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Bayesian and classical biomass allometries for open grown valonian oaks (*Q. ithaburensis* subs. *macrolepis* L.) in a silvopastoral system

Dimitrios Zianis · **Anastasia Pantera** ·
Andreas Papadopoulos · **Maria Rosa Mosquera Losada**

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Abstract Allometric models predicting aboveground woody biomass for open grown valonian oak (*Q. ithaburensis* subs. *macrolepis* L.) trees growing in a Mediterranean silvopastoral system were built based on Bayesian and classical statistical techniques. The simple power model $M = aD^b$ was used for predicting aboveground woody biomass (M), stem (M_S) and branch (M_B) biomass through tree diameter (D). An informative Bayesian approach (IB) based on prior information about a and b and increasing variance of predicted values in relation to D was applied on 25 destructively sampled trees for estimating M. Non-informative Bayesian (NB), log-linear regression (LR) and non-linear regression were also built for M, M_S and M_B. Quite similar M distribution was derived from LR and NB across the D range, totally different from IB predictions which provided biologically sound estimates. Tree height, stem length and crown length did not substantially improve predictions for M, M_S and M_B. Comparisons to oak trees growing in closed stands indicated that open-grown oaks sustain much less stem biomass but maintain larger branch biomass than forest-grown counterparts. Comparisons to published values for open-grown green ash trees supported the hypothesis that open grown broadleaved specimens may sustain similar M values, irrespectively of species, growth conditions and tree size. On the contrary, allocation pattern of organic matter to stem and branches seems to vary by species and/or site conditions. Finally, predictions for $b = 2.67$ derived from a theoretical model was not supported by this dataset.

Keywords Mediterranean agroforestry · Carbon stocks · Regression · Scaling · Greece

Introduction

Silvopastoral systems are considered to be one of the most prominent agroforestry practice in the Mediterranean landscape and may considered to be both a source or a sink of carbon depending on their function and structure (Montagnini and Nair 2004; Schoeneberger 2009). Additionally, agroforestry systems are reported to provide important opportunities for adaptation and mitigation of climate change (Gitay et al. 2002, p. 37). Murthy et al. (2013) report that carbon

D. Zianis (✉)
Department of Forestry and Natural Environment
Management, TEI of Thessaly, 43100 Karditsa, Greece
e-mail: dzianis_2000@yahoo.com

A. Pantera · A. Papadopoulos
Department of Forestry and Natural Environment
Management, TEI Stereas Elladas, 36100 Karpenissi,
Greece

M. R. Mosquera Losada
Crop production Department, Escola Politécnica Superior
– Campus Lugo, Universidade de Santiago de
Compostela, 27002 A Coruña, Spain

stocks in tree biomass in such a system is generally much higher than a treeless land, but empirical estimates are rather limited (Makungwa et al. 2013; Zhou et al. 2014). One of the main carbon pool in a silvopastoral system is expected to be the aboveground woody biomass (M) of tree species located in a specific area, although several other components may significantly contribute to carbon storage. Biomass estimates for agroforestry systems and therefore allometric equations that relate tree M to the diameter at breast height (D) and/or tree height (H) are rather limited. Specifically for Mediterranean silvopastoral systems, such information is largely missing from the literature.

On the other hand, a vast amount of tree allometries were developed for closed forest stands. Linear regression analysis on logarithmically transformed biomass data and non-linear regression have extensively been used to derive an empirical equation between M and D or H. The aforementioned approaches have been based on the classical statistical theories, but nowadays Bayesian theorem is rapidly emerging in ecological studies and specifically in forest biomass research (Zapata-Cuartas et al. 2012; Tredennick et al. 2013; Zell et al. 2014; Zianis et al. 2016). Bayes rule can be used to obtain probability distributions for the predicted biomass values as well as for the scaling parameters of allometric relationship (Gilks et al. 1995; McCarthy 2007, pp. 119–120; Gelman et al. 2014, p. 355).

The theoretical background on tree allometry originates with the proposition that tree stem is considered to be an ideal geometric object and therefore $M \propto V \propto D^2 H$, where V is stem volume. Biomechanical constraints assume that $H \propto D^{\gamma}$ or $M \propto D^{b=2+\gamma}$ and under fractal geometry $2 < b < 3$. An integrated approach based on the fractal distribution of tree branching system was presented by (West et al. 1997; WBE hereafter) and predicted that $M \propto D^{2.67}$ and $M \propto H^4$, applicable for trees growing across the globe. Analyses on a plethora of empirical aboveground biomass allometries indicated that the value of b is statistically different from the theoretical estimate of 2.67 (Muller-Landau et al. 2006; Zianis 2008; Navar 2010 to cite but a few).

Many empirical relationships were reported for trees growing in closed forest stands and plantations but equations for open grown trees are largely missing (Kort and Turnock 1999; Zhou et al. 2014). Trees growing in open-canopy conditions are expected to present different architectural and structural characteristics and in turn different size-shape relationships than specimens in more closed-canopy environments. Direct exposure to wind forces and snow loads, less competition for light, water and nutrient resources, as well as absence of mechanical support from neighboring trees result in more expanded crown size, sharper trunk taper and larger wood specific gravities (Enquist and Niklas 2001; Zhou et al. 2011) than closed-canopy trees (Zhou et al. 2014). Proportionally, much more organic matter tends to be allocated in branch biomass in comparison to trees growing in high density forested stands.

The main objective of this study was to report potential deviation of predicted values obtained by classical and Bayesian allometries for aboveground biomass of tree compartments for valonian oak (*Q. ithaburensis* subs. *macrolepis* L.) specimens growing in an open-canopy Mediterranean silvopastoral ecosystem. Secondly, the obtained biomass estimates were compared to published values for open-grown ash trees. Thirdly, the differences in the allometric relationships between open-canopy and closed-canopy trees for *Quercus* genus reported in the literature were analyzed. Finally, theoretical predictions from WBE model were validated against empirical values obtained by the analyzed dataset.

Materials and methods

Study area

The studied forest is located in the western part of central Greece and about 23 km west of Agrinio town. The heterogeneity of the landscape, consisting of agricultural, grazing and forested lands, characterizes the studied silvopastoral system. In the study area, valonia oaks are found on shallow calcareous soils in all aspects within an elevation range from 70 to 400 m above sea level. Mean yearly rainfall amounts to 938.5 mm and mean yearly temperature is 16.8 °C (National Meteorological Service for the period 1956–2012). The forested stands cover an area of more than 4400 ha while partially forested area amounts to 3300 ha. The stands are even-aged and range from 200 to 240 years. Stand density ranges from 50 to 60 trees per hectare.

Biomass measurements

Twenty five valonian oak trees were selected and cut down. Diameter at breast height (1.3 m above ground) was measured before cutting and tree height (H), stem (S_L) and crown length (C_L) were recorded after cutting the tree. Branches were separated from the stem after felling. Fresh weights were measured separately for stem and for each of the main branches (up to four for some trees). Two discs were removed from the stem at 0.3 m from the base and the base of crown. The fresh weight of discs was measured in the field and their dry weight was determined (oven dried at 80 °C until a constant weight was reached) in the laboratory. The oven dried biomass over the fresh weight (measured in the field) from each disc was therefore determined and their average value was applied to the stem fresh weight to obtain dry stem biomass (M_S). For each branch, a disc was removed near its base (about 5 cm from the insertion point for large branches and about 2 cm for small branches) and the oven dried biomass over the fresh weight from each disc was determined. This value was multiplied by the fresh branch weight to derive dry weight for each branch. The summation of branches' dry weight was therefore obtained (M_B). Total aboveground tree woody biomass (M) was the sum of M_S and M_B.

Classical modeling techniques

Two different frameworks were used to model the allometric relationships in our datasets: the classical regression and the Bayesian analysis. Under the classical framework two different approaches were used (Payandeh 1981; Chiyenda and Kozak 1982), namely the intrinsically linear regression of logarithmically transformed data (LR), which assumes a multiplicative error and thus

$$\ln Y = \ln a + b \ln X \tag{1}$$

and the intrinsically nonlinear regression (NLR), assuming an additive error term where

$$Y = aX^b \tag{2}$$

A bias is introduced when predictions from LR are back transformed to the ordinal scale and thus a correction factor should be used (Sprugel 1983). In NLR, a weight function, usually based on a negative power of X, is introduced to avoid negative predictions of Y. The most appropriate approach (either LR or NLR), was selected using the corrected Akaike information criterion (A) proposed by Xiao et al. (2011),

$$A = 2k - 2\ln(L) + 2k(k+1)/(n-k-1) \tag{3}$$

where k, n and L denote the number of parameters, the sample size and the corresponding likelihood of the model, respectively. The regression with the lowest A value was selected as the most appropriate empirical model.

In the case of Eq. 1, appropriate formulae should be used in order to predict the mean response for diameter D at normal scale by the following equation:

$$M = e^{(\ln a + b \ln D + v/2)} \tag{4}$$

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

$$v = M_{se}\left(1 + [1, \ln D](\mathbf{X}'\mathbf{X})[1, \ln D]'\right) \tag{5}$$

denotes 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. We used the method by Zou et al. (2009) for the estimation of predicted intervals (specifically, Eqs. 3 and 4 from the aforementioned reference for $n = 1$):

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

$$\text{Upper limit of } M = M \exp\left[\left(z^2_{1-a/2}v + (v/2)^2\right)^{1/2}\right] \tag{7}$$

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

Tree height (H), stem length (S_L) and crown length (C_L) were also used as regressor variables for predicting M, M_S and M_B under the LR, NLR and NB approaches. For the NLR approach (i.e., Eq. 2), the iterative procedures in the free software environment R (R Development Core Team 2011) provided the 95% predicted values of M based on the *nls* command.

Bayesian modeling techniques

In the Bayesian context, the parameters in statistical models are allowed to follow pre-specified probability distributions, not assumed to be fixed points as suggested by the classical method. Thus, previously empirical information and/or theoretical expectations are easily incorporated in the modeling approach (McCarthy 2007, p. 23).

The first step for building an informative Bayesian model of aboveground woody dry biomass (M) was the specification of prior distributions for the allometric parameters. To this end, a large compendium of published a and b values was used based on several databases for forested stands (Ter-Mikaelian and Korzukhin 1997; Eamus et al. 2000; Zianis and Mencuccini 2003; Jenkins et al. 2004; Zianis et al. 2005; Pilli et al. 2006; Zianis 2008; Navar 2009; Henry et al. 2011; Zapata-Cuartas et al. 2012). Thus,

$$a \sim \mathrm{Log-Normal\ distribution}\ (-2.0,\ 0.5),$$
$$b \sim \mathrm{Normal\ distribution}\ (2.35,\ 0.1).$$

Furthermore, following Zianis et al. (2016) the variance (v) of the predicted M_i at a specified D_i was modelled as

$$v_\mathrm{i} \propto \ \mathrm{M}_\mathrm{i}^c = g\left(aD_\mathrm{i}^b\right)^c$$

and according to Ducey et al. (2009) $c = 1.5$ for trees growing in an Amazonian region. In the absence of further information about its value for open-grown trees, the aforementioned estimate for c was used in our dataset. The variance in logarithmic scale may be determined as $z = \ln(1 + v/M^2)$, as reported in Thomopoulos and Johnson (2003). Based on the aforementioned priors and relationships, the following informative Bayesian (IB) approach was built:

$$M_i \sim \mathrm{Log-Normal}\ (\mu_\mathrm{i},\ z_\mathrm{i}),$$

where μ_i is the $\ln\left(aD^b\right)$, z_i is the $\ln(1 + v_i/M_\mathrm{i}^2)$, v_i is the $g\left(aD_i^b\right)^c$, g is the uniform distribution (0.01, 0.05).

For comparison, the following non-informative Bayesian method (NB) was developed based on the most commonly used log-linear regression, with non-informative priors about the parameters:

$$\ln M_\mathrm{i} \sim \ \mathrm{N}(\ln a + b \ln D_i, v)$$

$\ln a$ is the uniform distribution $(-4, -1)$, b is the uniform distribution (1.5, 3.5) and, v is the gamma distribution (0.1, 0.01), while predictions at normal scale were derived as, M_i is the log-normal distribution ($\ln M_i$, v).

For stem (M_S) and branch biomass (M_B) the above non-informative Bayesian formulation was also used. Specifically, aboveground woody biomass (M) was replaced by M_S and M_B so as to derive non-informative Bayesian allometries for these compartments. Informative Bayesian for M_S–D and M_B–D relationships could not be built since there is not adequate knowledge about the distribution of allometric parameters for open-grown trees. Additionally, Zhou et al. (2014) reported that the biomass of these two tree compartments for open grown ash specimens deviate by a high degree in comparison to forested trees. Thus, having used the probability distributions of a and b from closed-canopy trees would bias the Bayesian analysis performed on our open-grown tree dataset.

WinBUGS, a free software (Lunn et al. 2000) based on Markov chain Monte Carlo methods (Spiegelhalter et al. 2007), was used in order to generate posterior distributions and in turn to draw estimates for parameters and predictions (via Gibbs sampler). A burn-in period of 2000 steps and 100,000 iterations with a step of 2, were used to obtain 98,000 estimations per variable or parameter. In cases where autocorrelation of MCMC chain was reported, it was eliminated by increasing the number of iterations to 200,000.

Goodness of fit criteria

The mean absolute percentage difference (P_D) between the predictions and the observed data is reported to be one of the most appropriate criterions for assessing model performance in tree allometric relationships (Parresol 1999; Zianis and Mencuccini 2003; Sileshi 2014) and was therefore used in this study. The absolute difference between observed and predicted values divided by the observed is calculated for each tree and the average value of these deviations is multiplied by 100 to define P_D, or

$$P_\mathrm{D} = 1/n \times \Sigma(|1 - P_\mathrm{i}/O_\mathrm{i}|) \times 100$$

where P_i and O_i denote predicted and corresponding observed biomass value for the ith tree ($i = 1$ to $n = 25$).

Values close to 0% indicate accurate predictions while to the best of our knowledge, there is not a published cut-off maximum value for rejecting models. It should be mentioned that for a specific diameter, absolute percentage difference may reach up to 80 or to 37% when the whole dataset is considered

(Ketterings et al. 2001). The lower the P_D the better the model, when comparing different models for the same dataset. The coefficient of determination (R^2) was only used as an indicative criterion since Sileshi (2014) reported several caveats related to this statistic.

Results

Stem diameter (D) for the sampled trees ranged from 3.18 to 99.4 cm, covering the size spectrum of the diameter distribution recorded in the forest management plans with $10 < D < 84$ cm. Tree height (H) varied from 1.65 to 12.5 m, stem length (S_L) from 0.6 to 3.9 m, and crown length (C_L) from 1.40 to 10.12 m. Aboveground woody biomass (M) covered four orders of magnitude from 0.51 to 4753 kg, branch biomass (M_B) varied from 0.18 to 4123 kg and stem biomass (M_S) from 0.33 to 884.50 kg. The means and the standard deviations of the aforementioned variables are reported in Table 1. Scatter plots of M, M_B and M_S against D are presented in Fig. 1a–c, while the plot of

Table 1 Dendrometric characteristic of 25 destructively sampled open-grown oak trees

Variable	Mean	Range	SD
Diameter at breast height (D cm)	32.77	3.18–99.4	26.4
Total tree height (H m)	7.54	1.65–12.50	3.72
Stem (S_L m)	1.99	0.60–3.90	0.88
Crown length (C_L m)	5.76	1.40–10.12	3.02
Aboveground woody biomass (M kg)	905.10	0.51–4753	1392.87
Branch biomass (M_B kg)	652.68	0.18–4123	1108.14
Stem biomass (M_S kg)	185.05	0.33–884.50	235.02

Standard deviation (SD) is also reported

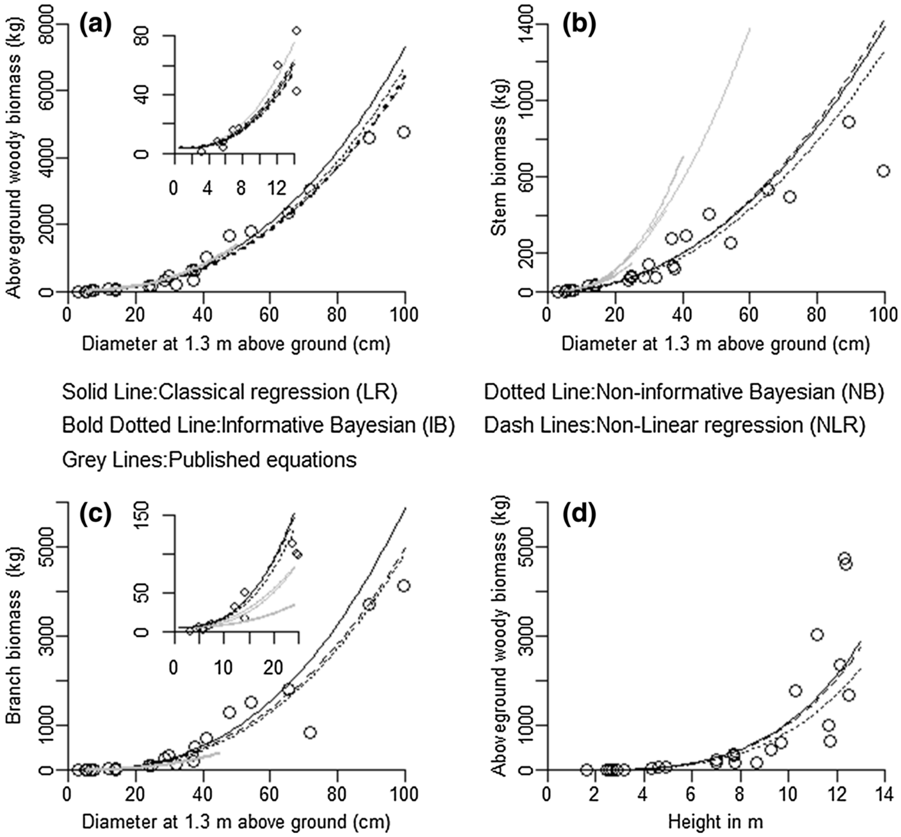

Fig. 1 Allometric relationships based on different regression techniques for **a** aboveground woody biomass against tree diameter, **b** stem biomass against tree diameter, **c** branch biomass against tree diameter and **d** aboveground woody biomass against tree height. *Insets* in **a** and **c** were provided for clarity. *Grey lines* depict published empirical allometries for oak specimens growing in closed stands. Raw biomass data collected from the studied area are shown with *open circles*

M against H is depicted in Fig. 1d. Using S_L and C_L as the regressor variables did not provide any strong allometric relationships for M, M_S or M_B under the three applied approaches (i.e., LR, NLR and NB).

Predictions of M

Within the classical statistical paradigm and based on the corrected Akaike criterion (Eq. 3), LR is supported against NLR (A equaled to 287.83 and 346.27, respectively), indicating that the analyzed M–D dataset follows a log-normal distribution with multiplicative error structure. As reported in Table 2, LR technique yielded slightly better predictions in M–D allometry, since P_D varied from 37 (LR) to 41% (IB), while size-shape scaling was not statistically different across the applied methods (the range of b values overlaps among the regression methods). The narrowest 5% credible interval for b was derived from the IB approach and the widest from the NB. Additionally, the inferences from LR and NB techniques were very similar as exemplified by the confidence and credible intervals, respectively, for the scaling parameters a and b. Across the D range, IB and NLR predict quite similar average M values, even though the mean b values for the two techniques differ by more than 0.07. The large relative difference of parameter a between the two approaches compensates for the discrepancy in b, resulting in small differences in M. For $D < 24$ cm, IB produced larger average M prediction than LR but smaller M values were obtained for bigger trees (e.g., for $D = 99.3$ cm the

Table 2 Empirical values for the scaling parameters in *M–D* and *M–H* allometries under the classical and Bayesian approaches

M–D allometry	a^A	SE a	b^A	SE b	R^2	P_D (%)^B
Classical approach						
Log-linear (LR)^C	−2.5524 (−3.1302 −1.9746)	0.2793	2.4688 (2.2913 2.6463)	0.0579	0.97	37
Nonlinear regression weighted (NLR)^D	0.1156 (0.0611 0.1970)	0.033	2.3682 (2.2207 2.5337)	0.077	0.97	38
Bayesian approach						
Non-informative Bayesian (NB)	−2.558 (−3.134 −1.974)	0.2928	2.47 (2.292 2.648)	0.09	0.97	37
Informative Bayesian (IB)	0.0835 (0.0539 0.1163)	0.0158	2.443 (2.351 2.552)	0.0524	0.96	41
M–H allometry	a^A	SE a	b^A	SE b	R^2	P_D (%)^B
Classical approach						
Log-linear (LR)^E	−1.8969 (−2.7089 −1.0870)	0.3925	3.7756 (3.3612 4.1900)	0.20	0.93	66
Nonlinear regression weighted (NLR)^F	0.1877 (0.077 0.3543)	0.065	3.7467 (3.3357 4.1925)	0.1970	0.93	65
Bayesian approach						
Non-informative Bayesian (NB)	−1.66 (−1.985 −1.126)	0.237	3.661 (3.375 3.879)	0.1319	0.94	65

Standard error (SE) for a and b, coefficient of determination (R^2) and mean absolute percentage difference (P_D) are also reported

[A] Mean value and credible or confidence intervals in parenthesis

[B] $P_D = 1/n \times \Sigma(|1 - P_i/O_i|) \times 100$

[C] Correction factor = 1.08

[D] Weight for the NLR in *M-D* allometry is D^{-4}

[E] Correction factor = 1.20

[F] Weight for the NLR in *M-H* allometry is H^{-8}. The R^2 for log-linear models are actually pseudo-R and is only an indicative value relative difference is 32%). In terms of uncertainty, wider prediction intervals were obtained from the IB for $D < 15$ cm, in relation to the LR and NB, but the reverse trend was derived for $D \geq 15$ cm.

A strong positive correlation ($R^2 = 95\%$) was obtained when the observed data were regressed against predicted M values derived from LR. The intercept was about 121 and the slope = 0.75 (Table 3). Similar statistics were derived from the NB regression. The corresponding figures for the IB method indicated a lower underestimation in comparison to the previous approaches since the intercept ≈ 114 and the slope equaled to 0.85. Quite similar results were reported for NLR (intercept ≈ 92 and slope = 0.87). In all cases, the variability in predicted M values explained more than 95% of the variability in the raw data, the intercept was not significantly different from zero, the slope was significantly different from one (at 95% level), but the overall underestimation was higher for LR and NB regressions.

In Fig. 2, the probability distributions of predicted M values, derived from the three regression techniques, are illustrated for different diameters. NLR was dropped from this analysis since it predicted very narrow normal distribution, implying unsound biological outputs. For small diameter ($D = 5.73$ cm; Fig. 2a), the 95% interval of M ranged from 1.33 to 24.6 kg for IB, while for LR and NB, M predictions varied from 2.4 to 14.5 kg. For tree diameter equal to 24.8 cm, the three approaches provided different probability distributions for M (Fig. 2b), even though LR and NB presented similar 95% upper limit (ca. 500 kg). For D close to the average value of raw diameters ($D = 37.30$ cm; Fig. 2c), LR predicted M to vary between 280.5 and 1453.2 kg and for NB the 95% M interval varied from 250.5 to 1,421.1 kg. The corresponding prediction interval for IB ranged from 331.40 to 970.90 kg. For the largest recording sampled tree ($D = 99.4$ cm; Fig. 2d), LR and NB provided practically identical log-normal probability

Table 3 Linear regression statistics for observed against predicted values derived from log-linear (LR), weighted nonlinear regression (NLR), non-informative Bayesian (NB) and informative Bayesian (IB) for different tree compartments. The coefficient of determination (R^2), F statistic and the p value are also reported. The confidence intervals at 95% level for the intercept and the slope are presented in the parentheses

Tree compartment	Intercept	Slope	R^2	F	P value
Total aboveground woody biomass (M)					
LR	121 (−23 to 267)	0.75 (0.68–0.83)	0.95	481	<0.001
NLR	92 (−44 to 229)	0.87 (0.79–0.94)	0.95	557	<0.001
NB	122 (−24 to 268)	0.75 (0.68–0.82)	0.95	481	<0.001
IB	114 (−29 to 258)	0.85 (0.77–0.94)	0.95	500	<0.001
Stem biomass (M_S)					
LR	43.7 (−3 to 93)	0.62 (0.50–0.73)	0.84	127	<0.001
NLR	45 (−1.75 to 92)	0.60 (0.48–0.70)	0.83	125	<0.001
NB	43 (−3 to 90)	0.62 (0.50–0.73)	0.84	127	<0.001
Branch biomass (M_B)					
LR	67.7 (−82 to 210)	0.73 (0.64–0.83)	0.92	270	<0.001
NLR	50 (−99 to 199)	0.86 (0.79–0.98)	0.92	277	<0.001
NB	63 (−87 to 213)	0.75 (0.66–0.85)	0.92	272	<0.001

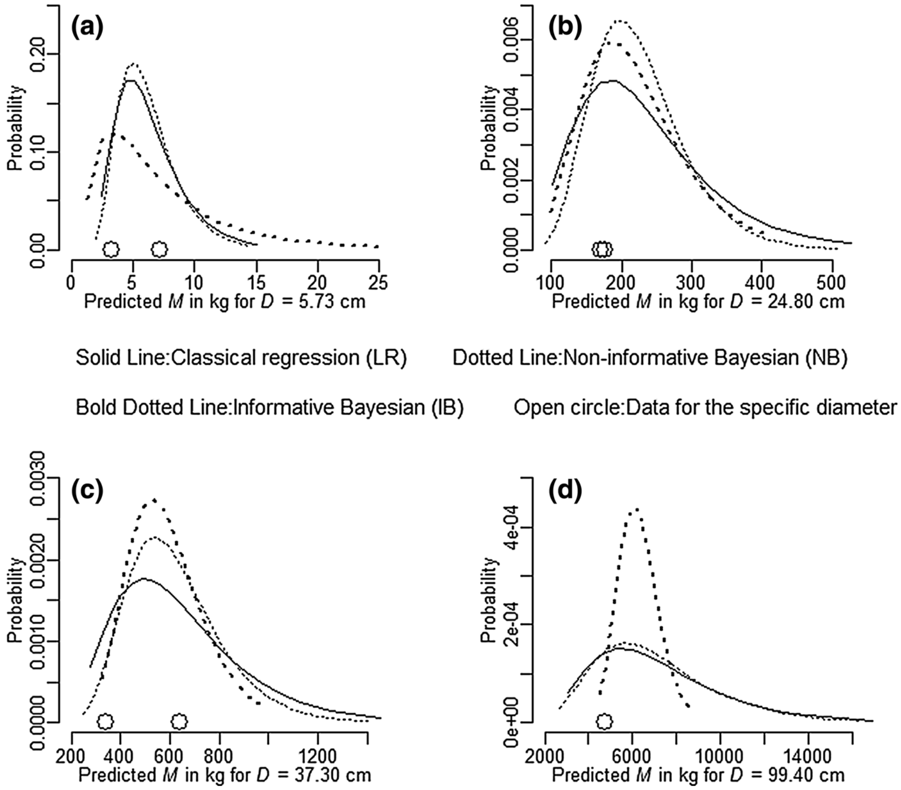

Fig. 2 Probability distributions for predicting aboveground woody biomass (M) derived from the three applied regression techniques at **a** $D = 5.73$ cm, **b** $D = 24.80$ cm **c** $D = 37.30$ cm and **d** $D = 99.40$ cm. The "superiority" of IB technique is depicted in **d** which is the only one to provide biologically sound upper limit for M

distributions for M, totally different than the one derived from IB. For LR and NB the 95% uncertainty level ranged from around 3000–17,000 kg (mean = 7179.23 kg) while for IB the range was between 4500 and 8600 kg (mean = 6308.10 kg).

The three applied regressions (LR, NB and NLR) provided quite similar predicted values for M, when H was used as the independent variable (Fig. 1d). The average absolute deviation was ca. 66%, while higher P_D values were derived for allometries developed for stem and branch compartments (80 and 70%, respectively). These results indicate that biased estimations may be obtained if allometric equation is solely based on H.

Predictions of M_S

As expected, LR and NB actually provided identical values for allometric parameters ln$a$ and b, which were not statistically different from the values obtained from NLR (Table 4). It is clearly illustrated in Fig. 1b that the three applied regression approaches for the studied oaks provided quite similar M_S values across the D spectrum. Even though the Akaike criterion showed that LR technique ($A = 234.27$) was better than NLR ($A = 293.86$), P_D indicated that there is no preference of one approach over the other (41.5% for LR and 42% for NLR; Table 4). The linear regression of raw M_S data against predicted values, derived from the three applied regressions (LR, NLR and NB), explained about 84% of the variability (Table 3). For LR, the intercept was ca. 44 and the slope equaled 0.62; for NLR the corresponding parameters were 45 and 0.60, while for NB the intercept was 43 and the slope was around 0.62. In all cases, M_S was underestimated, the intercepts were not significantly different from zero but the slopes were significantly different from one (Table 3). Including S_L, C_L or H did not substantially improved predictions (results not shown).

Predictions of M_B

The bias in M_B–D allometry was around 60% (P_D in Table 4) for all the applied methods. Irrespective of the regression technique, M_B predictions were similar

Table 4 Empirical values for the scaling parameters in M_S–D and M_B–D allometries under the classical and Bayesian approaches

M_S–D allometry	a[A]	SE a	b[A]	SE b	R^2	P_D (%)[B]
Classical approach						
Log-linear (LR)[C]	−2.6007 (−3.2100 to1.9914)	0.2945	2.1167 (1.9295 2.3039)	0.0904	0.95	41.5
Nonlinear regression weighted (NLR)[D]	0.0755 (0.0432 0.1207)	0.0208	2.1388 (1.9754 2.3066)	0.0866	0.95	42
Bayesian approach						
Non-informative Bayesian (NB)	−2.5990 (−3.2050 to 1.9880)	0.3000	2.1160 (1.9290 2.3030)	0.0944	0.94	42
M_B–D allometry	a*	SE a	b*	SE b	R^2	P_D (%)
Classical approach						
Log-linear (LR)[E]	−3.5154 (−4.3213 to 2.7093)	0.3896	2.6140 (2.36634 2.8617)	0.1197	0.94	61
Nonlinear regression weighted (NLR)[F]	0.0454 (0.0211–0.083)	0.015	2.5198 (2.3821 2.7520)	0.1000	0.94	60
Bayesian approach						
Non-informative Bayesian (NB)	−3.429 (−3.956 to 2.692)	0.3353	2.589 (2.36–2.762)	0.105	0.94	60

Standard error (SE) for a and b, coefficient of determination (R^2) and mean absolute percentage difference (P_D) are also reported

[A] Mean value and credible or confidence intervals in parenthesis

[B] $P_D = 1/n \times \Sigma(|1 - P_i/O_i|) \times 100$

[C] Correction factor = 1.09

[D] Weight for the NLR in M_S–D allometry is $D^{-4.5}$

[E] Correction factor = 1.17

[F] Weight for the NLR in M_B-D allometry is $D^{-4.5}$. The R^2 for non-linear models are actually pseudo-R and is only an indicative value

for small trees ($D \leq 25$ cm; inset in Fig. 1c), but LR provided the largest values for bigger trees (Fig. 1c). NB and NLR predicted quite similar M_B values across the D range. The observed M_B data were linearly regressed against predictions derived from the three approaches (Table 3). The value of R^2 was equal to 92, irrespective of the applied method. For LR, the intercept was 68 (−82 to 210) and the slope was 0.73 (0.64– 0.83). The corresponding values for NB were 63 (−87 to 213) and 0.75 (0.66–0.85). For NLR, the intercept equaled 50 (−99 to 199) and slope 0.86 (0.79–0.98). For the three applied regressions, the confidence intervals for the intercepts included zero but the value of one was not included in the confidence intervals of the slopes. Inserting tree height (H), as a second independent variable did not substantially improve the predictions ($P_D = 55.1\%$) Comparisons to published equations developed for trees growing in American and European oak forest stands, indicates that branch biomass fells below the analyzed open-grown trees, across the D range (grey lines in Fig. 1c).

Discussion

The results presented in this article complement tree biomass allometry for open-grown trees. One of the main finding illustrates that both the classical and Bayesian regressions explained much of the variability inherent in aboveground biomass compartments of open grown valonian trees (Fig. 1). However, it should be pointed out that the informative Bayesian model (IB) provided biologically sound predictions while LR and NB approaches failed to derive realistic probability distributions for total above ground woody biomass.

The 'biological' inconsistency of LR and NB is clearly depicted in Fig. 2d, where both techniques predict an upper limit (at 95% level) of M around 16 ton. For a tree with $D = 99.40$ cm; such a tree is expected to collapse under its own weight. The probability distribution from IB seems to follow a more realistic pattern than LR and NB, as illustrated in Fig. 2a–d. Not enough data were available to empirically support this finding, but bearing in mind that trees sustain similar amount of aboveground organic matter, irrespective of the growing environment (closed stands versus open grown trees in Fig. 1a; Zhou et al. 2014), direct comparisons to published data from trees growing in forest stands can be made. For example, Brown (1997) reported that a tree (tropical species) with $D = 97.3$ cm attained 4386.60 kg of M (including foliage) while for a specimen with $D = 99.50$ cm the corresponding value was 8962.30 kg. The predictions obtained from LR and NB greatly diverge from these observed values, providing unsound uncertainty predictions, but IB approach derived biologically sound M values (for $D = 99.40$ cm, M ranges from 4523 to 8675 kg; Fig. 2d).

Thus, a coherent analysis for tree biomass allometries should not be based solely on mean predicted values but on their associated uncertainties, as well. Within the classical framework of log-transformed data, linear regressions (LR approach) on different datasets, each one containing several destructively sampled trees, are needed in order to make statistically sound inferences about biomass variability for a specific diameter. However, such an approach is not feasible and rarely (if ever) being applied due to monetary and time restrictions. In Bayesian analysis this restriction is overcome, since biomass variance is modeled in a way that reflects its heteroscedasticity property and derived credible intervals are directly associated with their probability, based on prior information and the collected biomass data (Ellison 2004; McCarthy 2007, pp. 27–29).

Larger bias was reported for open-grown valonian oaks in relation to specimens growing in forested ecosystems. The value of P_D ranged between 37 and 41%, depending on the regression approach used for the studied species (Table 2), while P_D is usually around 20% for forest trees. A larger degree of variability of M for a specific D is therefore expected for open-grown trees. Similar results were derived for stem and branch biomass, even though R^2 values were quite high (Table 4). As clearly illustrated by Sileshi (2014), R^2 should be used in conjunction to other goodness-of-fit statistics to test the performance of empirical allometric models and the results in this article support this recommendation.

The obtained large deviations between observed and predicted biomass values are in accordance to the outcomes recently presented by Zhou et al. (2014), who developed aboveground woody biomass equations for coniferous and broadleaved open-grown trees. The value of R^2, for M–D, M_S–D and M_B–D allometries was equal to 0.97, 0.95 and 0.89, respectively, for green ash trees. Direct comparisons with the predicted values presented in the aforementioned article could not be made, since the lower predicted value for green ash trees with $D < 15$ cm provides negative biomass estimate, implying bias in their empirical models. However, the raw data by Zhou et al. (2014) for D ca. 15 cm corresponded to M around 80 kg (see Fig. 2a3 in Zhou et al. 2014), which is quite similar to our dataset (for $D = 14.33$ cm $M = 80.71$ kg; Fig. 1a). The value of M_S for green ash, at the specific diameter, was about 40 kg (see Fig. 2a1 in Zhou et al. 2014) and close to the valonian oak data (for $D = 14.33$ cm $M_S = 31.87$ kg; Fig. 1b), while the M_B for green ash ranged from 40 to 100 kg (see Fig. 2a2 in Zhou et al. 2014), including the value of 50.84 kg found in the valonian oak dataset (Fig. 1c).

Green ash and valonian oak trees sustained similar M values for D $\approx$ 28.5 cm (for oak $M = 351.99$ kg; for ash $320 < M < 420$ kg). Stem biomass (M_S) for oaks was smaller (for $D = 28.7$ cm $M_S = 71.28$ kg; Fig. 1b) in comparison to ash trees (M_S ranged from ca. 220–260 kg; see Fig. 2a1 in Zhou et al. 2014). On the other hand, M_B for oaks was larger than ash trees for trees with similar stature. For $D \approx 42$ cm, both species sustained ca. 1000 kg of M. Organic matter was equally allocated to stem and branch compartments for ash trees (around 500 kg) but not for valonian oaks ($M_S \approx 216$ kg and $M_B \approx 714$ kg). These results support the line of reasoning presented by Zhou et al. (2014) suggesting that more organic matter is allocated to branch compartment for open-grown trees in relation to stem, than in close-canopy counterparts.

This preliminary comparison between ash and valonian oak trees puts forward the hypothesis that open grown broadleaved specimens may sustain similar total aboveground woody biomass, irrespective of species, growth conditions and tree size. As a corollary, a 'global' allometric equation for M–D relationship may hold valid for ecosystems including open grown trees. This kind of equation may be developed based on the concept of generalized regressions (Pastor et al. 1984) or on pooled data regression (Zapata-Cuartas et al. 2012). On the contrary, allocation pattern of organic matter to stem and branches seems to vary by species and/or site conditions and therefore 'local' oriented empirical equations should be developed in cases where predictions on M_S and M_B are needed. To robustly test these hypotheses, extensive biomass datasets originating from different sites and covering several tree species should be analyzed on a statistically sound framework (based on Bayesian modeling).

Comparisons against published equations for trees growing in forested stands illustrated small differences in M. For example, setting $D = 14$ cm the three analyzed techniques yielded a value of M between 52.5 and 60 kg, while the corresponding M prediction from a *Q. conferta* stand in Greece derived a value of 71 kg (grey line in the inset at Fig. 1a). A value of 60 kg, for the same D, was reported for several oak trees growing in UK. For $D = 50$ cm, the British oak trees sustain 1383 kg of M (grey line in Fig. 1a), while across the three approaches M ranged between 1181 and 1316 kg. The published equations are reported in Zianis et al. (2005).

Comparisons to published equations built for stem and branch compartments for oak trees growing in closed European and American stands presented similar patterns as the ones provided by Zhou et al. (2014) for ash trees. For example, predictions of M_S for several oak species growing in the northern American forests (Ter-Mikaelian and Korzukhin 1997), diverge upwards (grey lines in Fig. 1b) in relation to the trees harvested from the studied ecosystem. Specifically, at $D = 40$ cm predictions for M_S ranged between 581 and 707 kg for American oaks, while the corresponding figure for the open-grown trees was around 200 kg. The ratio of stem biomass from closed-grown trees over open-grown specimens increases linearly from small ($D = 5$ cm; ratio ≈ 1.44) to average stature trees ($D = 35$ cm; ratio ≈ 3) and remains constant for larger trees.

Thus, oak trees growing in closed canopies sustain much larger stem biomass than open-grown counterparts (Fig. 1b), but maintain smaller branch biomass (Fig. 1c) across the diameter range. Extensive tree crowns and sharper trunk morphology for open-grown specimens may explain these trends. These findings infer that forest-derived equations should not be applied for estimating stem and branch biomass for open canopy trees. Aboveground woody biomass seems not to be differentiated between open-grown and forest-grown oak trees (relative difference less than 10% as illustrated in Fig. 1a), but the relative difference for open-canopy and closed-canopy ash trees attained a value of 18% (Zhou et al. 2014). Whether forest-derived equations could be used potentially for predicting total aboveground woody biomass for open-grown trees is not clearly demonstrated from the analyses on these two broadleaved species (valonian oak and green ash) and further research is needed.

Surpassingly, tree height did not significantly contribute in capturing much of the variability in woody biomass, either as a sole independent variable (Fig. 1d) or in combination to stem diameter. Additionally given the multicollinearity caveat (Zianis and Radoglou 2006) originating from the strong relationship between H and D, interpretation of predictions when both variables are used should be anticipated with skepticism. Neither stem length nor crown length provided accurate biomass predictions for different tree compartments.

The credible (Bayesian approaches) or confidence (classical approaches) intervals for the scaling exponent in M–D allometry did not include the value of 2.67, predicted by the WBE theoretical model. This result strongly supports similar outcomes from trees growing in forested stands, where b was statistically different than the theoretical value (Zapata-Cuartas et al. 2012; Sileshi 2014). The WBE model failed to predict the exponent in M–H allometry under the NB regression. The empirical value was equal to 3.661 (Table 2) and statistically different (at 95% level) from the theoretical one which is equal to four. The confidence intervals from LR and NLR include the value of four, but on average the model diverged from the empirical estimates (3.7756 for LR and 3.7467 for NLR). Therefore, analyses on empirical studies imply that a specific numeric value for the allometric exponent may not well represent the flexibility found in tree biomass allometry, which possibly originates from the accumulative effect of biotic and abiotic agents acting upon tree size-shape relations. Rather, a probability distribution may better describe the stochastic nature of the allometric equation in open-grown trees.

Conclusions

The IB and NB equations developed may be used to predict aboveground woody biomass for open-grown valonian oaks based on the diameter distributions of sampling plots compiled in the forest management plans of the studied ecosystem. Assuming that uncertainty is equally or even more important than merely predicting average values, it is recommended that future allometric models should report associated probability distribution for predicted tree biomass estimates. Informative Bayesian regression is considered to be more appropriate than classical statistical approaches (such as log-linear or non linear regressions) or non-informative Bayesian technique for deriving the variance of the predictive distribution. Large errors in predicting the biomass of stem and branch compartments are expected from the implementation of the derived models based on D, but not substantial improvement was obtained by inserting tree linear dimensions in the regressions (such as tree height, stem and/or crown length). Given that more biomass data for open-grown trees would become available, informative Bayesian regressions may provide better predictions for stem and branch compartments. Finally, the theoretical WBE model which assumes a specific value for the exponent in M–D allometry (i.e., $b = 2.67$) was not supported by our findings.

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References

Brown S (1997) Estimating biomass and biomass change of tropical forests. A primer. Forestry paper, vol 134. FAO, Rome

Chiyenda SS, Kozak A (1982) Some comments on choosing regression models for biomass prediction equations. For Chron 58:203–204

Ducey MJ, Zarin DJ, Vasconcelos SS, Araújo MM (2009) Biomass equations for forest regrowth in the eastern Amazon using randomized branch sampling. Acta Amazon 39:349–360

Eamus D, McGuinness K, Burrows W (2000) Review of allometric relationships for estimating woody biomass for Queensland, The Northern Territory and Western Australia. National Carbon Accounting System Technical Report 5b. Australian Greenhouse Office, Canberra

Ellison AM (2004) Bayesian inference in ecology. Ecol Lett 7:509–520

Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. Nature 5:655–660

Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB (2014) Bayesian data analysis, 3rd edn. Chapman and Hall, Boca Raton

Gilks W, Richardson S, Spiegelhalter D (eds) (1995) Markov chain Monte Carlo in practice. Springer, Berlin

Gitay H, Suarez A, Watson R, Dokken DJ (eds) (2002) Climate change and biodiversity—IPCC Technical Paper V. Intergovernmental panel on climate change. Available at: https://www.ipcc.ch/pdf/technical-papers/climate-changes-biodiversity-en.pdf. Accessed 5 Aug 2016

Henry M, Picard N, Trotta C, Manlay RJ, Valentini R, Bernoux M, Saint-André L (2011) Estimating tree biomass of sub-Saharan African forests: a review of available allometric equations. Silva Fenn 45(3B):477–569

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2004) Comprehensive database of diameter-based biomass regressions for North American tree species. GTR NE-319 USDA

Ketterings QM, Noordwijk CMY, Ambagau R, Palm CA (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. For Ecol Manag 146:199–209

Kort J, Turnock R (1999) Carbon reservoir and biomass in Canadian prairie shelterbelts. Agrofor Syst 44:175–186

Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Stat Comput 10:325–337

Makungwa SD, Chittock A, Skole DL, Kanyama-Phiri GY, Woodhouse IH (2013) Allometry for biomass estimation in jatropha trees planted as boundary hedge in farmers' fields. Forests 4:218–233

McCarthy MA (2007) Bayesian methods for ecology. Cambridge University Press, Cambridge

Montagnini F, Nair PKR (2004) Carbon sequestration: an underexploited environmental benefit of agroforestry systems. Agrofor Syst 61:281–295

Muller-Landau HC, Condit RS, Chave J, Thomas SC, Bohlman SA, Bunyavejchewin S et al (2006) Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecol Lett 9:575–588

Murthy IK, Gupta M, Tomar S, Munsi M, Tiwari R et al (2013) Carbon sequestration potential of agroforestry systems in India. J Earth Sci Clim Change 4:1–7

Navar J (2009) Allometric equations for tree species and carbon stocks for forests of northwestern Mexico. For Ecol Manag 257:427–434

Navar J (2010) Methods of assessment of aboveground tree biomass. In: Maggy Ndombo M, Momba B. (eds) Biomass InTech. Available: http://www.intechopen.com/books/biomass/methods-of-assessment-of-aboveground-tree-biomass. Accessed 09 Feb 2015

Parresol BR (1999) Assessing tree and stand biomass: a review with examples and critical comparisons. For Sci 45:573–593

Pastor J, Aber JD, Melillo JM (1984) Biomass prediction using generalised allometric regressions for some Northeast tree species. For Ecol Manag 7:265–274

Payandeh B (1981) Choosing regression models for biomass prediction equations. For Chron 57:229–232

Pilli R, Anfodillo T, Carrer M (2006) Towards a functional and simplified allometry for estimating forest biomass. For Ecol Manag 237:583–593

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/

Schoeneberger MM (2009) Agroforestry: working trees for sequestering carbon on agricultural lands. Agroforest Syst 75:27–37

Sileshi GW (2014) A critical review of forest biomass estimation models, common mistakes and corrective measures. For Ecol Manag 329:237–254

Spiegelhalter DJ, Thomas A, Best NG, Lunn D (2007) OpenBUGS User Manual version 3.0.2. MRC Biostatistics Unit, Cambridge

Sprugel DG (1983) Correcting for bias in log-transformed allometric equations. Ecology 64:209–210

Ter-Mikaelian MT, Korzukhin MD (1997) Biomass equations for sixty-five North American tree species. For Ecol Manag 97:1–24

Thomopoulos NT, Johnson AC (2003) Tables and characteristics of the standardized lognormal distribution. In: Proceedings of the Decision Sciences Institute (ed. Decision Sciences Institute) pp 1031–1036

Tredennick AT, Lisa Patrick Bentley LP, Hanan NP (2013) Allometric convergence in savanna trees and implications for the use of plant scaling models in variable ecosystems. PLoS ONE 8:e5824

West BG, Brown HJ, Enquist JB (1997) A general model for the origin of allometric scaling laws in biology. Science 276:122–126

Xiao X, White EP, Hooten MB, Durham SL (2011) On the use of log transformation versus nonlinear regression for analysing biological power laws. Ecology 92:1887–1894

Zapata-Cuartas M, Sierra AC, Alleman L (2012) Probability distribution of allometric coefficients and Bayesian estimation of aboveground tree biomass. For Ecol Manag 277:173–179

Zell J, Bösch B, Kändler G (2014) Estimating above-ground biomass of trees: comparing Bayesian calibration with regression technique. Eur J For Res 133:649–660

Zhou X, Brandle JR, Awada TN, Schoeneberger MM, Martin DL, Xin Y, Tang ZH (2011) The use of forest-derived specific gravity for the conversion of volume to biomass for open-grown trees on agricultural land. Biomass Bioenerg 35:1721–1731

Zhou X, Schoeneberger MM, Brandle JR, Awada TN, Chu J et al (2014) Analyzing the uncertainties in use of forest-derived biomass equations for open-grown trees in agricultural land. For Sci 60:1–18

Zianis D (2008) Predicting mean aboveground forest biomass and its associated variance. For Ecol Manag 256:1400–1407

Zianis D, Mencuccini M (2003) Aboveground biomass relationships for beech (*Fagus moesiaca* Cz.) trees in Vermio Mountain, Northern Greece, and generalised equations for *Fagus* spp. An For Sci 60:439–448

Zianis D, Radoglou K (2006) Comparison between empirical and theoretical biomass allometric models and statistical implications in stem volume predictions. Forestry 79:477–487

Zianis D, Muukkonen P, Mäkipää R, Mencuccini M (2005) Biomass and stem volume equations for tree species in Europe. Silva Fenn Monogr 4:5–63

Zianis D, Spyroglou G, Tiakas E, Radoglou K (2016) Bayesian and classical models to predict aboveground tree biomass allometry. For Sci 62:247–259

Zou GY, Taleban J, Huo CY (2009) Confidence interval estimation for log-normal data with application to health economics. Comput Stat Data Anal 53:3755–3764