Study data sets

We compiled data sets with diameter at breast height (DBH), height (H), and crown area (CA) of trees with a DBH >10 cm in five contrasted tropical forests: in the South-West Pacific (New Caledonia, NC), South-East Asia (Indonesia, ID), South Asia (India, IN), eastern Amazonia (French Guiana, FG), and equatorial Africa (Cameroon and Gabon, CM-GA) (Fig. 1). The compiled data sets combine measurements from 4148 trees belonging to 538 species originating from published data sets (Indonesia from Harja et al. 2012, India from Antin et al. 2013 and French Guiana from both Birnbaum 2001 and Sabatier et al. 1997), and from original unpublished data sets (from New Caledonia and equatorial Africa). The tree sampling method differed among the five data sets, and was either based on sampling of (1) selected tree species, (2) species adult stature (notably to distinguish canopy species from sub-canopy species) (Gourlet-Fleury et al. 2005), (3) the position of the tree crown in the vertical canopy layer at the time of sampling according to a crown light exposure index (Dawkins 1963) (notably distinguishing canopy trees from sub-canopy trees, corresponding to the Dawkins's indices 4/5 and 1/2/3,



Fig. 1 Location of the five study sites. The Indonesia site includes the islands of Sumatra and Kalimantan islands. The rainforests are in *green* on the map; the GIS layer was downloaded from The Nature Conservation website (http://maps.tnc.org/index.html) (color figure online)

respectively), (4) DBH classes, and (5) trees according to slope classes (Table 1). It should be noted that, except for India, the majority of the sampled trees belonged to species that reach the canopy when mature.

#### **Tree measurements**

In all data sets, three dimensions (DBH, H, and CA) were measured in the field. In IN and NC, the crown area was computed from the cumulated projected area of four quarters of an ellipse, which were approximated from four orthogonal radii defined from the distance from the trunk to the vertical projection of the crown edge. In ID, FG, and CM-GA, crown area was computed as the area of a circle with a radius estimated as the arithmetical average of two diameters of the crown projection in two perpendicular directions, including the largest diameter. When the crown was considered to be symmetrical, the radius was estimated in only one direction measurement (in CM-GA). Tree crown areas were measured using a standard measuring tape (in ID, IN, and FG) or a laser rangefinder device (in NC and CM-GA). Tree heights were measured at all sites as the vertical distance from the ground to the highest point of the tree crown using a graduated pole for small trees (in IN), a clinometer and a standard measuring tape (in ID, IN, and FG), or a laser rangefinder (in NC and CM-GA). Differences in the methods used to measure the crown area could lead to over-estimation of crown area in ID, FG, and CM-GA, but have no effect on the allometric scaling exponent, apart from preventing a comparison of the intercept of the allometries.

# Tree DBH, height, and crown area distribution in the data sets

The distribution of DBH reflected the combination of both the particular forest structure and the sampling strategy at each study site. In fact, the IN data set was a quasi-random sample of the forest and its DBH distribution reflected a majority of small trees (median = 17 cm). The distribution of DBH was less skewed towards small trees in the four other data sets (26 cm < median < 31 cm). Conversely, the data sets from CM-GA and FG contained a high proportion of large trees (third quartiles of 53 and 47 cm, respectively, see Fig. 2 and Table 2). As a consequence, H distribution was characterized by a higher proportion of tall trees in these two data sets (medians of 21 and 27 m and third quartiles of 30 and 33 m, respectively, see Fig. 2 and Table 2). Logically, the distribution of CA was also heterogeneous among sites, and was characterized by a higher proportion of small-crown trees in the NC data set (median of 15  $m^2$ ) and a higher proportion of large crowns

Table 1 Five tropics	nl forest areas studied	and their site char	acteristics					
Biogeographic region	Country	Anthropogenic impact	Forest types	Sampling area	Sampling strategy	Elevation (m)	Mean rainfall (mm year <sup>-1</sup> )	Dry season (months)
South-West Pacific	New Caledonia (NC)	Undisturbed	Montane evergreen forest	Plot	Crown light exposure species adult stature	200-850	1700	4
South-East Asia	Indonesia (ID)							
	Sumatra	Disturbed	Mixed agroforests	Plot	Crown light exposure tree species	0-100	2000	3
	Kalimantan	Disturbed	Mono-cultural stands	Stand	Crown light exposure tree species	100 - 300	3400	3
South-Central Asia	India (IN)	Undisturbed	Wet montane evergreen monsoon forests	Plot	Crown light exposure species adult stature slope classes	300-600	5000	5
Amazonia	French Guiana (FG)	Undisturbed	Dense lowland evergreen tropical rainforest	Plot	Crown light exposure	10–50	4000	2
Equatorial Africa	Cameroon-Gabon (CM-GA)	Undisturbed	Lowland evergreen and semi-evergreen moist forests	Plot	DBH classes	100–700	1800	4
The dry season is the	in number of calendar	months with avera	ge rainfall <100 mm					



Fig. 2 DBH, tree height, and crown area distributions of all trees with  $DBH \ge 10$  cm at the five study sites: Indonesia (ID), New Caledonia (NC), India (IN), Cameroon-Gabon (CM-GA), and French Guiana (FG)

Table 2       Distribution of the         diameter at breast height		DBH			Heigl	ht		Crow	n area	
(DBH), height, and crown area at each site		Q1	Median	Q3	Q1	Median	Q3	Q1	Median	Q3
	New Caledonia	17	28	39	11	15	21	8	15	28
	Indonesia	17	26	38	11	16	23	17	31	58
	India	13	17	28	13	17	22	15	25	48
	French Guiana	19	31	47	21	27	33	26	52	96
	Cameroon-Gabon	17	30	54	15	21	30	20	50	113

Q1 first quartile, Q3 the third quartile. See Table 1 for a list of abbreviations used for the sites

in the CM-GA and FG data sets (median of 50 and 52 m<sup>2</sup>, respectively). The IN and ID data sets contained a higher proportion of intermediate crowns (median of 25 and  $31 \text{ m}^2$ , respectively, see Fig. 2 and Table 2).

# Sub-sampling of canopy and sub-canopy trees

At each site, we sub-sampled the data set according to the position of the trees in the canopy layer: (1) canopy trees (i.e., trees whose crown was entirely exposed to light at the time of sampling); and (2) sub-canopy trees (i.e., trees whose crown was partially or poorly exposed to light at the time of sampling) (Table 3). These two sub-samples were selected using a site-specific threshold related to canopy height. When the exposure of the crown to light (sensus Dawkins 1963) was known (NC, ID, IN, and FG), the mean height of the recorded canopy trees was computed, otherwise the canopy height was extracted from some of our unpublished data for CM-GA. Thus, a tree was considered to be a canopy tree when its height was greater than or equal to 16 m in NC, 17 m in ID, 24 m in IN, 25 m in CM-GA, and 28 m in FG.

#### **Fitting allometries**

Allometries were fitted based on: (1) all the trees taken together; and (2) representative sub-samples of trees from the canopy and the sub-canopy layer. Because of missing data, DBH-H, DBH-CA, and H-CA relationships were fitted on slightly different data sets (i.e., 4148 individuals of 538 species, 4097 of 492 species, and 3431 individuals of 446 species, respectively). Allometric relationships were fitted to power functions using ordinary least-squares regression on log-transformed data:  $y = b \times x^a \Leftrightarrow$  $log(y) = log b + a \times log x$  where y was alternatively H or CA, and x was alternatively DBH or H. In the allometry, a is the scaling exponent and b is the intercept. In this study, we checked that power functions acceptably rendered the allometries and compared their variability through the comparison of scaling exponents and intercepts of the log-log-linear regression, even though this has been questioned, especially with respect to DBH-H allometry (Picard et al. 2015). As the relationship between allometric variables is theoretically bidirectional, with errors on all the variables, this could require fitting allometries using a 
 Table 3 Description of the data

 sets in the five geographical

 sites

	Indonesia (ID)	New Caledonia (NC)	India (IN)	Cameroon–Gabon (CM–GA)	French Guiana (FG)
All trees	664 (11)	830 (105)	1600 (71)	661 (156)	342 (148)
Canopy trees	290 (11)	546 (89)	315 (35)	252 (77)	319 (137)
Sub-canopy trees	374 (11)	284 (71)	1285 (70)	409 (119)	23 (22)

Only trees with a DBH  $\geq 10$  cm were considered. At each site, we distinguished trees whose crown was entirely exposed to light at the time of sampling (canopy trees) and trees whose crown was partially or poorly exposed to light at the time of sampling (sub-canopy trees). Numbers in brackets indicate the corresponding number of species in each data set

linear regression model of the reduced major axis (RMA) type, (see Sokal and Rohlf 2012). However, assuming that the estimated uncertainty on the DBH (typically  $\leq 1$  cm) was far lower than on the *H* and CA, and that the uncertainty on *H* was lower than on the CA, we chose to use an ordinary least-squares (OLS) regression (Henry and Aarssen 1999).

For all the fitted allometric relationships, the conditions of normality and homoscedasticity of residuals were checked with a Kolmogorov–Smirnov test and Breusch– Pagan test, respectively. The significance of the scaling exponents and intercepts was checked with Student's t tests (Sokal and Rohlf 1981). A standard variance decomposition procedure (ANOVA type I sum of squares) was used to determine the relative contribution of independent variables (DBH and H) to the variance of the dependent variables (CA and H).

As our study only concerned the allometries of trees with DBH  $\geq 10$  cm and  $H \geq 4$  m, we calculated the predicted intercept of the dependent variables (*H* and CA) for DBH = 10 cm (Int10) and H = 4 m (Int4), which was the lower limit of the independent variable. A correction factor  $e^{\left(\frac{MSE}{2}\right)}$ , where MSE is the mean square error of the fitted linear model (Baskerville 1972), was applied to back-transformed predicted values, so as to remove the bias from predictions made on log-transformed data (Chave et al. 2005; Mascaro et al. 2014).

# Testing for inter-site variability and intra-site variability of allometries

Using the whole data set (i.e., all the trees), we tested whether the scaling exponent of allometries varied among the five study sites. We also tested the significance of the interaction sites-DBH and sites-H (i.e., covariance analysis) using an F test to evaluate the additional amount of variance explained by the interaction term. When the interaction term was significant for either scaling exponents or intercepts, we applied inter-site pairwise comparisons (Student's test with a Bonferroni correction for the P value adjustment in the case of multiple testing). To facilitate the comparison of intra-site variability among allometries and between CA and H, coefficients of variation were calculated for: (1) each allometry with the rootmean-square error expressed as a percentage of the mean of the explained variable, and (2) CA and H with the standard deviations expressed as a percentage of the mean. Within each site, we used a t test to compare the observed scaling exponents of the DBH-CA and DBH-H allometries in the whole data set with the scaling exponent predicted by the MTE (West et al. 1999; Brown et al. 2004). Finally, we tested variations in the three allometries within each site according to the position of the tree crowns (i.e., canopy vs. sub-canopy trees) through a t test applied to the scaling exponents.

We also assessed how the observed scaling exponent varies during tree ontogeny using DBH as a proxy, and using a two-step breakpoint procedure applied to the allometric regression of all the trees in the five biogeographic areas. The first step used a Davies' test (Davies 1987) with adjusted P values for multiple comparisons to identify significant variations in the scaling exponent of each log-linear relationship for 1000 regularly spaced DBH values. The second step used the DBH value of the most significant breakpoint as an initial value of a segmented regression (Muggeo 2003). All statistical analyses were conducted with the R software (3.1.2, R Development Core Team 2014) and the "segmented" add-on package (Muggeo 2008) for the two-step breakpoint procedure.

# Results

# Site-wise allometric relationships

All allometric relationships between DBH, H, and CA (Fig. 3) followed a log-linear model (*F* tests, P < 0.001), all scaling exponents, and intercepts being highly significant (*t* tests, P < 0.001). For all the fitted allometric relationships, the conditions of normality and homoscedasticity of residuals were fulfilled, respectively, with P < 0.050 (Kolmogorov–Smirnov test) and P > 0.050 (Breusch–Pagan test). The fit of the log-linear model was better for DBH-CA and DBH-*H* allometries (0.51 < R2 < 0.68) than



Fig. 3 Log-linear allometric relationships for all trees with a DBH  $\geq$  10 cm at the five study sites, between **a** stem diameter at breast height (DBH) and crown area, **b** DBH and tree height, and **c** tree height and crown area

for H-CA allometry (0.18 < R2 < 0.44). Except for the DBH-CA allometry in NC and ID, the site-wise scaling exponents of the DBH-CA and DBH-*H* allometries were significantly lower than predicted by the MTE (scaling exponent = 4/3; *t* test, *P* < 0.050, Table 3).

According to the general allometric models (including all trees at all sites), DBH explained 52 % of *H* variability and 49 % of CA variability, while *H* only explained 32 % of the variation in CA. The proportion of variance explained by DBH in the DBH-CA and DBH-*H* allometries was also more uniform among sites (56–59 and 50–68 %, respectively) compared to the variability of the variance portion explained by *H* in the *H*-CA allometry (18–44 %, Table 3). The scaling exponents varied far less across sites for the DBH-CA allometry (1.212–1.354) than the DBH-H (0.374–0.631) and H-CA allometries (0.828–1.795). At each site, the comparison between the coefficients of variation of the three allometries showed that the dispersion of points was higher for the DBH-CA and H-CA allometries than for the DBH-H allometry (Table 4). For a given range of DBH, the coefficient of variation of CA was three-to-five times higher than the coefficient of variation of H, depending on the sites, for both canopy trees and subcanopy trees (Table 5).

When computed at each site separately, Davies' test revealed significant breakpoints for all the allometric relationships (P < 0.050) except for the DBH-CA and *H*-CA allometries in the NC and ID data sets. Compared to the DBH-CA and DBH-*H* allometries, all the significant breakpoints of the *H*-CA allometries occurred within a narrow range of *H* across sites (12.8–14.5 m). Moreover, in the IN site, there was consistency between the breakpoints of the DBH-CA and DBH-*H* allometries (DBH = 15.5 and 17.6 cm, respectively), which was not the case in the other data sets.

#### Inter-site variations in allometric relationships

The scaling exponent of the DBH-CA allometry revealed no significant variations (F test, P = 0.091) across the five study sites. The scaling exponent of the mean DBH-CA allometry (across all sites) was 1.237 (with a confidence interval ranging from 1.198 to 1.275), i.e., significantly lower than the MTE prediction of 4/3. However, the scaling exponents of the DBH-H and H-CA allometries showed highly significant inter-site variations (F test, P < 0.001; Table 3). According to the post-hoc pairwise comparison tests, the majority of pairs of sites showed significantly different scaling exponents (t test, P < 0.050), except the pairs ID/IN and NC/CM-GA for the DBH-H allometry and the pair FG/CM-GA for the H-CA allometry. On the other hand, inter-site homogeneity was also observed in DBH-CA scaling exponents when the comparison was limited to the sub-samples of canopy trees. However, inter-site heterogeneity was observed for the sub-canopy trees, since only four pairs out of ten displayed no significant differences (ID/NC, ID/IN, NC/IN, and NC/CM-GA).

Pairwise comparison between site intercepts distinguished three groups of DBH-CA allometric relationships (Table 4): CM–GA, FG, and IN displayed the highest intercepts, ID had an intermediate intercept value, and NC had the lowest intercept. There was no congruence between these differences and the variation in the method of crown measurement which differentiated IN and NC from the rest. For the DBH-*H* allometry, besides the NC/IN pair, pairwise intercepts differed significantly (*F* test, P < 0.05). Finally,

	DBH-	CA allc	ometry					DBH-	H allor	netry				
	RSE	$R^2$	CV	Intercept	Int10	Slope	BreakP	RSE	$R^2$	CV	Intercept	Int10	Slope	BreakP
NC	0.60	0.59	12.81	0.169 (0.131–0.219)	4.57	1.354 <sup>j</sup> (1.277–1.431)	18.470	0.28	0.51	7.40	2.689 <sup>i</sup> (2.419–2.988)	8.76	$0.496^{i***} (0.464-0.528)$	80.340
Ð	0.58	0.59	8.15	0.427 <sup>i</sup> (0.324–0.564)	11.09	1.341 <sup>jk</sup> (1.256–1.426)	33.150	0.33	0.50	7.79	2.066 (1.766–2.417)	9.35	$0.632^{j***}$ (0.585-0.680)	39.18**
NI	0.63	0.56	9.44	0.6315 <sup>ijb</sup> (0.540–0.739)	13.73	$\begin{array}{c} 1.256^{ij**} \\ (1.203-1.308) \end{array}$	15.50**	0.25	0.67	5.78	2.562 <sup>i</sup> (2.406–2.727)	11.20	$0.6243^{j***}$ (0.604-0.645)	17.55***
FG	0.59	0.57	7.02	$0.811^{\rm k}$ (0.554–1.186)	15.73	$1.212^{i*}$ (1.101–1.323)	79.32*	0.20	0.59	3.86	6.187 (5.436–7.045)	16.82	0.4254*** (0.388-0.463)	13.94*
CM GA	0.76	0.57	7.74	0.718 <sup>jk</sup> (0.540–0.958)	16.63	1.24 <sup>ik</sup> * (1.158–1.322)	27.21*	0.25	0.68	5.21	3.617 (3.293–3.973)	11.96	$0.5069^{i***}$ (0.480–0.533)	36.48***
			H-CA	allometry										
			RSE	$R^2$		CV Inte	rcept				Int10	Slope		BreakP
NC			0.76	0.22		12.50 0.33	(3 <sup>1j</sup> (0.098-	-1.150)			3.36	1.462 (	1.049–1.876)	12.12
Ð			0.89	0.18		11.58 3.29	4 (2.254-	4.814)			14.59	0.828 ((	).693–0.963)	36.32
N			0.80	0.29		12.05 0.95	i7 <sup>j</sup> (0.748–	1.224)			1.45	1.182 (	(.094 - 1.269)	$14.50^{***}$
FG			0.72	0.37		8.54 0.15	i7 <sup>i</sup> (0.071–	0.349)			2.33	1.76 <sup>i</sup> (1	.516-2.003)	$14.12^{*}$
CM GA			0.86	0.44		8.75 0.22	3 <sup>i</sup> (0.141–	0.353)			3.87	1.795 <sup>i</sup> (	1.645 - 1.946)	$12.83^{***}$
Residual confidence height ( $I$ ** $P < 0$ .	standar se interv f) and 010, ** as follo	d error al in bi crown *P < 0	(RSE) ackets area (C .001. R < 0.02	, squared coefficient of 1 are given for the five sites A) for DBH = $10 \text{ cm} a$ esults of the <i>t</i> tests on the esults of the <i>t</i> tests on the	The second regression is the second regression is the second $H = 1000$ shope parallel to $2001$ . The second regression is the second regression	n ( $\mathbb{R}^2$ ), coefficient of vai 'aledonia (NC), India (IN) 4 m, respectively. <i>Brea</i> trameter versus expectation <i>e letters</i> ( <i>i</i> , <i>i</i> , <i>k</i> ) indicate	iation (CV), Indonesii ), Indonesii <i>kP</i> stem d ons based c the results	7 = RM a (ID), G liameter on the m	$(SE/\bar{y})$ . Central at the tetaboli	in %,) Africa break c theor	intercepts, and scalin (CM-GA), and French point given by Davies y of ecology (MTE = hoc test hetween the s	g expoi i Guiana s' test, 1.333 fo	tent (or scaling exponents) (FG). Int10 and Int4 are the <i>P</i> value ( <i>P</i> ): $P < 0.100$ , *1 or DBH-CA and 0.666 for D of the intercents ( <i>t</i> test)	with their e predicted P < 0.050, BH-H) are



Table 5Coefficient ofvariation (%) of tree crown areaand height, calculated for eachof the five study sites, for alltrees and each individual treesub-sampled

	Crown	area		Height	t	
	All	Canopy	Sub-canopy	All	Canopy	Sub-canopy
New Caledonia	102	85	81	42	23	24
Indonesia	124	112	87	47	26	25
India	126	89	84	46	23	29
French Guiana	94	-	_	29	-	_
Cameroon–Gabon	125	87	111	41	15	29

Table 6 Differences in the scaling exponent of the allometric relationships found for canopy trees and sub-canopy trees

	DBH-0	CA alloi	netry			DBH-I	H allom	etry			H-CA	allomet	ry		
	NC	IN	ID	CM GA	FG	NC	IN	ID	CM GA	FG	NC	IN	ID	CM GA	FG
Canopy trees	1.495	1.581	1.716	1.446	1.156	0.212	0.318	0.273	0.21	0.403	1.367	2.014	0.547	3.089	1.635
Sub-canopy trees	1.240 ***	1.223 ***	1.351 ***	1.007 ***	-	0.287 ***	0.511 ***	0.287 NS	0.367 ***	-	0.729 **	0.611 ***	0.718 NS	1.314 ***	-
Delta (%)	17	23	21	30	-	35	61	5	75	_	47	70	31	57	_

Delta = [(canopy trees - sub-canopy trees)/canopy trees]  $\times$  100. The significance of differences was tested with an *F* test: *NS* non-significant, \*\* *P* < 0.010, and \*\*\* *P* < 0.001

three groups were separated from the intercepts of the *H*-CA allometry: CM–GA/FG/NC, IN/NC, and ID (NC was assigned to two groups due to the large confidence interval around the estimated intercept).

For a reference DBH of 10 cm (Int10, i.e., census threshold), the estimated mean crown size was ranked in ascending order from NC, ID, IN, and FG to CM–GA, and increased from 4.57 to 16.63 m<sup>2</sup>. Ranking was almost the same for mean tree height at DBH = 10 cm, and mean *H* values ranged from 8.76 to 16.82 m. For a height threshold of 4 m (Int4), the estimated mean CA was in ascending order from FG, NC, and CM–GA, to IN and ID, and ranged from 2.33 to 14.59 m<sup>2</sup> (Table 4).

# Variability between allometries of canopy and subcanopy trees

When the analysis was limited to either canopy trees or sub-canopy trees, all allometries between DBH, *H*, and CA fitted the log-linear model well (*F* tests, P < 0.001). The scaling exponents and intercepts were highly significant (*t* tests, P < 0.001) except for the FG sub-canopy trees, because too few were sampled (23 trees, Fig. 3).

The scaling exponent differed significantly (*t* test, P < 0.010) between canopy trees and sub-canopy trees for the allometries in NC, IN, CM–GA, and FG, while the scaling exponent of canopy and sub-canopy trees differed only for the DBH-CA allometry in the ID data set. The scaling exponent of the DBH-CA and *H*-CA allometries increased systematically from the sub-canopy trees to the

canopy trees, while the scaling exponent of the DBH-H allometry systematically decreased (Table 6; Fig. 4). A higher contrast in scaling exponents between canopy tree and sub-canopy tree sub-samples was observed for the DBH-H and H-CA allometries compared to the DBH-CA allometry (Table 6; Fig. 4).

# Discussion

# Towards a better understanding of the 3D structure of trees and stands

The three-dimensional forest structure and its dynamics are usually approximated by considering the DBH as a proxy for both the vertical expansion and the horizontal expansion of trees. However, if the DBH increases continuously with the age of the tree due to xylem expansion, a few quantitative data are available to infer height and crown dimensions from the DBH parameter alone and, hence, to understand which changes in resource allocation may co-vary with the DBH increment. If the collection of DBH-H measurements from all over the world has significantly increased in the last decade, incorporating crown dimensions in a large-scale study of tree allometry remained challenging as crown area is one among the most complicated parameters to acquire in the field. Nevertheless, the recent interest in tree allometries between crown and stem dimensions shows that the crown is a key parameter in assessing and monitoring tropical

Fig. 4 Allometric relationships (log-log-linear regressions) of stem diameter at breast height (DBH) with crown area (*first column*), height (*second column*), and height with crown area (*third column*) at the five sites investigated. At each site, relationships were computed and plotted for canopy trees and sub-canopy trees, separately



forest structure and dynamics (e.g., Muller-Landau et al. 2006; Bohlman and Pacala 2012; Goodman et al. 2014). In fact, to our knowledge, the present paper is the first attempt to provide a worldwide picture of crown allometries of tropical trees using data collected in five different biogeographic areas.

Our data set was compiled from tree inventories in five parts of the world, with different climates, topographical conditions, disturbance levels, types of tropical forests, pools of species, and DBH size distributions. Such heterogeneity is favorable to test the stability of tree allometries at inter- and intra-site scales. However, the different sampling designs used in these inventories prevented us from exploring all aspects of inter- and intra-site variations in the allometries. For instance, the imbalance between canopy and sub-canopy trees in the data sets did not allow analyzing the influence of species adult stature on the scaling exponent and intercept values of allometries, as evidenced in former studies (e.g., King 1990, 1996; Kohyama et al. 2003; Yamada et al. 2005; Bohlman and O'Brien 2006; Antin et al. 2013). The inter-site difference in sampling may also have influenced results relating to intercept values or breaking points, which failed to reveal any easily interpretable pattern.

#### Inter-site stability of DBH-CA allometry

The scaling exponent of the DBH-CA allometry remained strikingly stable across the five biogeographic areas for both the whole data set and the sub-set of canopy trees. We acknowledge that a relatively low P value of the F test (0.091) was found and that the failure to reject the null hypothesis may result from a lack of power (may be due to strong intra-site variability). However, the small range of variation observed for the scaling exponents of DBH-CA allometries (1.212–1.354) includes the mean value (1.311) found in Kalimantan (Borneo, Indonesia) by Kohyama et al. (2003) as well as the value of 1.28 reported by Farrior et al. (2016) for Barro Colorado (Panama). It is also close to the value reported by Muller-Landau et al. (2006) (1.36)for the same site. Moreover, this inter-site stability is somewhat puzzling, as it was observed across a set of different forest environments featuring several strong causes for variations in stand structure. In addition, the inter-site variability of the average crown area computed for trees with a DBH of 10 cm (i.e., the intercept of the scaling relationship) highlights the heterogeneity of the types of forest in our data set. Finally, our results on DBH-CA allometry did not clearly reject the prediction of the metabolic theory of ecology (MTE), since the inter-site range of variation in scaling exponents included the value of 4/3 and two sites yielded values that did not differ significantly from the MTE predictions.

The convergence towards a universal scaling exponent of the DBH-CA allometry in tropical trees has been observed notwithstanding the impressive variability of tree shapes and sizes observed across species and environments (e.g., Barthélémy and Caraglio 2007; Clark et al. 2015) and which call for interpretations that are still largely lacking (or, at best, incomplete) in the literature. Scaling between stem diameter and total leaf area has been proposed to be one consequence of the mechanical constraints exerted by the leaves on the stems that support them (Niklas 1992; Westoby et al. 2002). This scaling relationship has also been interpreted by hydraulic constraints (expressed by the pipe-model theory, see Shinozaki et al. 1964), as the result of the hydraulic supply through stems, which may determine the size of the leaves deployed by the stems (Westoby et al. 2002; Westoby and Wright 2003). Another possible explanation for this allometric scaling is metabolic constraints. Based on the assumption that similar amounts of photosynthates are produced per unit crown area (Olson et al. 2009), the scaling between DBH and CA would be expected to result from the metabolic demand of living cells in the stem for a given quantity of leaves as photosynthetic sources (Niklas 1994; Enquist 2002). All these, by no means mutually exclusive explanations, contribute to the MTE, which predicted fixed allometries for an idealised individual tree (West et al. 2009; Smith et al. 2013; Bentley et al. 2013). However, the stability of tree allometric scaling relations predicted by these theoretical predictions has often been invalidated by empirical studies, suggesting that intra-specific (Poorter et al. 2003; Bohlman and O'Brien 2006) and inter-site variability (Coomes et al. 2003; Muller-Landau et al. 2006) in tree architectural development lead to substantial deviations from theoretical predictions. Likewise, variations in allometries are expected to reflect the magnitude of the actual responses of trees to the availability of resources as well as to local spatial crowding (Iwasa et al. 1985; King and Maindonald 1999; Poorter et al. 2003; Kitajima et al. 2005).

Moreover, the overall inter-site stability of scaling exponents of DBH-CA allometries contrasted significantly with the high inter-site variability found for scaling exponents of the two other allometries studied (DBH-*H* and the H-CA). These inter-site differences are in agreement with the results of several previous studies showing that DBH-H allometry is subject to strong inter-site variability. This variability may be due to environmental conditions (Nogueira et al. 2008; Feldpausch et al. 2011; Vincent et al. 2012), forest structure, such as the proportion of trees with a small or large DBH (Molto et al. 2014), as well as the floristic composition, because some biogeographic areas may be dominated by families with particularly tall tree species (Banin et al. 2012). The average height reached at a given ontogenetic stage by the subpopulation of 'dominant' (i.e., the most vigorous) trees is known to be a proxy for site productivity and, to some extent, to be independent of stand density (Vanclay 1992; Skovsgaard and Vanclay 2008). In contrast to the intrinsic interdependency of DBH and age, the height of a tree is an adjustable parameter which, in a given species, depends to a great extent on the abiotic environment. In line with the previous empirical studies (Muller-Landau et al. 2006; Coomes and Allen 2009; Pretzsch and Dieler 2012), our results concerning DBH-H allometries once again clearly reject the prediction of a universal scaling exponent, such as that made by the MTE.

# Change in CA and H allometries as evidence of tree "liberation"

Our results support the hypothesis that the transition of a tree from the sub-canopy to the canopy layer leads to an increase in the DBH-CA scaling exponent and to a bigger decrease in the DBH-H scaling exponent. These concomitant variations could be linked to the fundamental architectural concept of metamorphosis (Hallé and Ng 1981), defined as the inner reprogramming of an expanding tree crown, in which the early branching pattern is repeated in each of the sub-crowns, thereby contributing to the development of the whole crown (Oldeman 1990). The height at which the architectural metamorphosis occurs is named the "liberation point" (Oldeman 1974, 1990; Cusset 1980; Hallé et al. 1978). This point marks a shift in resource allocation towards less investment in vertical stem growth to the benefit of thickening of the bole base to support the horizontal expansion of the crown, to maximize light interception (Richards 1996; Henry and Aarssen 1999; Montgomery and Chazdon 2001; King et al. 2005). The resulting asymptotic growth in height has been reported in the other studies (Thomas 1996; Yamada et al. 2005; Bohlman and Pacala 2012). The increase in the DBH-CA scaling exponent evidenced here has long been suggested to be another likely consequence of the liberation point connected with the decrease in the scaling exponent of the DBH-H allometry (Oldeman 1974; Richards 1996). However, among the few case studies on the topic, only a small number supported an increase in crown area when trees reach the canopy (Wyckoff and Clark 2005; Russo et al. 2007; Antin et al. 2013), while Muller-Landau et al. (2006) concluded the reverse.

Some authors have suggested that wood density explains the trade-off between effective vertical stem expansion and horizontal crown expansion (Anten and Schieving 2010). Species with high wood density were found to have more slender (and shorter) stems, but larger crowns than similarly sized trees of species having lower wood density (e.g., Kohyama and Hotta 1990; Kohyama et al. 2003; King et al. 2005; Poorter et al. 2008; Iida et al. 2012). However, it has been shown that this pattern weakens in tall trees (>17-18 m) (King et al. 2006; Iida et al. 2012), suggesting that it rather reflects inter-species trade-offs in resource allocation than a direct, overall effect of liberation.

# Evidence of crown plasticity

The high intra-site variability of the scaling exponent of the DBH-CA allometry compared to the relative stability of the scaling exponent of the DBH-H allometry suggests a high level of plasticity in the crown development for a given DBH. This variability in the lateral crown expansion could be explained by the combined ontogeny, asymmetrical competition for light, canopy shyness, and inter-specific differences in architectural patterns. First, for a given type of crown architecture, canopy trees are characterized by complex lateral branching processes, due to the multiple processes of architectural adjustment and compensation that crowns initiate when and after the trees reached the canopy layer (Oldeman 1990; Barthélémy and Caraglio 2007). These processes often result in a large fragmented crown whose fragmentation tends to increase with senescence (Hallé et al. 1978; Rutishauser et al. 2011). Second, the crown architecture of sub-canopy trees varies among species depending on their adult stature, and sub-canopy species have been shown to invest more in the width and depth expansion of their crown, unlike canopy species, which invest more in the height (e.g., Poorter et al. 2006; Bohlman and O'Brien 2006; Osunkoya et al. 2007; Iida et al. 2011). Third, in a closed canopy forest, competition for light and space is strongly asymmetrical depending on the irregular structure of the vegetation surrounding a given tree (Umeki 1995; Purves et al. 2007; Strigul et al. 2008), leading to locally highly variable lateral crown expansion. Finally, measuring crown dimensions becomes more difficult as tree size increases, since large crowns tend to be irregular and fragmented.

### Conclusion

To our knowledge, the present study is the first to evaluate and compare the main tree dimensions (DBH, *H*, and CA) across the tropics. In contrast to DBH-*H* allometry, intersite variability of the scaling exponent of DBH-CA allometry was strikingly low compared to intra-site variability. This inter-site stability suggests that, despite great diversity in tree crown architecture, some universal constraints would be sufficiently strong to shape the range of possible scalings between crown area and stem diameter. Such constraints seem to determine stand-level DBH-CA allometry patterns, irrespective of the biogeographic context, even though they are known-and confirmed here-to be locally modified by inter-species differences and by the morphological plasticity of individual trees. Our results also showed that the scaling exponent of DBH-CA and DBH-H allometries changed in opposite directions when computed for canopy or sub-canopy trees. This switch supports the hypothesis of enhanced biomass allocation for crown expansion once a tree reaches direct light. Finally, our findings suggest that the relative importance of errors linked to the prediction of crown dimensions from DBH, which is substantial for individual trees, may decrease at regional scales. Our results also suggest that calibration over a small number of reference sites seems to be sufficient to predict stand structure variables (e.g., mean quadratic DBH) and AGB using crown dimensions extracted from remotely sensed data. DBH-CA allometry is indeed a fundamental link in combining field and zenithal information to better understand, model, and map the spatio-temporal variability of stand structure and AGB in complex tropical forests.

**Author contribution statement** EB conceived the study, collected data from New Caledonia, compiled the data sets, analyzed the data, and led the writing of the manuscript. PC conceived the study and actively contributed to the writing. PB conceived the study, actively contributed to the writing, and was involved in the New Caledonian field work. TI revised the manuscript and was involved in the field work in New Caledonia. PP commented on the manuscript and was involved in the field work in the field work in Cameroon and Gabon. CA, GV, and RP commented on the manuscript. HV, TB, and VH were involved in the field work in New Caledonia. NB, VD, BS, NT, NGK, DZ, and ML performed the field work in Cameroon and Gabon.

Acknowledgments This study was funded by the Direction for Economic and Environmental Development (DDEE) of the North Province of New Caledonia. Data acquisition for IRD plots (data from Africa) was supported by Eramet, IRD-PPR FTH-AC, the World Bank, WWF, EIT-Climate KIC, the African Development Bank, and COMIFAC. We thank the Institut Agronomique néo-Calédonien (IAC) for co-funding E. Blanchard's Ph.D. We are grateful to the many field workers, technicians, engineers, and researchers who contributed to the long-term monitoring of the plots used in the analyses. We also thank Santiago Trueba-Sanchez (IRD) and two anonymous reviewers for their helpful comments on the manuscript.

#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

#### References

- Aiba SI, Kohyama T (1996) Tree species stratification in relation to allometry and demography in a warm-temperate rain forest. J Ecol 84:207–218. doi:10.2307/2261356
- Anten NPR, Schieving F (2010) The role of wood mass density and mechanical constraints in the economy of tree architecture. Am Nat 175:250–260. doi:10.1086/649581

- Antin C, Pélissier R, Vincent G, Couteron P (2013) Crown allometries are less responsive than stem allometry to tree size and habitat variations in an Indian monsoon forest. Trees Struct Funct 27:1485–1495
- Asner GP (2009) Tropical forest carbon assessment: integrating satellite and airborne mapping approaches. Environ Res Lett. doi:10.1088/1748-9326/4/3/034009
- Attocchi G, Skovsgaard JP (2015) Crown radius of pedunculate oak (Quercus robur L.) depending on stem size, stand density and site productivity. Scand J For Res 30:289–303. doi:10.1080/ 02827581.2014.1001782
- Baccini A et al (2012) Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nat Clim Change 2:182–185. doi:10.1038/nclimate1354
- Banin L et al (2012) What controls tropical forest architecture? Testing environmental, structural and floristic drivers. Glob Ecol Biogeogr 21:1179–1190. doi:10.1111/j.1466-8238.2012.00778.x
- Barbier N, Couteron P, Proisy C, Malhi Y, Gastellu-Etchegorry JP (2010) The variation of apparent crown size and canopy heterogeneity across lowland Amazonian forests. Glob Ecol Biogeogr 19:72–84
- Barthélémy D, Caraglio Y (2007) Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Ann Bot Lond 99:375–407. doi:10.1093/aob/ mcl260
- Baskerville GL (1972) Use of logarithmic regression in the estimation of plant biomass. Can J For Res 2:49–53. doi:10.1139/x72-009
- Bastin JF, Barbier N, Couteron P, Adams B, Shapiro A, Bogaert J, De Canniere C (2014) Aboveground biomass mapping of African forest mosaics using canopy texture analysis: toward a regional approach. Ecol Appl 24:1984–2001. doi:10.1890/13-1574.1
- Bastin JF et al (2015) Seeing Central African forests through their largest trees. Sci Rep 5:13156. doi:10.1038/srep13156
- Bentley LP et al (2013) An empirical assessment of tree branching networks and implications for plant allometric scaling models. Ecol Lett 16:1069–1078. doi:10.1111/ele.12127
- Birnbaum P (2001) Canopy surface topography in a French Guiana forest and the folded forest theory. Plant Ecol 153:293–300. doi:10.1023/a:101756380925
- Bohlman S, O'Brien S (2006) Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island, Panama. J Trop Ecol 22:123–136
- Bohlman S, Pacala S (2012) A forest structure model that determines crown layers and partitions growth and mortality rates for landscape-scale applications of tropical forests. J Ecol 100:508–518. doi:10.1111/j.1365-2745.2011.01935.x
- Bouvier M, Durrieu S, Fournier RA, Renaud J-P (2015) Generalizing predictive models of forest inventory attributes using an areabased approach with airborne LiDAR data. Remote Sens Environ 156:322–334. doi:10.1016/j.rse.2014.10.004
- Broadbent EN, Asner GP, Pena-Claros M, Palace M, Soriano M (2008) Spatial partitioning of biomass and diversity in a lowland Bolivian forest: linking field and remote sensing measurements. For Ecol Manag 255:2602–2616. doi:10.1016/j.foreco.2008.01.044
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789
- Chave J et al (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99. doi:10.1007/s00442-005-0100-x
- Chave J et al (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Change Biol 20:3177–3190. doi:10.1111/gcb.12629
- Clark ML, Clark DB, Roberts DA (2004) Small-footprint lidar estimation of sub-canopy elevation and tree height in a tropical rain forest landscape. Remote Sens Environ 91:68–89. doi:10. 1016/j.rse.2004.02.008

- Clark DB, Hurtado J, Saatchi SS (2015) Tropical rain forest structure, tree growth and dynamics along a 2700-m elevational transect in Costa Rica. PLoS One 10:e0122905. doi:10.1371/journal.pone. 0122905
- Coomes DA, Allen RB (2009) Testing the metabolic scaling theory of tree growth. J Ecol 97:1369–1373. doi:10.1111/j.1365-2745. 2009.01571.x
- Coomes DA, Duncan RP, Allen RB, Truscott J (2003) Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. Ecol Lett 6:980–989. doi:10. 1046/j.1461-0248.2003.00520.x
- Coomes DA, Holdaway RJ, Kobe RK, Lines ER, Allen RB (2012) A general integrative framework for modelling woody biomass production and carbon sequestration rates in forests. J Ecol 100:42–64. doi:10.1111/j.1365-2745.2011.01920.x
- Couteron P, Pélissier R, Nicolini EA, Dominique P (2005) Predicting tropical forest stand structure parameters from Fourier transform of very high-resolution remotely sensed canopy images. J Appl Ecol 42:1121–1128. doi:10.1111/j.1365-2664.2005.01097.x
- Cusset G (1980) Les paramètres intervenant dans la croissance des arbres: la relation hauteur-diamètre de l'axe primaire aérien. Candollea 35:231–255
- Davies RB (1987) Hypothesis testing when a nuisance parameter is present only under the alternative—linear model case. Biometrika 74:33–43
- Dawkins HC (1963) The productivity of tropical highforest trees and their reaction to controllable environment. Commonwealth Forestry Institute, Oxford
- Enquist BJ (2002) Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. Tree Physiol 22:1045–1064
- Farrior CE, Bohlman SA, Hubbell S, Pacala SW (2016) Dominance of the suppressed: power-law size structure in tropical forests. Science 351:155–157. doi:10.1126/science.aad0592
- Fauset S et al (2015) Hyperdominance in Amazonian forest carbon cycling. Nat Commun. doi:10.1038/ncomms7857
- Feldpausch TR et al (2011) Height-diameter allometry of tropical forest trees. Biogeosciences 8:1081–1106. doi:10.5194/bg-8-1081-2011
- Feldpausch TR et al (2012) Tree height integrated into pantropical forest biomass estimates. Biogeosciences 9:3381–3403. doi:10. 5194/bg-9-3381-2012
- Goodman RC, Phillips OL, Baker TR (2014) The importance of crown dimensions to improve tropical tree biomass estimates. Ecol Appl 24:680–698
- Gourlet-Fleury S, Blanc L, Picard N, Sist P, Dick J, Nasi R, Swaine MD, Forni E (2005) Grouping species for predicting mixed tropical forest dynamics: looking for a strategy. Ann For Sci 62:785–796. doi:10.1051/forest:2005084
- Hajek P, Seidel D, Leuschner C (2015) Mechanical abrasion, and not competition for light, is the dominant canopy interaction in a temperate mixed forest. For Ecol Manag 348:108–116. doi:10. 1016/j.foreco.2015.03.019
- Hallé F, Ng FSP (1981) Crown construction in mature Dipterocarp trees. Malays For 44:222–223
- Hallé F, Oldeman R, Tomlinson P (1978) Tropical trees and forests: an architectural analysis. Springer, Berlin
- Harja D, Vincent G, Mulia R, van Noordwijk M (2012) Tree shape plasticity in relation to crown exposure. Trees Struct Funct 26:1275–1285
- Heineman KD, Jensen E, Shapland A, Bogenrief B, Tan S, Rebarber R, Russo SE (2011) The effects of belowground resources on aboveground allometric growth in Bornean tree species. For Ecol Manag 261:1820–1832. doi:10.1016/j.foreco.2011.02.005
- Henry H, Aarssen L (1999) The interpretation of stem diameterheight allometry in trees: biomechanical constraints, neighbour effects, or biased regressions? Ecol Lett 2:89–97

- Iida Y, Kohyama TS, Kubo T, Kassim AR, Poorter L, Sterck F, Potts MD (2011) Tree architecture and life-history strategies across 200 co-occurring tropical tree species. Funct Ecol 25:1260–1268. doi:10.1111/j.1365-2435.2011.01884.x
- Iida Y, Poorter L, Sterck FJ, Kassim AR, Kubo T, Potts MD, Kohyama TS (2012) Wood density explains architectural differentiation across 145 co-occurring tropical tree species. Funct Ecol 26:274–282. doi:10.1111/j.1365-2435.2011.01921.x
- Iwasa Y, Cohen D, Leon JA (1985) Tree height and crown shape, as results of competitive games. J Theor Biol 112:279–297. doi:10. 1016/s0022-5193(85)80288-5
- Jacobs MR (1955) Growth habits of the eucalyptus. Forestry and timber Bureau, Canberra
- Kennel P, Tramon M, Barbier N, Vincent G (2013) Canopy height model characteristics derived from airbone laser scanning and its effectiveness in discriminating various tropical moist forest types. Int J Remote Sens 34:8917–8935. doi:10.1080/01431161.2013. 858846
- King DA (1990) Allometry of samplings and understorey trees of Panamanian forest. Funct Ecol 4:27–32. doi:10.2307/2389648
- King DA (1996) Allometry and life history of tropical trees. J Trop Ecol 12:25–44
- King DA (2005) Linking tree form, allocation and growth with an allometrically explicit model. Ecol Model 185:77–91. doi:10. 1016/j.ecolmodel.2004.11.017
- King DA, Clark DA (2011) Allometry of emergent tree species from saplings to above-canopy adults in a Costa Rican rain forest. J Trop Ecol 27:573–579. doi:10.1017/s0266467411000319
- King DA, Maindonald JH (1999) Tree architecture in relation to leaf dimensions and tree stature in temperate and tropical rain forests. J Ecol 87:1012–1024. doi:10.1046/j.1365-2745.1999.00417.x
- King D, Davies S, Supardi MN, Tan S (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. Funct Ecol 19:445–453
- King DA, Davies SJ, Tan S, Noor NSM (2006) The role of wood density and stem support costs in the growth and mortality of tropical trees. J Ecol 94:670–680. doi:10.1111/j.1365-2745.2006.01112.x
- Kitajima K, Mulkey SS, Wright SJ (2005) Variation in crown light utilization characteristics among tropical canopy trees. Ann Bot Lond 95:535–547. doi:10.1093/aob/mci051
- Kohyama T, Hotta M (1990) Significance of allometry in tropical saplings. Funct Ecol 4:515–521. doi:10.2307/2389319
- Kohyama T, Suzuki E, Partomihardjo T, Yamada T, Kubo T (2003) Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. J Ecol 91:797–806. doi:10.1046/j.1365-2745.2003.00810.x
- Lang AC et al (2010) Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. For Ecol Manag 260:1708–1715
- Lindenmayer DB et al (2012) Interacting factors driving a major loss of large trees with cavities in a forest ecosystem. PLoS One 7:e41864. doi:10.1371/journal.pone.0041864
- Lines ER, Zavala MA, Purves DW, Coomes DA (2012) Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. Glob Ecol Biogeogr 21:1017–1028. doi:10.1111/j.1466-8238.2011.00746.x
- Lutz JA, Larson AJ, Freund JA, Swanson ME, Bible KJ (2013) The importance of large-diameter trees to forest structural heterogeneity. PLoS One 8:e82784. doi:10.1371/journal.pone.0082784
- Mäkelä A, Valentine HT (2006) Crown ratio influences allometric scaling in trees. Ecology 87:2967–2972. doi:10.1890/0012-9658(2006)87[2967:criasi]2.0.co;2
- Mascaro J, Litton CM, Hughes RF, Uowolo A, Schnitzer SA (2014) Is logarithmic transformation necessary in allometry? Ten, onehundred, one-thousand-times yes. Biol J Linn Soc 111:230–233. doi:10.1111/bij.12177

- Molto Q, Herault B, Boreux JJ, Daullet M, Rousteau A, Rossi V (2014) Predicting tree heights for biomass estimates in tropical forests—a test from French Guiana. Biogeosciences 11:3121–3130. doi:10.5194/bg-11-3121-2014
- Montgomery RA, Chazdon RL (2001) Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82:2707–2718
- Moravie MA, Durand M, Houllier F (1999) Ecological meaning and predictive ability of social status, vigour and competition indices in a tropical rain forest (India). For Ecol Manag 117:221–240. doi:10.1016/s0378-1127(98)00480-0
- Muggeo VM (2003) Estimating regression models with unknown break-points. Stat Med 22:3055–3071
- Muggeo VM (2008) Segmented: an R package to fit regression models with broken-line relationships. R news 8:20–25
- Muller-Landau HC et al (2006) Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecol Lett 9:575–588. doi:10.1111/j.1461-0248.2006. 00904.x
- Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago
- Niklas KJ (1994) Plant allometry: the scaling of form and process. University of Chicago Press, Chicago
- Nogueira EM, Fearnside PM, Nelson BW, Barbosa RI, Hermanus Keizer EW (2008) Estimates of forest biomass in the Brazilian Amazon: new allometric equations and adjustments to biomass from wood-volume inventories. For Ecol Manag 256:1853–1867. doi:10.1016/j.foreco.2008.07.022
- Oldeman RAA (1974) L'architecture de la forêt guyanaise. ORSTOM, Paris

Oldeman RAA (1990) Forests: elements of silvology. Springer, Berlin

- Olson ME, Aguirre-Hernández R, Rosell JA (2009) Universal foliagestem scaling across environments and species in dicot trees: plasticity, biomechanics and Corner's rules. Ecol Lett 12:210–219
- Osada N, Tateno R, Hyodo F, Takeda H (2004) Changes in crown architecture with tree height in two deciduous tree species: developmental constraints or plastic response to the competition for light? For Ecol Manag 188:337–347. doi:10.1016/j.foreco. 2003.08.003
- Osunkoya OO, Omar-Ali K, Amit N, Dayan J, Daud DS, Sheng TK (2007) Comparative height-crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. Am J Bot 94:1951–1962. doi:10.3732/ajb.94.12.1951
- Palace MW, Sullivan FB, Ducey MJ, Treuhaft RN, Herrick C, Shimbo JZ, Mota-E-Silva J (2015) Estimating forest structure in a tropical forest using field measurements, a synthetic model and discrete return lidar data. Remote Sens Environ 161:1–11. doi:10.1016/j.rse.2015.01.020
- Picard N, Rutishauser E, Ploton P, Ngomanda A, Henry M (2015) Should tree biomass allometry be restricted to power models? For Ecol Manag 353:156–163. doi:10.1016/j.foreco.2015.05.035
- Ploton P, Pélissier R, Proisy C, Flavenot T, Barbier N, Rai S, Couteron P (2013) Assessing aboveground tropical forest biomass using Google Earth canopy images. Ecol Appl 22:993–1003
- Ploton P et al (2016) Closing a gap in tropical forest biomass estimation: taking crown mass variation into account in pantropical allometries. Biogeosciences 13:1571–1585. doi:10. 5194/bg-13-1571-2016
- Poorter L, Bongers F, Sterck FJ, Woll H (2003) Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. Ecology 84:602–608. doi:10.1890/0012-9658(2003)084 [0602:aorfts]2.0.co;2
- Poorter L, Bongers L, Bongers F (2006) Architecture of 54 moistforest tree species: traits, trade-offs, and functional groups. Ecology 87:1289–1301. doi:10.1890/0012-9658(2006)87 [1289:aomtst]2.0.co;2

- Poorter L et al (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89:1908–1920. doi:10.1890/07-0207.1
- Pretzsch H, Dieler J (2012) Evidence of variant intra-and interspecific scaling of tree crown structure and relevance for allometric theory. Oecologia 169:637–649
- Proisy C, Couteron P, Fromard F (2007) Predicting and mapping mangrove biomass from canopy grain analysis using Fourierbased textural ordination of IKONOS images. Remote Sens Environ 109:379–392. doi:10.1016/j.rse.2007.01.009
- Purves DW, Lichstein JW, Pacala SW (2007) Crown plasticity and competition for canopy space: a new spatially implicit model parameterized for 250 North American tree species. PLoS One 2:e870. doi:10.1371/journal.pone.0000870
- Putz FE, Parker GG, Archibald RM (1984) Mechanical abrasion and intercrown spacing. Am Midl Nat 112:24–28. doi:10.2307/ 2425452
- Quesada CA et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9:2203–2246. doi:10.5194/bg-9-2203-2012
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed 17 June 2016
- Read JM, Clark DB, Venticinque EM, Moreira MP (2003) Application of merged 1-m and 4-m resolution satellite data to research and management in tropical forests. J Appl Ecol 40:592–600. doi:10.1046/j.1365-2664.2003.00814.x
- Richards PW (1996) The tropical rain forest, 2nd edn. Cambridge University Press, Cambridge
- Russo SE, Wiser SK, Coomes DA (2007) Growth-size scaling relationships of woody plant species differ from predictions of the metabolic ecology model. Ecol Lett 10:889–901. doi:10. 1111/j.1461-0248.2007.01079.x
- Rutishauser E, Barthelemy D, Blanc L, Nicolini E-A (2011) Crown fragmentation assessment in tropical trees: method, insights and perspectives. For Ecol Manag 261:400–407. doi:10.1016/j.foreco. 2010.10.025
- Saatchi SS et al (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. Proc Natl Acad Sci USA 108:9899–9904. doi:10.1073/pnas.1019576108
- Sabatier D, Grimaldi M, Prevost MF, Guillaume J, Godron M, Dosso M, Curmi P (1997) The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. Plant Ecol 131:81–108. doi:10.1023/a:1009775025850
- Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A quantitative analysis of plant form—the pipe model theory: I. basic analyses. Jpn J Ecol 14:97–105
- Singh M, Evans D, Friess DA, Tan BS, Nin CS (2015) Mapping above-ground biomass in a tropical forest in Cambodia using canopy textures derived from Google Earth. Remote Sens 7:5057–5076. doi:10.3390/rs70505057
- Skovsgaard JP, Vanclay JK (2008) Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. Forestry 81:13–31. doi:10.1093/forestry/cpm041
- Slik JWF et al (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. Glob Ecol Biogeogr 22:1261–1271. doi:10.1111/geb.12092
- Smith AR, Lukac M, Hood R, Healey JR, Miglietta F, Godbold DL (2013) Elevated CO2 enrichment induces a differential biomass response in a mixed species temperate forest plantation. New Phytol 198:156–168. doi:10.1111/nph.12136
- Sokal RR, Rohlf FJ (1981) Biometry: the principles and practice of statistics in biological research, 2nd edn. W. H. Freeman, San Francisco

- Sokal RR, Rohlf FJ (2012) Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co, New York
- Sterck FJ, Bongers F (2001) Crown development in tropical rain forest trees: patterns with tree height and light availability. J Ecol 89:1–13
- Strigul N, Pristinski D, Purves D, Dushoff J, Pacala S (2008) Scaling from trees to forests: tractable macroscopic equations for forest dynamics. Ecol Monogr 78:523–545. doi:10.1890/08-0082.1
- Taubert F, Jahn MW, Dobner H-J, Wiegand T, Huth A (2015) The structure of tropical forests and sphere packings. Proc Natl Acad Sci USA 112:15125–15129
- Thomas SC (1996) Asymptotic height as a predictor of growth and allometric characteristics Malaysian rain forest trees. Am J Bot 83:556–566. doi:10.2307/2445913
- Thomas SC, Martin AR, Mycroft EE (2015) Tropical trees in a windexposed island ecosystem: height-diameter allometry and size at onset of maturity. J Ecol 103:594–605. doi:10.1111/1365-2745. 12378
- Umeki K (1995) Modeling the relationship between the asymmetry in crown display and local environment. Ecol Model 82:11–20. doi:10.1016/0304-3800(94)00081-r
- Vanclay JK (1992) Assessing site productivity in tropical moist forests—a review. For Ecol Manag 54:257–287. doi:10.1016/ 0378-1127(92)90017-4

- Vincent G, Caron F, Sabatier D, Blanc L (2012) LiDAR shows that higher forests have more slender trees. Bois et Forêts des Trop 314:51–56
- West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. Nature 400:664–667
- West GB, Enquist BJ, Brown JH (2009) A general quantitative theory of forest structure and dynamics. Proc Nat Acad Sci USA 106:7040–7045. doi:10.1073/pnas.0812294106
- Westoby M, Wright IJ (2003) The leaf size-twig size spectrum and its relationship to other important spectra of variation among species. Oecologia 135:621–628. doi:10.1007/s00442-003-1231-6
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Syst 33:125–159. doi:10.1146/ annurev.ecolsys.33.010802.150452
- Wyckoff PH, Clark JS (2005) Tree growth prediction using size and exposed crown area. Can J For Res 35:13–20. doi:10.1139/x04-142
- Yamada T, Ngakan OP, Suzuki E (2005) Differences in growth trajectory and strategy of two sympatric congeneric species in an Indonesian floodplain forest. Am J Bot 92:45–52. doi:10.3732/ ajb.92.1.45
- Zolkos SG, Goetz SJ, Dubayah R (2013) A meta-analysis of terrestrial aboveground biomass estimation using lidar remote sensing. Remote Sens Environ 128:289–298. doi:10.1016/j.rse.2012.10.017