

Towards a functional and simplified allometry for estimating forest biomass

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Abstract

Aboveground tree biomass (M) can be estimated using a power function in the form of $M = aD^b$ where a and b are the scaling coefficient and scaling exponent, respectively, and D the tree breast-height diameter. Both a and b are reported to vary with species, site and age. However West et al. [West, G.B., Brown, J.H., Enquist, B.J., 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400, 664–667] suggested that M should scale against D with a universal exponent ($b = 8/3$), because the scaling exponent would depend on an optimal tree architecture. Moreover a should be related with the wood density (ρ) [Enquist, B.J., West, G.B., Charnov, E.L., Brown, J.H., 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401, 907–911].

We collected 49 datasets of different species (most from the literature) with individual data of diameter, mass and tree height. We analysed the height-diameter relationship and estimated b and a for each dataset, in order to test whether: (i) the scaling exponent may be considered universal or, conversely, dependent on species, tree stage or site and (ii) a was correlated with wood density. Analysis of the height diameter relationship for each species and site generally allowed a juvenile, an adult and a mature stage to be identified. b appeared to be related to tree stage but independent of species and site. The mean a value was also correlated with the wood density. We estimated tree biomass using different b exponents for each stage, deriving a from ρ . This approach was applied to a validation dataset and an average relative difference of 21.4% from the observed values was obtained.

This would suggest that total forest aboveground biomass can be estimated by using functional allometry (i.e., universal b parameters), potentially avoiding any destructive tree sampling.

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1. Introduction

Estimating tree and forest biomass is essential for assessing ecosystem yield and carbon stock in compliance with the Kyoto Protocol on greenhouse gas reduction (Brown, 2002; Körner, 2005).

Because measuring tree biomass in the field is extremely time consuming and potentially limited to a small tree sample size, empirical relationships have been used to estimate total biomass from predictive biometric variables such as breast-height diameter (D) or height (H) (Curtis, 1967; Loetsch and Haller, 1973; Wirth et al., 2004). Generally these empirical relationships are analytically represented as power functions because it has long been noted that a growing plant maintains

the proportions between different parts. This function assumes the following form (Niklas, 1994; Kaitaniemi, 2004):

$$M = aD^b \quad (1)$$

with M total aboveground dry tree biomass, D the diameter at breast-height and a and b is the scaling coefficient and scaling exponent, respectively.

Although it is generally known that the scaling exponent b is between 2 and 3 (Zianis and Mencuccini, 2004), it is also commonly believed that a species-specific equation (i.e., with different coefficients a and b) has to be used because trees may differ in architecture as well as wood density (Ketterings et al., 2001). Thus until now, allometry has essentially been based on empirical relationships (Zianis et al., 2005).

A completely different approach was proposed by West et al. (1999), who presented a general model, known as the WBE model, to estimate values of scaling exponents using a

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functional (i.e., process-based) relationship (Enquist et al., 1999; Enquist, 2002). The model proposes that evolution by natural selection has resulted in an optimal fractal-like vascular network. As a result of this general principle, organisms should exhibit a common set of quarter-power scaling relationships with body mass. According to the WBE model, the above-ground biomass of tree species should scale against stem diameter with $b = 8/3$, independently of species, site and age (West et al., 1999). The universal structure of the vascular network proposed at tree level by West et al. (1999) has recently been empirically demonstrated (Anfodillo et al., 2006).

The theoretical and practical consequences of the WBE approach have been hotly debated (Chambers et al., 2001; Van Noordwijk and Mulia, 2002; Makarieva et al., 2003; Bokma, 2004; Kozłowski and Konarzewski, 2004; Niklas, 2006a), but a recent study based on a world-wide list of 279 biomass allometric equations showed that the use of a universal value for the scaling exponent ($b \approx 2.67$) should provide a rough estimate of tree biomass (Zianis and Mencuccini, 2004). The authors proposed another empirical exponent ($b \approx 2.36$), but they also underlined that the use of a universal value of b (either 2.36 or 2.67) is not acceptable, implying that the ratio of M and D for trees growing in different environmental conditions cannot be constant. Nevertheless they noted that there is a general convergence of the scaling exponents despite the multitude of factors affecting tree growth in different sites.

Niklas (1995), based on first-order biomechanical principles, reported that the allometry between D and H may change during tree ontogeny, implying that different scaling relationships should be obtained for trees differing in size. Indeed, it is widely known that the rate of growth in tree height relative to the rate of growth in trunk diameter decreases with increasing tree size and age as a consequence of the decreasing absolute rate of growth in height (Niklas, 1995). Ketterings et al. (2001) hypothesized that the scaling exponent between M and D depends on the relationship between H and D . This theory, also proved mathematically by Zianis and Mencuccini (2004), suggested that the relation between M and D depends on the ontogenetic stage. The WBE model, as noted by Anfodillo et al. (2006), seems to be strictly applicable only to actively-growing plants (i.e., with elevated increment in height). On the contrary, it should not be applied to big trees because plant biomass cannot scale at the same rate in relation to diameter when the tree height does not increase significantly. This has to be carefully considered when using or testing allometric equations within an ontogenetic perspective.

The estimation of parameter a represents a further crucial aspect when applying the model and using the scaling equations in practice, which has been discussed very little in other studies (Chambers et al., 2001). According to the WBE model, the scaling coefficient could or could not be species and site dependent and is in general group-specific constant (Niklas et al., 2003). Indeed both Niklas (1994) and Zianis and Mencuccini (2004) speculated on the relationship between a and the average wood density; considering that more than 80% of total aboveground biomass is the stem biomass, a can be estimated as the product of total aboveground volume with wood density.

The main aims of our work were: (i) to analyse in detail the relationship between M and D in different ontogenetic stages in order to test if the functional approach of WBE is supported by empirical data; (ii) to test the performance of a functional-based approach to estimate the aboveground tree biomass; (iii) to suggest possible causes of variation of the parameter a .

2. Material and methods

A dataset with raw individual data of diameter, height and aboveground dry tree biomass of 1278 trees, belonging to 49 different datasets and regarding 26 broadleaved and 11 coniferous species, was gathered from the literature or directly by the authors (Appendix A).

For each original dataset the distribution of the height-diameter ratio (HDR) was first analysed. To identify the outliers or observations affected by possible measurement errors, individuals with a distance greater than 3 *interquartile* ranges from the median were excluded from the subsequent analyses (SAS Institute Inc., 1990). Tree height versus diameter was plotted in order to recognise different growth stages (Philip, 1994; Bond, 2000).

To describe the height-diameter growing function, the *Chapman–Richards* function was applied to each dataset (Richards, 1959; Fekedulegn et al., 1999):

$$H = 1.3 + n(1 - e^{-qD})^t \quad (2)$$

where n , q and t are the parameters to be estimated. Where this function failed to converge, we adopted the *Weibull* function (Peng, 2001):

$$H = 1.3 + g(1 - e^{-iD^m}) \quad (3)$$

Parameters were estimated using the Marquardt method (Motulsky and Ransnas, 1987). The goodness of fit of each height-diameter model was evaluated analysing (i) the coefficient of determination R^2 , (ii) the distribution of studentized residuals (scaled version of residuals that are obtained by dividing each residual by its standard error) and (iii) the curve fitting (Sit, 1994). To obtain the most homogeneous band of studentized residuals and to improve the curve fitting, a weighting factor was also introduced (Carroll and Ruppert, 1988; Huang and Titus, 1992):

$$W = \frac{1}{D^k} \quad (4)$$

with $k = 0.5$, 1 or 2, depending on the distribution of observations in different datasets.

The presence and correct position of the inflection point indicates a complete dataset where it was possible to distinguish a juvenile, adult and mature growth stage. The tree stages can easily be identified by plotting the relative height increment (i.e., dH/dD , indicated as RHI) against its first-order derivative, which represents the rate of variation of RHI (Fig. 1). In fact:

- I. The juvenile stage is placed before the RHI maximum, i.e., where there is an increasing rate of growth as indicated by the positive value of its partial derivative.

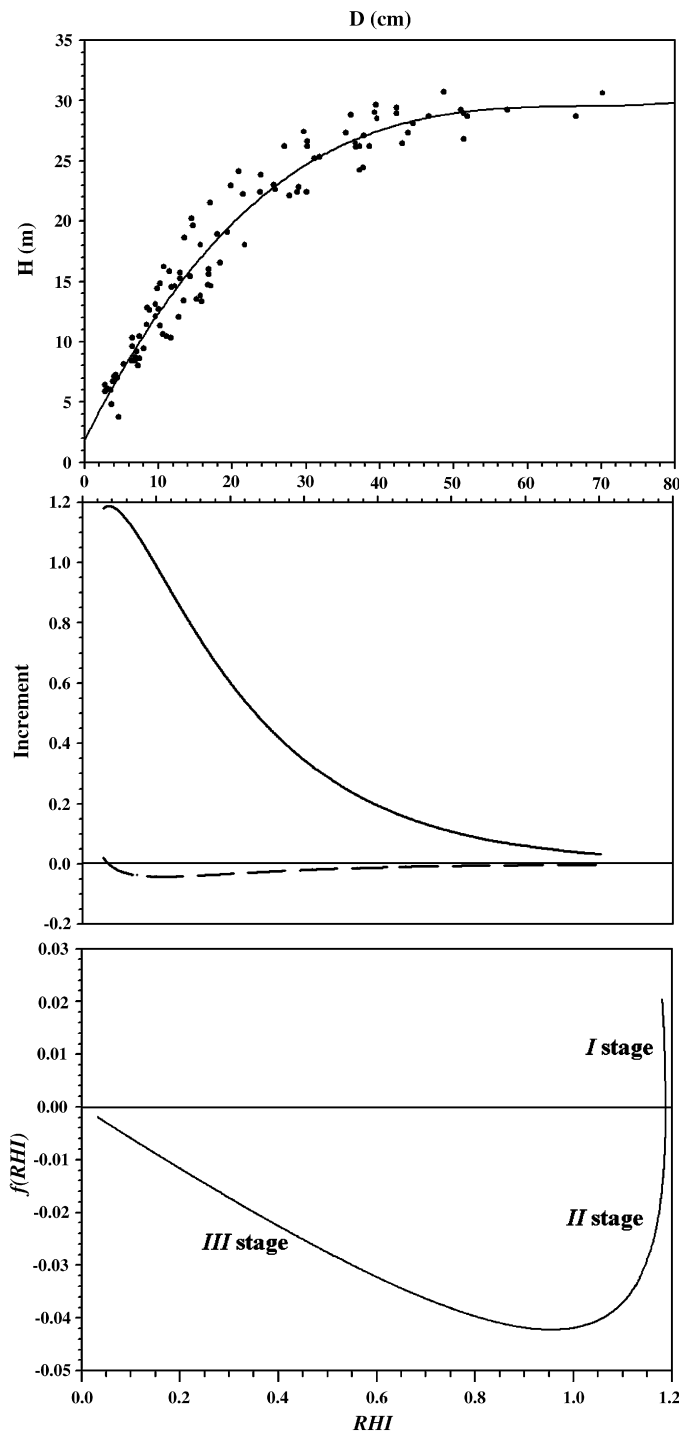


Fig. 1. An example of the height-diameter analysis for the dataset of Joosten et al. (2004) relative to 113 plants of *Fagus sylvatica*: (a) scatter plot and curve fitting of height (H) against diameter at breast-height (D); (b) plot of the first partial derivative of the function, that is the relative height increment (RHI) and the second partial derivative of the function (dashed line), that is the first partial derivative of the RHI ($f(RHI)$); (c) plot of the RHI against its first partial derivative, highlight the juvenile (I), adult (II) and mature (III) stage.

II. The adult stage, between the maximum and the point of inflection of the RHI, is characterized by a decreasing RHI and ends where the second partial derivative (negative) reaches its minimum.

III. In the mature stage both RHI and its partial derivative tend towards zero.

2.1. Analyses of parameters b and a

Because of *heteroscedasticity* of the data, Eq. (1) was logarithmically transformed into linear form, as:

$$\ln M = \ln a + b \ln D \tag{5}$$

Although this transformation introduces a systematic bias that is generally corrected with a correction factor estimated from the standard error (Finney, 1941; Yandle and Wiant, 1981; Sprugel, 1983), it has become conventional practice in allometric studies (Niklas, 2006b).

Once the three stages had been detected, the least-square regression technique was applied, stage by stage, to each dataset and $\ln(a)$ and b were estimated through Eq. (5). As proposed by Niklas (1994, 2006b), given that D is subject to natural variations and measurement errors and is therefore not an independent variable (Kaitaniemi, 2004), we used the *reduced major axis* model II regression (RMA) and estimated b_{RMA} as:

$$b_{RMA} = \frac{b_{LS}}{r_{yx}} \tag{6}$$

where b_{LS} is the value of b estimated by the least square model I regression and r_{yx} is the correlation coefficient determined from least square regression (Henry and Aarssen, 1999). We excluded any datasets where b_{RMA} was not significant.

Statistical differences between empirical b_{RMA} values of each stage were preliminarily tested comparing the 95% confidence intervals for b_{RMA} (Niklas, 1994).

In order to compare the mean b_{RMA} values of each stage, leaving out one observation at a time from each dataset (distinguished stage by stage), a series of *jackknife* samples was derived, equal to the original number of trees (Efron and Tibshirani, 1993). For each sample the corresponding b_{RMA} value was estimated and the three mean b_{RMA} values were then calculated. A basic F -test and Scheffé's test were then applied to both the means and the least square means of b_{RMA} values of these pseudo-replications (Sit, 1994). Because of the unequal number of replications a weighting factor was introduced, equal to the number of trees for each sample (Stehman and Meredith, 1995).

Grouping by stage and applying Eq. (5) with the same slope (previously estimated mean b_{RMA} value), we obtained a bundle of parallel straight lines corresponding to different datasets and a values and compared them at log scale. We tested, for each stage, the correlation between the intercept of the straight lines ($\ln a$) and ρ (Appendix B) (Giordano, 1980, 1988). Because specific ρ values distinguished by ontogenetic stage were not available, a constant wood density was assumed for each species. Parameter a , whose values depend on the units of M , D and ρ , was estimated for each species and for the mature and adult stages (where we had enough observations), as:

$$\ln a = \alpha + \beta \rho \tag{7}$$

where ρ is expressed as $t \text{ m}^{-3}$.

2.2. Estimation of total aboveground biomass

To test the performance of the approach in predicting M for a given value of D , Eq. (1) was applied to each tree by using the previously estimated mean b values (considering b as constant values) for each stage and deriving a from Eq. (7). For the juvenile stage, where we did not have a sufficient number of samples, the mean of the estimated a values was used, calculated for the datasets where a juvenile stage was recognised. The estimation was calculated by means of the confidence limits of the prediction and relative difference (RD) between the predicted and corresponding actual (measured) biomass values:

$$\text{relative difference} = \frac{|M_p - M_r|}{M_r} \times 100 \quad (8)$$

where M_r and M_p are the observed and predicted tree biomass, respectively.

In order to be able to apply the model in the cases where the height-diameter ratio could not be analysed, a simplified approach was proposed to distinguish the three stages by a “diametric threshold” expressed by the mean minimum diameter of the adult and mature stages: the former distinguishes the juvenile from the adult and the latter the adult from the mature stage. The studies excluded from previous analyses (where it was not possible to distinguish the three stages by the height-diameter ratio), composed of eight different datasets with at least five observations, were used to validate this simplified approach.

3. Results

The *Chapman–Richards* or *Weibull* functions were applied to 49 datasets: in 18 of these there were either not enough data to analyse the height-diameter relationship or it was not possible to recognize the correct position of the point of inflection because of the inhomogeneous distribution of samples (Appendix A). Thus 31 datasets were used to estimate parameters a and b , eventually excluding the functions where the following procedure indicated a b parameter not significantly different from zero.

3.1. Estimation of parameters b and a

We used 30 (one dataset included only the juvenile and adult stages), 17 and 6 datasets to estimate the b_{RMA} for mature, adult and juvenile stages, respectively (Table 1).

About 90% of the obtained b_{RMA} values were not statistically different from one another (Fig. 2). While the 95% confidence limits of the mean b_{RMA} values did not permit the three stages to be distinguished, both the F -test ($F = 4.66$, $P = 0.01$) and Scheffé’s test applied to the mean values highlighted a significant difference between the three stages. The test applied to the least square means demonstrated a difference only between the juvenile value of 2.08 and the other values, 2.64 and 2.51 for the adult and mature stages,

respectively (Table 2). All the b_{RMA} values estimated for the adult stage were not statistically different from that predicted by the WBE model (2.67), while 14 out of 30 values estimated for the mature stage were significantly different from the theoretical one. In the juvenile stage the six values had very wide confidence limits considering the small number of observations.

Plotting the empirical values of $\ln a$ and b estimated through the linear regression stage by stage showed a significant negative relationship between the two parameters for each stage (Fig. 3).

Applying the three mean b_{RMA} values previously estimated for each stage in Eq. (5), three bundles of parallel straight lines were obtained for each stage, with R^2 always higher than 0.70. The estimated $\ln a$ values were significantly correlated with the average wood density of each species in the mature ($r = 0.49$, $P = 0.006$) and adult ($r = 0.61$, $P = 0.009$) stage, whereas no significant correlation could be found for the juvenile stage ($r = 0.51$, $P = 0.304$).

Excluding possible outliers by analysis of the distribution of the studentized residuals, two linear regression functions were derived for the mature (9) and adult (10) stages, respectively (Fig. 4):

$$\begin{aligned} \ln a &= -3.12 + 1.11 \times \rho, \\ R^2 &= 0.56 \quad (n = 26, F = 32.3, P < 0.0001) \end{aligned} \quad (9)$$

$$\begin{aligned} \ln a &= -3.51 + 1.27 \times \rho, \\ R^2 &= 0.61 \quad (n = 15, F = 21.8, P = 0.0004) \end{aligned} \quad (10)$$

The mean $\ln a$ value calculated for the juvenile stage was -1.638 , and the mean standard error was 0.0589.

3.2. Estimate of total aboveground biomass

The predicted aboveground biomass of each dataset was estimated using the three mean b_{RMA} values (2.08, 2.64 and 2.51 for the juvenile, adult and mature stage, respectively), while parameter a was estimated with Eq. (9) and Eq. (10) (Table 3). RD obtained with the proposed approach was below 30% in 23 out of 31 studies. Excluding dataset $n^\circ 24$ (Jokela et al., 1981) with an RD value above 100%, the actual values of biomass (considering the average RD value (\bar{X}) 20.8%, S.E. 3.0%) should fall within the range $+14.7\%$ – 26.9% of the estimated one ($\bar{X} \pm t_{95}\text{S.E.}$). The mean relative differences observed for each stage were 25.7%, 9.3% and 26.8% for the mature, adult and juvenile stage, respectively.

The minimum mean values of diameter were 15.8 cm (S.E. = 1.5 cm) and 9.5 cm (S.E. = 1 cm) for the mature and adult stages, respectively. The total aboveground biomass estimated applying the simplified approach to the validation dataset (Table 4) gave an RD between 0.4% and 75.8%, with a mean value of 21.4%.

Table 1

Datasets used to analyse parameter b , distinguished in adult, mature and juvenile stage (the reported number of plants can be lower than the total available plants of each dataset, because of the exclusion of outliers by the analysis of studentized residuals)

Number dataset	b -Value	N	R^2	Author	Species
Adult					
1	2.39	12	0.92	Bartelink (1997)	<i>F. sylvatica</i>
2	2.35	9	0.96	Bartelink (1996)	<i>P. memziesii</i>
3	2.58	4	0.99	Cannell (1982)	<i>A. alba</i>
4	2.24	8	0.81	Cannell (1982)	<i>C. japonica</i>
5	3.03	4	0.97	Cannell (1982)	<i>F. sylvatica</i>
6	2.67	8	0.97	Cannell (1982)	<i>P. banksiana</i>
7	2.93	7	0.98	Cannell (1982)	<i>P. mariana</i>
8	2.64	10	0.95	Cannell (1982)	<i>P. memziesii</i>
9	2.73	29	0.92	Cannell (1982)	<i>P. sylvestris</i>
10	3.27	5	0.97	Cannell (1982)	<i>S. robusta</i>
11	2.32	12	0.92	Chroust (1985)	<i>P. sylvestris</i>
12	2.26	6	0.96	De Filippo Roia (1976)	<i>P. abies</i>
13	2.84	9	0.92	Hajny (2003)	<i>F. sylvatica</i>
14	2.37	5	0.89	Hajny (2003)	<i>P. abies</i>
15	2.88	8	0.96	Vanninen et al. (1996)	<i>P. sylvestris</i>
16	2.50	27	0.94	Joosten et al. (2004)	<i>F. sylvatica</i>
17	2.88	55	0.88	Wirth et al. (2004)	<i>P. abies</i>
Mature					
1	2.57	9	0.98	Bartelink (1997)	<i>F. sylvatica</i>
2	2.49	10	0.99	Bartelink (1996)	<i>P. memziesii</i>
3	2.52	9	0.99	Cannell (1982)	<i>A. alba</i>
4	2.20	17	0.94	Cannell (1982)	<i>C. japonica</i>
5	2.78	8	0.98	Cannell (1982)	<i>F. sylvatica</i>
6	2.57	14	0.96	Cannell (1982)	<i>P. mariana</i>
7	2.37	5	0.97	Cannell (1982)	<i>P. memziesii</i>
8	2.42	14	0.96	Cannell (1982)	<i>P. nigra_</i>
9	2.55	13	0.91	Cannell (1982)	<i>P. sylvestris</i>
10	2.25	11	0.97	Cannell (1982)	<i>Q. ilex</i>
11	2.93	5	0.91	Cannell (1982)	<i>S. robusta</i>
12	2.39	38	0.98	Chroust (1985)	<i>P. sylvestris</i>
13	2.49	25	0.96	Colleselli (1973)	<i>L. decidua</i>
14	2.56	10	0.99	Martin et al. (1998)	<i>A. rubrum</i>
15	2.59	10	0.98	Martin et al. (1998)	<i>B. lenta</i>
16	2.47	7	0.98	Martin et al. (1998)	<i>C. arya</i> sp.
17	2.67	9	0.99	Martin et al. (1998)	<i>L. tulipifera</i>
18	2.69	9	0.99	Martin et al. (1998)	<i>Q. alba</i>
19	2.63	11	0.96	De Filippo Roia (1976)	<i>P. abies</i>
20	2.53	9	0.99	Ellenberg et al. (1986)	<i>F. sylvatica</i>
21	2.26	22	0.98	Hajny (2003)	<i>F. sylvatica</i>
22	2.36	17	0.89	Hajny (2003)	<i>P. abies</i>
23	2.35	12	0.98	Jokela et al. (1981)	<i>B. papyrifera</i>
24	2.49	6	0.99	Santa Regina and Tarzopna (2001a)	<i>F. sylvatica</i>
25	3.21	6	0.95	Vanninen et al. (1996)	<i>P. sylvestris</i>
26	2.4	64	0.99	Joosten et al. (2004)	<i>F. sylvatica</i>
27	2.3	61	0.94	Wirth et al. (2004)	<i>P. abies</i>
28	2.4	15	0.96	Woods et al. (1991)	<i>P. mariana</i>
29	2.4	16	0.99	Woods et al. (1991)	<i>P. tremuloides</i>
30	2.2	12	0.97	Zianis and Mencuccini (2003)	<i>F. moesiaca</i>
Juvenile					
1	2.02	9	0.83	Bartelink (1997)	<i>F. sylvatica</i>
2	2.00	8	0.88	Cannell (1982)	<i>P. banksiana</i>
3	1.32	12	0.97	Cannell (1982)	<i>P. sylvestris</i>
4	2.19	17	0.85	Chroust (1985)	<i>P. sylvestris</i>
5	2.59	7	0.84	Hajny (2003)	<i>F. sylvatica</i>
6	2.36	10	0.91	Wirth et al. (2004)	<i>P. abies</i>

4. Discussion

As expected, the analyses of the height-diameter ratio generally presented a sigmoid pattern with different stages

(Huang and Titus, 1992; Peng, 2001), however the possibility of distinguishing three stages strictly depends on the diameter distribution range of the samples. Unfortunately the sampling criteria adopted by different authors often excluded the first

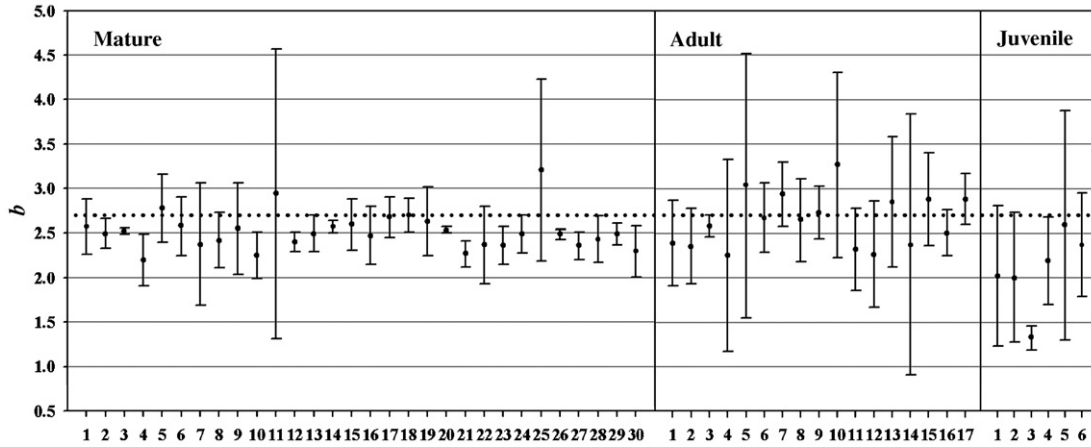


Fig. 2. Average values of parameter *b* of each dataset, distinguished stage by stage (the progressive number of the dataset is reported in Table 1, a dotted line indicates the theoretical *b* value).

Table 2
Differences between *b*_{RMA} means and least squares (LS) means estimated with the *jackknife* procedure (the probability values refer to the LS means comparison)

Stages comparison	Difference between means (<i>P</i> = 0.05)	Difference between LS means	Probability (Pr > <i>t</i>)
Adult–mature	0.339504	0.122094	0.60
Adult–juvenile	0.751178	0.550868	0.02
Mature–juvenile	0.411675	0.428774	0.03

crucial stage of tree growth (Parresol, 1999), leading to an incomplete diameter series where no inflection point could be detected. The same bias can occur in managed even-aged stands or in coppice formations, where the height-diameter ratios hardly have a sigmoid shape. In these cases the proposed simplified method based on diameter values to distinguish the different stages could overcome the problem.

4.1. Analyses of parameters *b* and *a*

The mean *b*_{RMA} value for the mature stage (2.64, S.D. ± 0.30), estimated from the 17 datasets in the adult stage, did not differ from the theoretical value (2.67) predicted by the WBE model. This result would substantially confirm, as suggested by Anfodillo et al. (2006), that the theoretical exponent proposed by West et al. (1999) can be correctly

applied to actively-growing plants. This condition is fulfilled when height increment is around its maximum.

The lower values of parameter *b* in young (2.08, S.D. ± 0.43) and mature stages (2.51, S.D. ± 0.21) compared to the theoretical one (2.67) might have different explanations. Very low *b* values are often reported in small plants (i.e., less than a few meters tall). Recently Reich et al. (2006) presented a wide dataset in which the whole-plant respiration rate (*R*) was correlated isometrically to total plant mass instead of to *M*^{3/4} as predicted by the WBE model. In small plants the RHI (usually called *α* exponent in the relationship *H* versus *D*) is very often close to 1 (instead of 2/3), thus leading to the parameter *a*^{*} (which indicates the degree of branch scaling as described by West et al. (1999) being about 2/3 (*α* = 2/3*a*^{*}). Since *n*_L (number of leaves or leaf area) ∝ *M*^{3/(1+3*a*^{*})} then *n*_L ∝ *M*¹. Because also *n*_L ∝ *D*² it follows that *M* should be proportional

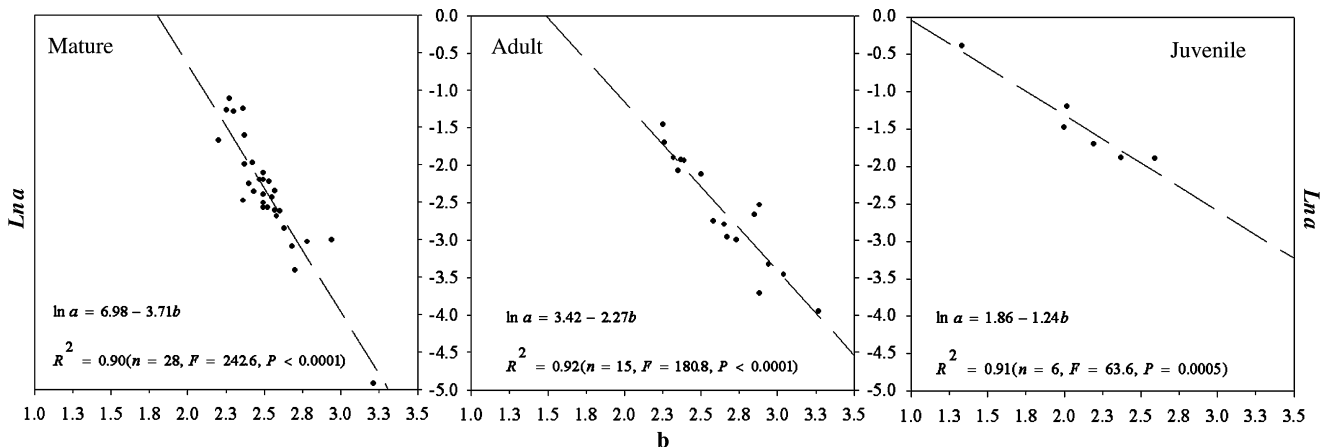


Fig. 3. Relation between *ln a* and *b* distinguished in mature, adult and juvenile stages, respectively.

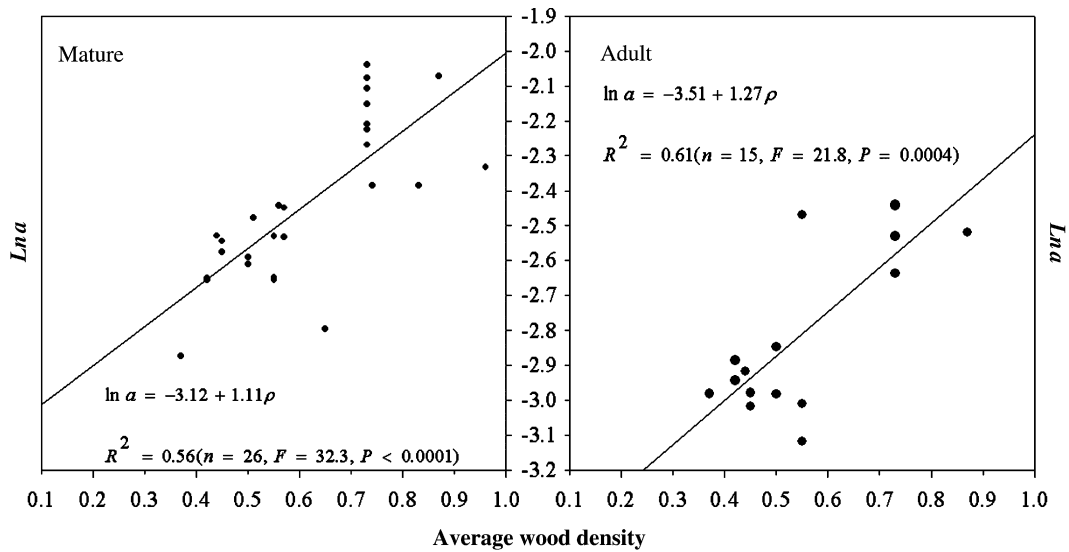


Fig. 4. Plot of $\ln a$ and average wood density values distinguished in mature and adult stages. The parameter $\ln a$ (t m^{-3}) was estimated considering the intercepts of the straight lines obtained with a constant slope in each stage.

to D^2 very close to the experimental data. West et al. (1999) very often underlined that predicted exponents may change if the conditions of the model are not fulfilled, as in small plants where stems are often green and can contribute to the total plant

assimilation, gravity is not so important as in taller plants and volume filling branching may not hold. However it has to be noted, for practical reasons, that the role of small plants in the total plant mass estimation of the whole data set is less than 1%, so they could even be eliminated from the data set and cause only a small effect on the biomass estimation.

Table 3
Actual and predicted values of total aboveground biomass (kg) estimated for 31 datasets

Author	Species	N	Actual	Predicted	RD
Bartelink (1997)	<i>F. sylvatica</i>	30	3340	3091	9.6
Bartelink (1996)	<i>P. memziesii</i>	19	3179	3262	6.8
Cannell (1982)	<i>A. alba</i>	13	4447	4038	9.5
Cannell (1982)	<i>C. japonica</i>	25	3251	4029	42.4
Cannell (1982)	<i>F. sylvatica</i>	12	11868	9632	30.6
Cannell (1982)	<i>P. banksiana</i>	16	410	402	1.2
Cannell (1982)	<i>P. mariana</i>	21	779	768	38.5
Cannell (1982)	<i>P. memziesii</i>	15	6780	7474	5.4
Cannell (1982)	<i>P. nigra</i>	14	6155	5813	8.3
Cannell (1982)	<i>P. sylvestris</i>	54	3306	3850	18.0
Cannell (1982)	<i>Q. ilex</i>	11	21616	30974	72.7
Cannell (1982)	<i>S. robusta</i>	10	1895	1750	26.4
Chroust (1985)	<i>P. sylvestris</i>	67	799	819	46.3
Colleselli (1973)	<i>L. decidua</i>	25	18774	27859	20.7
Martin et al. (1998)	<i>A. rubrum</i>	10	4582	4215	13.1
Martin et al. (1998)	<i>B. lenta</i>	10	3229	3540	24.8
Martin et al. (1998)	<i>Carya</i> sp.	7	5478	6530	5.6
Martin et al. (1998)	<i>L. tulipifera</i>	9	5703	5893	25.2
Martin et al. (1998)	<i>Q. alba</i>	9	4858	7293	2.1
De Filippo Roia (1976)	<i>P. abies</i>	17	12621	12167	8.9
Ellenberg et al. (1986)	<i>F. sylvatica</i>	9	4334	3647	9.7
Hajny (2003)	<i>F. sylvatica</i>	38	43755	38699	28.7
Hajny (2003)	<i>P. abies</i>	22	8683	8070	13.9
Jokela et al. (1981)	<i>B. papyrifera</i>	12	811	1407	135.1
Santa Regina and Tarzopna (2001a)	<i>F. sylvatica</i>	6	1752	1719	20.7
Vanninen et al. (1996)	<i>P. sylvestris</i>	14	5741	6701	2.5
Joosten et al. (2004)	<i>F. sylvatica</i>	91	51980	47953	22.3
Wirth et al. (2004)	<i>P. abies</i>	126	54570	30179	27.1
Woods et al. (1991)	<i>P. mariana</i>	15	899	907	52.1
Woods et al. (1991)	<i>P. tremuloides</i>	16	3237	3000	33.0
Zianis and Mencuccini (2003)	<i>F. moesiaca</i>	12	4896	4080	8.6

The reason why mature trees have a slightly lower b value (2.52) may be different. Considering the general dimensional analysis, the volume of a stem is $V \propto D^2H$, where H is tree height: since mature plants are approaching their maximum height and the annual longitudinal increment is usually very low (ΔL virtually 0 compared to the whole tree height), further increases of total mass with diameter must be progressively lower. Lateral branches may continue to grow and leaves form, but their growth rate does not compensate for the reducing stem growth.

Indeed in very big plants the parameter α is usually lower than $2/3$ indicating a sharp stem tapering (for example 0.6) thus leading to $a^* = 1.1$. Since $D \propto M^{3a^*/2(a^*+3)}$ (West et al., 1999) it follows that $D \propto M^{0.40}$, i.e., $M \propto D^{2.5}$ very close to the value of b for big plants.

Chambers et al. (2001), based on the WBE model, estimated the aboveground biomass of 315 Amazonian trees, using the theoretical value of 2.67 and a scaling coefficient of -2.30 . This model resulted as being reasonable at predicting the mass of small trees, but greatly over predicted the mass of large trees. Zianis and Mencuccini (2003), comparing different allometric equations to estimate the aboveground biomass for *Fagus* sp., also obtained inaccurate predictions using the values proposed by Chambers et al. (2001). We argued that a lower value of the scaling exponent, i.e., 2.52, could be adopted for the mature stage, using different a values. The lower RD observed for the adult stage (9.3%) than the juvenile and mature one, suggests that the theoretical b value (2.67) should only be used for actively-growing plants belonging to this stage.

Zianis and Mencuccini (2004), considering the distribution of b values collected from the literature using the least square model I regression, estimated an empirical $b = 2.36$,

Table 4
Actual and predicted biomass (kg) computed for eight studies used for the validation of the simplified model

No.	Author	Species	<i>N</i>	Actual	Predicted	RD
1	Bonazza (1979)	<i>A. alba</i>	21	20419	14147	16.9
2	Cannell (1982)	<i>P. glauca</i>	8	334	281	16.9
3	Martin et al. (1998)	<i>Q. prinus</i>	8	5149	5821	16.4
4	Martin et al. (1998)	<i>Q. rubra</i>	7	4602	5982	0.4
5	Damiani (1980)	<i>P. abies</i>	24	14534	16739	7.9
6	Pellinen (1986)	<i>F. sylvatica</i>	14	18052	15281	26.3
7	Van Hees and Bartelink (1993)	<i>P. sylvestris</i>	12	1268	1735	10.7
8	Vyskot (1982)	<i>L. decidua</i>	15	3591	5440	75.8

statistically different from 2.67. The difference in our result is mainly due, in our opinion, to the analysis of the dataset as a whole, without splitting into different stages. Indeed, as also suggested by Niklas (1995), different scaling relationships should be applied for trees of different size or age. The use of the least square model I—instead of RMA model II regression—to determine the scaling exponent can also partially explain the differences in our result and should be examined further (Kaitaniemi, 2004).

Considering the empirical values estimated for each dataset stage by stage, a resulted as strongly correlated with b . As observed by Zianis and Mencuccini (2004), this negative correlation, also predicted by Niklas (1994), has long been recognised but no biological interpretation has been proposed (White and Gould, 1965). The correlation between a and b could simply arise from the choice of measurement units, the algebraic equation itself, or the limited data field. However, both Zianis and Mencuccini (2004) and our study suggest that there would be only a limited number of M – D equations for a particular value of a .

Using a constant b value for each stage, we directly derived a as the value of the intersect of each straight line. The basic assumption is that functions belonging to the same stage should have the same slope. This approach highlighted the significant correlation between the scaling coefficient and wood density without falling into an indirect compensation between a and b , given the strong correlation between the two parameters. Since ρ was estimated from the literature, we could not account for the site-specific conditions that strongly affect ρ (Ketterings et al., 2001). However, in accordance with the WBE model, the scaling coefficient should be correlated with the particular conditions of the system under investigation (West et al., 1999) and, at least for the mature and adult stage, it could be directly derived from ρ . In this case, the use of a constant a value, -2.30 as reported by Chambers et al. (2001), could not be correct. The lack of significant correlation for the juvenile stage could be due both to an insufficient number of observations (only six available datasets) and to the use of a unique ρ value for the three stages. In fact, even if a recent study suggests that total tree height and D are not correlated with wood density (Nogueira et al., 2005), ρ could differ between juvenile and mature or adult trees because of the different amount of juvenile wood.

Using this functional approach we overcame the bias related to the log transformation of data. Indeed we did not need to

transform D – M data to improve the homogeneity of residual error variances, but could directly apply Eq. (1).

4.2. Estimation of total aboveground biomass

The method provides a good balance between few data requirements and acceptable biomass predictions (the relative difference based on the validation dataset is 21.4%). The main advantage of this approach is that it is not based on destructive sampling methods but requires only the height-diameter ratio in order to assess the three stages, and average wood density for estimating parameter a . Furthermore, the use of an “empirical diameter threshold” to assess the different stages permits the model to be directly applied where there is not enough height-diameter data or in uneven-aged forests without any specific measurements, as required by other models (Noordwijk and Mulia, 2002).

The average relative difference value of the validation dataset falls within the previously estimated confidence limits, suggesting that the accuracy of the estimate can be known. On the contrary, applying an empirical approach, where b depends on the analysed dataset, there could be difficulty in verifying the estimate accuracy.

The lower relative difference observed for the adult stage compared to the mature one suggests that the accuracy of the estimate may be improved, both in relation to a better evaluation of the b value and the correlation with ρ . In the same way, a larger dataset relative to the juvenile stage would probably also allow a regression function to be assessed for this stage.

Our analysis suggested that the WBE model predicts exactly the general allometric b exponent between M and D in actively-growing plants (condition of validity of the WBE model). In the juvenile and mature stages, for different reasons, the values of b may change and this can negatively affect tests aimed at comparing the WBE predictions.

Parameter a was negatively correlated with the scaling exponent b in accordance with previous studies and this correlation is strengthened if we consider each dataset stage by stage.

Our approach differs from those previously published, offering a concrete application of a functional instead of empirical allometric equation. Unlike other methods, it uses a mathematical function that links different variables, explaining this relationship with a “cause and effect relationship” (Niklas, 1994). This was predicted and interpreted, at least for the adult stage, by the WBE model.

The proposed approach offers a satisfactory estimate of the total aboveground biomass without requiring destructive sampling and permits the confidence limits of the estimation to be predicted, which is crucial not only for traditional forest applications but also for implementing the Kyoto Protocol requirements.

Further research, based on empirical data, is needed to verify and theoretically explain the b value for the juvenile and mature stages, to improve knowledge on the a – ρ relationship, where smaller RD values are expected if different values of density are used for each ontogenetic stage, and to test the usefulness of this approach for aboveground biomass estimation.

Appendix A

Selected studies with complete individual data for diameter, mass and height. The number of trees (N), average values of D , H , and M , and the result of the height-diameter analysis are indicated.

Author	Data source ^a	Species	N	D	H	M	Height-diameter analysis ^b
Anfodillo (unpublished data)	PC	<i>L. decidua</i>	6	25	11	333	No point of inflexion
Anfodillo (unpublished data)	PC	<i>P. abies</i>	7	21	9	185	No point of inflexion
Anfodillo (unpublished data)	PC	<i>P. cembra</i>	8	25	8	195	No point of inflexion
Bartelink (1997)	PC	<i>F. sylvatica</i>	38	13	12	112	Correct
Bartelink (1996)	PC	<i>P. memziesii</i>	23	17	14	148	Correct
Bonazza (1979)	RP	<i>A. alba</i>	26	33	25	873	No point of inflexion
Cannell (1982)	RP	<i>A. alba</i>	16	28	21	389	Correct
Cannell (1982)	RP	<i>B. pendula</i>	18	13	14	77	Failed
Cannell (1982)	RP	<i>C. japonica</i>	30	19	13	122	Correct
Cannell (1982)	RP	<i>F. sylvatica</i>	23	28	23	748	Correct
Cannell (1982)	RP	<i>P. banksiana</i>	30	6	6	15	Correct
Cannell (1982)	RP	<i>P. glauca</i>	8	11	9	42	No point of inflexion
Cannell (1982)	RP	<i>P. mariana</i>	30	10	9	32	Correct
Cannell (1982)	RP	<i>P. memziesii</i>	18	24	21	456	Correct
Cannell (1982)	RP	<i>P. nigra</i>	35	20	15	209	Correct
Cannell (1982)	RP	<i>P. sylvestris</i>	63	12	11	59	Correct
Cannell (1982)	RP	<i>Q. ilex</i>	17	36	12	1338	Correct
Cannell (1982)	RP	<i>S. robusta</i>	12	15	14	162	Correct
Chroust (1985)	OL	<i>P. sylvestris</i>	81	6	6	11	Correct
Colleselli (1973)	RP	<i>L. decidua</i>	28	41	20	737	Correct
Damiani (1980)	RP	<i>P. abies</i>	30	35	23	575	No point of inflexion
De Filippo Roia (1976)	RP	<i>P. abies</i>	25	30	21	558	Correct
Dibona (1981)	RP	<i>F. sylvatica</i>	29	26	22	506	Failed
Ellenberg et al. (1986)	OL	<i>F. sylvatica</i>	9	23	21	482	Correct
Hajny (2003)	RP	<i>F. sylvatica</i>	47	26	21	986	Correct
Hajny (2003)	RP	<i>P. abies</i>	26	28	23	420	Correct
Jokela et al. (1981)	PC	<i>B. papyrifera</i>	15	15	16	58	Correct
Ketterings et al. (2001)	OL	<i>Tropical sp.</i>	29	22	16	318	Failed
Martin et al. (1998)	OL	<i>A. rubrum</i>	11	23	21	429	Correct
Martin et al. (1998)	OL	<i>B. lenta</i>	10	23	22	323	Correct
Martin et al. (1998)	OL	<i>Carya_ sp</i>	10	27	23	561	Correct
Martin et al. (1998)	OL	<i>Cornus sp.</i>	4	7	7	7	Failed
Martin et al. (1998)	OL	<i>L. tulipifera</i>	10	31	28	608	Correct
Martin et al. (1998)	OL	<i>Q. alba</i>	10	30	19	537	Correct
Martin et al. (1998)	OL	<i>Q. prinus</i>	10	28	20	555	No point of inflexion
Martin et al. (1998)	OL	<i>Q. rubra</i>	9	30	21	520	No point of inflexion
Pellinen (1986)	OL	<i>F. sylvatica</i>	19	32	26	998	No point of inflexion
Santa Regina and Tarzopna (2001a)	OL	<i>F. sylvatica</i>	7	19	15	251	Correct
Santa Regina and Tarzopna (2001b)	OL	<i>P. sylvestris</i>	7	22	12	166	No point of inflexion
Van Hees and Bartelink (1993)	OL	<i>P. sylvestris</i>	12	18	11	106	No point of inflexion
Vanninen et al. (1996)	OL	<i>P. sylvestris</i>	18	25	18	325	Correct
Vyskot (1982)	OL	<i>L. decidua</i>	17	17	16	228	No point of inflexion
Vyskot (1983)	OL	<i>P. sylvestris</i>	16	11	12	40	Failed
Joosten et al. (2004)	PC	<i>F. sylvatica</i>	116	23	18	563	Correct
Wirth et al. (2004)	PC	<i>P. abies</i>	147	21	19	419	Correct
Woods et al. (1991)	OL	<i>P. mariana</i>	31	12	11	55	Correct
Woods et al. (1991)	OL	<i>P. tremuloides</i>	31	14	14	137	Correct
Zaccoletti (1977)	RP	<i>A.alba</i>	40	36	21	579	Failed
Zianis and Mencuccini (2003)	DP	<i>F. moesiaca</i>	16	19	19	341	Correct
Total			1278				

^a PC: personal communication; RP: reported in the publication; DP: digitised from published paper; OL: available on-line.

^b The height-diameter relation of each dataset was analysed by the *Chapman–Richards* or the *Weibull* function and, as reported in Fig. 1, the “a point of inflexion” was distinguished. The results are reported as: Failed: the non-linear regression procedure failed to converge and no further analysis was performed; “No point of inflexion”: the non-linear regression procedure converged but no point of inflexion was detected; Correct: the non-linear regression procedure converged and the point of inflexion was distinguished.

Appendix B. Average values of wood density, expressed as the ratio between mass and volume at 12% moisture content, used to test the correlation with parameter *a* (Giordano, 1980, 1988)

Species	Average wood density (t m ⁻³)
<i>A. alba</i>	0.44
<i>C. japonica</i>	0.37
<i>F. moesiaca</i>	0.73
<i>F. sylvatica</i>	0.73
<i>L. deciduas</i>	0.65
<i>P. abies</i>	0.45
<i>P. mariana</i>	0.42
<i>P. memziesii</i>	0.50
<i>P. nigra</i>	0.56
<i>P. sylvestris</i>	0.55
<i>P. tremuloides</i>	0.51
<i>Q. ilex</i>	0.96
<i>S. robusta</i>	0.87
<i>P. banksiana</i>	0.42
<i>A. rubrum</i>	0.57
<i>B. lenta</i>	0.74
<i>B. papyrifera</i>	0.62
<i>Carya</i> sp.	0.83
<i>L. tulipifera</i>	0.57
<i>Q. alba</i>	0.75
<i>P. cembra</i>	0.45
<i>P. glauca</i>	0.45
<i>Q. prinus</i>	0.75
<i>Q. rubra</i>	0.66

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