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Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests

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Abstract

Estimates of forest biomass are needed for tracking changes in C stocks, as well as for other purposes. A common method for estimating forest biomass is through use of allometric equations which relate the biomass of individual trees to easily obtainable non-destructive measurements, such as diameter. A common form is $B=aD^b$ for biomass B , diameter D and parameters a and b . Field data collected in Sumatra and compared with previously published data show that the values of a and b vary between sites. This variation is likely to be the major source of uncertainty if biomass estimates are produced using equations that are not calibrated for individual sites. However, calibration by collection of B and D data for each site is unrealistic, requiring destructive measures. Methods of choosing values for a and b are, therefore, proposed that do not require destructive measurements. The parameter b can be estimated from the site-specific relationship between height (H) and diameter, $H=kD^c$ as $b=2+c$. The parameter a can be estimated from the average wood density (ρ) at the site as $a=r\rho$, where r is expected to be relatively stable across sites. The allometric equation proposed is therefore $B=r\rho D^{2+c}$. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Above-ground biomass; Allometric biomass equation; Breast height diameter; Carbon stocks; Secondary forest; Wood density

1. Introduction

Estimation of above-ground biomass is an essential aspect of studies of C stocks and the effects of deforestation and C sequestration on the global C balance. Weighing tree biomass in the field is undoubtedly the most accurate method of estimating above-

ground tree biomass, but it is an extremely time consuming and destructive method, generally limited to small areas and small tree sample sizes.

Allometric equations for relating tree diameter at breast height (D) or other easily measurable variables to standing volume of wood or total biomass C, and nutrient stocks are commonly used for forest inventories and ecological studies. Whittaker and Marks (1975) and Pardé (1980) provide reviews. Recent applications and estimations of tropical forest biomass

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are included in Uhl et al. (1988), Brown et al. (1989), Brown and Lugo (1992), Brown et al. (1997) and Schroeder et al. (1997).

When estimating the above-ground biomass of a forest, the use of species-specific equations are preferred because trees of different species may differ greatly in tree architecture and wood density. However, due to the great number of different tree species in humid, tropical rainforests and the enormous efforts needed to develop these equations, species-specific equations for the humid tropics are virtually unavailable while relatively few mixed-species equations have been developed.

Brown et al. (1989) analyzed data from five studies in the humid tropics (1500–4000 mm rainfall per year). A total of 168 trees were cut and weighed and an allometric equation for predicting biomass was obtained. Despite the fact that a sample of 168 trees is not likely to be representative of the many different tree species and forest types present in the humid tropics, the biomass equation fitted to these data is widely used (e.g. Anderson and Ingram, 1993; Hairiah et al., 1999). This might not lead to large errors when the same equation is used to estimate growth rates because repeated measurements over time at the same site assume a relatively constant forest composition and site specificity. However, estimated errors should be addressed when biomass equations are used to monitor and compare absolute C balances of different sites. With the current interest in obtaining financial rewards for the amount of C sequestered in terrestrial biomass, the uncertainties and biases involved in using these simple tools certainly are of more than academic interest.

A protocol for forest biomass assessment based on the use of these allometric relationships will involve four steps: (1) choosing a suitable functional form for the allometric equation; (2) choosing suitable values for any adjustable parameters in the equation; (3) field measurements of the input variables such as tree diameter; and (4) using the allometric equation to give the above-ground biomass of individual trees and summation to get area estimates. Several authors (e.g. Overman et al., 1994; Araújo et al., 1999) compare competing models for step 1. Although the statistical methods used are not always clear, the general conclusion is that alternative models that appear to 'fit' the data give predictions of very similar

quality. Brown et al. (1995) discuss uncertainty due to measurement errors, transect size, fraction of the above-ground biomass considered, and site selection. These are uncertainties introduced in step 3. In this paper we consider the uncertainty or estimation error introduced in step 2. The paper uses original data collected in a field study in Indonesia together with the data reported in Brown (1997) to estimate the size of error introduced at step 2 relative to other sources of uncertainty, and suggests ways of reducing it.

2. Field study in Indonesia

2.1. Study site

All data were collected in mixed secondary forests in Sepunggur (1°29'S, 102°14'E) which is located 31 km southeast of Muara Bungo, the capital of sub-district Muara Bungo, Bungo Tebo, Jambi Province, Sumatra, Indonesia. These forests are dominated by human introduced latex producing *Hevea brasiliensis*, and naturally occurring wood species (*Mallotus*, *Eugenia*, *Mastixia*, *Styrax*, and *Dactylocladus* spp.) and fruit species (*Phitecellobium*, *Parkia*, and *Artocarpus* spp.).

Twelve of the 29 trees that contributed to the allometric equation developed for the region were taken in the foothill zone dominated by inceptisols and entisols. The remaining 17 trees were taken from the penepain zone dominated by oxisols and ultisols. Soils in both areas are very acidic (pH 4–4.5) and have a moderately low to very low fertility. Both areas have an average annual rainfall of nearly 3000 mm; 7–9 months are wet (>200 mm rainfall per month) and less than 2 months per year are dry (<130 mm rainfall). The mean maximum temperature varies from 30.0°C in January to 32.3°C in May and October. The mean minimum temperature varies from 22.1°C in July and September to 22.7°C in April and May. Climate, vegetation, soils, and land use were described by Van Noordwijk et al. (1998).

A land-use survey in Sepunggur showed that the secondary forests covering these soil types are rarely older than 60 years (Ketterings et al., 1999). Virtually all primary forest was logged in the past 20 years. In a study of forest composition and above-ground nutrient stocks in Sepunggur, 79 different species were

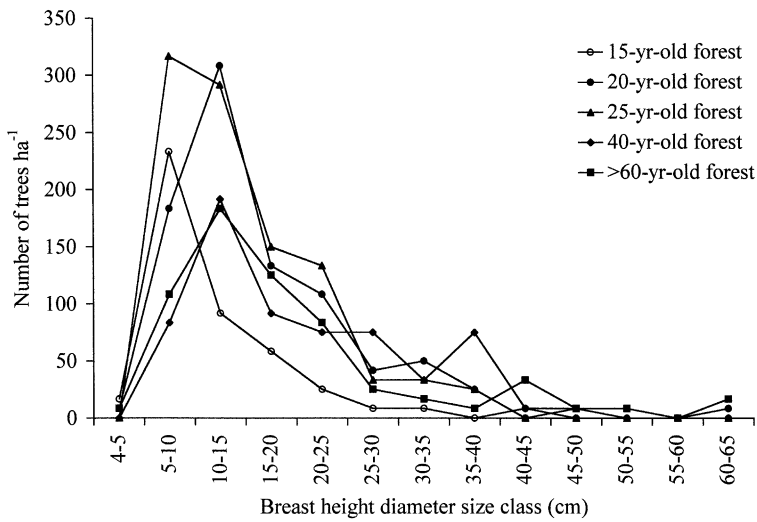


Fig. 1. Frequency distribution of tree diameter at breast height (*D*) for five mixed secondary forests in Sepunggur, Sumatra.

identified in 30 m × 40 m plots within five forests of different age (Ketterings, 1999). The mean *D* ranged from 14 to 20 cm. All *D* distributions were positively skewed (Fig. 1) with most trees in the 5–20 cm *D* class. Only four trees of a total of 429 trees present in the 0.6 ha had a *D* > 50 cm and no trees had a *D* > 65 cm (Ketterings, 1999). Tree *H* ranged from 4 to 34 m and was slightly positively skewed at each of the five locations (Fig. 2). Mean *H* varied from 13 to 16 m.

2.2. Data collection

To develop an allometric equation for the region, trees were selected based on their *D* (5–50 cm), *H* (0–34 m), and species. Due to the high value given by farmers to fruit producing trees, destructive sampling of these trees was not possible. The small-scale farmers of Sepunggur generally spare these fruit trees when slashing and burning the secondary forest and they are thus not likely to contribute to deforestation and CO₂ emission.

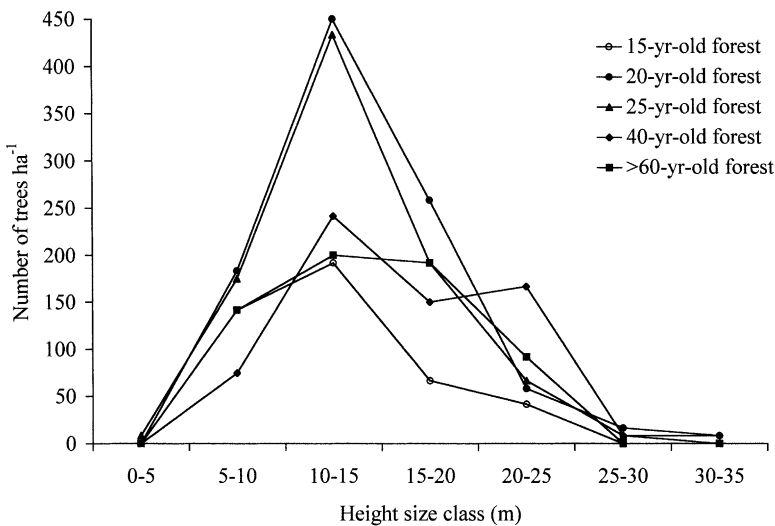


Fig. 2. Height distribution for five mixed secondary forests in Sepunggur, Sumatra.

Prior to cutting the trees, D was measured and local tree names were recorded. Tree height was measured with a measuring tape after cutting the trees. Each tree was separated into four fractions: (1) leaves, (2) twigs ($D < 3.2$ cm), (3) small branches ($3.2 < D < 6.4$ cm), and (4) large branches and stems with $D > 6.4$ cm. These fractions were chosen based on the observation that tree components showed varying burning percentages and nutrient concentrations. We estimated the weight of the basal stem remaining after cutting the tree by measuring its height and diameter, calculating the volume, and multiplying it with the density of the fraction > 6.4 cm in diameter. Subsamples of all fractions were collected in the field and stored in sealed plastic bags to prevent loss of moisture. Wet weights were recorded immediately upon arrival in the laboratory.

An estimate of the average wood density was obtained by combining values for specific species reported in southeast Asian literature (Prosea, 1994, 1995, 1996) and densities estimated by completely emerging 3–4 cm thick slices of the > 6.4 cm wood fraction in water and determining the ratio of increase in water volume to dry wood weight. A combination of reported and measured wood densities was used due to loss in transportation of a fraction of the subsamples prior to density measurements. All data are expressed on the basis of 105°C dry weights. Results on the tree component fractionations and nutrient contents were reported in Ketterings (1999). In this publications we focus on overall above-ground biomass estimates.

3. Choosing a functional form for the allometric equation

Allometric biomass equations aim to relate tree biomass (B) to quantities (V_i) that can be easily and nondestructively measured on trees:

$$B = f(V_1, V_2, \dots) \quad (1)$$

The most commonly used functions are polynomials and power models of the form $f(V) = aV^b$ and their combinations. Polynomials have the disadvantage that the shape may be biologically unreasonable (e.g. with a minimum within the range of V being considered). The power function form is widely found within biology (Huxley, 1932) and has some attractive interpretations (see below). It is important, however, to emphasize that these are empirical relationships cho-

sen because they ‘fit’. Causton and Venus (1981) show that it is not possible for power relationships to hold between the sizes of all plant parts and the total.

Of the variables V_i considered, the commonest used are H and D . Several authors have shown that the inclusion of H in the power equation generally gives only a slight improvement in the fraction of variance explained by the model for a given site. This can be understood from the normally close relationship between D and H within a given site. Niklas (1994) found that $H = 1.70D^{0.535}$ (for H in meter and D in centimeter; converted from $H = 20.6D^{0.535}$ for both H and D expressed in m) applies to a wide range of plant sizes. If D and H for trees of a given environmental condition are related by $H = kD^c$, the equation $B = aD^bH$ becomes $B = akD^{b+c}$. We show below why H may be important when comparing different sites. However, to develop an allometric equation for forests in Sepunggur, we consider a model of the form:

$$B = aD^b \quad (2)$$

which is equivalent to

$$\log(B) = \log(a) + b \log(D) \quad (3)$$

Fig. 3a shows this to be reasonable for the Sumatra data ($7.6 < D < 48.1$ cm) and Fig. 3b shows the same for the data ($5.0 < D < 48.5$ cm) from Brown (1997).

The pattern of variation in biomass of individual trees about the regression line is important if we want to find efficient methods of estimating the parameters a and b , obtain valid estimates of errors of these estimates, and quantify the error in using the resulting equation for prediction. It makes no difference whether the individual trees are considered to vary by an amount (with a mean of zero) added to Eq. (2) or to Eq. (3), the latter corresponding to multiplicative errors (varying around a mean of one) applied to Eq. (2). What is most important is the variance of these deviations. Figs. 4a and b show that the standard deviation of biomass is proportional to its mean, or the variance proportional to the square of the mean for the Sumatra data and the data compiled in Brown (1997), respectively. Thus the model may be written as

$$B_i = \mu_i + \varepsilon_i \quad \text{with} \quad \mu_i = aD_i^b \quad \text{and} \quad \text{var}(\varepsilon_i) = \phi\mu_i^2 \quad (4)$$

where B_i is the biomass of tree i , D_i its breast-height diameter, μ_i the mean biomass of all trees with diameters

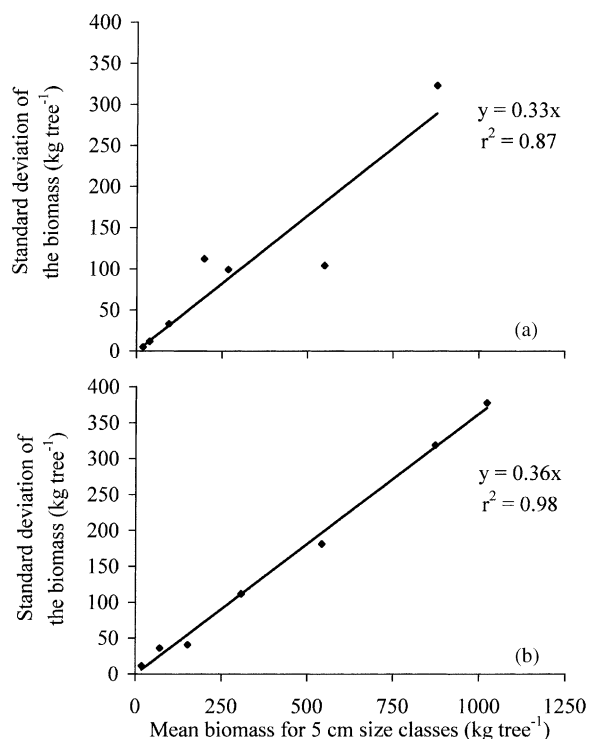
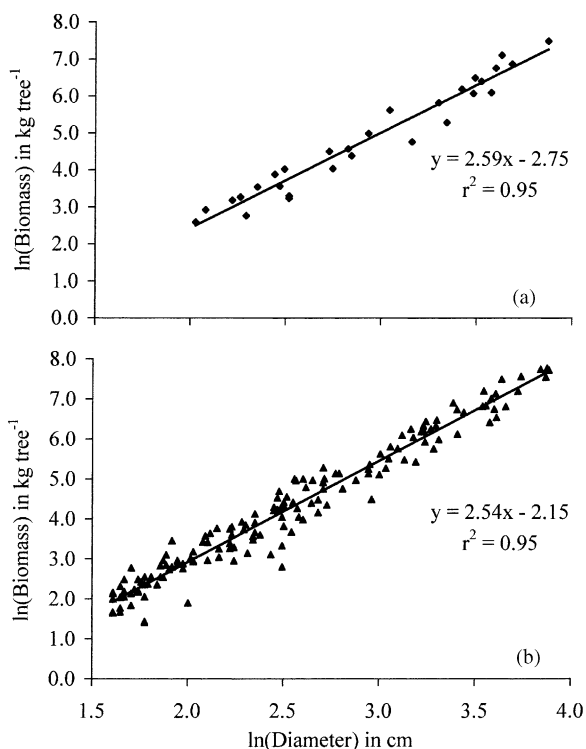


Fig. 3. Logarithmically transformed diameter versus above-ground biomass for (A) 29 calibration trees from Sepunggur, Sumatra, and (B) the combined data sets ($D < 50$ cm) reported in Brown (1997). The straight lines imply that a power model ($B = aD^b$ in which D is the diameter at breast height) is appropriate.

Fig. 4. The standard deviation of tree biomass per 5 cm diameter size class as a function of the mean biomass for (A) 29 calibration trees from Sepunggur, Indonesia, and (B) the combined data sets ($D < 50$ cm) reported in Brown (1997).

D_i , a and b are parameters to be estimated and ϕ the ‘dispersion parameter’, also to be estimated. The model of Eq. (4) has the form of a ‘generalized linear model’ (McCullagh and Nelder, 1989), allowing standard methods to be used to estimate parameters a , b , and ϕ together with their standard errors. The calculations were done using Genstat 5 release 3 (Genstat, 1993).

Table 1 shows the biomass data of the 29 trees cut and weighed for this study. Table 2 lists the local names as well as the scientific names and wood densities of the Sepunggur trees. Using these data to estimate the parameters of Eq. (4) led to the following model for trees ($7.6 < D < 48.1$ cm) in mixed secondary forest in Sepunggur:

$$B \text{ (kg per tree)} = 0.066D^{2.59} \tag{5}$$

The standard errors for a and b were 0.021 and 0.106, respectively, while the dispersion parameter ϕ was estimated as 0.101.

If the model is fitted making the usual assumptions that the variance is constant and does not change with the mean, the default assumption in most regression software, the estimates obtained are the parameter a of 0.014 (S.E.=0.010) and the parameter b of 3.05 (S.E.=0.204). The relatively large differences in fitted parameters assuming different mean–variance relationships show the importance of using an appropriate model for both the mean and variance components of the model. Furthermore, the standard errors of parameter estimates are only correct if a realistic description of the variance is included in the model.

4. Sources of error

Table 3 shows the estimates of a , b , and ϕ for the data from Sumatra as well as those derived for the four

Table 1

Biomass data (kg per tree) of 29 trees in secondary forest stands in the Sepunggur area, Jambi Province, Sumatra (AGB: above-ground biomass, D : breast-height-diameter, H : tree height, \varnothing : diameter in cm). All weights are expressed on 105°C dry weight basis (see Table 2 for species identification)

Local name	H (m)	D (cm)	Leaves	Twigs ($\varnothing < 3.2$)	Small branches ($3.2 < \varnothing < 6.4$ cm)	Large branches and stems ($\varnothing > 6.4$ cm)	Standing	Total
Buluh	12.3	7.6	2.0	1.8	4.7	2.1	2.7	13.3
Kubung	10.5	8.0	0.8	2.2	4.9	9.4	1.4	18.7
Kayu kacang	10.1	9.2	0.7	2.9	8.1	10.6	1.8	24.1
Balik angin	8.5	9.6	0.6	4.7	8.2	10.6	2.1	26.3
Mahang	7.2	9.9	0.5	2.2	7.8	4.3	1.1	15.9
Nilao	11.0	10.5	2.0	3.3	11.4	16.0	1.7	34.4
Kelat	14.0	11.5	2.2	5.3	3.0	35.3	2.7	48.5
Unidentified	12.5	11.8	3.2	6.5	4.5	16.6	4.3	35.1
Mahang	14.6	12.1	1.3	10.4	10.9	30.7	2.7	56.0
Balik angin	10.5	12.4	2.8	2.6	3.0	14.0	3.0	25.4
Unidentified	12.5	12.4	1.0	2.3	7.2	14.5	2.2	27.2
Meranti	14.3	15.3	5.8	15.0	13.3	53.7	2.7	90.4
Mahang	8.6	15.6	7.2	8.3	23.1	16.2	2.2	56.9
Patang buah	11.8	16.9	2.2	7.5	8.3	76.6	2.7	97.3
Balik angin	10.6	17.2	9.9	3.5	31.7	29.4	6.3	80.7
Mahang	11.0	18.8	3.9	10.3	40.4	87.9	4.6	147.1
Kemenyan	20.7	21.0	3.0	4.1	5.1	258.1	6.0	276.3
Jirak	16.7	23.6	2.1	3.0	10.8	97.5	3.9	117.3
Mahang	22.9	27.1	22.8	2.2	18.3	283.0	11.4	337.7
Buluh	11.4	28.3	7.8	10.1	12.0	156.4	11.0	197.4
Buluh	20.2	30.6	13.1	26.3	70.0	369.0	12.9	491.3
Medang	20.6	32.5	5.8	14.4	80.0	318.6	16.5	435.3
Kedungdung	25.4	32.8	19.0	23.3	57.0	538.9	24.2	662.4
Kubung	20.2	33.9	7.9	18.6	108.0	450.4	23.4	608.4
Medang	32.4	35.7	17.2	38.7	39.2	339.8	11.8	446.8
Medang	28.2	36.6	24.9	33.9	101.4	687.2	20.2	867.6
Medang	23.6	37.7	29.5	37.6	113.6	980.8	63.4	1224.9
Medang	26.1	39.8	13.7	22.1	146.7	755.7	27.4	965.5
Maribungan	24.0	48.1	35.2	30.0	145.3	1495.2	95.0	1800.7

sets reported in Brown (1997). A fifth set reported in Brown (1997) was eliminated from the study because it contained only two trees. Throughout the analyses data were restricted to trees of $D < 50$ cm as the number of larger trees was too small to be able to check the validity of the models. It is clear that the parameters a vary between data sets ($p < 0.001$) and there is evidence that parameters b do also ($p = 0.09$). When the estimates derived from our Sumatra trees were used to predict biomass at the four sites in Brown (1997), the total biomass estimates were 73, 50, 59, and 76% of the observed values, respectively. Likewise, when the models fitted to the Brown (1997) data were used to predict the biomass of the Sepunggur trees, the estimates were 124, 192, 164, and 118% of the true value, respectively.

These errors should be put into the context of other errors induced by the use of these equations. Assuming D is measured without error, the components of error in the predicted tree biomass are: (1) the error due to the fact that an individual tree has a biomass which deviates from the average of all trees of that D , (2) the error due to the fact that the a and b parameters used are estimates based on relatively small sample sizes, and (3) the error due to the fact that the relationship used may be the wrong one, or the parameter values used are not appropriate for that site. Each of these errors is measured by a variance: V_{tree} , V_{estimate} , and V_{model} , for errors 1, 2, and 3, respectively.

For a tree of diameter D , Eq. (4) gives

$$V_{\text{tree}} = \varphi B D_i^2 = \varphi a^2 D_i^{2b} \quad (6)$$

Table 2

Local, family, genus name and wood densities (g cm^{-3}). Family and genus identifications are based on Sidiyasa et al. (1986) and Heyne (1950)

Local name	Family	Genus	Wood density (Prosea, 1994, 1995, 1996) ^a	Wood density (Sepunggur) ^b
Kayu kacang	<i>Olacaceae</i>	<i>Strombosia</i> spp.	0.64–1.22	0.61
Balik angin	<i>Euphorbiaceae</i>	<i>Mallotus</i> spp.	0.37–0.83	0.43–0.54
Mahang	<i>Euphorbiaceae</i>	<i>Macaranga</i> spp.	0.27–0.82	0.49–0.91
Nilao	Unknown	Unknown	n.r.	0.35
Buluh	<i>Rhizophoraceae</i>	<i>Ginetrosnesia</i> spp.	n.r.	0.53
Kelat	<i>Myrtaceae</i>	<i>Eugenia</i> spp.	n.r. ^c	0.48
Meranti	<i>Dipterocarpaceae</i>	<i>Shorea</i> spp.	0.30–0.86	0.65
Patang buah	<i>Euphorbiaceae</i>	<i>Baccaurea</i> spp.	0.63–0.95	0.73
Medang	<i>Melastomataceae</i>	<i>Dactylocladus</i> spp.	0.41–0.61	n.d.
Jirak	<i>Celastraceae</i>	<i>Celastrus</i> spp.	n.r.	n.d.
Kemenyan	<i>Styracaceae</i>	<i>Styrax</i> spp.	n.r.	n.d.
Kedungdung	<i>Anacardiaceae</i>	<i>Pentaspadon</i> spp.	0.49–0.83	n.d.
Maribungan	<i>Rosaceae</i>	<i>Parinari</i> spp.	0.63–1.01	n.d.
Kubung	<i>Cornaceae</i>	<i>Mastixia</i> spp.	0.38–0.77	0.47

^a Some species were not reported in these references (n.r.).

^b Due to transportation problems, several samples were lost before wood density could be measured (n.d.).

^c Brown (1997) mentioned a density of 0.65 kg dm^{-3} .

The V_{estimate} for a specific D is determined from the covariance matrix of the fitted parameters a and b :

$$V_{\text{estimate}}(D_i) = \left(\frac{B_i}{a}\right)^2 (V_{aa} + a^2 \ln(D_i)^2 V_{bb} + 2a \ln(D_i) V_{ab}) \quad (7)$$

where V_{aa} (S.E._a^2), V_{bb} (S.E._b^2), and V_{ab} ($\text{S.E.}_a \times \text{S.E.}_b \times \text{correlation}_{(ab)}$) are the elements of the covariance matrix, and B_i is the biomass of a tree with a diameter D_i .

V_{model} is difficult to estimate as it depends on the range of sites or environmental conditions over which the model might be used and on the range of

alternative models that might be considered. However, a conservative, order-of-magnitude estimate can be found by looking at the five data sets available (the four reported in Brown (1997) and the data set from Sepunggur) and fitting the model of Eq. (4) to each. For any diameter D , V_{model} was estimated as the variance of the five predicted biomass values. Fig. 5 shows the relative size of these three components of the error. V_{estimate} is small. Its size depends on the size of the data set used to calibrate the model, as well as on the D distribution in the calibration set. The small size of V_{estimate} suggests we could have used fewer trees to calibrate the model without losing much information. V_{tree} is large, as expected. However, these error

Table 3

Fitting parameters of a power model $B_i = \mu_i + \varepsilon_i$ with $\mu_i = aD_i^b$ and $\text{var}(\varepsilon_i) = \phi\mu_i^2$ (see text) to data of four sources ($D_i < 50$ cm) as compiled by Brown (1997) and trees from Sepunggur, Sumatra. B_i is the biomass (kg per tree) of a tree with diameter D_i . ϕ is the dispersion parameter

	n	D -range (cm)	a (S.E.)	b (S.E.)	ϕ
Brown 1	37	6.4–48.5	0.2360 (0.0701)	2.300 (0.102)	0.161
Brown 2	15	10.0–38.0	0.1172 (0.0581)	2.627 (0.176)	0.082
Brown 3	32 ^a	9.8–48.1	0.0997 (0.0358)	2.627 (0.122)	0.088
Brown 4	71	5.0–41.3	0.1393 (0.0197)	2.437 (0.065)	0.080
Sepunggur	29	7.6–48.1	0.0661 (0.0208)	2.591 (0.106)	0.101

^a One tree in this data set ($D=14.8$ cm and $B=433.2$ kg) appeared to be an erroneous measurement. This tree was excluded from the statistical analyses.

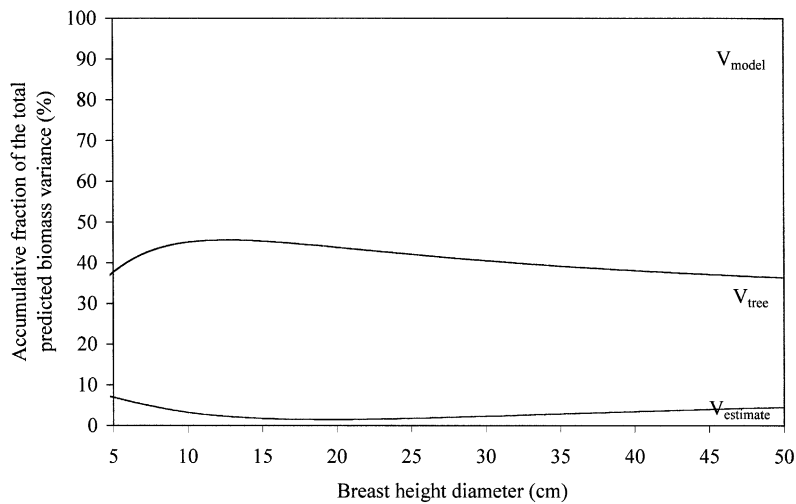


Fig. 5. Accumulated fraction of the total predicted biomass variance in each of the three error components (V_{model} is the variance introduced when applying different models to trees of a similar D ; V_{tree} the variance introduced by the scatter of biomass around the regression line for trees with a similar diameter; V_{estimate} the variance introduced by uncertainty in the estimated parameters).

variances apply to use of the model to predict biomass of single trees. The usual application is to estimate the total biomass in a stand by summing the biomass of individual trees. The relative contribution of V_{tree} will then decrease as the number of trees in the sum is increased. The extent of the reduction depends on the D distribution of the population to which the model is applied, but it will always get smaller as the stand area increases, so for large stands V_{tree} can be made arbitrarily small. V_{model} does not depend on the size of the calibration set or the population to which the model applies. It depends on the extent to which the values of a and b are appropriate for the site to which the model is being applied. It is a major source of error in biomass estimates, and so strategies for reducing it are needed.

5. Reducing the model error

Because V_{model} depends on the difference between the 'true' values of a and b at the site for which biomass estimates are required, and the values used in other models, this component of error can be reduced by reducing this difference. One strategy for doing this is calibrating the model at each site it is to be used. This is, however, expensive and impractical, due to the destructive nature of the calibration.

Furthermore, it is not clear what is meant by a 'site' in this context. If an estimate for a large forest stand is needed, is that a single site or not? This strategy would require obtaining calibration data sets from different sub-sites, comparing the values of a and b obtained for each sub-site and only using single values for the whole site when no differences are found.

Another strategy for reducing V_{model} is finding characteristics of the site (e.g. soil type, species mixture) which allow selection of values of a and b from a catalogue. This may be feasible in future, but at present we do not know what characteristics may be important, and do not have the data to build such a catalogue.

A third strategy is finding auxiliary measurements that may be cheap to obtain for a particular site but allow the a and b parameters to be tuned to that location. Two of these, tree D versus H relationships and wood density are suggested here.

6. Height

If we model tree shape by any simple geometric model, such as a cone, then the volume, and hence biomass, is proportional to D^2H . If, furthermore, the relationship $H=kD^c$ holds, then we have $B=aD^{2+c}$. Thus we hypothesize that the parameter b in Eq. (5)

can be taken as $2+c$, where c is estimated from the relationship between D and H at the site. Data needed for determining such a relationship are easy to collect, requiring only height and diameter of a calibration sample of trees. The Sepunggur data set yielded

$$H = kD^c = 2.54D^{0.62} \quad (8)$$

where H is tree height in meters and D expressed in centimeters. The standard errors for k and c are 0.74 and 0.09, respectively, so the global equation of Niklas (1994) cited above is well within the 95% confidence interval for each parameter. The value of 2.59 for the parameter b of the biomass power equation (5) and 0.62 for the parameter c of Eq. (8) are consistent with taking $b=2+c$. We therefore suggest that the form of equation to use is

$$B = aD^{2+c} \quad (9)$$

with c estimated from a site-specific relationship between D and H . Calibration of the parameter c for the site only requires data on D and H for a sample of trees, and, once calibrated, only tree diameters are needed.

The observation that D and H tend to be related (site-specifically) has led to the omission of height measurements in many data sets, including the data sets compiled in Brown (1997). Thus, we cannot use data currently available to test if using height to calibrate models to sites leads to a reduction in V_{model} . We suggest these measurements should be standardized in future research.

7. Wood density

The biomass of a tree equals the product of the volume and the density. We hypothesize that the parameter a for a given location may be estimated as

$$a = r\rho \quad (10)$$

where r is a parameter that is constant over a wide range of conditions and ρ the average wood density for the site.

The lower value of the estimated parameter a for the Sepunggur trees as compared to the models fitted to the Brown data (Table 3) may be explained by differences in wood density. Unfortunately, wood density measurements were not obtained from all 29 trees in

the Sepunggur data set. We estimated an average wood density of the Sepunggur trees by combining reported and measured data and obtained an average value of 0.60 kg dm^{-3} ($0.53\text{--}0.67 \text{ kg dm}^{-3}$) with a range across species from 0.35 to 0.91 kg dm^{-3} (Table 2). A similar spread in density was obtained for other mixed forests: tree density measurements by Brown et al. (1995) in the Amazonian forest (Rondonia, Brazil) ranged from 0.52 to 0.80 kg dm^{-3} with an average tree density of $0.67 \pm 0.09 \text{ kg dm}^{-3}$ ($n=8$). The average density in the data sets of Brown (1997) was 0.71 kg dm^{-3} . Brown and Lugo (1984) reported a value of 0.62 kg dm^{-3} as a global average for tropical forests. Uhl et al. (1988) used a value of 0.71 kg dm^{-3} , which had been determined as the mean value of 30 common tree species in Paragominas, Para State, Brazil, while Brown (1997) (data from Reyes et al., 1992) mentioned an arithmetic mean of 0.57 kg dm^{-3} and a range of $0.40\text{--}0.69 \text{ kg dm}^{-3}$ for 428 species in Asia. Wood density may also strongly depend on location, climate, and possibly management. Although we recognize that the most accurate estimate of wood density of a mixed forest is one that is weighed according to relative frequency of species biomass in the forest, our calibration set was roughly representative with respect to species mix in Sepunggur and thus we used the density estimate of our calibration set for further analyses.

When we assume that the wood density affects the parameter a of the power equation we derive the following equations:

$$B \text{ (kg per tree)} = r\rho D^{c+2} \quad (11)$$

If we use the data from Sepunggur to estimate the value of r , we obtain r as $0.066/0.60=0.11$. Hence the model we propose is

$$B \text{ (kg per tree)} = 0.11\rho D^{2+c} \quad (12)$$

in which both c and ρ are parameters which can be estimated for each site relatively easily. Options for estimation of ρ are either from wood samples or from published values for the species present at that site. Eq. (12) is very similar to the equation by Brown et al. (1995) developed in Amazonian forests of $B=0.062\rho(0.1(\pi/4)D^2H)=0.049\rho D^2H$. If we use the value of k from Eq. (8) then (12) is equivalent to $B=0.042\rho D^2H$. The advantage of Eq. (12) over this is that it does not require H , which is easy to measure in a

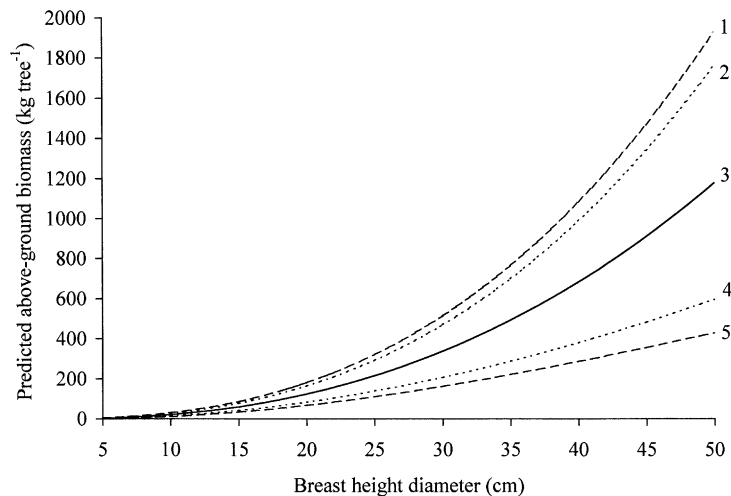


Fig. 6. Model variance (expressed as predicted value \pm the standard deviation of the model error) introduced when assuming a wood density of 0.71 kg dm^{-3} (Eqs. (1) and (5)) and a density of 0.60 kg dm^{-3} (Eqs. (2) and (4)). Eq. (3) is the predicted biomass using the equation developed for trees from Sepunggur, Sumatra (see text).

sample of trees, but can be difficult to collect for an inventory of all trees within a stand of closed forest.

Adjustment of the wood density (from 0.71 to 0.60 kg dm^{-3}) in each of the Brown equations of Table 3, reduced V_{model} from 54–63 to 36–51% of the total variance (Fig. 6) and the absolute uncertainty from ± 48 –62 to ± 41 –52% of the predicted biomass. Further improvement is expected with the incorporation of a site-specific D versus H relation.

8. Conclusions

We propose the following equation as the most appropriate equation for an 8–48 cm D tree in secondary forest in Sumatra: $B \text{ (kg per tree)} = 0.066D^{2.59}$ with D measured in cm. The uncertainty in biomass estimates using this equation for the region was largely determined by errors introduced by the scatter in the biomass of individual trees of a similar D and to a lesser extent by uncertainty in the estimated parameters. Estimated uncertainties became very large when similar models developed for the humid tropics were applied to trees of a specific D . Thus, the biggest improvement in predictions can be obtained by better understanding when to apply which model. Site-specific ρ and D versus H relations were two factors whose incorporation into the model could reduce

estimate errors. Assuming that wood density affects the parameter a of the power function and that the above-ground biomass is proportional to D^2H , we converted our site-specific model into a more flexible model: $B \text{ (kg per tree)} = 0.11\rho D^{2+0.62}$. Adapting the Brown equations to reflect a lower average ρ reduced model errors to 36–51% of the total uncertainty and the absolute uncertainty to ± 41 –52% of the predicted biomass of individual trees. Our results supported the hypothesis that ρ can explain part of the variation in models and should be included as a calibration variable, where cutting and weighing of the trees is not possible to obtain a site-specific equation. Further validation of the model is needed to determine if our hypotheses hold for data sets other than those compiled by Brown (1997) and the set measured for this study. Furthermore, forest stand D distributions should be included to estimate uncertainty for forest stands rather than individual trees.

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