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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.

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:

$$B = a\,\rho D^b \tag{1}$$

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: $(\mathrm{d}B/B) = b(\mathrm{d}D/D)$. 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:

$$B = a\,\rho D^b H^c \tag{2}$$

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: $(\mathrm{d}B/B) = b(\mathrm{d}D/D) + c(\mathrm{d}H/H)$. 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; EngoneObiang 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 aboveground biomass is proportional to stem biomass (which is the rationale behind biomass expansion factors) and that stem volume is a cone leads to:

$$B = a\,\rho D^2 H \tag{3}$$

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):

$$H = \alpha - \beta\exp(-\gamma D) \tag{4}$$

Integrating the Mitscherlich equation into (3) gives:

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