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On simplifying allometric analyses of forest biomass

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Abstract

Tree biomass plays a key role in sustainable management and in estimating forest carbon stocks. The most common mathematical model in biomass studies takes the form of the power function $M = aD^b$ where a and b are the allometric coefficients to be determined by empirical data, and M the total aboveground tree dry biomass for a specific diameter at breast height, D.

In this study the development and comparison of three methods for simplifying allometric equations of aboveground biomass estimation are reported. Based on the criterion of the relative difference (RD) between observed and predicted biomass data, the small trees sampling scheme (SSS) predicted quite accurate estimates for raw data reported in 10 studies. The SSS equation was based on the hypothesis that information provided in published allometric equations, in conjunction with two pairs of empirical M–D values, are enough to obtain reliable predictions for aboveground stand biomass. In addition, predictions of M based on theoretical values of b were also tested with the RD criterion, but reliability of predictions in 10 studies is questioned. Finally, fractal geometry was used to develop a 'reductionist' model for M estimation and implications from its implementation in biomass studies are discussed. We totally based our investigation on a metadata set derived from published aboveground biomass allometric studies conducted for different species spanning the globe.

Keywords: Allometric equations; Aboveground biomass; Carbon stocks; Fractal geometry; Biomechanics

1. Introduction

After an absence of about 30 years from scientific research, forest biomass appears to be regaining its historical significance. Rapid, easily implemented methods are needed for the assessment of standing biomass in order to estimate the carbon sequestration by forest ecosystems. Estimates of biomass are required for assessing the amount of primary energy obtainable from the forests as an alternative to fossil fuels. For scientific purposes, standing biomass is a fundamental state variable in several ecological and ecophysiological models.

Traditionally, the determination of aboveground tree biomass has been related to insure sustainable planning of forest resources, and foresters applied different methods to obtain such estimations. Undoubtedly, the most commonly used mathematical model for biomass studies takes the form of the power function:

$$M = aD^b \tag{1}$$

where a and b are the scaling coefficients, M the total aboveground tree dry biomass and D the diameter at breast height. In most cases variability of M is largely explained by the variability of D. Values of a and b are

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reported to vary with species, stand age, site quality, climate, and stocking of stands. Baskerville (1965) investigated allometric equations for balsam fir (*Abies balsamea* M.) based on sampled trees selected from plots with different stem densities. He concluded that stand density had no significant effect on the allometric relations, and a single expression was developed for all trees regardless of density. Cannell (1984) analysed the woody biomass of 640 forest stands, spanning the globe, and concluded that the proportion of branches also influences the total aboveground wood biomass for any given basal area at breast height and mean tree height.

The standard method to obtain estimates for the coefficients a and b is by the least-square regression of log-transformed data for D and M measured from destructively sampled trees that represent the diameter range within the stands under investigation. This is a laborious and time consuming approach and it would be difficult to implement it at a national level. Moreover, difficulties arise, as the geographical area for which the obtained equation is valid should be determined.

Alternative to empirical approaches, biomechanical principles of tree structure and ecophysiological models based on the fractal properties of tree branching networks (West et al., 1999), have been used to obtain estimates for the scaling exponent in Eq. (1). The West et al. (1999) fractal model predicts that the aboveground biomass of tree species should scale against stem diameter on average with $b = 8/3$ (i.e. ≈ 2.67), independent of the structural and morphological characteristics of the trees under investigation. The question of whether an analysis of the existing information on M–D allometry provides support for this theory immediately arises.

The main objectives of this study are threefold:

(a) To test whether the exponent of the allometric relationship, b, is linearly dependent on the exponent in the H–D relationship (hypothesis suggested by Ketterings et al. (2001); H denotes the tree height).

(b) To test the performance of a theoretical and an empirical b value. The theoretical value was derived from a recent model (see West et al., 1999); the empirical equals the average of published b values from different studies.

(c) To present and validate two new methods (the SSS method and the 'reductionist model') which simplify the allometric relation between M and D. The first one is based on the sampling of the smallest trees only of a stand. The second was developed by applying the theory of fractal geometry to the underlying relationships between the variables describing tree size and shape.

Associated errors involved in the simplification procedures are also reported. We totally based our investigation on a metadata set derived from published aboveground biomass allometric studies conducted for different species spanning the globe.

2. Materials and methods

2.1. Compilation of data

Two types of data were employed for our analyses. We first compiled a world-wide list of biomass allometric equations including all the statistical parameters reported in the following section. We then selected those publications, from which raw individual-level data for M and corresponding D could be extracted.

2.1.1. Allometric studies

The interest in the estimation of aboveground tree biomass has resulted in a voluminous amount of literature published throughout the world. During our reference search, we applied no particular selection criteria to exclude certain species or sites. For all cases included in this meta-database, aboveground dry biomass (including stem, bark, branches and leaves) had been regressed against diameter at breast height D (either at 1.30 or 1.37 m above ground). The following information was recorded from each study: species and region for which the equation was developed, a and b values, coefficient of determination R^2, and D range of the harvested trees—whenever this last information was available. The total number of compiled equations is 279. Of these, 62 allometric equations were developed in Australia, 28 in countries from the tropical zone, 20 in Europe and 169 in the USA (Appendix A). The majority of the American equations was obtained from a review paper written by

Ter-Mikaelian and Korzukhin (1997). Thirty-three broadleaved species belonging to 15 genera were found in 122 different studies, while 21 coniferous tree species from 8 genera were recorded in 67 studies. Species growing in tropical regions and Australia are generally referred to as 'tropical' in this study, and in total provided 90 allometric equations. In 54 studies, the D interval of the sampled trees was not given, while in 2 studies estimates of the parameter a were not reported and thus only 223 equations were used for the development of the simplifying method (SSS, see Section 2.2.4). The present study is not to be considered an exhaustive review of aboveground biomass equations at a world-wide scale, since a lot of information is believed to exist in 'grey' literature of forestry and related institutes not widely available. However, the collected information is assumed to represent an unbiased sample of the M–D relationships for tree species growing at the global scale.

2.1.2. Raw individual-level data

For some publications a table containing the empirical tree-level information could be found. However, when M–D data were not provided in the original articles, appropriate graphs were scanned and subsequently digitised in order to obtain M and D values. Prof. Gower (University of Wisconsin, USA) kindly provided unpublished data for aspen species growing in USA. Hence, original tree-level data from nine different studies concerning seven different species—four coniferous and three broadleaved—and one study based on various tropical tree species were available to us (see Table 1 for details).

In addition, 13 more studies, which provided the M–D and H–D relations, were reviewed (Table 2) for calibrating the 'reductionist' model described in Section 2.2.2.

2.2. Theory

2.2.1. The theory of tree mass–diameter allometry

A brief discussion of allometric analysis will follow in order to pinpoint basic assumptions made by the least-square regression method for computing the parameters in Eq. (1). Since M–D relationships seem to conform to a power mathematical function, the raw data are usually (decision depends on the error structure) logarithmically transformed and the linear (in the parameters) logarithmic relationship is therefore obtained:

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

This transformation is appropriate when the standard deviation of M at any D increases in proportion to the value of D. When this situation exists, it implies that values of M can be measured more precisely at low than at high values of D (Zar, 1996). The least-square regression technique is applied to the transformed data and estimates for ln a and b are obtained. In many cases, log-transformation of real data results in homoscedasticity of the dependent variable M, a prerequisite for the regression methods. However,

Table 1
Raw data reported in these studies were used for the validation of the SSS method, the empirical, the theoretical and the 'reductionist' models[a]

No.	Author	Species	Region	a	b	b^*	D range (cm)	R^2	R^{2*}	N
1	Woods et al. (1991)	Spruce	USA	0.1062	2.3574	0.8486	2.9–23	0.9835	0.9071	31
2	Gower (pers. commun.)	Aspen	USA	0.036	2.785	0.5938	5.8–23.7	0.9915	0.9183	8
3	Woods et al. (1991)	Aspen	USA	0.1061	2.4151	0.6847	0.9–35.4	0.9942	0.9784	32
4	Lim (1979)	Scots pine	UK	0.196	2.2055	0.4324	6.3–25.6	0.9809	0.8025	22
5	Santa Regina and Tarazona (2001a)	Scots pine	Spain	0.2375	2.0291	0.6469	2.5–36.5	0.9914	0.8986	7
6	Santa Regina and Tarazona (2001b)	Beech	Spain	0.1315	2.432	0.5602	4–34.5	0.9983	0.886	7
7	Jokela et al. (1981)	Paper birch	USA	0.0809	2.3595	0.4926	7.1–23.1	0.9704	0.7604	15
8	Menguzzato and Tabacchi (1986)	Douglas fir	Italy	0.1413	2.2996	0.3733	8.7–26.8	0.9493	0.9994	69
9	Cerny et al. (2000)	Norway spruce	Czech Republic	0.2161	2.1864	0.5256	13.4–41.5	0.9858	0.903	11
10	Ketterings et al. (2001)	Tropical species	Indonesia	0.0639	2.5866	0.6094	7.6–48.1	0.9522	0.6852	29

[a] a and b are the allometric coefficients for M–D relationship with R^2 the coefficient of determination; b^* is the scaling exponent in H–D relationship and R^{2*} the corresponding coefficient of determination. N denotes the number of the sampled tress per study.

Table 2
Thirteen studies on tree size–shape relation were reviewed for the calibration of the equation between the scaling exponents b and b^* found in *M–D* and *H–D* relationships, respectively (see Section 2.2.2)

No.	Author	Species	b^*	b
1	Cantiani (1974)	*A. alba*	0.3814	2.2716
2	Makela and Vanninen (1998)	*P. sylvestris*	0.8802	2.6931
3	Vanninen et al. (1996)	*P. sylvestris*	1.0746	2.7017
4	Parresol (1999)	*Q. phellos*	0.2596	2.1702
5	Taras (1980)	*P. clausa*	0.5024	2.3789
6	Menguzzato and Tabacchi (1988)	*P. radiata*	0.7725	2.2936
7	Menguzzato and Tabacchi (1988)	*Eucalyptus* ssp.	0.6443	2.2644
8	Baldini et al. (1989)	*P. pinaster*	0.3459	2.0392
9	Whittaker and Woodwell (1968)	*P. rigida*	0.5699	2.3373
10	Whittaker and Woodwell (1968)	*Q. coccinea*	0.6783	2.19
11	Whittaker and Woodwell (1968)	*Q. alba*	0.5629	2.1666
12	Tahvanainen (1996)	*Salix* ssp.	0.8188	2.54
13	Zianis and Mencuccini (unpublished data)	*F. moesiaca*	0.5317	2.3087

even though the linear relation of Eq. (2) is mathematically equivalent to Eq. (1), they are not identical in a statistical sense (Zar, 1968). This inconsistency has long been recognised (Finney, 1941), but concern of its potential impact on estimates of biomass is relatively recent (Madgwick, 1970; Mountford and Bunce, 1973; Sprugel, 1983). Several procedures for correcting bias in logarithmic regression estimates have been advocated (Baskerville, 1972; Beauchamp and Olson, 1973; Yandle and Wiant, 1981; Sprugel, 1983).

A second important point in biomass studies is that researchers rarely validate the obtained relationship *M–D* with data other than the ones that were used in regression analysis. Chiyenda and Kozak (1982) pointed out that if models are to be used for prediction purposes, they should be evaluated with new data. The validity of the relation is usually tested by the coefficient of determination in Eq. (2), R^2, and the standard error of the estimate is computed for the entire dataset of the transformed data. However, high values of R^2 and low values of the standard error of the estimate (typically obtained in allometric studies) do not guarantee precision of the estimate when values are back transformed to the linear scale.

The fact that b is constant over the D interval, implies that an unchanging ratio is maintained between rates of growth in M and D. One might expect then that a and b be negatively related to one another, since high values of both a and b would result in large values of biomass for large diameters that possibly approach the safety limits imposed by mechanical self loading. A negative relationship between the scaling coefficients has long been recognised in zoological studies, but White and Gould (1965) concluded that no biological interpretation can be deduced from this relation. They pointed out that the self-correlation of a and b simply arises from the choice of measurement units, the algebraic equation itself, and the limited field (a, b) of the collected equations. However, this mathematical artefact provides the basic tool in simplifying allometric analysis of forest biomass. Since a and b are restricted to a certain relationship, then, inevitably, *M–D* relationships can be described by a restricted number of allometric equations. Thus, for a particular value of a, only a limited range of values for b can be obtained, and this suggests that there is a limited number of *M–D* equations despite the diversity of factors acting on each stand. In other words, information on the allometric parameters provided by published equations could be useful in estimating a and b for the stand under investigation.

2.2.2. Fractal geometry and tree size–shape relation

In this section, some insights provided by fractal geometry (Mandelbrot, 1983) and from the biomechanical principles of tree structure are presented and a ‘reductionist’ method for estimating forest M is developed. According to simple dimensional analysis, the volume of a tree is $V \propto D^2H$. Moreover, dimensional analysis assumes that the cross-section of the stem at breast height is an idealised geometric object (circle, ellipse, etc.), and its area A is related to the perimeter P by $A \propto P^2$. Diameter (which is also a linear dimension of the cross-section) is related to A by $A \propto D^2$. However, this is not completely true for real trees since the stem cross-section at any height has a non-standard shape that is only approximated by ideal objects. Mandelbrot (1983) suggests that the description of natural objects falls beyond the principles provided by Euclidean geometry and introduced the neologism (and related concepts) of fractal geometry to facilitate the understanding of the form and shape of such objects. Based on fractal geometric analysis, several techniques have been developed to quantify the dimension of trees, and the usefulness of fractal geometry in ecological studies has been demonstrated several times (e.g. Zeide and Gresham, 1991; Zeide and Pfeifer, 1991; Zeide, 1993, 1998; Osawa, 1995; Berezovskava et al., 1997). For the sake of simplicity—since no information is yet available—the dimension of the stem volume may be approximated by the third power of its linear dimension. On the other hand, it is generally acknowledged (Mandelbrot, 1983; Zeide and Gresham, 1991; Zeide and Pfeifer, 1991; Zeide, 1993, 1998; Osawa, 1995) that a positive number between 2 and 3 is a better estimation of the tree's crown dimension, and it is assumed that the overall shape of a tree (stem and crown) may posses a similar fractal dimension. In mathematical terms:

$$V \propto D^d H^h \tag{3}$$

where d and h are positive numbers with $2 < d + h < 3$. Theoretically, tree shapes and particularly tree crowns can be described as hybrid objects of surface and volume, since they are neither three-dimensional solids, nor two-dimensional photosynthetic surfaces (Zeide, 1998)—indentations and gaps are the main characteristics of their structure.

Following biomechanical principles, the scaling of H with respect to D has been examined principally in terms of stress and elastic similarity models (McMahon and Kronauer, 1976). Niklas (1994) reported that H scales as the 0.535 power of D for a wide range of plant sizes. If $H \propto D^{b*}$ with $0 < b^* \leq 1$, then Eq. (3) becomes

$$V \propto D^d D^{hb*} = D^{d+hb*} \tag{4}$$

Furthermore, if tree biomass is assumed to be proportional to V (with tree density as the proportionality constant) then $M \propto D^{d+hb*}$ and in conjunction with Eq. (1):

$$b = d + hb^* \tag{5}$$

Thus the hypothesis put forward by Ketterings et al. (2001) (that the scaling coefficient between M and D depends on the scaling coefficient between H and D) has been proved. In practical terms, the allometric exponent in H–D relationship, namely b^*, can be used to estimate the allometric parameters in Eq. (1), and subsequently estimate the M value for a given D; the procedure is straightforward and its applicability was tested using the original data reported in 10 studies.

2.2.3. *Theoretical versus empirical equations*

According to West et al. (1999) model, D is related to M through $D \propto M^{3/8}$, indicating that the scaling exponent b in Eq. (1) equals 2.67 (see also Enquist et al., 1998). The average b value from the compiled empirical equations (b_{emp}) was compared to the theoretical one (b_{theo}). Both the theoretical and empirical b values were used to test their performance in predicting M for a given D for the compiled studies (Table 1). For this procedure an estimate for the parameter a is also needed. The coefficient a was calculated—following an approach similar to Chave et al. (2001)—using the formula $a = M/D^b$ with the two values of b, for all the M–D pairs reported in each study summarised in Table 1. The two average values for a_{theo} and a_{emp} (corresponding to the theoretical and empirical value of b) were computed for each dataset and subsequently applied in Eq. (1) in order to predict M from D. In practice, the implementation of this approach is primarily restricted by the fact that several trees spanning the entire D range of the stand under investigation have to be destructively sampled. Thus, the feasibility of an alternative approach (i.e. estimating a_{theo} and a_{emp} from M–D measurements made only on small trees and corresponding b values), was tested.

2.2.4. *Small trees sampling scheme*

The small trees sampling scheme (SSS) was developed to simplify allometric analyses irrespective of tree species and forest site. It is widely known that the standard deviation of tree biomass is linearly related to the mean biomass of the particular D class.

Accordingly, the standard error of the M per tree is smaller in lower D classes compared with the standard error of M at upper range of D, implying that the variability around the regressed line increases in proportion to mean size. Moreover, Chave et al. (2001) supported that the biomass values of the smallest trees strongly affected the values of the coefficients in the allometric relation between M and D. Motivated by these observations, we investigated the potential to develop biomass equations based on sample trees of small size, since destructive sampling of several trees spanning the entire D range of a stand under investigation is extremely time consuming.

The rational for this approach is that additional constraints to derive a valid estimate of the 'true' allometric equation may be obtained by making use of the published information related to the 223 compiled biomass equations. We classified the 223 compiled equations into three groups according to the class that each species belonged to, namely conifer, broadleaved, and tropical species. A further classification took place based on the D interval over which these equations hold. Such an approach was considered to be useful since the calibration of the scaling parameters in Eq. (2) is based on the average value of $\ln D$ and $\ln M$, implying that the range of the independent variable D in Eq. (1) affects the shape of the regressed line. Compiled equations whose lower and upper endpoints of the D interval differed by less than 2 cm were classified into the same category. In total, 223 allometric relations were examined with this method.

The approach proposed here is based on the hypothesis that valid estimates for the scaling coefficients in Eq. (1) can be obtained from only two values of D and the corresponding M. Let (D_1, M_1) and (D_2, M_2) be the two pairs of the empirical values recorded in a given stand. Based on the 223 biomass equations, D_1 and D_2 can also be used to derive the values $\hat{M}_{J,1}$ and $\hat{M}_{J,2}$ with J ranging from 1 to 223. For each of the 223 equations, the difference between M_1 and $\hat{M}_{J,1}$ (as well as between M_2 and $\hat{M}_{J,2}$) can easily be computed. The equation with the smallest deviation between observed M and predicted $\hat{M}$ is selected. Thus, two equations (unless the same one is selected for both cases) are available from the two pairs of the empirical values. The selected equations may or may not be close to the 'true' regressed equation which could be developed by the least-square method if several M–D pairs covering the entire D interval were available. There are nine different logical combinations that can occur for the b values between the two selected equations and the 'true' regressed relation (summarised in Table 3).

Table 3
The nine different combinations for the b values between the two selected equations and the regression curve (developed from several trees)[a]

1. $b_1 = b_{\mathrm{reg}}$ and $b_2 = b_{\mathrm{reg}}$
2. $b_1 = b_{\mathrm{reg}}$ and $b_2 > b_{\mathrm{reg}}$
3. $b_1 = b_{\mathrm{reg}}$ and $b_2 < b_{\mathrm{reg}}$
4. $b_1 > b_{\mathrm{reg}}$ and $b_2 = b_{\mathrm{reg}}$
5. $b_1 > b_{\mathrm{reg}}$ and $b_2 > b_{\mathrm{reg}}$
6. $b_1 > b_{\mathrm{reg}}$ and $b_2 < b_{\mathrm{reg}}$
7. $b_1 < b_{\mathrm{reg}}$ and $b_2 = b_{\mathrm{reg}}$
8. $b_1 < b_{\mathrm{reg}}$ and $b_2 > b_{\mathrm{reg}}$
9. $b_1 < b_{\mathrm{reg}}$ and $b_2 < b_{\mathrm{reg}}$

[a] b_1 denotes the allometric exponent obtained from the compiled equation that predicts the closest value to M_1, for D_1. b_2 denotes the allometric exponent obtained from the compiled equation that predicts the closest value to M_2, for D_2. b_{reg} is the 'true' b value that would be obtained by least-square regression, if many sampled trees spanning the entire D range were available.

We speculated a priori that the simple mathematical averages of a and b obtained from the two selected equations can be used to correctly predict M for higher diameters.

The performance of each model was tested using the criterion of relative difference between the actual and the corresponding predicted values of biomass (RD) for a specific diameter. It was calculated as

$$\mathrm{RD} = \frac{|M - \hat{M}|}{M} \qquad (6)$$

where M and $\hat{M}$ denote the real and the predicted biomass for a particular diameter, respectively. In addition, the following statistical test, reported in Zar (1996), was computed to compare predicted values from different models: $t = (\hat{M}_{\mathrm{reg}} - \hat{M}_{\mathrm{SSS}})/S_{\hat{M}_{\mathrm{reg}} - \hat{M}_{\mathrm{SSS}}}$, where $\hat{M}_{\mathrm{reg}}$ and $\hat{M}_{\mathrm{SSS}}$ stand for the biomass values predicted by the regression and SSS equation, respectively. For the calculation of $S_{\hat{M}_{\mathrm{reg}} - \hat{M}_{\mathrm{SSS}}}$ see Zar (1996, p. 368).

The obtained equations for each study were also plotted and a visual analysis performed for evidence of systematic under—or over—estimation across 10 different datasets.

3. Results

3.1. Predictions based on the 'reductionist' model

To calibrate Eq. (5), data on scaling coefficients from 23 case studies (given in Tables 1 and 2) were analysed and the following relationship has been obtained (Fig. 1):

$$b = 1.9262 + 0.6972b^* \quad (R^2 = 0.4197, P < 0.001) \tag{7}$$

Interestingly, a significant negative relationship between a and b was obtained from the metadata set of 277 compiled equations:

$$a = 7.0281b^{-4.7558} \quad (R^2 = 0.6984) \tag{8}$$

when M is expressed in kg and D in cm (Fig. 2).

The empirical parameters in Eq. (7) were employed for each b^* reported in 10 studies (Table 1), and corresponding estimates for the allometric exponent b were derived; subsequently these values were applied to Eq. (8) and the coefficient a was obtained for each study. The summarised results for M estimation and the RD criterion for the 'reductionist' model, were calculated for each study. The RD values in 8 out of 10 studies was below 30%. In studies 5 and 7 (Table 1) the RD was ca. 48 and 41%, respectively. A preliminary analysis failed to identify any relation between magnitude of RD and other specific characteristics for each study (family of species, number of sampled trees, D range). Unfortunately, the 10 datasets reviewed do not provide essential information to develop testable hypotheses for disentangling the

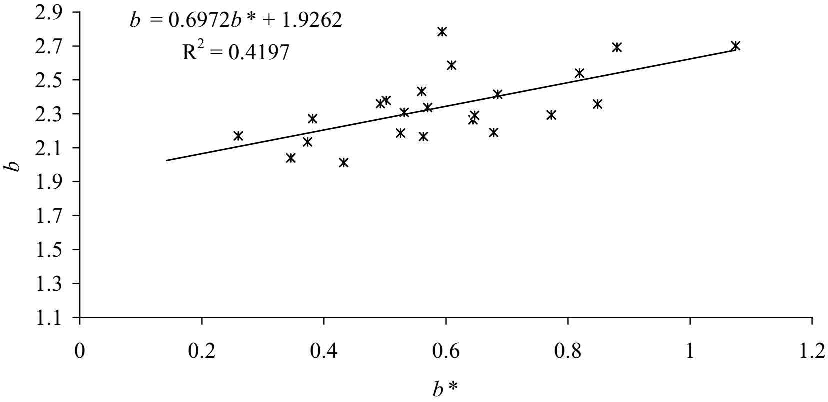

Fig. 1. Calibration of Eq. (5) based on 23 studies (see Tables 1 and 2).

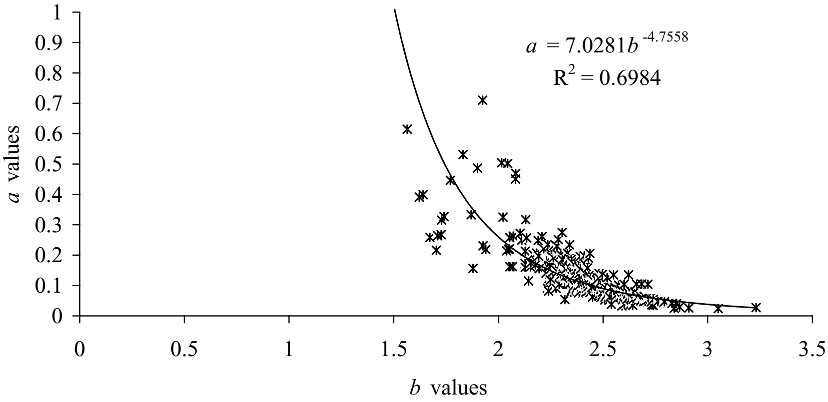

Fig. 2. Relation of a and b values reported in 277 compiled studies (see Appendix A). M is measured in kg and D in cm. The regression line is also depicted.

observed variability of RD and further analysis did not take place. However, despite the high degree of uncertainty reported in two studies, the application of this approach may provide acceptable predictions for aboveground biomass estimates if more information on the factors affecting the parameters in the b–b^* and a–b relationships was available. The summation of the empirical parametric values in Eq. (7) equals 2.6234 and this outcome supports that $2 < d + h < 3$ (see Section 2.2.2). Had we had more datasets available for analysis, a deeper insight in the interpretation of the coefficients in Eq. (5) might be possible. We speculate that further research, based on empirical data, would be important to test the usefulness of this 'reductionist' approach for aboveground biomass estimation.

3.2. Predictions based on theoretical and empirical allometric coefficients

The average b value calculated from the 279 compiled studies was statistically different from the theoretical one (2.67) and equals 2.3679 (Table 4).

About 69% of the recorded b values fall within the range 2.18–2.54, and about 13% from 2.68 to 2.80 (Fig. 3).

The reduced major axis technique was also applied to the collected b. However, the calculated average for the distribution of 279 studies was still significant lower than 2.67 (Zianis and Mencuccini, unpublished data). In each study, several M–D pairs were used to obtain an average theoretical value of a, a_{theo}, when $b_{\text{theo}} = 2.67$ (theoretical model) and an average empirical value of a, a_{emp}, when $b_{\text{emp}} = 2.36$ (empirical model). The RD estimates indicated that the empirical models gave better predictions than the theoretical in all studies but one (study 2, Table 1). This pattern of deviation is expected, since the b estimate obtained by the regression method (b_{reg}) is 2.785, which is closer to b_{theo} than to b_{emp}. In study 5, $b_{\text{reg}} < b_{\text{emp}} < b_{\text{theo}}$ and a similar trend of RD for the three models was observed, $\text{RD}_{\text{reg}} < \text{RD}_{\text{emp}} < \text{RD}_{\text{theo}}$ (RD_{emp} and RD_{theo} denote the average RD value for the empirical and theoretical equation, respectively, and RD_{reg} stands for the RD computed from the regression model). The dependency of RD_{emp} (and RD_{theo}) on the deviation between b_{reg} and b_{emp} (or b_{reg} and b_{theo}) leads to the conclusion that M predictions

Table 4
Statistics for the b values reported in 279 allometric equations (see also Fig. 3)

Mean	2.3679
Standard error of mean	0.0163
Standard deviation	0.27
Variance	4.71
Skewness	−1.016
Standard error of skewness	0.146
Kurtosis	2.774
Standard error of kurtosis	0.291

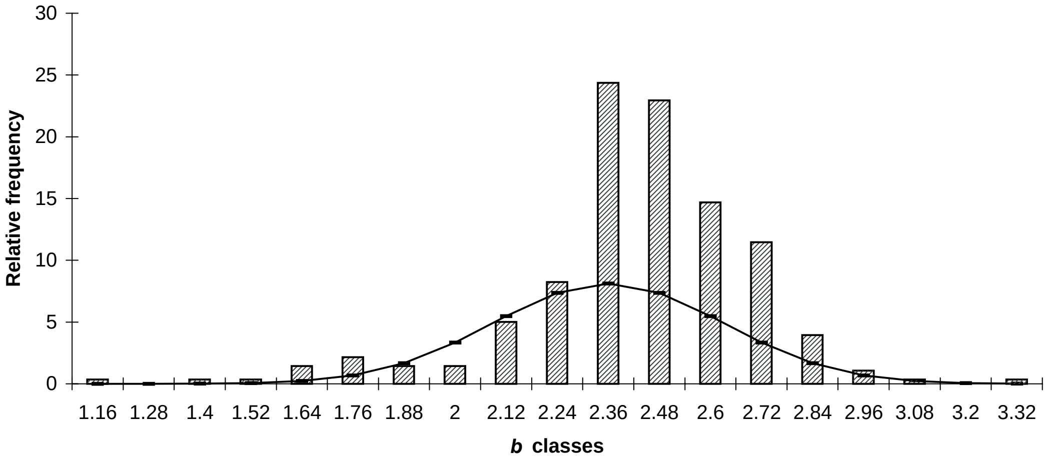

Fig. 3. Relative frequency distribution of b values superimposed on the normal curve.

made either by the theoretical or the empirical model are largely affected by the size–shape relationship (viz. b_{reg}) of the trees whose biomass is to be estimated.

Finally, the performance of the theoretical and empirical models, based on M–D pairs recorded for small trees only, was also tested. The same pairs that were used for the calibration of SSS equation (see next section), were employed in Eq. (1) with b_{theo} and b_{emp}, and an average value for a_{theo} and a_{emp} was computed for each study. The comparison between empirical and theoretical predictions, indicated that the empirical models more accurately predicted M. Applying the empirical estimated values to the entire stand, the larger deviation of predicted biomass estimates is about 30% of true biomass (studies 2 and 10, Table 1) in comparison to 128% (study 3, Table 1), obtained from the theoretical model. In conclusion, moderately accurate predictions for the biomass of the stand can be made if one estimates the parameter a in Eq. (1) from M–D pairs measured on small trees and uses $b = 2.3679$.

3.3. Application of SSS

The main practical application of SSS is apparent: to have the allometric relationship for the entire D range one has to sample only small trees. All other predictions are based on these data. To illustrate the SSS approach, Woods et al. (1991) dataset on Black spruce was used. The method includes the following steps:

1. Identify the D range of the given dataset, namely $2.9 < D < 23$ cm. Thus, all the equations developed for conifer species with a lower endpoint of the D interval between 0 and 3 cm (and with upper endpoint of D interval between 21 and 25 cm) are selected for the next step. In this example, 6 equations out of 67 (compiled in the meta-database) were selected.
2. Choose the two smallest trees, namely $D_1 = 2.9$ cm, with $M_1 = 0.95$ kg and $D_2 = 4.1$ cm, with $M_2 = 3.54$ kg. Calculate the predicted $\hat{M}_{J,1}$ and $\hat{M}_{J,2}$ values for the two diameters D_1 and D_2 based on the selected six relations and find the equation that corresponds to the smallest difference between the real and the predicted biomass values for each diameter.
3. Calculate the average value of a and b parameters obtained from the two equations and apply the computed averages in Eq. (1) to estimate M for the entire D range.

Biomass predictions calculated with the SSS method (hereafter called SSS equation) were compared with raw data (reported in Woods et al. (1991)) and the corresponding regressed values. A power function has also been fitted to the two pairs of M–D data. The regression and the power functions were fitted with the least-square technique using 31 and 2 pairs of M–D values, respectively. No bias correction factor was introduced (see Section 2.2.1). The SSS equation was based on two points of M–D values (the same as the power function) following steps 1–3.

The average RD was quite similar for the regressed and SSS values (13 and 14%, respectively), indicating that if both functions were applied to the entire stand, the same degree of standard error due to the prediction equations would be obtained. As expected, the power function based on two pairs does not provide acceptable predictions. Two other pairs of M–D were used to test the applicability of SSS method. If $D_1 = 2.9$ cm with $M_1 = 0.95$ kg and $D_2 = 4.1$ cm with $M_1 = 5.25$ kg the modelled average value of RD is about 14% for the SSS equation, indicating that biomass variability of small trees (compare with M–D values in step 2) may not largely affect the results obtained by this method. It is expected that a reasonable number of sampled trees (not less than three) for each diameter would give better results. Mean values of M–D variables were available for the 4 and 5 cm diameter classes, based on four and three sampled trees, respectively. These values were implemented in SSS and an average RD of 16% (close to 13% obtained with the regression method based on 31 trees) was computed.

The SSS method was also applied to the 10 studies presented in Table 1, based on two M–D pairs with minimum difference in D. The potential of using the biomass of the two smallest trees in each study was tested and the results are presented in Table 5.

The average RD values for the regression, the SSS method and the power function in each dataset are reported; the diameters of the smallest two trees D_1, D_2 used in the SSS equation and for calibrating the power function are depicted in the last two columns.

Table 5

Summary of the average RD values for three different models (RD_{reg} for the regression, RD_{SSS} for the SSS model and RD_P for the power function) computed for 10 studies; the diameters of the smallest trees used in calibrating the SSS model and the power function are reported in the last two columns[a]

No.	Region	RD_{reg}	RD_{SSS}	RD_P	D_1 (cm)	D_2 (cm)
1	USA	0.1339	0.1452	2.6530	2.9	4.1
2	USA	0.0862	0.0905	0.1468	5.8	8.5
3	USA	0.1533	0.1838	0.7650	0.9	1.2
4	UK	0.0947	0.0928	0.0891	6.3	9.8
5	Spain	0.1303	0.2104	0.6116	17.5	19.1
6	Spain	0.0552	0.0784	1.2456	16.2	17.6
7	USA	0.1091	0.182	0.4812	7.1	8.9
8	Italy	0.0993	0.1096	1.5823	8.77	8.8
9	Czech Republic	0.0734	0.0743	0.2829	13.4	17.2
10	Indonesia	0.2865	0.3159	0.3474	7.8	9.8

[a] Study number as in Table 1.

It should be noted that in the fifth and sixth datasets the two trees with the smallest D differ by 15 and 4 cm, respectively; the use of trees that differ less than 2 cm in D seemed to improve the predictions (data not shown). In the 10th study, the raw data were collected from various tropical species with different wood anatomy and crown architecture and it is speculated that tree-to-tree biomass variability would be large for a given D. Thus, two D classes were used for the smallest five trees spanning from 7.6 to 9.9 cm; the SSS method was applied to the average D and M values per diameter class and quite reliable biomass estimates are obtained for the entire D interval as indicated by the comparison of the RD between the regressed and SSS equations presented in Table 5.

To resume: based on sampling trees that belong to neighbouring diameter classes (differences less than 3 cm), and following steps 1–3, one can obtain the allometric coefficients for Eq. (1). Applying this equation to the entire D range of the stand under investigation, quite reliable M predictions are computed. The larger is the size of the sacrificed trees, the more are the individuals to be harvested per each D. Small trees yield compatible accurate biomass predictions for the entire D range, but it should be noted that trees with $D < 1$ cm may provide unreliable estimates as adequate information does not exist in the dataset of the compiled equations for these D classes. Finally, the D range of the trees whose M is to be estimated with the SSS is the most important criterion in selecting the appropriate compiled equations, i.e. equations developed for a similar diameter range.

4. Conclusions and discussion

In this study the following three simplifying methods for estimating aboveground forest biomass were investigated:

(i) The development of a 'reductionist' model based on theoretical insights provided by fractal geometry and on empirical estimates from H–D allometry. Two straightforward equations were calibrated from the compiled studies and applied to 10 datasets to demonstrate the overall performance of this model. The results indicated that the scaling exponents in tree size–shape relationships could provide only rough estimations of M values for tree stands. It is speculated however, that this approach may result in adequate predictions if additional variables were available for the calibration of Eq. (5); appropriate datasets were not available to us to robustly test this hypothesis. The basic assumption made in this model is that the fractal dimension of different tree species has a value between 2 and 3. Since data on the fractal geometry of trees are not yet recorded in forest inventory databank (not are likely to ever be), the calibration of Eq. (5) was based on datasets collected from different species and biomes, missing valuable information for a given species growing at a specific site. Finally, another factor that could account for the large deviations between modelled and raw M values (observed in studies 5 and 7, Table 1) is the average value of wood density, which is supposed to have small variability in a given stand; if this postulation does not hold true, then Eq. (5) should be modified. Niklas (1994, p.165:172), based on first-order biomechanical principles, reported that the allometry between D and M changes during tree ontogeny, implying that different scaling relations should be obtained for trees differing in size (or age). This observation may result from the fact that trees of the same species growing in similar environment, but differing in size, may possess different fractal dimensions. Thus, it is supported that the potentiality of fractal geometry has not been fully investigated and further research is necessary to reveal its value in forest biomass studies.

(ii) The comparison between predicted and observed M values when theoretical ($b = 2.67$) and empirical ($b = 2.3679$) scaling exponents are applied in Eq. (1). The values given from the RD criterion implied that, in general, empirical models provide better biomass predictions than the theoretical West et al. (1999) model. Future studies using several species growing at several sites may bring about a better understanding of the factors influencing the magnitude of the deviation between predicted and observed biomass values. The theoretical model of West et al. (1999) performed with reasonable levels of accuracy (except in study 5, Table 1), but its applicability is questioned, since a large number of sampled trees are needed for its calibration. The main disadvantage in accepting a universal value of b—either it be 2.3679 or 2.67—results from the fact that no flexibility is allowed for different datasets, implying that the ratio of the specific growth rates of M and D ($(1/M)\,\mathrm{d}M/\mathrm{d}t$ and $(1/D)\,\mathrm{d}D/\mathrm{d}t$) for different tree species growing in totally diverse environments should remain constant, contrary to our understanding of ecophysiological and ecological processes. Therefore, the acceptance of a constant value of b should be viewed as tentative, and applicable only for rough predictions of M. If more accurate estimates of aboveground forest biomass are needed, the SSS method seems a better—meaning less effort and compatible predictions—approach.

(iii) The development of the SSS approach, in which the allometric relationship between M and D for the entire D range can be obtained from destructively sampling of small trees and from information provided in published equations. Raw data of D and corresponding M from 10 studies were used to test the applicability of the SSS approach. Results presented in Table 5 indicate that the SSS equation provides a good balance between acceptable biomass predictions and low data requirements. It is based on destructively sampling small trees whose D values differ by no more than 3 cm. If larger trees are used, then the number of sampled individuals per D class should increase to account for increased variability in M at larger tree sizes. A procedure for the estimation of the standard error in SSS is not currently available, but it is obvious (Table 5) that is likely to be close to the standard error obtained from the standard regression equation and should fall within acceptable intervals. Moreover, the accumulated error in predicting M from D tends to be lower for sites with a large number of trees (see Woods et al., 1991), implying that the implementation of the SSS allometric equation at the stand level may result in quite accurate predictions for aboveground biomass. Since no criterion was used in order to validate the SSS method, i.e. the raw data obtained from the 10 studies (Table 1) were randomly chosen—its broad applicability should be warranted. If this hold true, then the SSS scheme may apply to other tree variables (i.e. stem biomass, branch biomass, leaf biomass, etc.) or to other life forms.

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Appendix A

Summary of the 279 allometric equations found in literature; 225 were used for the development of the SSS method.

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
1	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer rubrum*	0.1262	2.3804	3–66
2	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.1789	2.334	10–52
3	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.2582	1.6728	0–10
4	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.197	2.1933	0–35
5	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.1394	2.3405	1–31
6	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.1317	2.3199	1–30
7	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.1651	2.2394	8–26
8	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.1618	2.3095	4–35
9	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.091	2.508	5–50
10	Ter-Mikaelian and Korzukhin (1997)	USA	*A. rubrum*	0.0755	2.5623	5–40
11	Martin et al. (1998)	USA	*A. rubrum*	0.087	2.574	6.3–52.4
12	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer saccharum*	0.1791	2.3329	3–66
13	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.1599	2.3376	1–41
14	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.1641	2.4209	1–50
15	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.2064	2.33	2–40
16	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.1252	2.48	2–40
17	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.1532	2.3924	1–34
18	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.1676	2.3646	4–34
19	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.1008	2.5735	5–50
20	Ter-Mikaelian and Korzukhin (1997)	USA	*A. saccharum*	0.1259	2.52	8–24
21	Ter-Mikaelian and Korzukhin (1997)	USA	*Acer spicatum*	0.204	2.2524	1–20
22	Martin et al. (1998)	USA	All species	0.0566	2.663	3.8–63
23	Johansson (1999)	Sweden	*Alnus glutinosa*	0.3251	2.022	0–40
24	Johansson (1999)	Sweden	*Alnus incana*	0.1086	2.337	0–36
25	Ter-Mikaelian and Korzukhin (1997)	USA	*Alnus rugosa*	0.2612	2.2087	3–9
26	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula alleghaniensis*	0.1588	2.3376	3–66
27	Ter-Mikaelian and Korzukhin (1997)	USA	*B. alleghaniensis*	0.1541	2.3666	1–27
28	Ter-Mikaelian and Korzukhin (1997)	USA	*B. alleghaniensis*	0.1684	2.415	1–55
29	Ter-Mikaelian and Korzukhin (1997)	USA	*B. alleghaniensis*	0.1188	2.451	3–29
30	Ter-Mikaelian and Korzukhin (1997)	USA	*B. alleghaniensis*	0.0872	2.587	5–21
31	Ter-Mikaelian and Korzukhin (1997)	USA	*B. alleghaniensis*	0.154	2.3753	5–50
32	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula lenta*	0.0629	2.6606	5–50
33	Martin et al. (1998)	USA	*B. lenta*	0.0564	2.726	7.8–39.6
34	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula papyrifera*	0.0882	2.562	0–30
35	Ter-Mikaelian and Korzukhin (1997)	USA	*B. papyrifera*	0.0612	2.6634	3–51
36	Ter-Mikaelian and Korzukhin (1997)	USA	*B. papyrifera*	0.0775	2.48	2–8
37	Ter-Mikaelian and Korzukhin (1997)	USA	*B. papyrifera*	0.3154	1.7284	0–15
38	Ter-Mikaelian and Korzukhin (1997)	USA	*B. papyrifera*	0.1545	2.3064	0–33
39	Ter-Mikaelian and Korzukhin (1997)	USA	*B. papyrifera*	0.1347	2.3634	1–34
40	Ter-Mikaelian and Korzukhin (1997)	USA	*B. papyrifera*	0.1074	2.4313	3–33
41	Ter-Mikaelian and Korzukhin (1997)	USA	*B. papyrifera*	0.1182	2.4287	5–32

Appendix A. (*Continued*)

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
42	Wang et al. (2000)	USA	*B. papyrifera*	0.1567	1.879	0.1–13
43	Ter-Mikaelian and Korzukhin (1997)	USA	*Betula populifolia*	0.1564	2.3146	3–24
44	Ter-Mikaelian and Korzukhin (1997)	USA	*B. populifolia*	0.1218	2.3123	1–23
45	Ter-Mikaelian and Korzukhin (1997)	USA	*Carya* spp.	0.0792	2.6349	5–50
46	Ter-Mikaelian and Korzukhin (1997)	USA	*Carya* spp.	0.0763	2.6209	5–40
47	Martin et al. (1998)	USA	*Carya* spp.	0.0472	2.762	8.2–52.3
48	Leonardi et al. (1996)	France	*Castanea sativa*	0.118	2.336	3–23.8
49	Leonardi et al. (1996)	Italy	*C. sativa*	0.137	2.247	1–36.1
50	Leonardi et al. (1996)	Spain	*C. sativa*	0.066	2.628	2–16.9
51	Martin et al. (1998)	USA	*Cornus florida*	0.0458	2.73	3.8–10.2
52	Ter-Mikaelian and Korzukhin (1997)	USA	*Fagus grandifolia*	0.2013	2.2988	3–66
53	Ter-Mikaelian and Korzukhin (1997)	USA	*F. grandifolia*	0.1958	2.2538	2–29
54	Ter-Mikaelian and Korzukhin (1997)	USA	*F. grandifolia*	0.1957	2.3916	1–60
55	Ter-Mikaelian and Korzukhin (1997)	USA	*F. grandifolia*	0.0842	2.5715	5–50
56	Ter-Mikaelian and Korzukhin (1997)	USA	*Fraxinus americana*	0.1535	2.3213	1–28
57	Ter-Mikaelian and Korzukhin (1997)	USA	*F. americana*	0.1634	2.348	4–32
58	Ter-Mikaelian and Korzukhin (1997)	USA	*F. americana*	0.1063	2.4798	5–50
59	Ter-Mikaelian and Korzukhin (1997)	USA	*Fraxinus nigra*	0.1634	2.348	4–32
60	Ter-Mikaelian and Korzukhin (1997)	USA	*Liriodendron tulipifera*	0.0365	2.7324	5–50
61	Ter-Mikaelian and Korzukhin (1997)	USA	*L. tulipifera*	0.0687	2.5153	5–40
62	Martin et al. (1998)	USA	*L. tulipifera*	0.0580	2.635	10.2–55.8
63	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus grandidentata*	0.0983	2.3773	1–34
64	Ter-Mikaelian and Korzukhin (1997)	USA	*P. grandidentata*	0.0785	2.4981	3–45
65	Ter-Mikaelian and Korzukhin (1997)	USA	*Populus tremuloides*	0.1008	2.4341	1–30
66	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.079	2.3865	1–32
67	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.0911	2.2759	1–26
68	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.0774	2.3466	5–33
69	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.0637	2.6087	3–51
70	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.1625	2.0673	0–15
71	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.1049	2.391	0–36
72	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.0928	2.4085	1–27
73	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.0726	2.4827	2–33
74	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.0527	2.5084	3–50
75	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.1231	2.242	3–36
76	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.2065	2.249	15–40
77	Ter-Mikaelian and Korzukhin (1997)	USA	*P. tremuloides*	0.1122	2.35	1–32
78	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus pensylvanica*	0.1556	2.1948	3–24
79	Ter-Mikaelian and Korzukhin (1997)	USA	*P. pensylvanica*	0.2159	1.7041	0–10
80	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus serotina*	0.0716	2.6174	5–50
81	Ter-Mikaelian and Korzukhin (1997)	USA	*P. serotina*	0.1225	2.4253	5–40
82	Ter-Mikaelian and Korzukhin (1997)	USA	*Prunus virginiana*	0.2643	1.7102	3–15
83	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus alba*	0.2022	2.1666	0–18
84	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. alba*	0.0293	2.8661	8–26

Appendix A. (*Continued*)

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
85	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. alba*	0.0579	2.6887	5–50
86	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. alba*	0.0472	2.701	5–40
87	Martin et al. (1998)	USA	*Q. alba*	0.0542	2.613	7–63.01
88	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus coccinea*	0.2482	2.19	0–23
89	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. coccinea*	0.0536	2.7147	8–28
90	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. coccinea*	0.1241	2.4395	5–40
91	Martin et al. (1998)	USA	*Q. coccinea*	0.0521	2.685	15–43.3
93	Canadell et al. (1988)	Spain	*Quercus ilex*	0.4864	1.9	5.3–19.8
94	Canadell et al. (1988)	Spain	*Q. ilex*	0.1399	2.413	5.3–24.4
95	Canadell et al. (1988)	Spain	*Q. ilex*	0.2208	2.217	5.3–24.4
96	Canadell et al. (1988)	Spain	*Q. ilex*	0.5308	1.831	5.3–30
97	Canadell et al. (1988)	Spain	*Q. ilex*	0.1253	2.433	6.6–24.4
92	Susmel et al. (1976) (cited in Canadell et al., 1988)	Italy	*Q. ilex*	0.2302	2.28	20–90
98	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus macrocarpa*	0.1447	2.282	6–25
99	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus prinus*	0.0554	2.7276	5–50
100	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. prinus*	0.0907	2.5344	5–40
101	Martin et al. (1998)	USA	*Q. prinus*	0.0258	2.91	10.6–57.5
102	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus rubra*	0.1335	2.422	5–34
103	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. rubra*	0.113	2.4572	5–50
104	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. rubra*	0.0643	2.6598	5–40
105	Martin et al. (1998)	USA	*Q. rubra* L.	0.0550	2.644	19.7–52
106	Ter-Mikaelian and Korzukhin (1997)	USA	*Quercus velutina*	0.0904	2.5143	7–27
107	Ter-Mikaelian and Korzukhin (1997)	USA	*Q. velutina*	0.0945	2.503	5–40
108	Ter-Mikaelian and Korzukhin (1997)	USA	Salicaceae	0.1619	2.0552	3–24
109	Ter-Mikaelian and Korzukhin (1997)	USA	Salicaceae	0.0616	2.5094	4–20
110	Ter-Mikaelian and Korzukhin (1997)	USA	*Ulmus americana*	0.0825	2.468	4–29
111	Ter-Mikaelian and Korzukhin (1997)	USA	*Abies amabilis*	0.0627	2.4921	31–90
112	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.0877	2.4017	3–51
113	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.0523	2.53	3–25
114	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.3908	1.6217	0–20
115	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.1746	2.1555	0–36
116	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.1075	2.3263	3–28
117	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.1598	2.1283	2–32
118	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.2575	2.0543	3–40
119	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.069	2.4975	3–40
120	Ter-Mikaelian and Korzukhin (1997)	USA	*A. balsamea*	0.0705	2.497	4–34
121	Wang et al. (2000)	USA	*Abies lasiocarpa*	0.0817	2.24	1–8.2
122	Ter-Mikaelian and Korzukhin (1997)	USA	*Chamaecyparis nootkatensis*	0.2498	2.1118	18–60
123	Ter-Mikaelian and Korzukhin (1997)	USA	*Larix laricina*	0.1265	2.2453	3–51
124	Ter-Mikaelian and Korzukhin (1997)	USA	*L. laricina*	0.1359	2.298	7–30
125	Ter-Mikaelian and Korzukhin (1997)	USA	*L. laricina*	0.0946	2.3572	2–31

Appendix A. (*Continued*)

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
126	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea abies*	0.2722	2.104	12–44
127	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea glauca*	0.0777	2.472	1–33
128	Ter-Mikaelian and Korzukhin (1997)	USA	*P. glauca*	0.0635	2.48	3–25
129	Ter-Mikaelian and Korzukhin (1997)	USA	*P. glauca*	0.1077	2.3308	0–39
130	Ter-Mikaelian and Korzukhin (1997)	USA	*P. glauca*	0.1601	2.2413	2–30
131	Ter-Mikaelian and Korzukhin (1997)	USA	*P. glauca*	0.1037	2.2907	2–32
132	Ter-Mikaelian and Korzukhin (1997)	USA	*P. glauca*	0.1643	2.248	2–25
133	Barney et al. (1978)	USA	*Picea mariana*	0.0331	2.59	1.4–8.5
134	Barney et al. (1978)	USA	*P. mariana*	0.0377	2.54	1.4–12.9
135	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	0.153	2.248	1–23
136	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	0.1444	2.2604	0–37
137	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	0.2626	2.0707	2–30
138	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	0.1683	2.1777	2–34
139	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	0.0963	2.4289	3–32
140	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	1.3836	1.544	2–15
141	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	0.0339	2.626	2–15
142	Ter-Mikaelian and Korzukhin (1997)	USA	*P. mariana*	0.1137	2.316	2–25
143	Ter-Mikaelian and Korzukhin (1997)	USA	*Picea rubens*	0.6149	1.5639	0–20
144	Ter-Mikaelian and Korzukhin (1997)	USA	*P. rubens*	0.1444	2.2604	0–37
145	Ter-Mikaelian and Korzukhin (1997)	USA	*P. rubens*	0.2066	2.183	1–35
146	Ter-Mikaelian and Korzukhin (1997)	USA	*P. rubens*	0.166	2.2417	1–31
147	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus banksiana*	0.2131	2.1283	0–38
148	Ter-Mikaelian and Korzukhin (1997)	USA	*P. banksiana*	0.2186	1.94	0–20
149	Ter-Mikaelian and Korzukhin (1997)	USA	*P. banksiana*	0.1093	2.3291	3–34
150	Ter-Mikaelian and Korzukhin (1997)	USA	*P. banksiana*	0.0919	2.4206	2–32
151	Ter-Mikaelian and Korzukhin (1997)	USA	*P. banksiana*	0.1747	2.2495	6–39
152	Zavitkovsi et al. (1981) (cited in Zavitkovsi et al., 1981)	USA	*P. banksiana*	0.1055	2.2738	4–19
153	Zavitkovsi et al. (1981)	USA	*P. banksiana*	0.1410	2.2278	4–18
154	Son et al. (2001)	Korea	*Pinus koraiensis*	0.1393	2.386	7–35.5
155	Forrest (1969) (cited in Keith et al., 2000)	Australia	*Pinus radiata*	0.2671	1.727	1.4–5.8
156	Forrest (1969)	Australia	*P. radiata*	0.0535	2.318	10.3–19.8
157	Forrest (1969)	Australia	*P. radiata*	0.0481	2.663	6.4–14.5
158	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus resinosa*	0.1003	2.3865	3–51
159	Ter-Mikaelian and Korzukhin (1997)	USA	*P. resinosa*	0.0847	2.3503	2–34
160	Ter-Mikaelian and Korzukhin (1997)	USA	*P. resinosa*	0.0778	2.4171	3–46
161	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus rigida*	0.104	2.3373	0–31
162	Ter-Mikaelian and Korzukhin (1997)	USA	*Pinus strobus*	0.0696	2.449	3–66
163	Ter-Mikaelian and Korzukhin (1997)	USA	*P. strobus*	0.1617	2.142	2–37
164	Ter-Mikaelian and Korzukhin (1997)	USA	*P. strobus*	0.6298	1.3475	0–15
165	Ter-Mikaelian and Korzukhin (1997)	USA	*P. strobus*	0.0755	2.3833	5–26
166	Ovington (1957)	UK	*Pinus sylvestris*	0.0398	2.64	0.5–22.7

Appendix A. (*Continued*)

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
167	Santa Regina et al. (1997)	Spain	*P. sylvestris*	0.2206	2.0519	2.5–36.5
168	vanLear et al. (1984)	USA	*Pinus taeda*	0.0695	2.5641	12.7–38.6
169	Bartelink (1996)	Netherlands	*Pseudotsuga menziesii*	0.1978	2.41	6.9–28.5
170	Ter-Mikaelian and Korzukhin (1997)	USA	*P. menziesii*	0.0808	2.5282	5–54
171	Ter-Mikaelian and Korzukhin (1997)	USA	*Thuja occidentalis*	0.2305	1.9269	3–51
172	Ter-Mikaelian and Korzukhin (1997)	USA	*T. occidentalis*	0.1148	2.1439	2–30
173	Ter-Mikaelian and Korzukhin (1997)	USA	*T. occidentalis*	0.091	2.234	4–31
174	Ter-Mikaelian and Korzukhin (1997)	USA	*Tilia americana*	0.0872	2.3539	4–47
175	Ter-Mikaelian and Korzukhin (1997)	USA	*T. americana*	0.0617	2.5328	5–50
176	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga canadensis*	0.0991	2.3617	3–51
177	Ter-Mikaelian and Korzukhin (1997)	USA	*T. canadensis*	0.1617	2.1536	2–34
178	Ter-Mikaelian and Korzukhin (1997)	USA	*T. canadensis*	0.0622	2.45	5–50
179	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga heterophylla*	0.257	2.1349	16–49
180	Ter-Mikaelian and Korzukhin (1997)	USA	*Tsuga mertensiana*	0.5038	2.0154	44–76
181	Clough and Scott (1989) (cited in Eamus et al., 2000)	Australia	*Bruguiera gymnorrhiza*	0.1858	2.3055	2.0–24
182	Clough and Scott (1989)	Australia	*Bruguiera parviflora*	0.1679	2.4167	2.0–21
183	Clough and Scott (1989)	Australia	*Ceriops targal* var. *australis*	0.1884	2.3379	2.0–18
184	Eamus et al. (2000)	Australia	*Erythrophloem chlorostachys*	0.0407	2.851	4.6–14.7
185	Eamus et al. (2000)	Australia	*Eucalyptus*	0.162	2.383	2.6–52.8
186	Eamus et al. (2000)	Australia	*Eucalyptus bleeseri*	0.1366	2.497	4.6–22.7
187	Ward and Pikersgill (1985) (cited in Eamus et al., 2000)	Australia	*Eucalyptus calophylla*	0.3985	1.64	2–11.5
188	Ward and Pikersgill (1985)	Australia	*E. calophylla*	0.2143	2.04	2–24.5
189	Eamus et al. (2000)	Australia	*Eucalyptus* combined	0.4506	2.082	3.15–60.34
190	Eamus et al. (2000)	Australia	*Eucalyptus* combined	0.1092	2.468	6.68–24.77
191	Grove and Malajczuk (1985)	Australia	*Eucalyptus diversicolor*	0.1179	2.47	2–40
192	Bennett et al. (1997) (cited in Keith et al., 2000)	Australia	*Eucalyptus globulus*	0.1466	2.3	7.5–22.8
193	Applegate (1982), Keith et al. (2000)	Australia	*Eucalyptus intermedia*	0.0394	2.6018	13.4–25.5
194	Ward and Pikersgill (1985)	Australia	*Eucalyptus maculata*	0.3328	1.87	2–11.5
195	Ward and Pikersgill (1985)	Australia	*E. maculata*	0.0812	2.47	2–24.5
196	Eamus et al. (2000)	Australia	*Eucalyptus miniata*	0.1581	2.426	2.6–50
197	Eamus et al. (2000)	Australia	*E. miniata*	0.2352	2.269	2.6–50

Appendix A. (*Continued*)

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
198	Eamus et al. (2000)	Australia	*E. miniata*	0.7103	1.925	2.6–50
199	Keith et al. (cited in Keith et al., 2000)	Australia	*Eucalyptus obliqua*	0.1287	2.353	25.4–78
200	Keith et al. (cited in Keith et al., 2000)	Australia	*E. obliqua*	0.0644	2.584	29.9–70.8
202	Keith et al. (cited in Keith et al., 2000)	Australia	*E. obliqua*	0.0350	2.642	21.1–55.3
203	Keith et al. (cited in Keith et al., 2000)	Australia	*E. obliqua*	0.2023	2.283	26.2–284
204	Snowdon et al. (2000)	Australia	*E. obliqua*	0.0929	2.445	19.95–186
205	Eamus et al. (2000)	Australia	*Eucalyptus papuana*	0.0437	2.79	11.7–44.2
201	Applegate (1982)	Australia	*Eucalyptus pilularis*	0.0464	2.6934	13.1–123.9
206	Applegate (1982)	Australia	*E. pilularis*	0.0491	2.6803	17.8–53.4
207	Eamus et al. (2000)	Australia	*Eucalyptus porrecta*	0.0811	2.512	7.5–24.9
208	Ward and Pikersgill (1985)	Australia	*Eucalyptus resinifera*	0.3262	1.74	2–11.5
209	Ward and Pikersgill (1985)	Australia	*E. resinifera*	0.0788	2.44	2–24.5
210	Eamus et al. (2000)	Australia	*Eucalyptus tetrodonta*	0.1774	2.351	2.7–52.10
211	Eamus et al. (2000)	Australia	*E. tetrodonta*	0.1861	2.348	2.7–52.8
212	Eamus et al. (2000)	Australia	*E. tetrodonta*	0.4686	2.083	2.7–52.9
213	Martin et al. (1998)	USA	*Oxydendrum arboreum*	0.0605	2.582	4.3–34.6
214	Eamus et al. (2000)	Australia	*Terminalia ferdinandiana*	0.1914	2.263	2.6–16.7
215	Eamus et al. (2000)	Australia	Tropical	0.0720	2.644	4–29.1
216	Eamus et al. (2000)	Australia	Tropical	0.1349	2.622	2.7–22.1
217	Nelson et al. (1999)	Brazil	Tropical	0.1357	2.4128	1.2–28.6
218	Nelson et al. (1999)	Brazil	Tropical	0.1627	2.37	1.2–26.8
219	Nelson et al. (1999)	Brazil	Tropical	0.0811	2.4257	5.1–38.2
220	Nelson et al. (1999)	Brazil	Tropical	0.0671	2.5996	2.3–25.3
221	Nelson et al. (1999)	Brazil	Tropical	0.1657	2.4206	1.5–12.2
222	Nelson et al. (1999)	Brazil	Tropical	0.1081	2.5105	1.6–24.8
223	Nelson et al. (1999)	Brazil	Tropical	0.0934	2.5392	1.6–21.8
224	Nelson et al. (1999)	Brazil	Tropical	0.1681	2.3651	1.5–28.6
225	Clough and Scott (1989)	Australia	*Xylocarpus granatum*	0.0823	2.5883	3.0–17
226	Kumar et al. (1998)	India	*Acacia auriculiformis*	0.2061	2.4369	n/a
227	Kumar et al. (1998)	India	*A. auriculiformis*	0.2746	2.3052	n/a
228	Morrison (1990)	USA	*A. saccharum*	0.5018	2.0444	n/a
229	Hughes (1971)	UK	*A. glutinosa*	0.0859	2.35371	n/a
230	Kumar et al. (1998)	India	*Artocarpus heterophyllus*	0.1792	2.2512	n/a
231	Kumar et al. (1998)	India	*Artocarpus hirsutus*	0.0464	2.7934	n/a
232	Snowdon et al. (2000)	Australia	Australian plantation	0.1059	2.3582	n/a
233	Westman and Rogers (1977) (cited in Eamus et al., 2000)	Australia	*Banksia aemula*	0.0528	2.5924	n/a

Appendix A. (*Continued*)

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
234	Hingston et al. (1981) (cited in Eamus et al., 2000)	Australia	*Banksia grandis*	0.1043	2.5	n/a
235	Glossop (1978) (cited in Grierson et al., 2000)	Australia	*B. grandis*	0.1152	2.4383	n/a
236	Morrison (1990)	USA	*B. alleghaniensis*	0.3168	2.1307	n/a
237	Hughes (1971)	UK	*Betula pendula*	0.2511	2.2865	n/a
238	Kumar et al. (1998)	India	*Casuarina equistifolia*	0.1040	2.7142	n/a
239	Hingston et al. (1981)	Australia	*E. calophylla*	0.0343	2.74	n/a
240	Glossop (1978)	Australia	*E. calophylla*	0.1458	1.1536	n/a
241	Grove and Malajczuk (1985)	Australia	*Eucalyptus diversicolour*	0.0535	2.74	n/a
242	O' Brien (1998) (cited in Keith et al., 2000)	Australia	*Eucalyptus grandis*	0.4458	1.771	n/a
243	O' Brien (1998)	Australia	*E. grandis*	0.1077	2.404	n/a
244	Barrett (1992) (cited in Grierson et al., 2000)	Australia	*E. maculata*	0.1905	2.43	n/a
245	Hingston et al. (1981)	Australia	*Eucalyptus marginata*	0.0252	2.84	n/a
246	Todd (2000) (cited in Grierson et al., 2000)	Australia	*E. marginata*	0.0241	3.0499	n/a
247	Todd (2000)	Australia	*E. marginata*	0.0271	3.2306	n/a
248	Todd (2000)	Australia	*E. marginata*	0.0872	2.4882	n/a
249	Glossop (1978)	Australia	*E. marginata*	0.0353	1.4219	n/a
250	Ward and Koch (1996)	Australia	*E. resinifera*	0.0934	2.4	n/a
251	Bartelink (1997)	Netherlands	*Fagus sylvatica*	0.0798	2.601	n/a
252	Santa Regina et al. (1997)	Spain	*F. sylvatica*	0.1326	2.4323	n/a
253	Grove (1988) (cited in Eamus et al., 2000)	Australia	Karri	0.1717	2.128	n/a
254	Kumar et al. (1998)	India	*Paraserianthes falcataria*	0.0538	2.6818	n/a
255	Snowdon et al. (2000)	Australia	Pine plantation	0.1179	2.2476	n/a
256	Ter-Mikaelian and Korzukhin (1997)	USA	*P. banksiana*	0.152	2.273	n/a
257	Green and Grigal (1978) (cited in Zavitkovsi et al., 1981)	USA	*P. banksiana*	n/a	2.38	n/a
258	Zavitkovsi and Dawson (1978)	USA	*P. banksiana*	n/a	2.19	n/a
259	Lieffers and Campbell (1984)	USA	*P. tremuloides*	0.1007	2.4343	n/a
260	Kumar et al. (1998)	India	*Pterocarpus marsupium*	0.0410	2.8286	n/a
261	Leonardi and Rapp (1982) (cited in Canadell et al., 1988)	Italy	*Q. ilex*	0.2187	2.0491	n/a
262	Ferres et al. (1980)	Spain	*Q. ilex*	0.2319	2.265	n/a
263	Snowdon et al. (2000)	Australia	Rainforest	0.1500	2.3698	n/a

Appendix A. (*Continued*)

No.	Author	Region	Species	*a*	*b*	*D* range (cm)
264	Barrett (1992)	Australia	Rainforest species	0.2344	2.34	n/a
265	Clough and Scott (1989)	Australia	*Rhyzophora apiculata*/*stylosa*	0.1049	2.6848	n/a
266	Snowdon et al. (2000)	Australia	Sclerophyll forest	0.1446	2.3501	n/a
267	Brown (1997) (cited in Chave et al., 2001)	Brazil	Tropical	0.0880	2.57	n/a
268	Higuchi et al. (1998) (cited in Chave et al., 2001)	Brazil	Tropical	0.1353	2.55	n/a
269	Araujo et al. (1999) (cited in Chave et al., 2001)	Brazil	Tropical	0.0780	2.65	n/a
270	Brown (1997)	Brazil	Tropical	0.1043	2.66	n/a
271	Brown (1997)	Cambodia	Tropical	0.0916	2.56	n/a
272	Overman et al. (1994) (cited in Chave et al., 2001)	Colombia	Tropical	0.1394	2.48	n/a
273	Brown (1997)	Costa Rica	Tropical	0.1636	2.32	n/a
274	Lescure et al. (1983) (cited in Chave et al., 2001)	Fr. Guiana	Tropical	0.0561	2.72	n/a
275	Brown (1997)	Indonesia	Tropical	0.1043	2.6	n/a
276	Ketterings et al. (2001)	Indonesia	Tropical	0.0661	2.591	n/a
277	Edwards and Grubb (1977) (cited in Chave et al., 2001)	New Guinea	Tropical	0.1353	2.36	n/a
278	Ovington (1957)	Puerto Rico	Tropical	0.0898	2.41	n/a
279	Snowdon et al. (2000)	Australia	Woodland trees	0.2350	2.2364	n/a

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