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Bayesian and Classical Models to Predict Aboveground Tree Biomass Allometry

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Total dry aboveground tree biomass (M) allometric equations were derived from 25 destructively sampled Hungarian oak (*Quercus frainetto* Ten.) trees, growing in the Chalkidiki peninsula (Northern Greece). The regression models were developed under Bayesian and classical statistical approaches. All approaches captured equally well the variability in the recorded M values across the diameter ($D_{1.3}$) range of the sampled trees. The informative Bayesian approach based on prior distributions about the allometric parameters and the size-dependent error variance provided quite accurate M predictions. The log-linear regression, nonlinear regression, and noninformative Bayesian approaches failed to predict M distribution when validation was performed against an independent data set previously collected from the study area. It was concluded that adaptation of the Bayesian theorem in tree allometry research is strongly supported. A published simplified Bayesian approach, based on a six-tree sample, was applied in our data set and was found to be a promising tool for allometric relationships. Further research is needed to robustly support or reject such an approach. Theoretical values of the slope in $M - D_{1.3}$ allometry were validated against the derived parameter. A number of scaling parameters, rather than a unique pair of them, may quite accurately describe tree biomass allometry.

Keywords: Bayesian tree allometry, aboveground tree biomass, power law, biomechanical models, *Quercus frainetto* Ten.

Tree biomass allometries have been developed mainly for two reasons: to estimate forest biomass at the stand, forest, or ecosystem level and, during the last decade, to validate predictions about tree functional-structural characteristics derived from theoretical models. Allometric theory implies proportionality between the relative growth rates of two size variables of an organism. Tree biomass allometry predicts that

$$M = aD_{1.3}{}^b \qquad (1)$$

where M is the total tree biomass or the biomass of the tree component (stem, bark, foliage, or branch) and $D_{1.3}$ is diameter at a specified height (usually at 1.3 m aboveground). Theoretical predictions on allometric exponent b originate with dimensional analysis, which ensures that the resulting equations are dimensionally compatible. For example, if stem biomass is to be predicted through Equation 1, the value of b is expected to lie close to 3, because stem shape can be approximated as a solid of revolution. However, when crown biomass is taken into consideration and total aboveground biomass is to be estimated, b is expected to lie between 2 and 3 because tree crown

resembles a fractal object with fractional dimension (Zeide 1998). Biomechanical models have also been used to study tree allometric relationships (Niklas 1994, Sileshi 2014). West et al. (1997) integrated biomechanical constraints with an optimum distribution system of biological resources and derived a model (metabolic scaling theory [MST]) that predicts several allometric relationships between structural and functional characteristics (e.g., for total aboveground $M \propto D^{8/3}$ or $M \propto H^4$), both within and among individual plants.

In practice, theoretical scaling models are rarely being applied to estimate tree biomass because empirical studies have produced a wide range of a and b values. Meta-analyses on $M - D_{1.3}$ allometric equations spanning the globe indicated that empirical parametric values are statistically different from the MST theoretical predictions (Muller-Landau et al. 2006, Zianis 2008, Návar 2010). However, Fehrmann and Kleinn (2006) supported the fact that tree diameter measured at fixed stem height is an inappropriate variable for describing relative diameter growth and therefore should not be used for validating allometric theoretical models. They empirically

demonstrated that MST predictions were corroborated when diameter at relative stem height was used as the independent variable. Similar conclusions were reported by Návar (2010).

Traditionally, data sets on $M - D_{1.3}$ pairs are logarithmically transformed to solve the nonnormality, and the heteroscedasticity problem and expected parametric values are derived through regression analysis by minimizing least-square errors or by maximum likelihood estimation. It should not escape our attention that the inherent drawbacks in logarithmic biomass regressions, mainly related to difficulties in estimating goodness-of-fit measures in the original scale, may lead to selecting an incorrect model. These kinds of problems arise because such measures are calculated on the logarithmic scale and are not directly comparable to those obtained in the normal scale. To a lesser extent and within the classical statistical paradigm, nonlinear and seemingly unrelated linear regressions have also been used to parameterize Equation 1. Packard and Boardman (2008) have questioned the appropriateness of log-linear regression and proposed that a nonlinear least-squares method (nonlinear regression) should also be used for developing allometric equations when variables related to biological phenomena are studied (see also Packard and Birchard 2008, Packard 2009, Packard et al. 2011).

Tree empirical allometric equations are used to obtain average M values for specific $D_{1.3}$ values. However, to derive biologically sound M predictions, stochasticity in terms of probability distribution should be appropriately selected and directly integrated in the allometric model. For example, if M is assumed to be normally distributed, then negative values might be predicted, especially for small-sized trees, jeopardizing the modeling approach. The vast majority of empirical biomass studies assumed a multiplicative error structure in M predictions and therefore the linear regression technique was applied in the logarithmic transformation of Equation 1. Green and Bullock (2014) referred to the importance of reporting model prediction error. Ignoring model error would result in confidence intervals that are too narrow, and model developers should provide users with methods to account for prediction error. Prediction intervals for M are rarely being documented in empirical studies. Zou et al. (2009) reported closed-form formulas to estimate prediction intervals for variables following a log-normal distribution. These formulas, based on the asymmetric variance pattern of predicted M, could be used to evaluate the uncertainties related to forest biomass estimation, when log-linear equations are applied to the diameter distribution of inventory plots. For the nonlinear regression technique, a weighted function is usually implemented to avoid unrealistic M prediction intervals.

Within a Bayesian framework, the quantification of uncertainty in tree biomass prediction for a specific $D_{1.3}$ can readily be modeled by inserting an equation for the variance, which may depend on the predicted M value. The flexibility of Bayesian analysis allows the use of any modeling approach (e.g., nonlinear regression), assuming any kind of error structure (e.g., randomly distributed, normal, or log-normal), to avoid the limitations usually imposed by classical statistical assumptions.

Recently, Zapata-Cuartas et al. (2012) compiled an $M - D_{1.3}$ data set of 257 tropical trees from various sources to illustrate the usefulness of Bayesian analysis for simplifying tree biomass allometry. They concluded that quite accurate M predictions are derived through Bayesian regression, even if a small sample of destructively compiled trees was used. A hierarchical Bayesian approach was also applied by Tredennick et al. (2013) to validate theoretical allometric models for tree species in savannah ecosystems, and the derived

empirical value of the scaling exponent in $M - D_{1.3}$ allometry supported the predictions from the MST model. Zell et al. (2014) have also used a Bayesian calibration approach to predict tree biomass.

The main objective of this article was to test the prediction performance for aboveground biomass allometric equations derived by the Bayesian and classical approaches for oak trees growing in the Chalkidiki peninsula (northern Greece). Two models were used in each approach, namely log-linear relationship and a simple power function. The derived parametric values were applied to a previously published raw data set for validating both M predictions and their associated uncertainty bounds. Moreover, the performance of a published simplified Bayesian method to derive M predictions was also tested. Finally, comparisons of empirical scaling exponents against theoretical values predicted by MST and biomechanical theories were made.

Materials and Methods
Study Area
The study was conducted at the Taxiarchis experimental forest, which is located on the central mountainous part of the Chalkidiki peninsula, approximately 70 km southeast of the city of Thessaloniki (40°25′N and 23°31′E). It consists of deciduous oak and beech natural stands in upper elevations and evergreen broadleaved (marquis) vegetation in lower elevations. In addition, Black pine plantations (*Pinus nigra* L.), Calabrian pines (*Pinus brutia* Ten.), and firs are included in the tree species composition. The Taxiarchis experimental forest is managed on a sustainable basis. A 10-year thinning cycle is applied removing 5% of the oak standing volume. At the time of the study, the mean tree density for trees with dbh greater than 6 cm was 1,260 ($\pm$994) trees ha^{-1}; the mean diameter and height were 15 cm and 16 m, respectively. The region has a transitional Mediterranean to continental climate with a 37-year mean annual temperature of 11.3° C. The mean annual precipitation is 777 mm, of which 265 mm fall from May to September. Bioclimatically, the region belongs to the sub-Mediterranean bioclimate with biologically dry days 0–27 while the Emberger's ombrothermic quotient $Q = 72$ mm ° C^{-2} (Mavromatis 1980), classifying the region in the Emberger's wet bioclimatic level with harsh winters. The Taxiarchis experimental forest is located on mica schist mixed with talc schist rocks with soil texture from sandy-clay to clay. The soil type in the oak stands is acid brown forest soils derived from the mica schist erosion (Matis and Alifragis 1983). The overstory species composition at the site under study is dominated by Hungarian oak (*Quercus frainetto* Ten.) coppice stands under conversion into high forest with about 44% cover area.

Calibration Data Set
Twenty-five Hungarian oak trees were destructively sampled during the growing period in 2013 and 2014. The dbh ($D_{1.3}$ in cm) was measured at 1.3 m aboveground before felling. The sampled trees were cut at the stump height (0.30 m), and, after felling, total tree height (H in m), diameter at 10% of H ($D_{0.1}$ in cm), and diameter at 50% of bole length ($D_{0.5}$ in cm) were recorded. Subsequently, the branches were removed from the stem, and fresh biomass was determined in the field using a hanging balance ($\pm$100 g) (crane scale model OCS-05-SP). Dead and epicormic branches were weighted separately from the live crown. For trees with $D_{1.3} \leq 15$ cm, the whole crown was taken to the laboratory, foliage was separated from branches, and dry weight was determined (oven-dried at

80° C until a constant weight was reached). For trees with $D_{1.3} > 15$ cm, subsamples from the lower, middle, and upper parts of each branch were selected for the determination of fresh and oven-dried biomass ratios. The leaves were removed from twigs and branches to determine the foliage/branch biomass ratio. The fresh biomass of the subsamples was measured with an electronic balance (± 50 g) (model Aspire A12) and was subsequently oven dried at 80° C until a constant weight was reached. Fresh/oven-dried biomass ratios of twigs, branches, and foliage were applied to estimate the total crown dry biomass.

The stem was divided into six sections (including the stump) after felling, and fresh biomass of each section was measured in the field. From each section, a stem disk 7 cm wide was removed, weighed, taken to the laboratory, and oven dried at 80° C until a constant weight was reached to determine the fresh/oven-dried biomass ratio. The ratio from each stem disk was applied to the corresponding stem section fresh biomass, and dry biomass values were therefore obtained; the summation of the six dry biomass values determined the stem biomass. The total aboveground tree biomass (M) was determined as the sum of the crown dry biomass (foliage + branches) and stem dry biomass. The sawdust during the stem cutting was not accounted for in the biomass calculations. Raw data are available from the authors on request.

Validation Data Set

Twenty-seven Hungarian oaks trees, originating from three pure even-aged coppice under-conversion stands at the Taxiarchis experimental forest, were destructively sampled after a stratified random sampling. The scatter plot of M against $D_{1.3}$, presented by Matis and Alifragis (1983), was scanned, and appropriate software was used to derive the corresponding values. $D_{1.3}$ varied from 2.2 to 19 cm, H from 2.2 to 14.7 m, and M from 3.4 to 164.9 kg. This data set was used mainly for testing the performance of our models, when extrapolation to lower diameters was performed.

Statistical Methods

Two different mathematical models had been used to describe the allometric relationship between M and $D_{1.3}$, namely log-linear equation and a simple power function. Thus, under the classical statistics framework the following two techniques were applied: linear regression on the logarithmic transformed data (LR), and weighted nonlinear regression (NLR) on normal scale. In addition, two Bayesian approaches based on noninformative (using the log-linear model) and informative (using the power function) priors about parameters and variance were also developed and applied in the compiled data sets. Finally, a simplified Bayesian approach for predicting M, based on six-tree sample, was tested. In the following sections, brief descriptions about these methods are reported.

Log-Linear Regression (LR)

The $M - D_{1.3}$ values from the 25 destructively sampled oak trees were logarithmically transformed for the ordinary least-squares technique to be applied, and the predictions on the logarithm of M were obtained through the following equation

$$\ln M = \ln a + b \ln D + \varepsilon \tag{2}$$

The error term ε implies that the data do not perfectly follow a straight line in the log-log plot, but rather deviations are normally distributed with zero mean and constant variance (σ^2). Assuming that $\ln M$ follows a normal distribution, inevitably M is log-normally distributed. It should be noted that Equation 1 is mathematically equivalent to Equation 2 but not in a statistical sense, because bias is introduced from the exponentiation of Equation 2, originating from the fact that the mean of a log-normal distribution is not directly obtained by exponentiating the mean of the corresponding normal distribution. Therefore, to reduce the bias, a correction factor should be used (Sprugel 1983), which, in general, has a positive biased effect (Smith 1993).Thus, the prediction of the mean response for diameter D, at normal scale, was obtained by the following equation

$$M_D = e^{(\ln a + b \ln D + v/2)} \tag{3}$$

where $e^{v/2}$ is the correction factor to eliminate the bias from log-transformation, and

$$v = M_{se}(1 + [1, \ln D](X'X)[1, \ln D]') \tag{4}$$

denoting the variance of the predicted value, M_{se} is the mean square error of the linear regression, and $\mathbf{X}$ is the design matrix of the linear regression. According to Zou et al. (2009), the estimation of predicted intervals could be based on the following formulas (application of Equations 3 and 4 in the aforementioned reference for $n = 1$)

$$\text{Lower limit of } M_D = M_D \exp[-(z^2_{1-a/2}v + (v/2)^2)^{1/2}] \tag{5}$$

$$\text{Upper limit of } M_D = M_D \exp[(z^2_{1-a/2}v + (v/2)^2)^{1/2}] \tag{6}$$

where $z_{1-a/2}$ denotes the respected quantile of the standard normal distribution.

Nonlinear Regression (NLR)

The standard fit method for NLR is similar to linear regression, but a curve is fitted to the data set instead of a straight line. Just as in the linear scenario, the sum of the squares of the horizontal and vertical distances between the line and the points are to be minimized. Several assumptions should hold valid for NLR regression to be applied. If nonconstant M variance is reported, weighted NLR may be used. All statistical analysis was performed using the R statistical package (R Development Core Team 2014) and MATLAB R2011b (MATLAB 2011).

Noninformative Bayesian Approach (NB)

In the Bayesian framework, the noisy realization of the data over the underlying allometric model is approximated through a posterior distribution of $\ln a$ and b rather than as point estimates of the allometric coefficients. Prior distribution over all parameters and the likelihood function of the data are prerequisites to obtain posterior distribution for the allometric coefficients under Bayes' theorem. Thus, uncertainty in parameters and variables is expressed on probabilistic terms

Posterior distribution $\propto$ likelihood X prior

The prior distribution reflects our knowledge of the parameters and/or variables under study, which is "updated" through the data to derive a posterior distribution (Van Oijen et al. 2005). If noninformative priors are to be used, then Bayesian credible intervals are expected to be numerically similar to classical confidence limits. To derive the expected parametric values as well as M predictions and

the associated probability distribution, the following model was developed

$$\ln M_i \sim N(\ln a + b \ln D_{1.3i}, \sigma^2)$$
$$\ln a \sim \text{uniform distribution } (-4, -1)$$
$$b \sim \text{uniform distribution } (1.5, 3.5) \text{ and}$$
$$\sigma^2 \sim \text{gamma distribution } (0.1, 0.01)$$

whereas predictions at the normal scale were derived as

$$M_i \sim \text{log-normal distribution } (\ln M_i, \sigma^2).$$

At this point it should be mentioned that Zapata-Cuartas et al. (2012) proposed a bivariate normal distribution for a and b to account for their close interrelationship (see also Sileshi 2014). However, as reported by White and Gould (1965), this is a statistical caveat and depends on the measurement unit of the "independent" variable (in our case for D).

A similar approach was applied for the $M - H$ relationship with the following priors for the allometric coefficients

$$\ln a \sim \text{uniform distribution } (-3, 3)$$
$$b \sim \text{uniform distribution } (0, 5)$$

For all the allometries, WinBugs software based on Markov chain Monte Carlo methods (Spiegelhalter et al. 2007) was used to generate posterior distributions and in turn to draw estimates for parameters and predictions (via Gibbs sampler). A burn-in period of 5,000 steps and 50,000 iterations was used to obtain 45,000 estimations per variable or parameter. In cases where autocorrelation of the Markov chain Monte Carlo was reported, it was eliminated by increasing the number of iterations to 200,000.

Informative Bayesian Approach (IB)

A priori distributions for the allometric coefficients could improve the precision of parameter estimates (Zapata-Cuartas et al. 2012), whereas modeling variance, based on previous studies, could provide reasonable credible intervals when extrapolation of M predictions beyond the $D_{1.3}$ range of the sampled trees is needed. A priori distributions for a and b were derived from studies conducted on a large compendium of biomass allometric equations (Ter-Mikaelian and Korzukhin 1997, Zianis and Mencuccini 2003, Jenkins et al. 2004, Zianis et al. 2005, Pilli et al. 2006, Zianis 2008, Návar 2009, Zapata-Cuartas et al. 2012). A preliminary analysis on these databases resulted in

$$a \sim \text{log-normal distribution } (-2.0, 0.5)$$
$$b \sim \text{normal distribution } (2.35, 0.1)$$

Because theoretical outcomes of different origins (dimensional analysis, biomechanics, fractal geometry, and others.) indicate that the $M - D_{1.3}$ relationship is better described through a simple power function (i.e., Equation 1) and letting M_i follow a log-normal distribution, predictions at normal scale were derived as

$$M_i \sim \text{log-normal } (\mu_i, z_i) \text{ where}$$
$$z_i = \ln(1 + \sigma_i^2/M_i^2)$$
$$\sigma_i^2 = g(aD_i^b)^c$$
$$g \sim \text{uniform distribution } (0.01, 0.05)$$

The aforementioned IB model was based on the assumption that M is log normally distributed with mean $\mu = \ln(aD^b)$ and variance z. Taking into account the well-known pattern of variance heterogeneity at normal scale (σ^2), it is expected that $\sigma^2 \propto M^c = g(aD_i^b)^c$.

Ducey et al. (2009) reported $c = 1.5$ for trees growing in an Amazonian region and in the absence of further information about its value, the aforementioned estimate was used for our data set. According to Thomopoulos and Johnson (2003), when the variance (σ^2) in normal scale is known, the variance in logarithmic scale may be determined as $z = \ln(1 + \sigma^2/M^2)$.

Simplified Bayesian Allometry

Recently, Zapata-Cuartas et al. (2012) proposed a methodology based on the small sample size used in a Bayesian regression to capture the variability in $M - D_{1.3}$ allometry. It was reported that values from six destructively sampled trees are enough for such an analysis. An approach similar to the proposed method was implemented in the oak data set by analyzing 15 sub-data sets, each one consisting of six trees. Subsamples 1 to 5 were deliberately based on "extreme" trees to better examine the performance of the model under "biased" conditions. Specifically, subsample 1 was based on the six smallest trees, the second subsample included six trees from the middle quantile, and the third subsample was based on the six largest trees. Subsample 4 consisted of six trees that had the maximum positive deviation from IB regression, which was based on the full data set, and the fifth subsample included six trees with the minimum negative deviation. Subsamples 6 to 15 included six randomly selected trees. It should be mentioned that a full analysis should have been made on 177,100 subsamples, each one consisting of six trees, produced by the 25 destructively collected trees. However, such an exercise was beyond the scope of this study, because much more empirical data are needed to thoroughly test the applicability of the proposed method.

Priors for $\ln a$ and b were set equal to -3.215 and 2.383, respectively (derived from Table 1 in Zapata-Cuartas et al. 2012). Because the errors in the log-scale are assumed to be normally distributed [$\varepsilon_i \sim N(0, \sigma^2)$], the prior for the variance was specified with a gamma distribution as recommended by McCarthy (2007). The following model was therefore developed

$$\ln M_i \sim \text{normal distribution } (\ln a + b \ln D_i, \sigma^2)$$
$$\ln a \sim \text{normal distribution } (-3.215, 3.103)$$
$$b \sim \text{normal distribution } (2.383, 0.058) \text{ and}$$
$$\sigma^2 \sim \text{gamma distribution } (0.1, 0.01)$$

whereas predictions at normal scale were derived as

$$M_i \sim \text{log-normal distribution } (\ln M_i, \sigma^2)$$

Goodness-of-Fit Criteria

Sileshi (2014) reviewed several criteria and indices for assessing model performance in tree allometric studies. The mean absolute percentage error or, according to Parresol (1999) and Zianis and Mencuccini (2005), the mean absolute percentage difference (P_D) between the predictions and the raw data was proposed to be used as one of the most appropriate criteria. Therefore, the absolute difference between the observed and predicted values divided by the observed value is calculated for each tree and the average value of these deviations is multiplied by 100 to define P_D, or

$$P_D = 1/n^* \sum (|1 - p_i/O_i|)^* 100$$

where P_i and O_i denote the predicted and corresponding observed biomass values for the ith tree ($i = 1$ to n where n is the total number of sampled trees), respectively. Values close to 0% indicate accurate predictions, whereas to the best of our knowledge, there is not a

Table 1. Dendrometric characteristics of 25 destructively sampled oak trees.

Variable	Mean	Range	SD	CV	SE
Diameter at 10% of height ($D_{0.1}$) (cm)	19.3	10.8–34.8	6.27	0.32	1.25
Dbh ($D_{1.3}$) (cm)	19.57	9.5–35.5	6.82	0.35	1.36
Diameter at 50% of bole length ($D_{0.5}$) (cm)	17.52	9.4–31.2	6.05	0.34	1.21
Total tree height (H) (m)	15.4	8.2–22.6	4.14	0.27	0.82
Aboveground biomass (M) (kg)	254.68	34.40–1,032.45	240.12	0.96	49.2

Standard deviation (SD), coefficient of variation (CV), and standard error (SE) are also reported.

published cutoff maximum value for rejecting models. It should be mentioned that for a specific diameter, the absolute percentage difference may reach up to 80% (unpublished analyses made by the first author to other data sets), and, clearly, the lower the P_D is, the better the model, when different models for the same data set are compared. As a rule of thumb, models with $P_D > 20\%$ may be regarded as not that accurate.

Moreover, the Furnival index (FI) was also used for model selection (Furnival 1961). The FI is a modified likelihood criterion that reflects both the size of the residuals and the possible departures from normality and homoscedasticity. In addition, the expected values of the allometric coefficients obtained from the classical statistical regressions (LR and NLR) and their corresponding mean square errors were used to estimate the corresponding likelihoods (the procedure is explicitly summarized in Ballantyne 2013). The Akaike information criterion corrected for small sample size (AICc) was calculated for each approach, and, subsequently, the algorithm proposed by Xiao et al. (2011) was applied to select either the log-linear or nonlinear model. The root mean square error (RMSE) and the coefficient of determination (R^2) were also used to this end (but with skepticism as explained in Sileshi 2014). For LR models, a

modified R^2 criterion, proposed by Payandeh (1981), was used as a better measure for goodness of fit and was calculated as

$$S = 1 - \sum (O_i - P_i)^2 / \sum (O_i - \text{average}(O))^2$$

where O_i and P_i are as in the equation above.

Results

Total Aboveground Dry Biomass (*M*) Predictions

Statistical parameters for biomass and dendrometric characteristics from the sampled trees are presented in Table 1. Dbh ($D_{1.3}$) for the harvested trees varied from 9.5 to 35.5 cm, covering the size spectrum recorded in the forest management plan (University Forest Administration and Management Fund 2013), tree height (H) ranged from 8.2 to 22.6 m, and *M* varied from 34.4 to 1,032.45 kg. As expected, scatter plots of the data showed that aboveground dry biomass is allometrically related to the dimensions of the tree (Figure 1). The regression techniques applied to the data indicated that strong relationships, in terms of R^2, were derived for most of the cases. Specifically, for the $M - D_{1.3}$ relationship, the four regression techniques applied yielded quite similar values for adjusted R^2 and RMSE (Table 2). For all the models, R^2, or *S* for the LR model (see section Goodness-of-Fit Criteria above), was 98% (Figure 2). The RMSE, calculated in normal scale, was about 31 for LR, NLR, and NB regressions, with minor differences among them, whereas for IB it was larger (about 35). The performance of each method was also tested based on the P_D criterion. Quite similar P_D values were obtained from the four models (for IB, $P_D = 9.25\%$ and about 7.5% for the rest), but very different ranges were calculated. The lower value for IB was 0.001% and was recorded at $D_{1.3} = 28.8$ cm, whereas for NB the corresponding value was 0.02% (at $D_{1.3} = 21.8$ cm). The lower value for the classical regressions varied from 0.16% (NLR at $D_{1.3} = 21.8$ cm) to 0.2% (LR at $D_{1.3} = 16.5$ cm). The highest value for IB was about 25% (at $D_{1.3} = 13.6$ cm), whereas the highest absolute percentage difference for the rest of the models was
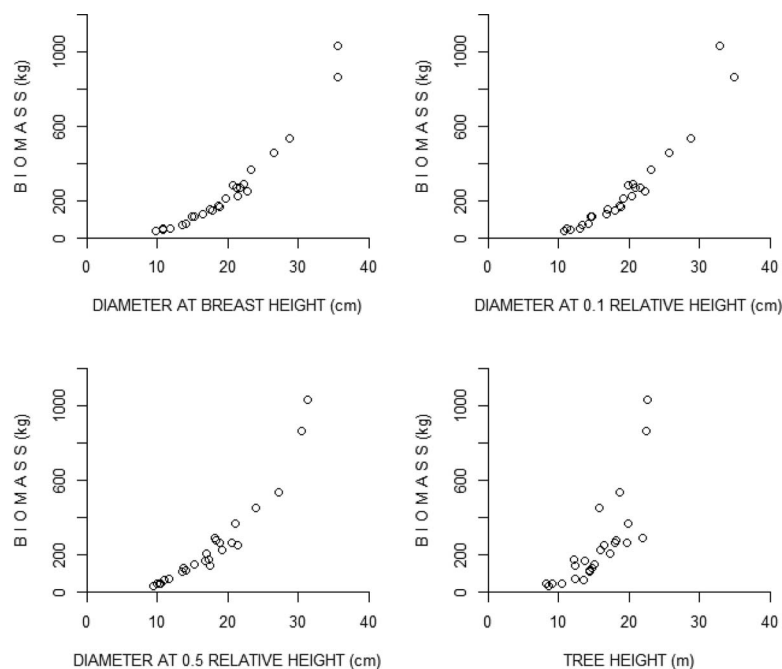

Figure 1. Scatter plots of total aboveground dry tree biomass (*M*) against tree dimensions. In all cases, an allometric relationship is being illustrated.

Table 2. Empirical values for the scaling parameters in $M - D_{1.3}$ and $M - H$ allometries under the classical and Bayesian approaches.

	$a*$	SE a	$b*$	SE b	R^2 or S	RMSE	P_D (%)†
$M - D_{1.3}$ allometry							
Classical approach							
LR	−2.4503 (−2.8025 to 2.0982)	0.1702	2.6086 (2.4879–2.7385)	0.0579	0.98	31.62	7.39
NLR ($w = D_{1.3}{}^{-5}$)	0.0866 (0.0558 to 0.1174)	0.0149	2.6087 (2.4885–2.7288)	0.0581	0.99	31.52	7.47
Bayesian approach							
NB	−2.4503 (−2.816 to 2.088)	0.1839	2.609 (2.485–2.733)	0.0579	0.98	31.76	7.59
IB	0.1341 (0.0967 to 0.1819)	0.0215	2.47 (2.365–2.575)	0.0524	0.98	35.18	9.25
$M - H$ allometry							
Classical approach							
LR‡	−2.5207 (−4.091 to 0.9503)	0.7591	2.8481 (2.2689–3.4272)	0.28	0.65	142.02	35.48
NLR ($w = H^{-6}$)	0.0775 (−0.0472 to 0.2023)	0.06	2.8886 (2.2913 3.4859)	0.2887	0.86	141.24	35.57
Bayesian approach							
NB	−2.203 (−2.959 to 0.8301)	0.5624	2.732 (2.224–3.019)	0.2099	0.64	143.76	36.79

SEs for a and b, coefficient of determination (R^2 or S), root mean square error (RMSE), and mean absolute percentage difference (P_D) are also reported.
* Mean value and credible or confidence intervals in parentheses.
† $P_D = 1/n \cdot \Sigma(|1 - P_i/O_i|) \cdot 100$.
‡ Correction factor = 1.07. R^2 for nonlinear models is actually pseudo-R and is only an indicative value.
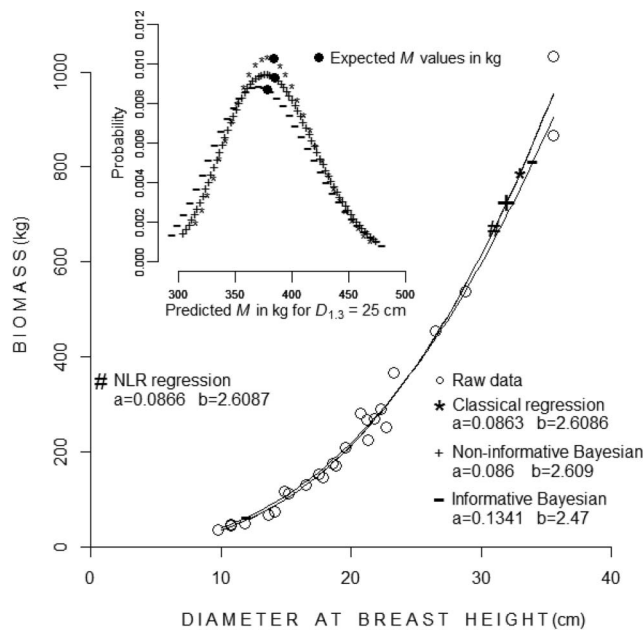

Figure 2. In the main graph, the four different modeling approaches provide very similar M estimates, despite different parametric values. Regression lines for the classical LR (*), NLR (#), and NB (+) approaches are practically indistinguishable, whereas the IB line (−) slightly diverges from them. In the inset, the probability distributions of the expected M values are presented, along with the mean M (black circles) estimations for $D_{1.3} = 25$ cm. The probability distribution for NLR has a very high peak (0.06) and was not included in the graph for clarity reasons.

about 18% (for all of them at $D_{1.3} = 22.7$ cm). It should be pointed out that the mean and median values were quite similar (less than 1 kg for the smallest trees and about 6 kg for the largest trees) for both Bayesian models.

On average, all models captured equally well the variability in recorded M values. Very small differences in predicted M values, for the recorded $D_{1.3}$ range of raw data, were derived from the LR, NLR, and NB models ($P_D < 3\%$ for intercomparisons). When comparisons were made against the IB predictions, the maximum P_D was 5% between the IB and LR models (less than 4% between the IB model and the rest of the models), and the largest absolute percentage difference reached up to 12%, calculated for the speci-

men with $D_{1.3} = 9.8$ cm (reported between the IB and LR models). Because $M - D_{1.3}$ values are strongly related, differences in predictions among the four models are becoming less pronounced as illustrated in Figure 3, where recorded M (observed) values were regressed against derived (predicted) values (Piñeiro et al. 2008). In all cases, R^2 was more than 98%, slopes were not significantly different from 1, and intercepts were not significantly different from 0. Predictions from the IB model slightly underestimated sampled trees with $M = >400$ kg or with $D_{1.3} = 25.5$ cm.

On the other hand, the IB approach performed slightly better in terms of standardized quantile plots (Figure 4). Specifically, three "outliers" are evident at the high end of the standardized residuals range for the IB model, but, otherwise, the standardized values for the IB approach fit the normal distribution very well. The rest of the models presented the characteristic "S" shape, which indicates leptokurtic (or "heavy tails") deviations that imply nonnormal error distribution. The model validation using the equivalence test as proposed by Robinson and Froese (2004) had not been performed because the prerequisite normality assumption is violated in our data set. As inferred by the quantile-quantile plots and clearly demonstrated in Figure 4, this is not the case for the four approaches analyzed. Statistical tests on the assumption of normality (e.g., the Shapiro-Wilks test, the Kolmogorov-Smirnov test, and the Anderson-Darling test) about the residuals had not been performed, because the database consisted of less than 30 entries and therefore biased results were to be expected.

Based on the analysis of the aforementioned goodness-of-fit criteria, no sound decision could be reached as to the most appropriate statistical model describing $M - D_{1.3}$ allometry. Thus, log-likelihood values were calculated for LR and NLR, and the algorithm reported in Xiao et al. (2011) was applied in our data set. The AICc value for LR and the power function were 217.84 and 248.53, respectively. Even though the absolute difference between the two estimates is not very large, according to the terminology of Burnham and Anderson (2002), there is "essentially no" support for accepting the NLR model. Similarly, the FI values supported LR (17.032) against NLR (17.164). Nonetheless, the power function incorporated within the Bayesian framework provided M values similar to those for the rest of the models (Figure 2), whereas the LR approach presented nonnormal standardized residuals as illustrated in the quantile plots (Figure 4), violating one of the assumptions in linear
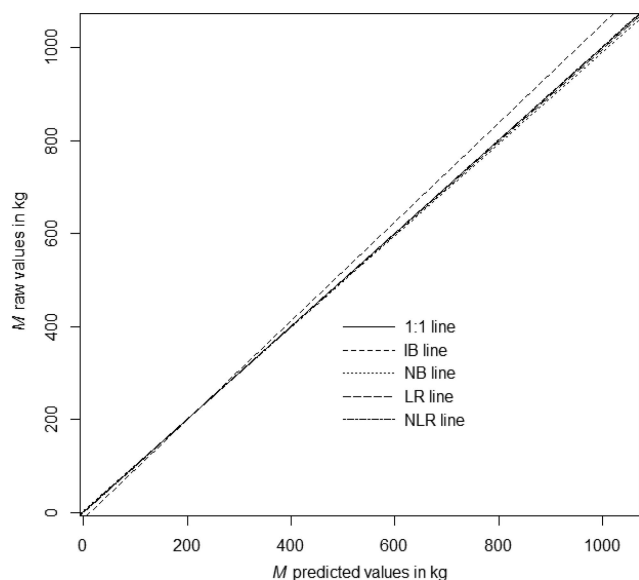
Figure 3. Raw *M* values regressed against predicted *M* values derived from the four techniques. In all cases, the slope is statistically similar to 1 and the intercept is similar to 0. IB slightly underestimated *M* for large trees.
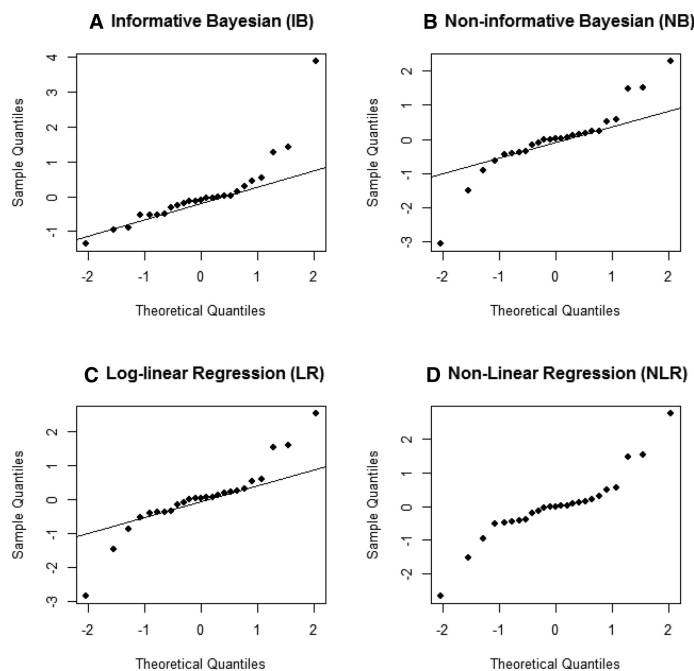

Figure 4. Quantile plots of standardized residuals for $M - D_{1.3}$ allometry from IB (A), NB (B), LR (C), and NLR (D). The IB approach performed slightly better than the LR, NLR, and NB approaches that present nonnormal error distribution.

regression. These findings directly contradict decisions based solely on the AICc, at least for the given data set.

To further illustrate the performance of the approaches developed, validation against the Matis and Alifragis (1983) data set, for $9 \leq D_{1.3} \leq 19.3$ cm, was performed. The analysis indicated that LR and NLR performed better ($P_D = 13.5\%$) than NB ($P_D = 15\%$) and IB ($P_D = 18\%$), even though the difference between IB and LR or NLR is less than 5%. The minimum relative percentage difference for NB was 0.02% at $D_{1.3} = 13.2$ cm, for LR was 1.6% and for NLR was 2.08% at $D_{1.3} = 15.1$ cm, and for IB was 3.4% at $D_{1.3} =$

9.0 cm. The largest value for all the models was obtained at $D_{1.3} = 10$ cm (IB = 48.2%, NB = 38%, and NLR and LR = 31%). Raw values from the aforementioned data set were regressed against the predicted *M* derived from the four approaches, and linear regressions indicated that the intercept, for all cases, was not statistically different from 0 (at the 95% level) but the slope was less than 1 (about 0.83 for all models). Thus, all approaches consistently underestimated the recorded *M* values, but with minor deviations (see the P_D values above). In all cases, more than 97% of the variability in raw data was explained by the modeled values.

The strong $M - D_{1.3}$ allometric relationship ($R^2 \geq 98\%$, irrespective of the method applied) implies that inserting *H* as a second variable does not substantially improve the total aboveground predictions. In addition, *H* was highly related to $D_{1.3}$ ($R^2 \geq 83\%$) and therefore was not included as a second independent variable in the allometric regression because the multicollinearity problem could lead to statistically unsound inferences. An allometric relationship was also obtained between *M* and *H*, based on the LR, NB, and NLR models (see Table 2 for parametric values). The *S* value for the unconstrained LR model was 0.65 (formula by Payandeh 1981; $R^2 = 0.83$ in logarithmic scale), P_D was 35% (minimum = 0.47 and maximum = 98%), and the residual standardized error in the logarithmic scale was 0.3933. For the NB model, $R^2 = 64\%$ and P_D was 37% (minimum = 0.95 and maximum = 121%), whereas for the weighted NLR model, $R^2 = 86\%$, and P_D was 35% (minimum = 7.6 and maximum = 129%). The AICc value for LR was 287.45 and was 320.78 for the power function, indicating that regression with multiplicative error structure (LR) was preferable over additive errors regression (NLR). LR was also supported by FI values. The $M - H$ allometric equation obtained could be applied, in conjunction with the light detection and ranging (LIDAR) data sets, to report tree biomass estimates at the stand or forest scale. In contrast, it cannot be readily used in existing forest inventory databases, since it is unusual to record tree height at the plot level, at least in Greek forest management plans.

Probability Distribution of Predicted *M*

Apart from predicting expected *M* values through empirical allometric equations, associated *M* intervals should be reported as well. The manifestation of the assumptions for modeling stochasticity in $M - D_{1.3}$ allometry is clearly illustrated in Figure 5, where extrapolation beyond the $D_{1.3}$ range of the raw data is depicted. Whereas classical regression and the NB method produced similar probability distributions for *M* at $D_{1.3} = 5$ cm, the IB approach derived a quite different *M* distributional shape, as well as a different average value of 7.44 kg that was very close to the raw value provided by Matis and Alifragis (1983) with *M* = 7.3 kg. NB and LR predicted a value of 5.78 kg with an absolute percentage difference of 21% in comparison to the aforementioned data. Different *M* probability distributions were also obtained from the three models at $D_{1.3} = 10$ cm (Figure 5B). LR and NB predicted an expected *M* value of about 35 kg, whereas IB predicted a value of 40 kg. The prediction interval for the IB model ranged from 25 to 60 kg, whereas a narrower range (28–45 kg) was derived for LR and NB. Most importantly, quite dissimilar probabilities are assigned to predicted *M* values. Although 81.65% of the observations should fell below the biomass of $e^{(\mu+\sigma)} = e^{(35+0.1058)} \approx 38.9$ kg according to LR and NB approaches, only three of six trees (i.e., 50%) sustain *M* values smaller than 39 kg. In contrast, the IB model predicts that 81.65% of observations should fell below $e^{(40+0.1702)} \approx 47.4$ kg,
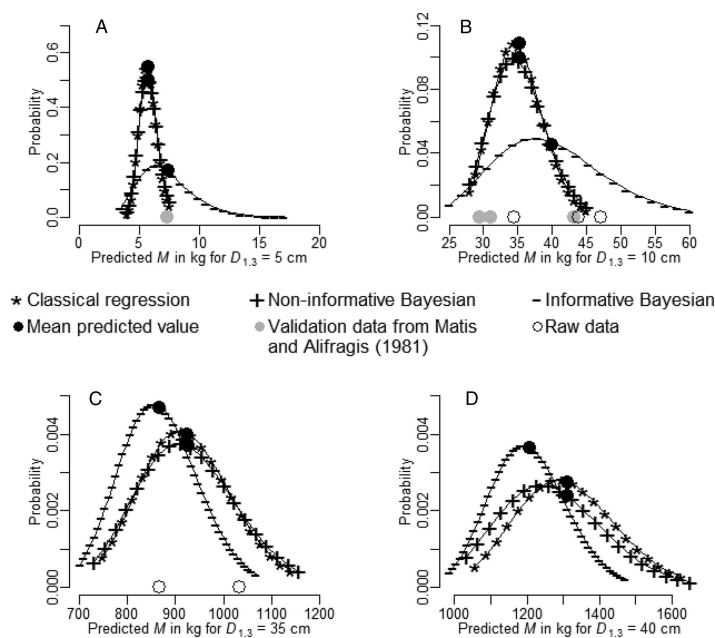
Figure 5. Probability distributions for predicted *M* values derived from three regression approaches. Predictions from NLRs presented very narrow and sharp *M* bands and were excluded for clarity reasons. A. Raw data from Matis and Alifragis (1983) validated the IB model. B. Raw data from our data set and Matis and Alifragis (1983) supported the IB model. C. LR and NB follow a similar distribution pattern that is quite different from that of IB. D. Raw values for $D_{1.3} = 40$ cm were not available, but analysis (not shown) on a "global" compendium consisted of more than 1,500 trees at the disposal of the first author, illustrated that no specimen from temperate studies with $D_{1.3} = 40$ cm sustains an *M* of more than 1,368 kg.

and raw data (validation plus calibration trees) indicate that 5 of 6 trees (i.e., 83%), fell within the predicted value (see Figure 5B). NLR presented a very narrow, and therefore a nonrealistic, distribution for all the diameters and was not included in the figure.

On the other hand, quite similar *M* probability distributions and average values from the IB, NB, and LR models were obtained at $D_{1.3} = 25$ cm, which is close to the average $D_{1.3}$ value of the sampled trees. The lower predicted value was around 300 kg, the mean was about 380 kg, and the upper value was about 470 kg, as illustrated in

the inset of Figure 2. LR and NB probability distributions followed a similar pattern for $D_{1.3} = 35$ cm but quite different from that obtained from the IB model, as illustrated in Figure 5C. The average *M* predicted value derived from IB was 866.2 kg and was lower than the corresponding predictions derived from LR and NB (about 926 kg). Lower predicted values were quite similar for the three models but differed in the upper estimates by 6% (1,136 kg for LR and NB and 1,069 for IB). Different distribution shapes and average predicted *M* values were also obtained when models were extrapolated to $D_{1.3} = 40$ cm. *M* for IB was 1,207 kg and around 1,310 kg for NB and LR, but neither calibration data from Matis and Alifragis (1983) nor raw data existed for this diameter, and, therefore, an inference about the performance of the models could not be made. However, analysis (not shown) on a "global" compendium, consisting of more than 1,500 trees at the disposal of the first author, illustrated that no specimen from temperate studies with $D_{1.3} = 40$ cm sustains an *M* of more than 1,368 kg. The *M* for the vast majority of the compiled trees fell between 536 and 1,200 kg. Thus, it is highly unlikely for LR and NB probability distributions to hold valid for the given oak data set at the given $D_{1.3}$.

Simplified Bayesian Allometry

The simplified Bayesian procedure proposed by Zapata-Cuartas et al. (2012), described above in detail in the section Simplified Bayesian Allometry, was applied in 15 subsamples, and the results are presented in Table 3. For seven of the derived allometries, the P_D criterion was less than 10%, for four of them it was less than 15%, and for the rest it varied between about 16 and 20%. The value for ln*a* ranged from -2.734 to -1.369, whereas *b* ranged from 2.27 to 2.706. It should be mentioned that classical regression produced, in most of the cases, very large P_D values. The power of the proposed approach is revealed in subsample 2, where $D_{1.3}$ ranged from 18.6 to 21.3 cm and P_D was 8%. Similar performance was obtained for subsample 10, where $D_{1.3}$ ranged from 20.7 to 22.7 cm and P_D was 9.6% with a minimum value of 0.5 and a maximum value of 26%. As expected, classical linear regression in the specific subsamples failed dramatically ($P_D = 50\%$.). Very accurate predictions were derived for "biased" subsamples as well (subsamples 2 to 5 in Table 3) but not for subsample 1 for which the six smallest trees were used ($P_D = 18\%$). In Figure 6A, an underestimation of simplified Bayesian allometry is shown for the specific subsample, but quite accurate

Table 3. Empirical values for the scaling parameters in $M - D_{1.3}$ allometry derived from the simplified Bayesian approach, applied to 15 subsamples.

Subsample no.	Remarks	$D_{1.3}$ range (cm)	*a*	*b*	SE *a*	SE *b*	P_D (%)	Minimum P_D (%)	Maximum P_D (%)
1	6 smallest trees	9.8–14.1	−1.657	2.27	0.4814	0.1948	18	1.5	39
2	6 middle trees	18.6–21.3	−2.088	2.492	0.6555	0.2182	8	0.04	22
3	6 largest trees	22.7–35.5	−2.15	2.516	0.6093	0.1817	8.5	0.3	22.5
4	6 "positive" trees*	14.9–35.5	−1.946	2.482	0.395	0.1256	16	0.75	37
5	6 "negative" trees*	11.8–22.7	−2.387	2.542	0.3533	0.1257	12.5	0.7	27.6
6	6 random trees	18.8–35.5	−2.285	2.579	0.5228	0.167	7.7	0.01	19.1
7	6 random trees	21.3–26.5	−2.165	2.513	0.6743	0.2148	8	0.24	19.6
8	6 random trees	11.8–21.2	−2.734	2.706	0.5503	0.1946	8.1	0.44	20
9	6 random trees	9.8–35.5	−2.021	2.462	0.3271	0.1105	8.5	0.3	21
10	6 random trees	20.7–22.7	−1.878	2.423	0.6841	0.2218	9.6	0.5	26
11	6 random trees	18.8–35.5	−2.285	2.579	0.5228	0.167	10.8	0.16	26.7
12	6 random trees	10.8–35.5	−2.242	2.575	0.3269	0.1099	13.4	0.99	30.6
13	6 random trees	14.9–35.5	−2.069	2.52	0.4065	0.1314	14.7	1.3	34.2
14	6 random trees	20.7–35.5	−1.588	2.364	0.5394	0.1616	18.5	4	44.4
15	6 random trees	20.7–35.5	−1.36c9	2.29	0.5211	0.1604	19.6	1.55	48.1

SEs for *a* and *b*, P_D, and the associated minimum and maximum values are also reported.
* Positive/negative trees stands for maximum positive and minimum negative deviation from IB regression, respectively.
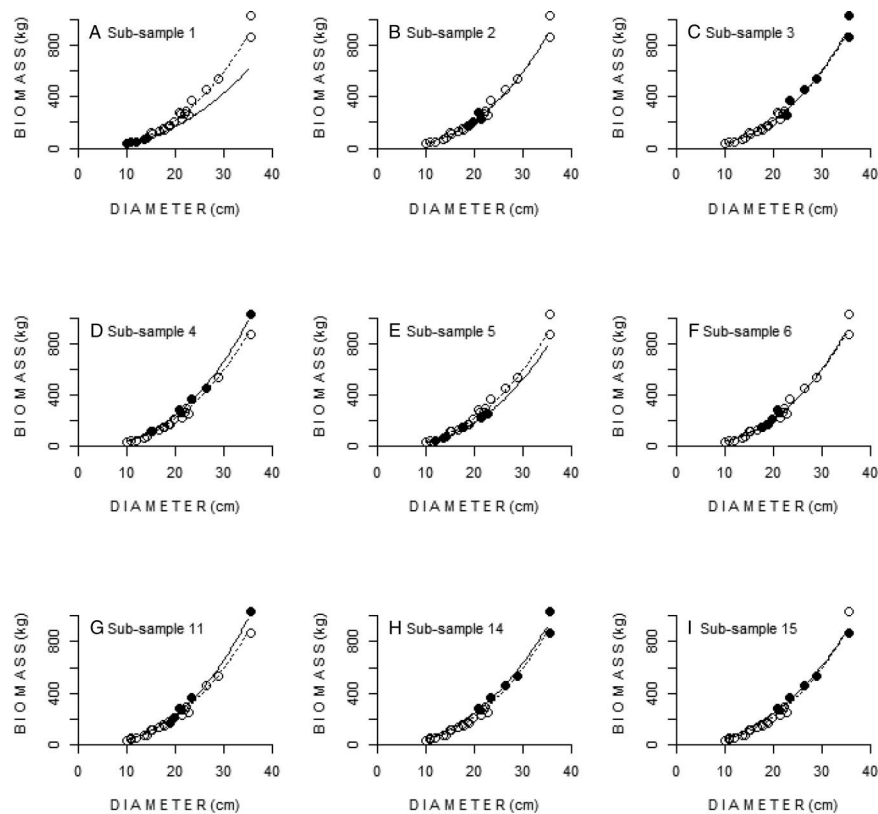
Figure 6. Regressions obtained through the simplified Bayesian approach (solid lines) based on six trees (closed circles). The dotted lines represent regression lines based on 25 trees (open circles).

estimations are illustrated for the rest of the predicted models (Figure 6B–I). The best result was reported for subsample 6 in which $D_{1.3}$ varied from 18.8 to 35.5 cm, with $P_D = 7.7\%$ (minimum = 0.01 and maximum = 19.1%). In subsample 9, the selected six trees covered the $D_{1.3}$ spectrum and $P_D = 8.5\%$ (minimum = 0.3 and maximum = 21%). A very strong linear relationship was derived when ln$a$ was regressed against b values for the 15 allometries (ln$a$ = −2.8449 + 5.0192b; $R^2 = 0.91\%$).

Validating Theoretical Models

Apart from the practical usefulness of the derived M allometries for estimating forest biomass, information related to their parametric values may be used for validating theoretical models. Comparisons based on confidence (classical regressions) and credible (Bayesian regressions) intervals indicated that a and b values were statistically similar (at the 95% level) for the LR, NLR, and NB models. Both the scaling coefficient (a or $e^{\ln a + v/2}$) and the scaling exponent (b) were quite similar for the aforementioned models as well as for their confidence intervals (Table 2). The mean value of parameter a was 0.08626 (0.0606−0.1227) for LR, 0.0866 (0.0558−0.1174) for the weighted NLR, and 0.086 (0.0598−0.1239) for NB, but for the IB regression attained a value of 0.1341 (0.0967−0.1819). None of the confidence or credible intervals for LR, NLR, or NB included the value of 0.1341 nor did the credible interval of IB include the value of 0.086. However, there is a partial overlap between the intervals of LR, NLR, NB, and IB. As expected, the b value for the IB regression was the smallest one (2.47), but quite similar average b values were derived for the rest of the models (2.6086 for LR, 2.6087 for weighted NLR, and 2.609 for NB). The confidence or credible intervals for LR (2.4879−2.7385), weighted NLR (2.4885−2.7288), or NB (2.485−2.733) did not include the value of 2.47 nor did the credible interval of IB (2.368−2.583) include the value of 2.6087. A partial overlap between the intervals of LR, NLR, NB, and IB is also evident for this parameter.

The central tendency of the allometric exponent (b) for LR, NLR, and NB was neither close to theoretical values predicted by the biomechanical models (stress = 2.5, elastic = 2.67, or geometric = 3) nor close to the value of 2.67 predicted by MST. However, the 95% confidence and credible intervals for the aforementioned approaches included both the stress and elastic models as well as the MST value. On the other hand, the b value derived from IB regression supports the stress model (0.03 difference in the scaling exponent) and the credible interval includes the value of 2.5 but rejects the other theoretical predictions. Niklas (1994) reported that a-b parametric values derived from reduced major axis regression should be used, when empirical equations are to be used for validating theoretical models. However, because R^2 is very high for the M − $D_{1.3}$ allometries obtained, the b value differs slightly ($b = 2.62$) in comparison to the one obtained by LR, and the interpretation of results remains valid.

Surprisingly, even if IB produced a and b values quite different from those for the rest of the models, very similar M predictions were obtained by the four approaches applied (see Figure 2). Following the same line of reasoning, we let a and b take values throughout their corresponding confidence or credible intervals and the combinations of a-b pairs were used to derive M predictions. These predictions were used to estimate goodness-of-fit statistics such as RMSE, R^2, and sum of squares of error (SSE). Interestingly, letting these estimates differ slightly from the ones corresponding to
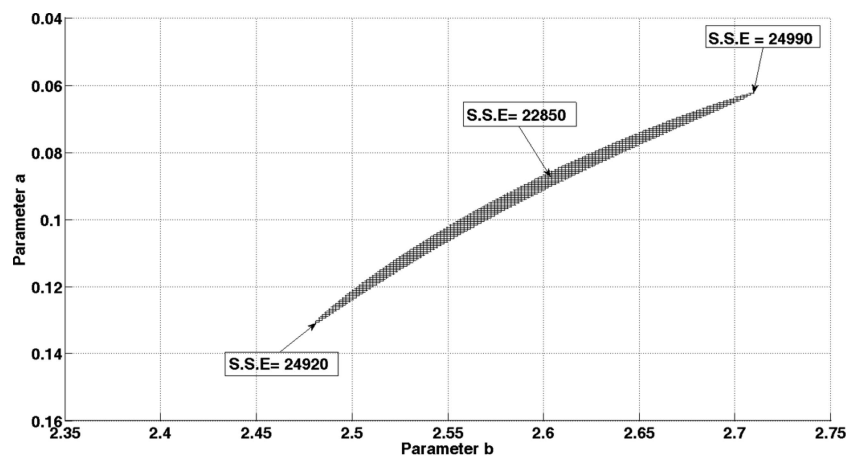
Figure 7. The parametric space of the normalization constant (*a*) is plotted against the space of the allometric exponent (*b*). The hatched area includes *a*-*b* pairs within which SSE for LR in the normal scale varies from 22,300 to 25,000. In other words, by letting residual error vary slightly around a given value, a group of *a* and associated *b* values may be derived. Thus, for the given empirical allometric relationship, no specific parametric *a*-*b* pair exists, but rather a group of them, which provide accurate *M* predictions.

the expected *a* and *b* values (i.e., assuming that one or more $M - D_{1.3}$ pair(s) enter the raw data set), a bunch of values for *a* was predicted for a given value of *b*. For example, if SSE varies from 22,500 to 25,000 (SSE = 22,850 for LR based on 25 trees), a specific relationship between *a* and *b* is depicted (Figure 7). It is therefore implied that there is no unique *a*-*b* pair that best describes $M - D_{1.3}$ allometry, but rather there is a whole spectrum of allometric parameters explaining *M* variability through $D_{1.3}$, for a given data set.

Fehrmann and Kleinn (2006) questioned the appropriateness of using the scaling exponent from the empirical $M - D_{1.3}$ allometry to validate the universal theoretical value derived from the MST model. They proposed that when the tree diameter is measured at relative tree height (their analysis was based on the diameter at $0.1H$), the empirical *b* value supports the theoretical exponent of 2.667. Following their analysis, the reduced major axis approach was used in our data set for $\ln(M) - \ln(D_{0.1})$ relationship, and the *b* value was 2.8773 (95% range, 2.6874–3.0806), statistically different from the MST prediction. In contrast, the 95% confidence limits of *b*, derived by NLR (or $M = aD_{0.1}{}^{b}$), supported the theoretical value (2.3818 − 2.9173; the mean was 2.6402, close enough to the MST prediction). Moreover, using the diameter at 50% of tree bole as the "independent" variable, the reduced major axis regression produced a log-linear slope equal to 2.6442 (95% confidence interval, 2.4596–2.8426) in line with the theoretical prediction. The NLR model (or $M = aD_{0.5}{}^{b}$) also corroborated the MST prediction (*b* = 2.7281 and 95% range of 2.4825–2.9932). Applying NB in both LRs (i.e., "independent" variables $D_{0.1}$ or $D_{0.5}$) produced ranges for the scaling exponent that included the value of 2.67.

To further test the validity of the biomechanical and MST predictions, $H - M$ allometry was analyzed under the three aforementioned approaches, namely LR, NLR, and NB. The reduced major axis for the $\ln(H) - \ln(M)$ relationship indicated that geometric similitude (*b* = 1/3) may best describe the variability in $H - M$ empirical allometry, since *b* = 0.3175 and varied from 0.2645 to 0.3813 at the 95% level. The mean *b* value from NLR was 0.2571, clearly supporting the elastic and MST predictions (*b* = 1/4), but stress (*b* = 1/5) and geometric models are just attainable because *b* ranged from 0.2009 to 0.3139. On the other hand, NB analysis for

the allometric slope failed to distinguish geometric, elastic, and MST predictions (*b* varied from 0.2268 to 0.348; mean = 0.2869), whereas the lower limit of the 95% confidence interval was close to that of the stress model. It is therefore implied from the above analyses that validation of theoretical predictions against empirical data sets largely depend not only on the applied regression technique, as explicitly stated in Sileshi (2014), but also on the variables analyzed.

Discussion

Four interesting findings were demonstrated in this study. First, the IB approach not only accurately estimated total aboveground biomass (*M*) of sampled trees (Figure 2) but also predicted biologically sound intervals for *M* both within and beyond the $D_{1.3}$ range of the 25 oak specimens. The LR, NLR, and NB approaches derived slightly better *M* estimates, in terms of goodness-of-fit criteria but failed to describe *M* probability distributions. The results indicated that even if the four approaches performed equally well around the middle range of $D_{1.3}$ (i.e., at $D_{1.3}$ = 25 cm) (Figure 2), the IB approach provided much more realistic uncertainty levels for *M*, when the derived empirical equations were extrapolated to lower (Figure 5A) and larger (Figure 5B) diameters. In addition, preliminary cumulative frequency analysis based on six trees with $D_{1.3}$ values close to 10 cm supported the probability distribution predicted by the IB approach (Figure 5B) but did not support outcomes from the rest of the approaches. Up-scaling *M* values from the tree to the plot level, without taking into consideration the pattern of associated uncertainty, may lead to large errors in estimating the variability of forest biomass, carbon stocks, and carbon fluxes and in turn jeopardize practical application of allometric equations, such as the quality assessment of the Kyoto protocol procedures. Future efforts in the study of tree allometry may incorporate Bayesian analysis, which is not merely a new statistical tool but rather a different theoretical context in statistics, providing the potential for drawing useful insights on theoretical grounds and resolving several issues on practical aspects. For example, one of the main properties in Bayesian allometry is that error modeling (perceived either intuitively or empirically) may be straightforwardly incorporated into the regression technique using either conjugate priors or previously studied formulations. In this study, *M* stochasticity was entered in the

model as a log-normal distribution (predetermining positive predicted values across tree size range), with a mean equal to the logarithm of $aD_{1.3}{}^b$ (as dictated by several theories), and variance was allometrically related to M (as reported in several empirical studies such as Ketterings et al. 2001, Ducey et al. 2009, Návar 2009). Thus, the theoretical prerequisites of tree biomass allometry were evenly integrated to empirical research outcomes under a Bayesian formulation, and biologically sound results were obtained.

The usefulness of the Bayes theorem in our data set is better illustrated through the second finding of our analysis, which is directly related to the simplified approach proposed by Zapata-Cuartas et al. (2012). When the performance of this approach is tested, quite accurate M predictions were obtained in most of the cases analyzed. However, for subsample 1, which consisted of the six smallest trees from the full data set, constant underestimation of the recorded M range was reported (Figure 6A) and the proposed approach yielded P_D of 18%, not an unusual value for biomass studies. Subsamples 14 and 15, based on six randomly selected trees, overestimated M values by about 19%. With use of the six trees in the middle of sampled $D_{1.3}$ range (subsample 2) or the six largest trees (subsample 3), the reported allometries were indistinguishable from the one built on 25 trees (Figure 6B and C). In all cases, the proposed approach performed better that the classical LR or NLR and therefore the potential of IB biomass modeling should be further studied. Hypotheses to be examined under the simplified Bayesian approach might be related to the appropriate number of sampled trees to be used, the range covered by the selected specimens, and the usefulness of adopting hierarchical models, mainly by incorporating additional information about the allometric parameters. Future research should be directed to developing formal standardized Bayesian techniques for simplifying tree allometry, by producing algorithms on selecting the most appropriate trees (by intuition, a couple of trees from the lower, middle, and upper stature specimens) rather than by collecting a large number of samples covering the whole $D_{1.3}$ range. Thus, a thorough study examining a large number of subsamples across several biomass data sets is needed to clarify in a standardized context the potentiality of Bayesian simplified regression in estimating forest biomass.

The third research finding is related to the analysis made in a classical statistical context. The main and perhaps the only dilemma in selecting the most appropriate model for tree biomass allometry is initiated by the assumptions made for uncertainty structure (either an additive error for nonlinear function or multiplicative error in LR). Xiao et al. (2011) provided a guideline to accept the model that better conforms to a given data set, based on computing raw data likelihoods by using underlying error probability distribution. In this study, AICc values supported the use of LRs but weighted NLR also provided accurate M predictions as well. Thus, based solely on AICc values, erroneous conclusions about the most appropriate model (power function versus log-linear) may be obtained. This is clearly illustrated in Figure 4, where LR did not perform better than NLR. Traditionally, linear regression is straightforwardly implemented by the simple expedient of log-transforming biomass data sets. However, paraphrasing Tukey (1957) as quoted in Packard et al. (2010), compressing and stretching data on the Procrustean logarithmic bed do not really contribute to resolving statistical issues related to modeling allometric relationships. We should bear in mind that the logarithm of a positive number x is a nonlinear transformation defined as $\ln(x) = \lim n(x^{1/n} - 1)$ for large n, implying that no coherent understanding may be reached for the underlying

rules and mechanisms governing tree shape-size relationships, under such a "random" transformation. As explicitly illustrated by Hui and Jackson (2007) and Packard and Boardman (2008), back transformation of predictions from log-linear functions may provide unbiased estimates for small independent values, but statistically significant errors are to be expected for large values of the "explanatory" variable. This is clearly illustrated in Figure 5D. With extrapolation of $D_{1.3}$ to 40 cm, LR predicted a maximum M value of more than 1,600 kg, which is believed to be not highly plausible. In addition, Lai et al. (2013) supported the fact that NLR estimates should be preferred for estimating forest biomass because big stature trees often dominate in natural stands. Beyond the statistical caveats inherent in log transformation, theoretical analysis (briefly presented in the Introduction and explicitly reported in Sileshi 2014) clearly supports the power function model for biomass allometry rather than back transformation of LR. The idiosyncratic nature of forest biomass estimation principally resulting from the interplay of biotic and abiotic factors, which in turn affects tree size-shape relationships, contributes to nonresolved statistical issues, and thus questions might arise about the appropriateness of the processes applied so far in empirical studies (Sileshi 2014).

A very surprising finding in this study, related to the not yet disclosed statistical properties of allometric relationships, lies in the fact that quite different a-b pairs may provide very similar M predictions (Figure 2). For example, classical regression ($a = 0.0863$ and $b = 2.6086$) provided M values statistically similar to those for the IB approach ($a = 0.1341$ and $b = 2.47$), which may not had been disclosed if Bayesian analysis were not used in the analysis. Such a property was actually implied by letting the SSE in LR to slightly vary, as illustrated in Figure 7. These outcomes directly contradict the acceptance of a fixed a-b pair and its associated statistical properties and indicate that a whole range of values in a-b parametric space may accurately describe M allometry for a specific data set. Thus, there is not enough statistical support to reject competing predictions originating from stress, elastic, and MST allometric theories, at least for the specific empirical $M - D_{1.3}$ relationship. The analysis on scaling parameters did not specifically aim to either reject or accept different allometric theories but rather to test whether the proposed theoretical values could be used for accurately predicting tree biomass. The empirically obtained average b value, under classical regressions and NB modeling, failed to provide adequate support for accepting any of the theoretical outcomes to be used for M predictions. In contrast, the b value derived from the IB approach fell very close to the one predicted by the stress similarity model, and it is therefore implied that quite accurate M predictions could have been derived if this model were to be applied in the given data set. Thus, the choice of regression technique influences the allometric parameters, in accordance with Sieg et al. (2009) and Sileshi (2014), and inevitably no coherent conclusions may be reached on the usefulness of allometric theories in predicting tree biomass for a given data set. The effect of the regression approach on the values of scaling slope was also illustrated in the $H - M$ relationship, because the reduced major axis exponent supported geometric similitude, NLR supported elastic and MST predictions, and NB failed to support any of the theoretical models.

In contrast, $M - D_{0.5}$ allometry was consistent with the MST predictions for the given oak data set, irrespective of the regression technique used. However, analysis made on $M - D_{0.1}$ by reduced major axis regression rejected the value of 2.67 (opposing the finding reported by Fehrmann and Kleinn 2006), whereas the 95%

confidence intervals for NLR included that value. Thus, the hypothesis put forward by Fehrmann and Kleinn (2006), that diameter at relative tree height should be used for validating MST predictions, seems to hold valid when the diameter is measured at 50% of the tree bole but is not supported when the diameter measurements are made at 10% of total tree height.

Last, one might take exception with the interpretation of the results presented in this study on the basis that a small number of specimens (25 trees) had been analyzed. A recent review by Sileshi (2014) indicated that extreme exponent values were associated with sample sizes of less than 50 trees. However, a visual inspection on Figure 2B of the aforementioned reference illustrates that a plethora of studies had sample sizes of less than 50 trees, but only a small fraction (about 75 studies) had more than 100 trees. Thus, it might be likely that reduced variability in the scaling exponent is depicted for studies with large numbers of sampled trees due to the fact that the number of them included in the analysis was not adequate. A more detailed approach is needed to thoroughly conclude this issue.

Conclusions

The predictive power of IB regression against the classical LR, NLR, and NB approaches for tree biomass estimation is illustrated in this study. The Bayesian approach provides the means to fully integrate the variance of the predicted M value in the modeling scheme. Thus, adaptation of the Bayesian theorem in tree allometry research is strongly supported, whereas the potential of the simplified Bayesian approach should be investigated in future forest biomass projects because monetary and time resources are dramatically reduced. The validity of theoretical allometric models depends on the variables analyzed ($M - D_{1.3}$ allometry supported different theoretical models than $M - H$ analysis) as well as on the applied regression technique. It also seems that there is no escaping the conclusion that a number of scaling parameters may quite accurately describe tree biomass allometry, rather than a unique pair of them.

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