



Should tree biomass allometry be restricted to power models?



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ABSTRACT

The increasing number of model types that are used to predict tree biomass from diameter, height and wood density has brought questioning about the biological relevance of complex allometries (i.e. non-power models). Statistical issues such as collinearity among predictors and unreliable coefficient estimates have also been associated with complex allometric models. Using a data set of 225 trees from central Africa, we assessed the relevance of simple allometry (i.e. power model) versus complex allometry to predict tree biomass. A complex allometric model of biomass was developed based on a model of resource partition between dbh and height growths. Although being a good model for biomass prediction, the power model was outperformed by the complex allometric model. A careful examination showed that the power model could be segmented into two pieces of power models. Using tree diameter and height as separated predictors improved the biomass prediction, irrespective of the collinearity between these two predictors. A critical value of 25% for the PRSE statistic used to assess the reliability of coefficient estimates corresponded to a significance level of 10^{-5} – 10^{-4} and was thus unreasonably low. We conclude that growth theories should be developed to explain allometric models, but that the arbitration between these models should ultimately rely on observed data, not on theories.

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1. Introduction

With the current interest in forest carbon stocks to mitigate greenhouse gas emissions, emphasis has been put on the statistical tools to estimate tree aboveground biomass (Eggleston et al., 2006). Among these tools are allometric equations i.e., in this context, mathematical models to predict the biomass of a tree from dendrometrical variables that are easier to measure and non-destructive, such as diameter at breast height (dbh), height, or wood density. The term ‘allometry’ was coined by Huxley and Teissier (1936) “to denote growth of a part at a different rate from that of body as a whole”. Because body size results from the temporal integration of its growth, this definition of allometry also implies relationships between body sizes, such as biomass, dbh and height for a tree. However, because many different model forms have been proposed for tree biomass equations, there is

concern that the common understanding of allometry in the IPCC guidelines departs from its original definition (Sileshi, 2014).

More specifically, Sileshi (2014) argued that “biologically implausible (...) equations have been published as allometric models”, where plausible models in his argument referred to power models based on a single predictor. Power models have played a central role in allometry because many growth data empirically turned out to align along a straight line when plotted in log–log scales (Stevens, 2009). However, to quote Gould (1966), “allometry is not confined to any form of mathematical expression, such as a power function”. In their seminal definition of allometry, Huxley and Teissier (1936) considered power models as a particular case of allometry that they called *simple* allometry. In contrast to this simple allometry, *complex* allometries that do not conform to the power model have also been developed (Nijhout and Wheeler, 1996; Bernacchi et al., 2000). Because complex allometric data do not exactly align along a straight line in log–log plots, complex allometry is also called *curvilinear* allometry.

A pending question then is whether tree biomass rather conform to simple allometry or to complex allometry (Temesgen

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et al., 2015). This question may be investigated empirically by assessing whether non-power models provide a better fit to data than power models. More importantly, growth theories may be developed to support one type of allometric models and be confronted to data. Because power models suppose a constant scaling across the whole ontogenic development of the individual, theories supporting simple allometry are mainly fractal-based. The self-similarity that is the basis of fractals solves the dimensional issues associated with the normalization coefficient of the power model (White and Gould, 1965). Nevertheless, the scaling is more likely to be constant only across a finite range of size such as dbh or height (Antin et al., 2013; Temesgen et al., 2015). Because many non-power models can bring nearly constant scaling across a wide range of scale, simple allometry may be confused with complex allometry.

Sileshi (2014) also argued that “statistically dubious equations (...) have been published as allometric models” and highlighted purported common statistical issues, such as collinearity among predictors and unreliable coefficient estimates (as measured by the PRSE statistic). These statistical considerations led the author to conclude that simple allometric models based on a single predictor (typically, dbh) should be preferred to models with several non-independent predictors (such as dbh and height). On the other hand, a growing body of literature highlighted the importance of height-diameter ratios as critical determinants of biomass, both for biomass prediction and for designing sampling strategies of biomass (Temesgen et al., 2011, 2015; Poudel et al., 2015).

Using a compilation of data sets on tree biomass in moist African forests, this study aims at revisiting the question of the form of biomass allometric equations and at addressing the following questions: (1) Based on observed data, does tree biomass rather conforms to simple allometry (i.e. power model) or to complex allometry (i.e. non-power model)? (2) Does simple allometry hold across the whole range of tree size, or can it be segmented into different allometries depending on the size range? (3) Should height be included as a predictor of biomass, in combination with dbh (i.e. using a combined predictor such as square dbh times height) or as a separate predictor? A complex allometric model of biomass was specifically developed in this study based on dbh and height growths. A simple rule of resource partition between dbh and height growths allowed us to derive a non-power model that closely approximates a power model on a wide range of tree size. Although the current study focuses on tree biomass, its approach readily extends to other tree attributes concerned by allometry, such as tree volume or nutrient content.

2. Materials and methods

2.1. Models

2.1.1. Power models or simple allometry

By definition, power models correspond to a relationship between two quantities where one quantity varies as a power of another. Considering that biomass B divided by the specific wood density ρ varies as a power of dbh D , one obtains for example the power model:

$$B = a \rho D^b \quad (1)$$

where a and b are parameters. Wood density ρ in (1) accounts for species differences. When monitoring a single tree across its ontogenic development, ρ is not separable from the a parameter and (1) then boils down to a power relationship between B and D . Both power models are equivalent with a proportional relationship between the biomass relative growth and the diameter relative growth: $(dB/B) = b(dD/D)$. Without further biological theory

explaining this proportionality in relative growth rates, and in particular when this proportionality relationship is empirically derived from data, there is no more biological plausibility in this model than in any other model empirically derived from data. However, some theories are able to derive this power model from lower-level assumptions, such as the metabolic scaling theory (West et al., 1997). This theory is fractal-based, and thus predicts a scaling coefficient b that remains constant along the whole ontogenic development of the plant.

Power models can be reparameterized using the log-transformation. For instance, the power model (1) is trivially equivalent with $\ln(B) = a' + \ln(\rho) + b \ln(D)$ where $a' = \ln(a)$. Re-parameterization is common practice in modelling and is even sometimes a necessity when original parameters are not identifiable and, contrary to Sileshi (2014), we argue that there is no mistake in doing it. Unlike Sileshi's (2014) statement, extensions of the one-entry power model (1) that include other predictors can also be given biological interpretations. For instance, the two-entries power model:

$$B = a \rho D^b H^c \quad (2)$$

where H is tree height and c another parameter, corresponds to a biomass relative growth rate that is a linear combination of the diameter and height relative growth rates: $(dB/B) = b(dD/D) + c(dH/H)$. Another example is the second order polynomial on log-transformed variables: $\ln(B) = a' + \ln(\rho) + b(\ln D) + c(\ln D)^2$. Provided that $c < 0$, which is a natural assumption to ensure that biomass does not increase to infinity, this latter model is equivalent after back-transformation with the log-normal model that has been used to model tree growth (e.g. Uriarte et al., 2004; Engone Obiang et al., 2013):

$$B = B_{\max} \exp \left\{ - \left[\frac{1}{Y} \ln \left(\frac{K}{D} \right) \right]^2 \right\}$$

where $B_{\max} = \rho \exp[a' - b^2/(4c)]$ (in the same unit as B) is the maximum biomass that an individual can reach, $K = \exp[-b/(2c)]$ (in the same unit as D) is the diameter where biomass reaches its maximum and $Y = 1/\sqrt{-c}$ (dimensionless) is a shape parameter that determines the breadth of the biomass function.

2.1.2. Geometric models

Geometric models follow from the fact that biomass is wood density times volume, and that tree volume can be assimilated to simple geometric shapes. For instance, assuming that total above-ground biomass is proportional to stem biomass (which is the rationale behind biomass expansion factors) and that stem volume is a cone leads to:

$$B = a \rho D^2 H \quad (3)$$

For instance, Chave et al. (2005) found a model of this type as being the most suitable for tropical moist forest stands. Contrary to the power model $B = a \rho D^b H^c$ where b and c are free parameters that can take any value, the exponents of D and H in geometric models are fixed. This difference is fundamental as it solves the dimensional issue of the a coefficient in power models.

Replacing measured tree height with a prediction of a height model based on dbh brings biomass equations that depend on dbh and wood density only. A common model for height is the Mitscherlich model (Banin et al., 2012; Kearsley et al., 2013):

$$H = \alpha - \beta \exp(-\gamma D) \quad (4)$$

Integrating the Mitscherlich equation into (3) gives:

$$B = \alpha^* \times \rho D^2 [1 - \beta^* \exp(-\gamma D)] \quad (5)$$

where the α parameter of the height model has been combined with the intercept parameter of the biomass–volume relationship: $\alpha^* = \alpha\alpha$ (these two parameters are not separately identifiable) and $\beta^* = \beta/\alpha$.

2.1.3. Growth models with biomass allocation

Geometric models for biomass can be combined with growth models for dbh and height to derive biomass equations that depend on dbh and wood density. Because growth models can account for biomass allocation among organs depending on the environment (Peters et al., 2014), these models can explain the different allometries that are observed for trees growing in different environments, such as smaller tapering for trees growing in open conditions (Archibald and Bond, 2003). A simple model is proposed here, where we deliberately favoured simplicity over realism. Diameter and height growths are supposed to compete for a common resource in carbohydrates R , that is used to increase the volume D^2H of the stem. Because $d(D^2H) = 2DHdD + D^2dH$,

$$\begin{aligned} 2DH \frac{dD}{dt} &= \alpha r R \\ D^2 \frac{dH}{dt} &= \beta(1-r)R \end{aligned}$$

where α and β are rates of transform of carbohydrates into wood volume, and r is the partition rate of the resource between diameter and height growth. The carbohydrate resource is supposed to be proportional to the foliage mass, i.e. to the basal area (according to the pipe-model theory; Shinozaki et al., 1964), and to light intensity that is supposed to be a function of height only. When expressed in square dbh units, its expression thus is: $R = D^2 \phi(H)$, where $\phi(H)$ is the spatial average of a dimensionless measure of the light intensity at a height H . Without loss of generality, we assume that $\phi(0) = 0$ (the carbohydrate resources of a tree tend to zero as its size tends to zero), that $\phi'(0) > 0$ and that ϕ has a maximum value that is normalized to 1. The vertical profile of the light intensity depends on the vertical distribution of the foliage, which in turns depends on the stand density and on the dbh distributions of trees within the stand. Deriving ϕ from stand characteristics is outside the scope of the current study and we shall subsequently assume that ϕ has some parametric form that summarizes the light environment of the forest.

Biomass partition is supposed to be optimized so that the resource is not limiting (Peters et al., 2014). In first approximation, the partition rate r is supposed to be proportional to the incremental resource that is provided by diameter or height, i.e.:

$$r = \frac{(\partial R / \partial D)}{(\partial R / \partial D) + (\partial R / \partial H)} = \frac{2\phi(H)}{2\phi(H) + D\phi'(H)}$$

This simple growth model with biomass allocation brings the following height–dbh differential equation:

$$\frac{dH}{dD} = \frac{\beta}{\alpha} \frac{2H}{D} \left(\frac{1}{r} - 1 \right) = (\beta/\alpha) \frac{H\phi'(H)}{\phi(H)} \quad (6)$$

The ratio β/α represents the height–dbh ratio of very small trees (i.e. the value of dH/dD at $H = 0$). For a tree growing in open conditions, $\phi(H) \equiv 1$ and only dbh growth occurs. The Mitscherlich model for height is obtained from (6) when the vertical light profile is given by: $\phi(H) = (e/\alpha)H \exp(-H/\alpha)$ (where $e = 2.718\dots$ is Euler's number; proof in Appendix A). In what follows, we assume that the light intensity exponentially increases as height increases (because light intensity obeys a Beer–Lambert law): $\phi(H) = 1 - \exp(-kH)$, where k is the parameter of the Beer–Lambert law. The solution of (6) then is:

$$H = \frac{f^{-1}((\beta/\alpha)kD + c)}{k} \quad (7)$$

where f is the function defined by $f(x) = \text{Ei}(x) - \ln(x) - \gamma$, Ei is the exponential integral function (Abramowitz and Stegun, 1964, Section 5.1.2, p. 228), $\gamma = 0.5772156\dots$ is Euler's constant (Abramowitz and Stegun, 1964, Section 6.1.3, p. 255), and c is an intercept parameter. When plugging the height model (7) into (3), it turns out that neither a and k , nor α and β are identifiable from dbh and biomass data. The biomass model actually has three parameters that can be estimated from data:

$$B = a^* \times \rho D^2 f^{-1}(b^* D + c) \quad (8)$$

where $a^* = a/k$ and $b^* = (\beta/\alpha)k$.

2.2. Data sets

Two data sets were used: a real data set obtained from the compilation of different data sets collected in moist African rain forests, and a simulated data set built from this latter data set. The real data set included 225 trees between 1.2 and 180 cm in dbh and was compiled from Djomo et al. (2010) (71 trees measured in Cameroon), Ebuy Alipade et al. (2011) (12 trees in the Democratic Republic of Congo), Henry et al. (2010) (41 trees in Ghana) and Ngomanda et al. (2014) (101 trees in Gabon). We selected these data sets on the basis of the following criteria: they originated from moist African forests; they included dbh, height, biomass and species or wood density data; they were publicly available in publications.

The simulated data set was obtained from the real data set by replacing every measured biomass B_i for the i th tree by a randomly drawn biomass $\rho_i \exp(a' + b \ln D_i + \varepsilon_i)$, where ρ_i is the wood density of the i th tree, D_i is its dbh, ε_i is drawn according to a Gaussian distribution with mean zero and standard deviation σ , a' and b are the estimated coefficients of the power model (1) fitted to the real data set, and σ is the residual standard deviation of this fitted power model. Therefore, the simulated data set has the same number of observations, with the same dbh, height and wood density values as the real data set. Moreover, simulated tree biomasses are on average the same as real biomasses.

However, the simulated data set strictly conforms to simple allometry, which remains an unknown hypothesis for the real data set. Controlling for simple allometry is necessary to assess the capacity of a statistical method to detect complex allometry. For example, there is a logical flaw in Sileshi (2014) when he concludes “that with current methods it is not possible to confidently tell whether heterogeneity in the exponent [of the power model] is an artefact or a reflection of its size-dependence”. His results are based on a real data set whose conformity to simple allometry remains unknown. To reach his conclusions, Sileshi should either have used a data set that conformed to simple allometry and for which current methods detected an heterogeneity of the exponent (false positive), or a data set that did not conform to simple allometry and for which current methods did not detect the heterogeneity of the exponent (false negative).

2.3. Statistical analysis

Both height–dbh models and biomass models were fitted to the data set from moist African forests. Three height models were fitted to the African data: the Mitscherlich model (4), the model (7) that results from the exponential light profile, and the power model:

$$H = aD^b \quad (9)$$

These height models were fitted using non-linear regression and generalized least squares, where a power model was assumed for the residuals ε : the standard error of ε for a tree with dbh D was assumed to be σD^z .

Two types of biomass models were fitted: with and without height as a predictor. Biomass models based on dbh alone were obtained by plugging the three aforementioned height models into (3), i.e. biomass models (1), (5) and (8), respectively. The biomass models that included height as a predictor were the two-entries power model (2), model (3), and the generalization of model (3) as a power model:

$$B = a\rho(D^2H)^b \quad (10)$$

Whereas models (3) and (10) combine dbh and height into a single predictor, model (2) uses dbh and height as separate predictors. This separation raises the issue of collinearity between dbh and height (Sileshi, 2014). All biomass models were fitted using non-linear regression on log-transformed data and ordinary least squares.

For each estimated coefficient, the T statistic of the Student test that tests if the coefficient is significantly different from zero was also provided. A relationship can be established between the T statistic and the percent relative standard error (PRSE) used by Sileshi (2014). By definition, the PRSE is the standard error of the parameter estimate divided by its absolute value, whereas the T statistic is the parameter estimate divided by its standard error, so that $PRSE = 1/|T|$. Sileshi (2014) considered that a coefficient estimate was unreliable if $PRSE > 25\%$, i.e. if $|T| < 4$. Sileshi's critical value of the PRSE thus corresponds to a significance level that ranges between 10^{-4} for a sample size of 100 observations to 7×10^{-5} for a sample size of 1000 observations. This significance level is several order less than the level of 5% that is commonly used in ecology.

Fitted models were compared to four existing pantropical models. Two of these existing models used height as a predictor, namely Chave et al.'s (2014) model 4: $B = 0.0673(\rho D^2 H)^{0.976}$, and Brown et al.'s (1989) model 4 for moist forests: $B = \exp[-2.4090 + 0.9522 \ln(\rho D^2 H)]$. The two other did not use height as a predictor, namely Chave et al.'s (2014) model 7: $B = \exp[-1.803 - 0.976E + 0.976 \ln \rho + 2.673 \ln D - 0.0299(\ln D)^2]$ where E is a climatic index tabulated by Chave et al. (2014), and Brown's (1997) model 3.2.4 for moist forests: $B = \exp(-2.134 + 2.530 \ln D)$.

Models were compared on the basis of different goodness-of-fit metrics, namely: the Akaike Information Criterion (AIC) and AIC weights (Burnham and Anderson, 2002); the mean relative error $\frac{1}{n} \sum_{i=1}^n (Y_i - \hat{Y}_i)/Y_i$; the mean absolute relative error $\frac{1}{n} \sum_{i=1}^n |Y_i - \hat{Y}_i|/Y_i$; and the relative root mean square error $\sqrt{\frac{1}{n} \sum_{i=1}^n [(Y_i - \hat{Y}_i)/Y_i]^2}$, where Y_i is the i th observation (biomass or height) and \hat{Y}_i is its model prediction. Whereas AIC was computed for fitted models only and relied on log-transformed data whenever log-transformation was used, the other metrics were computed for all models and relied on untransformed data.

To assess the effects of the collinearity between dbh and height in model (2), we fit model (2) to the data set from African moist forests using linear regression on log-transformed data and ordinary least squares. The variance inflation factor (VIF) was computed for each predictor. This model fit was then compared with partial least squares (PLS) regression. We also computed the residuals ε of the linear regression of log-transformed height with respect to log-transformed dbh: $\ln(H) = a + b \ln(D) + \varepsilon$. The null correlation between residuals and predicted values in the linear model ensures that the correlation between ε and $\ln(D)$ is null. We then used $\ln(D)$ and ε as predictors of the log-transformed biomass in a linear regression and compared its fit to the PLS regression.

A segmented regression was fitted to the data set from African moist forests to test for a breakpoint in the simple allometry. The power model (1) was fitted using linear regression on log-transformed data, then a breakpoint was sought in this linear regression (Muggeo, 2003). Difference in slopes between the two pieces of linear regressions was tested using the Davies (2002) test.

To further investigate the differences in allometry depending on tree size, we also fitted the power model (1) to subsets with successive removal of smaller diameter trees: the power model (1) was first fitted using linear regression on log-transformed data to the whole data set of African moist forests; then the power model was refitted to the subsets of trees with dbh greater than a threshold d , with $d = 5, 15, 25$ and 35 cm. If allometry conformed to the power model on the whole dbh range, then the coefficients a_d and b_d of the power model should be the same (within to estimation variability) for all thresholds d . Accounting for the estimation variability of a_d and b_d is not straightforward because the subset with dbh threshold d encompasses all subsets with greater dbh thresholds, so that the estimates of a_d and b_d for the different d are not mutually independent. Therefore, we used a Monte Carlo technique. A data set that conforms to simple allometry was simulated as depicted in Section 2.2. The coefficients of the power model were estimated for all d for this simulated data set. The simulation of the data set was reiterated 5000 times. Let \tilde{a}_{di} and \tilde{b}_{di} be the estimates of the coefficients of the power model for dbh threshold d and for the i th simulated data set. The values of a_d and b_d for the moist African data set were compared to the empirical 95% confidence intervals of \tilde{a}_{di} and \tilde{b}_{di} , respectively.

All analyses were made using the R software. Non-linear regressions were made using the 'nlsLM' function of the 'minpack.lm' package for ordinary least squares and the 'gnls' function of the 'nlme' package for generalized least squares. Segmented regression was made using the 'segmented' package.

3. Results

3.1. Is complex allometry suitable?

Power model (9) for height and power model (1) for biomass correspond to simple allometry, whereas models (4) and (7) for height and models (5) and (8) for biomass correspond to complex allometry. For both height and biomass, and whatever the goodness-of-fit metric used, the two complex allometry models provided a similar quality of fit and outperformed the power model (Fig. 1 and Table 1). Two of the estimated coefficients had a $PRSE > 25\%$, yet were significantly different from zero (p -values < 0.005 ; Table 2). The fitted models provided a better fit to the data than existing biomass equations (Table 1).

3.2. Is the segmentation of simple allometry relevant?

The segmented linear regression of log-biomass with respect to log-dbh for the data set of African moist forests found a breakpoint at $\ln(D) = 3.24$ (std. err. 0.42), i.e. for a dbh of 25.5 cm (Fig. 2). The difference of slopes between the two pieces of lines was significant (Davies' test, p -value = 0.04). The fitted segmented regression had the following expression:

$$\ln(B/\rho) = \begin{cases} -1.911 + 2.610 \ln(D) & \text{for } \ln(D) \leq 3.24 \\ -1.059 + 2.347 \ln(D) & \text{for } \ln(D) > 3.24 \end{cases}$$

with a residual standard error of $\sigma = 0.379$. After back-transformation, including the bias correcting factor of $\exp(\sigma^2/2)$, the expression of the segmented biomass equation is:

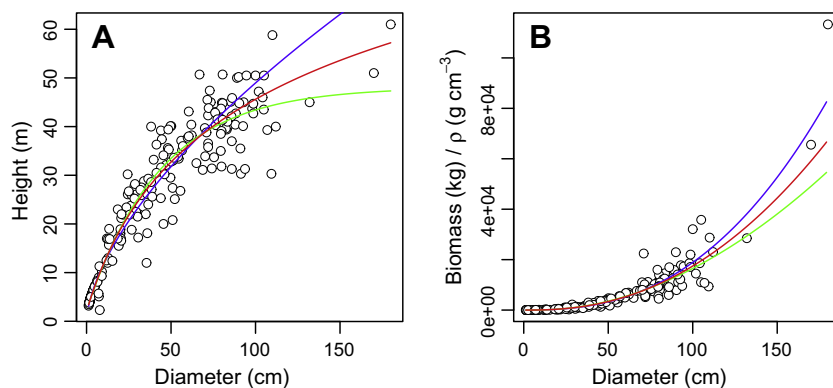


Fig. 1. Height (A) and biomass (B) versus diameter for 225 trees from moist African forests, and their prediction according to different models: (A) Blue line: power model (9); green line: Mitscherlich model (4); red line: model (7) that results from the exponential light profile. (B) Blue line: power model (1); green line: biomass model (5) that results from the integration of (4) into (3); red line: biomass model (8) that results from the integration of (7) into (3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Goodness-of-fit metrics for height and biomass models fitted to the data set from moist Africa forests, and for existing pantropical biomass models. For all models: MRE is the mean relative error, MARE is the mean absolute relative error, and RRMSE is the relative root mean square error. For fitted models: σ is either the standard deviation of residual errors if the model was fitted using ordinary least squares, or the intercept coefficient of the power model for the standard deviation of errors if the model was fitted using generalized least squares (in that case z is the exponent of this power model), and AIC_w is the AIC weight.

Model	σ	z	AIC	AIC _w	MRE	MARE	RRMSE
<i>Height models</i>							
(4)	0.192	0.86	1062.7	0.73	−0.033	0.118	0.280
(7)	0.188	0.87	1064.6	0.27	−0.037	0.118	0.283
(9)	0.182	0.90	1087.8	0.00	−0.041	0.128	0.290
<i>Biomass models without height</i>							
(1)	0.385		213.0	0.01	−0.076	0.310	0.436
(5)	0.377		204.6	0.47	−0.072	0.303	0.425
(8)	0.377		204.4	0.52	−0.073	0.304	0.427
Chave et al.'s (2014) model 7					−0.331	0.444	0.643
Brown's (1997) model 3.2.4					−0.250	0.433	0.639
<i>Biomass models with height</i>							
(2)	0.375		201.9	1.00	−0.069	0.286	0.402
(3)	0.405		235.1	0.00	−0.074	0.290	0.396
(10)	0.385		212.6	0.00	−0.068	0.276	0.388
Chave et al.'s (2014) model 4					−0.278	0.380	0.530
Brown's (1997) model 4					−0.402	0.474	0.653

$$B = \begin{cases} \rho \times 0.159D^{2.610} & \text{for } D \leq 25.5 \\ \rho \times 0.373D^{2.347} & \text{for } D > 25.5 \end{cases}$$

When fitting the power model (1) to subsets of the moist African forests data set with successive removal of smaller diameter trees, the power exponent b had a trend to decrease while the intercept $\ln(a)$ had a trend to increase as the minimum diameter of the subset increased (red lines in Fig. 3). For a minimum dbh of 5, 15 or 25 cm, the exponent b was smaller than expected under the hypothesis of simple allometry, as shown by the 95% confidence interval of b for simulated data sets that conform to simple allometry (Fig. 3A). Correspondingly, for these dbh thresholds, the intercept $\ln(a)$ was greater than expected under the hypothesis of simple allometry (Fig. 3B).

3.3. How height should be included?

Including height as a variable D^2H combined with dbh prevented the issue of collinearity between height and dbh, but brought little improvement as compared to models based on dbh

alone (model (10) in Table 1). The AIC of the power model based on D^2H was 212.6, thus giving a probability of 55% for this model to be better than the power model (1) based on dbh alone, and a probability of less than 1% for this model to be better than any of the complex biomass models based on dbh alone. On the contrary, using dbh and height as separate predictors brought substantial improvement: the AIC of the two-entries power model (2) was 201.9, thus giving a probability of 65% for this model to be better than any of the complex biomass models based on dbh alone.

Log-transformed dbh was strongly correlated with log-transformed height (Pearson's correlation coefficient: 0.98) and, consequently, the VIF of these predictors in the linear regression that predicted log-transformed biomass was very high (VIF = 23.0). Yet, the coefficients associated with $\ln(D)$ and $\ln(H)$ were significantly different from zero (Table 3). The PRSE associated with $\ln(H)$ was greater than 25%. However, in the present

Table 2

Estimates of the coefficients of the height and biomass models fitted to the data set from moist Africa forests. Dbh is in cm, height in m, and biomass (in kg) is divided by wood density (in g cm^{-3}). $|T|$ is the inverse of PRSE and italic text highlights PRSE > 25%.

Model	Parameter	Estimate	Std. error	T	p -value
<i>Height models</i>					
(4)	α	48.07	2.11	22.8	< 0.001
	β	45.84	2.06	22.3	< 0.001
	γ	0.0229	0.0017	13.6	< 0.001
(7)	β/α	123.1	5.8	21.3	< 0.001
	k	0.0657	0.0045	14.7	< 0.001
	c	0.136	0.007	19.9	< 0.001
(9)	a	2.765	0.040	70.0	< 0.001
	b	0.624	0.006	98.4	< 0.001
<i>Biomass models without height</i>					
(1)	a	0.167	0.010	16.9	< 0.001
	b	2.527	0.018	140.8	< 0.001
(5)	α^*	1.704	0.106	16.1	< 0.001
	β^*	0.924	0.011	86.2	< 0.001
	γ	0.0338	0.0054	6.2	< 0.001
(8)	a^*	0.435	0.058	7.5	< 0.001
	b^*	17.64	5.52	3.2	0.002
	c	0.256	0.057	4.5	< 0.001
<i>Biomass models with height</i>					
(2)	a	0.101	0.015	6.7	< 0.001
	b	2.228	0.084	26.6	< 0.001
	c	0.487	0.133	3.7	< 0.001
(3)	a	0.0460	0.0012	37.0	< 0.001
(10)	a	0.0625	0.0041	15.2	< 0.001
	b	0.965	0.007	140.9	< 0.001

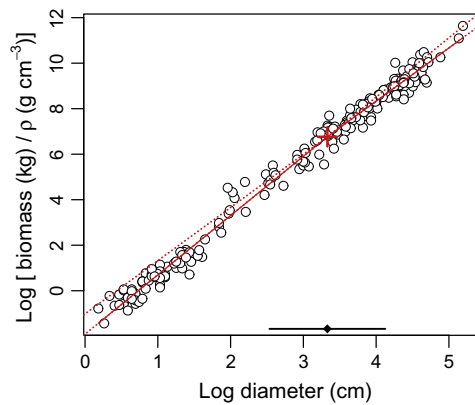


Fig. 2. Segmented regression of log-transformed biomass on log-transformed diameter, fitted to a data set of 225 trees from moist African forests. The red dot indicates the detected breakpoint and the red lines are the two fitted pieces of lines. The black horizontal line and point indicate the 95% confidence interval of the breakpoint. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

case, the critical value of 25% for the PRSE corresponded to a confidence level of 8.6×10^{-5} . Replacing $\ln(H)$ with the residuals ε of the linear regression of $\ln(H)$ with respect to $\ln(D)$ suppressed the collinearity (VIF became equal to one) but changed nothing to the overall performance of the model. The coefficient associated with $\ln(D)$ increased from 2.228 to 2.527, whereas that associated with the other predictor ($\ln(H)$ or ε) did not change. The correlation between the scores on the first component of the PLS regression and $\ln(D)$, and the correlation between the scores on the second component of the PLS regression and ε were both > 0.99 in absolute value. Therefore, there was almost no difference between the outcome of the PLS regression and that of the linear regression using $\ln(D)$ and ε as predictors.

4. Discussion

All results concur to show that simple allometry, although fitting the data very closely, does not hold after careful examination (Poorter and Sack, 2012). The fit of the power model to data subsets with successive removal of smaller trees consistently brought constant coefficients when the data set conformed to simple allometry (simulated data set, see black dots in Fig. 3). Therefore, contrary to Sileshi (2014) who argued that this method could not detect size-dependence in allometry, we interpret the decrease of

the b coefficient and the concomitant increase of the a coefficient in Fig. 3 as some size-dependence of allometry. This result was confirmed by the segmented regression that found a lower exponent b (and correspondingly a higher a) of the power model for larger trees. The same outcome of the segmented regression was obtained for the height-dbh model (results not shown here to save space). The fit of complex allometric models that outperformed simple allometric models was consistent with the conclusion that tree biomass did not exactly conformed to the power model (Nijhout and German, 2012). Temesgen et al. (2015) also noted the need to localize height-diameter relationships and to account for tree height variation within diameter classes in order to improve the predictive abilities of biomass equations.

Although not being exact, simple allometry still provided a very good fit to data. Accordingly, the segmented regression was close to non-significance at confidence level 95% (p -value = 4%). The point is that complex allometric models are hardly distinguishable from a straight line in log–log plots on a large range of dbh, thus advocating that they may have often been confused with simple allometry. To make a parallel with another power model in a very different context, the between-sample variance in density of organisms in a study area is often expressed as a power model of the overall mean density, which is known as Taylor's (1961) law. However, if the spatial distribution of organisms is described by a spatial point process, it is possible to analytically derive the relationship between the variance of density and its mean (Stoyan and Stoyan, 1994), and this relationship is not a power relationship, although being very close to it on a large range of scales (Picard and Favier, 2011). Therefore, it cannot be excluded that power models have often been selected in ecology because a line can fit many patterns in log–log scales, regardless of the fact that a complex relationship provides a better fit (compare Enquist and Niklas, 2001; Coomes et al., 2003, for another example). Simple models have also been popular among foresters because dbh and bole volume have long been the sole information collected in the field. Inclusion of total height and wood density have only been recently proposed (Brown et al., 1989) and assessed in tropical forests.

The concomitant increase of the intercept b with decreasing exponent a in Fig. 3 is expected for the power model. Going back to Hersh (1931) who established a negative power relationship between the two coefficients in simple allometry, many authors have found this relationship (e.g., Sileshi, 2014; Zianis and Mencuccini, 2004), both for ontogenetic allometry (i.e. size of individuals of the same species at different development stages) and for phylogenetic allometry (i.e. size of individuals of different species at the same development stage). Biological interpretations of this relationship have been proposed and contested (White and

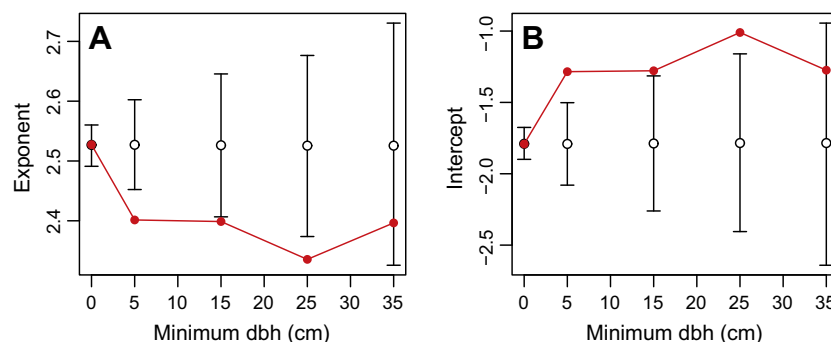


Fig. 3. Changes of the coefficients of the linear model $\ln(B/\rho) = a' + b \ln(D)$ with successive removal of smaller diameter trees (i.e. >0 , >5 , >15 , >25 , >35 cm) and refitting of the model: (A) Exponent b , (B) Intercept a' . Black lines and dots correspond to the simulated data set according to simple allometry; whiskers indicate the 95% confidence intervals for 5000 simulated data sets. Red line and dots correspond to the observed data set from moist African forests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3

Fit of the two-entries power model (2) for biomass using linear regression on log-transformed data and ordinary least squares. The data set contains 225 trees from central African moist forests. Predictors are either $\ln(D)$ and $\ln(H)$ (with collinearity between them), or $\ln(D)$ and the residuals ε of the linear regression of $\ln(H)$ with respect to $\ln(D)$ (no collinearity).

Parameter	Estimate	Std. error	T	p-value	PRSE	VIF	σ	AIC
<i>Collinearity: predictors are $\ln(D)$ and $\ln(H)$</i>								
$\ln(a)$	−2.291	0.148	−15.4	< 0.001	6.5		0.375	201.9
b	2.228	0.084	26.6	< 0.001	3.8	23.0		
c	0.487	0.133	3.7	< 0.001	27.4	23.0		
<i>No collinearity: predictors are $\ln(D)$ and ε</i>								
$\ln(a)$	−3.182	0.385	−8.2	< 0.001	12.1		0.375	201.9
b	2.527	0.017	144.6	< 0.001	0.7	1		
c	0.487	0.133	3.7	< 0.001	27.4	1		

Gould, 1965) but it could also be a mere sampling effect. The estimators of slope and intercept in linear regression are negatively correlated. For instance, for the tree biomass data set from African moist forests, the correlation between the estimates of $\ln(a)$ and b with linear regression on log-transformed data was -0.90 . Therefore, when estimating the coefficients of the power model using linear regression on log-transformed data and back-transforming the intercept a (but not the exponent b), a non-linear relationship between a and b appear that is only due to sampling (Appendix A).

When included as a separate predictor in addition to dbh, height significantly improved the prediction of biomass. From a prediction viewpoint, including height implies that any error on the measurement of height will propagate to the tree-level, then to the plot-level estimate of biomass (Garber et al., 2009; Fortin and DeBlois, 2010). Such error propagation may act as a caveat for the inclusion of height. Nevertheless, from a biological viewpoint, height is expected to be a determinant of biomass because trees with the same dbh but different tapering are expected to have different allometries (Nogueira et al., 2008; Temesgen et al., 2015). Therefore, height is a necessary predictor to account for specific differences in plant architecture or phenotypic plasticity in growth depending on growing conditions (Callaway et al., 1994; Archibald and Bond, 2003). Crown size may be another predictor to describe this plasticity in growth (Goodman et al., 2014; Kohyama et al., 2003). The coefficients associated with height had a PRSE greater than 25% (or, equivalently, a $|T|$ statistic less than 4). According to Sileshi (2014), this would mean that these coefficients are unreliably estimated and should lead to reject height as a predictor of biomass. However, the p -values of the test of significance of these coefficients were 10^{-3} or less, thus much less than the significance level of 5%. Using a critical value of 25% for the PRSE as Sileshi (2014) recommended actually corresponds to very low significance levels of the test ($< 10^{-4}$ for a sample size > 100 observations). Because such low levels go in hand with high type II error, we strongly discourage the use of a critical value of 25% for the PRSE. Consistently, we conclude that the coefficient associated with height was reliably estimated.

Including height as a predictor in addition to dbh raises the issue of collinearity between these two predictors. Collinearity is a concern but, in opposition with Sileshi (2014), its effects should not be exaggerated (Mason and Perreault, 1991). Collinearity has no impact on the overall regression model and associated statistics such as R^2 , F ratios and associated p -values. It also has no impact on predictions made using the overall model as long as the new data set for which predictions are made has the same type of predictor correlations as the data set used for model fitting. For trees, this condition is most likely to hold since the correlation between dbh and height follows from ontogeny. Contrary to what Sileshi (2014) said, selecting predictors on the basis of a threshold value for their VIF is not appropriate (O'Brien, 2007). What matters first

is whether the coefficients are significantly different from zero; if not, then collinearity and VIF should be inspected. In the present case, the coefficient associated with height was highly significant despite its inflated variance, and there was no reason for rejecting height as a predictor even if it was strongly correlated with dbh. The results of the PLS regression and of the regression using the residuals ε as a predictor in place of height confirmed this result.

Collinearity between height and dbh simply means that the coefficients associated with height and dbh cannot be interpreted separately (Mason and Perreault, 1991). The PLS regression showed that the main effect of tree size on biomass was captured by dbh. Height acted as a correcting variable: the positivity of the coefficient associated with height meant that, given two trees with the same dbh, the higher had a greater biomass. Accounting for differences in biomass for trees with the same dbh is precisely what is expected from the inclusion of height as a predictor in the model.

The model for resource partition between dbh and height growths that we developed in this study was coarse, but we deliberately aimed at showing that even the simplest theories can bring complex allometric models that fit data. The light profile function ϕ summarized the average light environment of the forest, and could be thus adjusted to account for different growing conditions. By changing ϕ , one may thus predict the differences in allometry that result from different growing conditions. An important point to highlight is that, whatever the light profile ϕ , the biomass allometry that results from the biomass allocation model cannot be a power model (proof in Appendix A). Therefore, this growth model is inherently incompatible with simple allometry. Many models for biomass allometry can be designed but we argue that the arbitration between these models should be made by measured data, not by theory. Thus, we strongly disagree with Sileshi (2014) that claim that models to fit to data should be *a priori* selected among those with a theoretical basis.

Models for resource partitioning, and more generally tree growth models predicting total aboveground biomass, need to be developed to better understand the relationships between biomass and tree characteristics such as height-diameter ratio, crown size or wood density. Such models would then allow one to relate tree-level variations in biomass to stand-level attributes such as stand density, local competition, moisture stress or nutrient availability (Temesgen et al., 2015). Such relationships could be investigated in even-aged monospecific stands to be then extended to uneven-aged or treated stands (Saint-André et al., 2005). They would eventually allow one to understand how climate or edaphic conditions across broad geographic areas control for variations in tree allometry (Callaway et al., 1994; Lines et al., 2012).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.05.035>.

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