Error propagation and scaling for tropical forest biomass estimates

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The above-ground biomass (AGB) of tropical forests is a crucial variable for ecologists, biogeochemists, foresters and policymakers. Tree inventories are an efficient way of assessing forest carbon stocks and emissions to the atmosphere during deforestation. To make correct inferences about long-term changes in biomass stocks, it is essential to know the uncertainty associated with AGB estimates, yet this uncertainty is rarely evaluated carefully. Here, we quantify four types of uncertainty that could lead to statistical error in AGB estimates: (i) error due to tree measurement; (ii) error due to the choice of an allometric model relating AGB to other tree dimensions; (iii) sampling uncertainty, related to the size of the study plot; (iv) representativeness of a network of small plots across a vast forest landscape. In previous studies, these sources of error were reported but rarely integrated into a consistent framework. We estimate all four terms in a 50 hectare (ha, where $1 \text{ ha} = 10^4 \text{ m}^2$) plot on Barro Colorado Island, Panama, and in a network of 1 ha plots scattered across central Panama. We find that the most important source of error is currently related to the choice of the allometric model. More work should be devoted to improving the predictive power of allometric models for biomass.

Keywords: above-ground biomass; allometric equation; error propagation; sampling; tropical forest

1. INTRODUCTION

Permanent sampling plots have long been used in ecological studies for assessing how much biomass is held in ecosystems (Olson *et al.* 1983; Fearnside 1996; Brown 2002). Tree AGB is strongly correlated with trunk diameter (Brown & Lugo 1992; Brown 1997; Clark *et al.* 2001*a*), and it is therefore possible to use forest inventory data to estimate the stocks and changes in AGB in those inventories. Recently, plot data have been influential in creating new hypotheses on the dynamic coupling between tropical forests and the atmosphere (Phillips & Gentry 1994; Phillips *et al.* 1998; Malhi & Grace 2000). It has been suggested that the tropical forest biome could be responding en masse to global change, leading to shifts in species composition and to an overall increase of the turnover rate (Phillips & Gentry 1994; Phillips *et al.* 1998; 2002*a,b*). This renewed interest in tropical forest inventories has also motivated a new literature on methodological aspects that have greatly improved our confidence in biomass data estimated from plots (Sheil 1995; MacDicken 1997; Condit 1998; Higuchi *et al.* 1998; Chave *et al.* 2001; Clark *et al.* 2001*a,b*; Clark 2002; Phillips *et al.* 2002*a*; Brown 2002).

Nevertheless, difficulties in assessing data quality in forest inventories lead to continuing debate on the functional

response of tropical forests to global change (Clark 2002; Chave *et al.* 2003; Baker *et al.* 2004*b*). The biomass stocks of tropical forests remain poorly resolved at the regional scale (Fearnside 1996; Houghton *et al.* 2001). Indeed, it is difficult to integrate site-specific and heterogeneously collected data to draw regional-scale conclusions about tree densities, turnover rates or biomass stocks of tropical forests, and it thus seems precarious to extrapolate such local data to larger scales without assessing how representative these data are. Dynamic global vegetation models of the new generation have made remarkable progress towards integrating ecological processes across scales for tropical forests (Hurtt *et al.* 1998; Bugmann & Solomon 2000; Foley *et al.* 2000; Cramer *et al.* 2001, 2004; Moorecroft *et al.* 2001), but these models need to be calibrated.

Figure 1 depicts one strategy for converting forest plot data into regional-scale AGB estimates (Brown *et al.* 1989; Brown 1997; Houghton *et al.* 2001). Each tree in a plot is measured, tagged and identified (Clark 2002; Phillips *et al.* 2002*a*); an allometric equation is used to relate its diameter to an AGB estimate (Brown 1997). The plot-level estimate is then summed over all the trees to obtain a stand-level AGB estimate. For carbon sequestration issues, the quality of this estimate depends on the plot size. In addition, the landscape-scale environmental variability should be integrated by replicating the measurement in other plots of the same forest (Clark & Clark 2000; Keller *et al.* 2001; Nascimento & Laurance 2002). These steps integrate a variety of techniques that all contain some
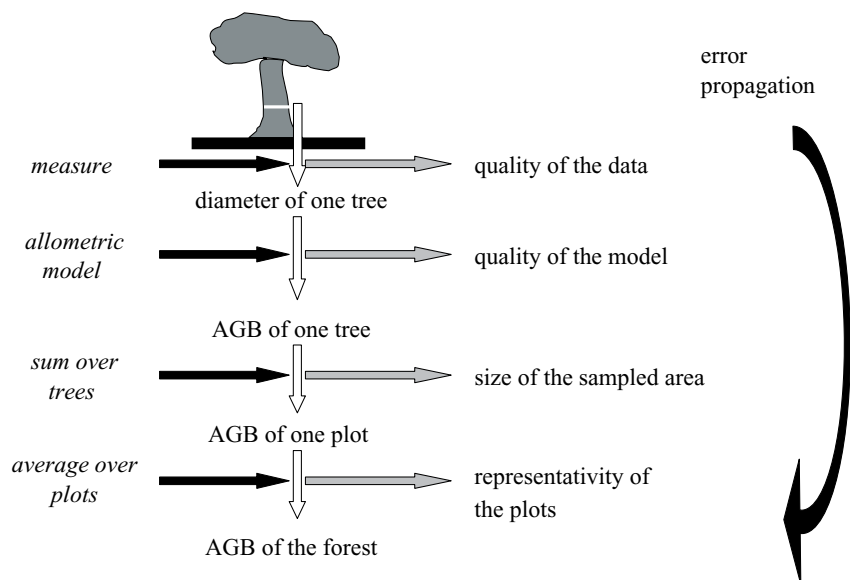
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Figure 1. The error propagation for estimating the AGB of a tropical forest from permanent sampling plots.

uncertainty, yet there is no consistent methodology for propagating uncertainty across scales (but see Ketterings *et al.* 2001). Because errors due to these problems add up, each needs to be quantified carefully and independently. In the present contribution, we assess the different sources of error associated with AGB estimates from forest inventories, and present calculated examples for a moist tropical forest of central Panama.

2. METHODS

(a) *Uncertainty on tree level AGB estimate*

The first potential source of error is the tree measurement process. Stems, of diameter 10 cm or greater, at 130 cm above the ground or above any trunk deformity, are tagged, located and their diameter D is measured. As any ecological variable, D is likely to be measured with some imprecision, and special conventions should be applied (Sheil 1995; Condit 1998; Phillips *et al.* 2002*a*). In particular, special attention should be paid to irregular-shaped trunks.

We denote the standard error associated with the diameter measurement as σ_D. It is expected to be an increasing function of D. When a height measurement H is also taken, the related error is denoted σ_H. These two error terms covary as D and H are positively correlated in most woody plants. Finally, a wood specific gravity value ρ (oven-dry weight over green volume; Chudnoff (1984)) can be associated with each tree, either by direct measurement (e.g. from tree cores) or using databases that provide the mean ρ for the species to which the tree belongs (Brown 1997; J. Chave, T. Baker and H. C. Muller-Landau, unpublished results). The corresponding error σ_ρ could be due to a misidentification of the tree, or to a variation in ρ within or among conspecific trees (Carvalho *et al.* 1995; Wiemann & Williamson 2002).

Errors in trunk diameter, height or density measurement all result in error in estimating the AGB, which is usually taken from an allometric model of the form AGB = $f(D,H,\rho)$. This error is propagated to the AGB estimate through the allometric model by expanding the model function f in Taylor series. In Appendix A, we compute the measurement s.d. for the AGB estimate, σ_M.

In addition, there is a second source of error due to the construction of the allometry: the model's parameters are usually estimated using a regression on the log-transformed variables:

$$\ln(\text{AGB}) = \ln\left(f(D,H,\rho)\right) + \xi. \tag{2.1}$$

The residuals ξ represent the departure from a perfect allometry, and are normally distributed. The s.d. σ of these residuals represents the uncertainty in the AGB estimation due to the allometry itself. Baskerville (1972) noticed the following bias: the expectation of AGB is $\langle \text{AGB} \rangle = f(D,H,\rho)\langle \exp(\xi) \rangle$, and it is incorrect to state that $\langle \exp(\xi) \rangle$ is equal to $\exp(\langle \xi \rangle) = \exp(0) = 1$. Indeed, the random variable $\exp(\xi)$ is log-normally distributed and the expectation of $\exp(\xi)$ is $\langle \exp(\xi) \rangle = \exp(\sigma^2/2)$. This last term is often called the correction factor, CF (Brown *et al.* 1989; Ter-Mikaelian & Korzukhin 1997; Hughes *et al.* 1999). An unbiased estimate of AGB is, therefore

$$\langle \text{AGB} \rangle = \text{CF} \times f(D,H,\rho). \tag{2.2}$$

The uncertainty on the estimate of AGB associated with the allometric model is measured by the s.d. $\sigma_A = \sqrt{\text{CF}^2 - 1} \times \langle \text{AGB} \rangle$. Thus, for a given allometric model, one can estimate both the expected AGB held in a tree and the s.d. of this estimate.

In the following, we assume that the measurement and the allometric uncertainties are independent sources of variability. The overall uncertainty on the AGB estimation of a single tree therefore is $\sigma_A + \sigma_M$.

(b) *Allometric model selection error*

Ideally, as is the case for temperate trees (Ter-Mikaelian & Korzukhin 1997), each species should have its own biomass equation, based on a large sample size. This programme is unrealistic for tropical forests. Tropical forest allometric models used for AGB estimation suffer from three important shortcomings: (i) they are constructed from limited samples; (ii) they are sometimes applied beyond their valid diameter range; (iii) they rarely take into account available information on wood specific gravity.

Many of the published models are based on harvest experiments performed in a single forest and based on, typically, less than 50 harvested trees. We suggest that the number of trees

used to calibrate allometric models is a major source of variation of the AGB estimate when different models are selected. We used several published allometric models to assess this problem of model selection. We selected six published allometric models reconstructed directly from the original datasets (trees 10 cm or more in diameter) with 39–187 sampled trees (Lescure *et al.* 1983; Yamakura *et al.* 1986*a*,*b*; Overman *et al.* 1994; Joyce in Brown 1997; Araújo *et al.* 1999; Chambers *et al.* 2001). All of these models were used to estimate AGB stocks outside the biogeographic zone where they were constructed, either alone, or included in pan-tropical allometric models. Further, they all used similar sampling strategies (but the dataset of Joyce cited in Brown 1997 remains poorly documented). To test for variation among allometric models' predictions, we use a pan-tropical equation that relates the AGB (in kilograms) to the trunk diameter (in cm) and the wood specific gravity (in grams per cubic centimetre) deduced from a compilation of 634 trees of diameter 10 cm or greater (J. Chave (and 11 others), unpublished results):

$$f(D, \rho) = \frac{\rho}{0.6} \exp(-3.742 + 3.450 \ln(D) \qquad (2.3)$$
$$- 0.148 \ln(D)^2).$$

We independently assessed the model selection effect by using a rarefaction technique on the pan-tropical dataset. A set of 10–400 trees was drawn at random from the sample of 634 trees, and it was used to construct a regression model from which we estimated the AGB of the 50 ha BCI plot. We replicated this procedure 1000 times, and computed the variance among our estimates. This enabled us to assess the true error associated with using a model constructed from an imperfect knowledge of the allometric relationships in tropical trees.

Second, many published allometric models lack reliable data for the largest diameter classes, so they cannot be used to estimate the AGB held in large trees (Clark & Clark 2000; Houghton *et al.* 2001). We therefore assessed the potential error caused by extrapolating the models beyond their range of applicability. This uncertainty is of the order estimated AGB for the largest trees, and more importantly, it does not average out for large sample sizes, because it reflects our limited knowledge of the model itself for the largest diameter classes. We attempted to minimize this uncertainty as much as possible. We used the pan-tropical equation to correct for the AGB of extrapolated trees for the other published models, as we have the best confidence in this equation for the largest trees.

Finally, few of these models use information on wood specific gravity, known to vary over a fivefold range in tropical tree species. Including wood specific gravity as a predictive variable improves the quality of the AGB estimate. For instance, in the BCI 50-ha plot, large trees tend to have a much lower wood density than small trees (see figure 2). We corrected the published allometric models by including a dependence on wood specific gravity of the form

$$\langle \text{AGB} \rangle = \text{CF} \times \frac{\rho}{\rho_{av}} f(D), \qquad (2.4)$$

where the AGB estimate is a linear function of tree-level wood specific gravity divided by the average specific gravity for the plot where the allometric equation was constructed. The parameter ρ_{av} is the ratio of the total oven-dry weight of the trees used to construct the equation, over their fresh volume. Multiplying directly the model by a factor ρ/ρ_{av} as above is only valid if the trees used to construct the original allometry all have the same
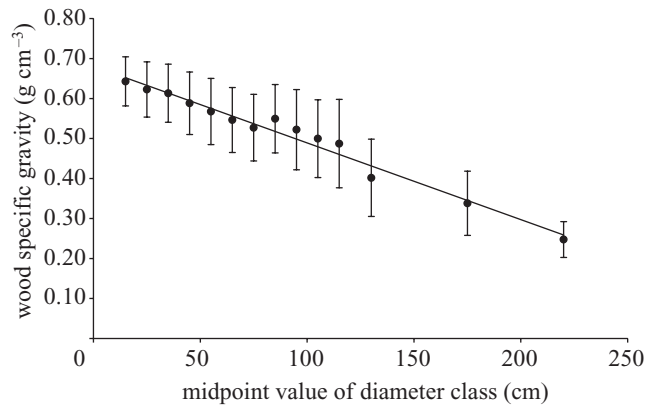
Figure 2. Wood specific gravity for different diameter classes in the BCI 50 ha plot. The decrease in wood density was significant across size classes ($p < 0.001$, $r^2 = 0.97$).

specific gravity. If, in this dataset, large trees have lighter wood than small trees, then this factor would induce a systematic bias. We used a compilation of tree harvest datasets and confirmed that there was no such bias (results not shown; J. Chave (and 11 others), unpublished results).

(c) *Minimal single plot size*

Tree plots are usually 0.2–100 ha in size (Houghton *et al.* 2001). Methodologies related to the establishment of plots have been covered in the literature (Sheil 1995; Condit 1998). More recently, the limitations of this methodology in relation to the estimation of AGB stocks and changes have also been covered (Clark *et al.* 2001*a*,*b*; Clark 2002; Phillips *et al.* 2002*a*). For assessing the uncertainty on the stand-level AGB estimate in one plot, one should consider how well the census has been performed, and how large the census was. We refer to this as the within-plot sampling uncertainty.

Methodological sources of error include the incorrect estimation of the plot area, trees missed, measured twice or dead trees counted as alive. In addition, tree-level errors average out in large plots, and for this reason too it is advisable to establish large permanent sampling plots. This aspect has been largely overlooked in the literature before the 1990s. Klinge & Rodrigues (1973) wrongly concluded that one 0.2 ha plot was enough to estimate tree AGB with good confidence, by assuming that the AGB was normally distributed among $10 \text{ m} \times 10 \text{ m}$ subplots. Since rare large trees contribute a large fraction of the overall AGB, the distribution of AGB across $10 \text{ m} \times 10 \text{ m}$ subplots is far from normal (Chave *et al.* 2003).

Lianas, multi-stemmed trees and re-sprouting trees are often not recorded during the censuses. This leads to an underestimation of the stand-level AGB. Correction factors have been computed in studies where this information is available, and the uncertainty on these correction factors contributes to the stand-level error. Similarly, BGB is usually estimated from other studies' averages (Malhi & Grace 2000; Houghton *et al.* 2001), more rarely from diameter–BGB allometries (Ovington & Olson 1970). In this study, we have no data on lianas or on BGB, and we cannot therefore consider errors in those areas.

In the Panama data, trees less than 10 cm in diameter (and 1 cm or more) were measured in the whole 50 ha BCI plot and in sub-plots of the Marena plot network of plots (see § 3). For trees less than 10 cm in diameter, we used a single equation modified from the model devised by Hughes *et al.* (1999) for a

moist tropical forest of south Mexico (Los Tuxtlas). The model was

$$f(D,\rho) = \frac{\rho}{\rho_{av}}\exp(-1.9703 + 2.1166\ln(D)). \qquad (2.5)$$

(d) *Landscape-scale representativity*

A single plot corresponds to one sample of the forest, and it is unlikely to represent the whole landscape-scale environmental variability. Among the possible biases, there is a tendency for researchers to select attractive forests (the 'majestic effect' of Sheil 1995) or to avoid disturbed forests. The landscape-level AGB estimate should be assessed by establishing a network of plots randomly distributed over the landscape, to assess the variability of forest types.

3. MATERIAL AND STUDY SITES

We quantified the uncertainty associated with the estimation of AGB of a single tree, assuming that the allometric method is unbiased, for the forest of the Panama Canal Zone, central Panama. We have already provided estimates of the AGB held in the 50 ha permanent sampling plot on BCI. We used diameter measurements for over 200 000 trees of diameter 1 cm or greater, combined with tree heights modelled from diameter–height regressions that had been developed for 80 common tree species. We used literature data on wood specific gravity for 123 species occurring in the BCI plot (Chave *et al.* 2003). Here, we use the BCI plot and reassess various sources of error in the previously published AGB estimate. In the present contribution, we use only the most recent census of the BCI plot, conducted during the year 2000.

We addressed the issue of within-plot sampling using sub-plots within the BCI plot. We also investigated the landscape-scale sampling problem, by using a network of 45 plots distributed across the watershed of the Panama Canal, henceforth called the Marena plots. These plots were originally set up to study the variation of floristic composition in forests across the north–south climatic gradient of this region (Pyke *et al.* 2001), spatial turnover in diversity (Condit *et al.* 2002) and differential forest response to drought (Condit *et al.* 2004). Each plot is 1 ha in size and has all trees of diameter 10 cm or greater tagged, mapped and identified to species or morphospecies, except for 154 trees out of 22 955 (0.7%) that remain unidentified. A total of 775 species or morphospecies were identified. In 35 of the plots, trees of diameter 1 cm or greater were censused in central sub-plots of 40 m × 40 m (0.16 ha), whereas all trees of diameter 1 cm or greater were censused in another 10 1 ha plots. Finally, trees of diameter 10 cm or greater were inventoried in nine additional smaller plots (0.32 ha each). This represented a total sampling effort of *ca.* 49 ha. These plots spanned a variety of environmental types and successional ages (Appendix B; see also Pyke *et al.* (2001); note that some errors in table 1 of Pyke *et al.* (2001) have been corrected in Appendix B).

4. RESULTS

(a) *Uncertainty on tree-level AGB estimate*

The uncertainty associated with the diameter measurement in the BCI forest was discussed in Condit *et al.*

(1993). To estimate rates of error, we performed a double-blind re-measurement of 1715 trees in 1995 and 2000 (Condit 1998) and fitted the discrepancies with a sum of two normal distributions. The first describes small errors and has an s.d. (SD_1) proportional to the trunk diameter; the second has a fixed larger s.d. (SD_2). The 1715 errors were best fit with $SD_1 = 0.0062 \times D + 0.0904$, $SD_2 = 4.64$ (all units in centimetres), with 5% of the trees subject to the larger error. For example, the diameter of a 30 cm tree has a typical error of 0.27 cm (95% probability) or of 4.63 cm (5% probability). The uncertainty associated with the height estimate is due to the inherent measurement problem of tree height. Tree heights were taken for over 1000 trees of diameter 10 cm or greater in 80 different species. Based on this dataset, we assume that the error in height is *ca.* 10% of the estimated value.

We assume an s.d. of 10% of the mean wood specific gravity for all species. This figure is based on 50 neotropical tree species for which more than six different estimates were available from a total of 43 literature sources (see Appendix C). A detailed report on this dataset is beyond the scope of the present publication and will be the topic of a forthcoming publication (J. Chave, T. Baker and H. C. Muller-Landau, unpublished results). For species missing wood specific gravity estimates, we used a mean of 0.58 g cm^{-3} and the same error of 10%.

The measurement error on the AGB can be deduced from the equations provided in Appendix A for the pantropical model used for trees of diameter 10 cm or greater. We find $\sigma_M = 0.165\langle AGB \rangle$ and $\sigma_A = 0.313\langle AGB \rangle$. Hence, the uncertainty on the AGB estimation of a single tree of diameter 10 cm or greater is 47% of the estimated AGB, partitioned into 31% due to the allometric model and 16% due to the measurement uncertainty. However, this error averages out at the stand level. For the model used for trees of diameter less than 10 cm (equation (2.5)), the uncertainties are $\sigma_M = 0.234\langle AGB \rangle$ and $\sigma_A = 0.547\langle AGB \rangle$, and this model predicts that 7.66 Mg ha^{-1} are in trees less than 10 cm in diameter.

(b) *Allometric model selection error*

The different allometric models estimated AGB from 215 to 461 Mg ha^{-1} with a mean of 347 Mg ha^{-1} and an s.d. of 77 Mg ha^{-1}, before correcting for variation in wood specific gravity (table 1).

Using the rarefaction method, we estimated the s.d. differently because of the choice of the allometric model (figure 3). For a sample size of 300 trees, we found a mean AGB estimate of 263 Mg ha^{-1} with an s.d. of 3.1% of the mean, but this figure increased to over 10% of the mean for samples of 50 trees or less.

Equations that included wood specific gravity predicted 218–334 Mg ha^{-1} in trees of diameter 10 cm or greater (mean: 284 Mg ha^{-1}, s.d.: 37 Mg ha^{-1} or 13% of the mean).

Next, we assessed the uncertainty due to the AGB estimation in large trees for the same eight allometric models. The extrapolated AGB represented 7–30% of the total AGB, depending on the model. We used the pan-tropical equation to correct for the AGB of extrapolated trees. In the 50 ha plot, 46 trees are larger than 148 cm in diameter, the larger diameter in the sample used to construct the

Table 1. AGB estimates (in megagrams per hectare) for the BCI 50 ha forest based on eight different equations involving diameter, developed for different forests.

(The AGB estimate for trees of diameter 10 cm or greater varied significantly among equations, even when the problem of using an equation beyond its acceptable range was corrected. We provide the reference for the original data, the region of this study, the number of trees of diameter 10 cm or greater, the maximal diameter. The column headed 'order' refers to the order of the polynomial regression of ln(AGB) versus ln(D) (chosen to minimize the variance in the residuals, Chambers *et al.* (2001)), and column CF provides the correction factor for this regression. max dbh, maximum stem diameter at breast height.)

reference	location	number of trees	max dbh	ρ_{av}	order	CF	uncorrected AGB	correction ρ/ρ_{av}	correction large trees + ρ/ρ_{av}
Araújo *et al.* (1999)	Para, Brazil	127	138	0.68[a]	2	1.070	375	307	315
Chambers *et al.* (2001)	Manaus, Brazil	161	120	0.69[b]	2	1.065	330	266	278
Overman *et al.* (1994)	Colombia	51	98.2	0.62[e]	1	1.046	351	292	274
Yamakura *et al.* (1986*a*,*b*)	Kalimantan, Indonesia	38	130.5	0.7[c]	1	1.074	461	334	310
A. Joyce, in Brown (1997)	Costa Rica	92	116	0.52[d]	1	1.028	215	218	220
Lescure *et al.* (1983)	French Guiana	187	118	0.66	1	1.080	428	322	288
Chave *et al.* (in prep.)	pan-tropical	634	148	0.6	1	1.092	324	278	268
Chave *et al.* (in prep.)	pan-tropical	634	148	0.6	2	1.091	293	260	260

[a] From species-level information, assuming a fresh wood specific gravity of 1.05.
[b] From a neighbouring forest, value published by Fearnside (1997).
[c] Estimated from information in Yamakura *et al.* (1986*a*,*b*) and in Suzuki (1999).
[d] Low-quality estimate from the value of the dominant species at La Selva (*Pentaclethra macroloba*).
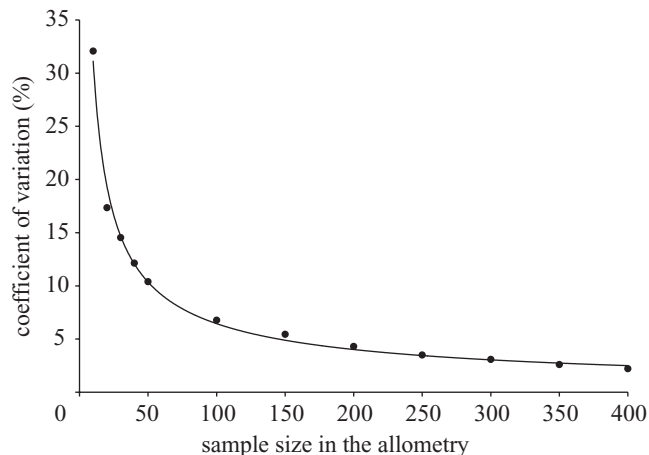[e] Estimated from combining allometric equations published in Overman *et al.* (1994).

Figure 3. Coefficient of variation (CV = 100 × s.e.m. over mean AGB) as a function of the sample size used to construct the allometric equation. Each point corresponds to the CV constructed from 1000 independent selections out of the pan-tropical dataset of 632 trees. For example, with allometric equations constructed from 50 trees, the s.e.m. was 10% of the mean AGB.

pan-tropical equation. The largest tree is a *Hura crepitens* of 246.8 cm in diameter. Approximately 17 Mg ha^{-1} was held in trees greater than 148 cm in diameter, which corresponds to the largest tree used to construct the pan-tropical model. The BCI forest has a high density of very large trees, and this problem is unlikely to be as important in other forests. When corrected for very large trees, the predicted AGB estimate for the BCI forest ranged between 220 and 315 Mg ha^{-1} (mean: 277 Mg ha^{-1}, s.d.: 30 Mg ha^{-1} or 11% of the mean). The 'best estimate' equation predicted 260 Mg ha^{-1} for trees of diameter 10 cm or greater, very close to the value reported in Chave *et al.* (2003).

Table 2. Uncertainty in the BCI 50 ha plot, and normality of the AGB estimates in sub-plots of various sizes.

(The normality test was performed on the skewness and on the kurtosis. Asterisks show the significance level of the normality test (*$p < 0.10$; **$p < 0.05$). For sub-plots of size 50 m × 50 m and greater, the distribution was normal (2000 census; cf. Chave *et al.* (2003)).)

sub-plot size (m)	number of plots	s.d.	skewness	kurtosis
10 × 10	5000	385.08	5.42	47.05
20 × 20	1250	187.64	2.57	10.62
25 × 25	800	149.44	1.88	5.34
20 × 50	500	119.52	1.54	3.47
50 × 50	200	77.55	0.57*	−0.24**
100 × 100	50	42.01	−0.06**	−0.12**

(c) *Minimal single plot size*

We used the BCI 50 ha plot to evaluate the stand-level sampling uncertainty, under the assumption that the allometric model is perfect. The tree-level uncertainties average out at the stand scale. For example, in a typical plot of one-quarter of a hectare, the error on the AGB estimate is 10% of the mean. In Chave *et al.* (2003), we assessed the uncertainty on our AGB estimate based on our limited sampling of the forest. We showed that the AGB held in the sub-plots of a 50 ha plot is not autocorrelated, even for very small sub-plots: two neighbouring sub-plots of size 10 m × 10 m to 100 m × 100 m are not significantly more similar in their AGB stock than two randomly chosen plots. We also developed a test of normality for the data. Table 2 gives the first moments of AGB distributions, together with tests of normality, for sub-plots of varying size. This shows that the size of one-quarter of a hectare is the minimal size such that the normality criterion is

satisfied in this forest, in agreement with Clark & Clark (2000, section 3.5). Although this figure might vary slightly with the stem density in the plot, it can be taken as a reasonable guideline. In Phillips *et al.* (1998), only two of the 68 plots (Queensland, Australia) were less than one-quarter of a hectare in size, so this constraint in the error assessment is not too stringent.

(d) *Landscape-scale representativity*

Several environmental factors, e.g. edaphic and topographic constraints or climatic gradients, might bias the extrapolation of AGB estimates to the landscape scale. This is a serious problem if the plot is located in a forest patch that is not representative of the surrounding forest. Recent studies suggest that a total sampling size of *ca.* 5 ha, or 20 plots of one-quarter of a hectare allows a landscape-scale estimation of the AGB with an error of ± 10% within 95% confidence (Clark & Clark 2000; Keller *et al.* 2001). On BCI, we used the AGB estimates from the 200 one-quarter of a hectare sub-plots to assess a similar measure of uncertainty on AGB, and we found that it was 7% of the mean (Chave *et al.* 2003). However, this estimate cannot be thought of as a landscape-scale one, as it results from a single plot measurement.

The landscape-scale variation of the AGB estimate for the BCI forest was therefore assessed using the Marena dataset, a network of plots scattered across the Panama Canal watershed (Appendix B). The mean BA in trees of diameter 1 cm or greater for the Marena plots was 31.3 ± 5.5 m^2 ha^{-1} (s.d. computed across plots), similar to the within-plot BCI value (30.6 ± 5.1 m^2 ha^{-1}). One plot was an outlier (plot 39: 56.2 m^2 ha^{-1}), owing to the presence of a massive *Ficus* (222 cm diameter) in a small plot. We estimated a landscape-scale AGB estimate of 245 ± 57 Mg ha^{-1} (see plot-level results in Appendix B). This high variance reflects the variability of environmental conditions, and of variations in forest disturbance history.

We then performed an ANOVA to assess whether the environmental factors accounted for part of this variability. First, we ran a linear model (SAS 8.02, SAS Institute Inc.) including annual rainfall, length of the dry season, plot age, and geology of the substrate, and excluding the outlying plot number 39. The geology factor was not significant ($n = 49$, $p = 0.16$), but the three other factors were significant ($p < 0.002$). Plot age alone explained only 14% of the variance, probably because of the broad and somewhat ambiguous definition of this parameter in our study. We re-ran the model with the climate data only, and found that both parameters were significantly correlated with the AGB estimate ($n = 54$, $p < 0.001$ for both variables) and explained 41% of the variance. The correlation between rainfall and AGB was positive, whereas that between length of the dry season and AGB was negative.

5. DISCUSSION

(a) *Relative importance of the sources of error*

We have assumed that the AGB stock of a forest is estimated from sampling plots that have been correctly set up and measured. We did not examine the importance of biases such as the measurement of trees at breast height when the stem is buttressed, although those can be present in some datasets. However, we did consider the error terms that are unavoidable in ecological studies: for example, imprecision on the measurements, and on the estimate of wood specific gravity. These are obvious sources of error, yet we contend that they are not the largest ones.

Analysing the structure of the existing allometric regressions, we found an intrinsic source of error not due to the size of the census plot, but to the sample available to construct the allometric model itself (i.e. harvested trees). For the 50 ha plot, an error of greater than 20% on the AGB estimate was due to the choice of the allometric equation. We then corrected these equations by including wood specific gravity and showed that AGB varied significantly across diameter classes. This reduced the error to *ca.* 13% of the mean. Because none of these equations was designed to estimate the AGB of trees beyond a limited range, we used a pan-tropical regression model (i.e. based on the largest sample size and with the broadest diameter range) to estimate the AGB of the largest trees. This also led to a significant reduction of the error, to *ca.* 10% of the mean AGB. Finally, we included wood specific gravity in the allometric equation, which resulted in a significant reduction the across-model variation.

This intermodel comparison was supplemented by a rarefaction study of a pan-tropical dataset of weighted trees. The quality of an AGB estimate should depend on the size of the dataset used to construct the allometric model. The dataset was a compilation of various literature studies, and the data might be heterogeneous. However, we suspect that the trend is a general one. This implies that allometric biomass models based on regional or pan-tropical compilations should be preferred to site-specific models based on small sample sizes.

The uncertainty resulting from the use of small plots (type 3 error) was also considered. We reinforce previous results advocating the use of plots at least 0.25 ha in size (Laurance *et al.* 1999; Clark & Clark 2000; Keller *et al.* 2001). For the uncertainty related to the representativity of a network of such plots in a landscape (type 4 error), we confirmed that an area of *ca.* 5 ha is necessary to estimate the landscape-scale AGB to within 10% of the mean.

As a synthesis of our results, we present a summary in table 3. For a total sampled area of 5 ha, our study reveals that the cumulated uncertainty on the estimate is *ca.* 20% of the mean, with only a small fraction due to measurement error (assuming unbiased measurement), 10% due to the allometric error and 10% due to the sampling error. With larger plots, one can reduce the sampling uncertainty but not the allometric uncertainty. We stress that such conclusions may vary, depending on the forest under study.

(b) *Comparison with other landscape-scale studies*

Several studies report results on AGB estimates for forests at the landscape scale. We compare our results to three similar studies: one at Los Tuxtlas Biological Station, southern Mexico (Hughes *et al.* 1999, 2000), one at La Selva Biological Station, Costa Rica (Clark & Clark 2000), and one in the Manaus region, central Brazilian Amazon (Nascimento & Laurance 2002).

The study done in Mexico used a nested sampling design to estimate the AGB in four plots *ca.* 0.79 ha in

Table 3. Summary of the sources of error in the AGB estimation of a tropical forest.
(Type 1 error refers to the error made in the estimation of the AGB held in a single tree; this error averages out in plots. Type 2 error is that caused by the choice of the allometric model. Types 3 and 4 are two types of sampling error, which can be minimized by large-sized, multi-plot, censuses. The reported values are examples for the forests of the Panama Canal watershed.)

error type		s.e.m. (percentage of the mean)	type of data
1. tree level error	trees > 10 cm diameter	48	BCI plot—pan-tropical allometric model
	trees < 10 cm diameter	78	
2. allometric model	before ρ correction	22	BCI plot—eight allometric models
	after ρ correction	13	
	after large tree correction	11	BCI plot—pan-tropical allometric model
3. within-plot uncertainty	0.1 ha plot	16	
	0.25 ha plot	10	
	1 ha plot	5	
4. among-plot uncertainty		11	Marena plots—pan-tropical allometric model
total	50 1 ha plots, after ρ and large tree corrections	24	—

size (Hughes *et al.* 2000; table 5). A mean AGB of 403 ± 50 Mg ha^{-1} was found for this forest. However, they report a very high density of large trees (as many as 23 trees greater than 70 cm in diameter per hectare), almost twice as high as the values commonly found in neotropical rainforests. Thus, it is possible that diameter measurements were not taken above buttresses, which would greatly overestimate the true AGB (Clark 2002).

The second study took place in the La Selva forest, characterized by the overdominance of one tree species (*Pentaclethra macroloba* (Willd.) Kuntze, Fabaceae), which constitutes over 35% of the AGB estimate (Clark & Clark 2000). Clark & Clark (2000) used three sampling designs to assess the landscape-scale variability (three 4–4.4 ha plots, 18 0.5 ha plots and 1170 0.01 ha plots). They report a low AGB estimate (160.5–186.1 Mg ha^{-1}) and an among-site sampling error of 4.2–8.4 Mg ha^{-1}, based on trees of diameter 10 cm or greater. Their sampling error is consistent with that found in the present study, and measurement error was minimized as much as possible. Though they did not account for the allometric error, and their allometric equation may significantly underestimate tree AGB, it is possible that the La Selva forest indeed holds less AGB than the forests of central Panama.

The third study took place in the forests of the central Amazon, in the BDFF project north of Manaus. This forest is characterized by the rarity of very large trees and the abundance of hardwood species. Nascimento & Laurance (2002) reported an AGB estimate of 325 ± 31 Mg ha^{-1} ($n = 20$ 1 ha plots). The AGB held in small trees (less than 10 cm in diameter) represented 21 Mg ha^{-1}. This study used an allometry comparable to ours, and suggests that the central Amazonian forests hold, on average, *ca.* 20% more AGB than the forests of central Panama, although the density of large trees is much lower. This is a clear illustration of the importance of including wood specific gravity in pan-tropical allometric models.

In general, the lack of standardization to estimate tropical forest AGB results in great difficulty in comparing the published values, and we hope that collaborative efforts will help resolve this problem. The collaborative project

summarized in Malhi *et al.* (2002) is an important step forward in this direction. Using the data of this project, Baker *et al.* (2004a) have reported results for 59 forest plots across Amazonia, for a total sampled area of *ca.* 80 ha. They investigated three regions: northwestern Amazonia, southwestern Amazonia, and central and eastern Amazonia, and found significant difference among these regions: using the equation of Chambers *et al.* (2001) they predicted 288, 258 and 347 Mg ha^{-1} in these regions, respectively. Using another equation, however, they consistently found AGB figures 20% lower, confirming the crucial importance of the choice of the allometric model.

(c) *Recommendations*

Using allometric models to convert tree diameter data into stand-level AGB estimates often leads to methodological errors, and we have therefore quantified those errors. Plots where very many large trees are recorded (e.g. more than 15 trees greater than 70 cm in diameter per hectare) should be double-checked. Only large enough stands should be included in the analysis (greater than 0.25 ha). These factors have fortunately been taken into account in the most recent AGB estimation protocol at the scale of a regional forest network (Baker *et al.* 2004b). Moreover, allometric equations constructed from very small sample sizes and from trees spanning a small diameter range should be avoided, and only equations based on at least 100 weighted trees should be used. Pan-tropical allometric models are, for the moment, the best available ones. The AGB of large trees should be carefully estimated, especially if their diameter exceeds the range for which the use of the allometric equation is valid. In this case, only a 'best guess' estimate can be produced. Wood specific gravity should be included in the allometric equation wherever possible. AGB held in life forms other than trees of diameter 10 cm or greater should also be estimated (in particular trees less than 10 cm in diameter, lianas, and bamboos, when present). This may represent as much as 10% of the total AGB stock. The landscape-scale variability and issues of spatial autocorrelation of the data should be carefully investigated.

APPENDIX A

The measurement uncertainty on diameter, height and wood density can be directly added to the model uncertainty: assuming the expected data D_e, H_e, ρ_e deviate by small amounts δD, δH, $\delta\rho$ normally distributed with zero mean and with standard deviations σ_D, σ_H, σ_ρ. This is propagated to the AGB estimate through the allometric model by expanding the model function f in the Taylor series. Moreover, we assume that $f(D, H, \rho) = f_1(D) f_2(H) f_3(\rho)$. The uncertainty on the estimate of AGB associated with the measurement is measured by the variance

$$\frac{\sigma_M^2}{AGB^2} = \frac{\sigma_D^2}{D^2}\left(\frac{\partial\ln(f)}{\partial\ln(D)}\right)^2 + \frac{\sigma_H^2}{H^2}\left(\frac{\partial\ln(f)}{\partial\ln(H)}\right)^2 + \frac{\sigma_\rho^2}{\rho^2}\left(\frac{\partial\ln(f)}{\partial\ln(\rho)}\right)^2$$
$$+ 2\frac{\sigma_{DH}}{HD}\frac{\partial\ln(f)}{\partial\ln(H)}\frac{\partial\ln(f)}{\partial\ln(D)} .$$

$\partial\ln(f)/\partial\ln(D)$ is the partial derivative of $\ln(f)$ with respect to $\ln(D)$, and $\sigma_{DH} = \langle\delta D\delta H\rangle$ represents the covariance between D and H. If, for example, the chosen model does not depend on the total tree height, then $\partial_H f = 0$, and height does not contribute to the measurement uncertainty. Most allometric models are of the form

$$f(D,H,\rho) = aD^\alpha H^\beta \rho^\delta.$$

For this class of models, the measurement error reads

$$\sigma_M = \langle AGB\rangle\left(\alpha^2\frac{\sigma_D^2}{D^2} + \beta^2\frac{\sigma_H^2}{H^2} + \delta^2\frac{\sigma_\rho^2}{\rho^2} + 2\alpha\beta\frac{\sigma_{DH}^2}{DH}\right)^{1/2}.$$

For example, if one assumes a 5% uncertainty on the measurement of diameter, 10% uncertainty on both height and wood density, a correlation coefficient of 0.8 between diameter and height, and a simple model $f(D,H,\rho) = aD^2H\rho$, the measurement uncertainty is 21.6% of the AGB. For the model $f(D,H,\rho) = aD^\alpha$, with α close to 2.5, it is 12.5% of the AGB.

APPENDIX B

Summary information for the 54 Marena plots, and for the BCI plot. Coordinates: x, y (UTM), elevation (m). Plot structure: size, number of trees, BA, fraction of BA in trees less than 10 cm in diameter. AGB: total AGB (megagrams per hectare), fraction of AGB in trees less than 10 cm in diameter. Age type: 1, young secondary forest; 2, old secondary forest; 3, old-growth forest. Geology: see legend in Pyke *et al.* (2001), table 2 (except symbol Tue: Marine rocks, Late Eocene, sandstone and siltstone). Climate: annual rainfall, and length of the dry season (interpolated from weather stations). UTM, universal transverse mercator coordinates.

plot number	UTMx	UTMy	elevation (m)	size (ha)	number of trees ≥10 cm	basal area (m² ha⁻¹)	% BA < 10 cm	AGB (Mg ha⁻¹)	% AGB < 10 cm	ρ_{av}	age category	geology type	rainfall (mm yr⁻¹)	dry season (days)
BCI	625 755	1 011 569	120	50	21 205	30.6	11.4	269	2.85	0.54	3	Tb	2530	135
1	614 857	1 031 786	20	1	400	34.2	12.2	257	4.08	0.45	1	Tct	2993	122
2	613 985	1 030 725	100	1	409	30.3	12.4	271	4.09	0.56	3	Tc	3072	123
3	614 674	1 023 802	180	1	366	37.9	5.9	297	1.8	0.43	2	Tc	3007	126
4	615 019	1 023 548	180	1	450	34.1	10.7	229	4.09	0.4	2	Tc	3000	127
5	637 158	1 012 428	40	1	364	28.4	11.1	243	3.33	0.51	1	Tgo	2414	136
6	637 984	1 012 395	30	1	480	22.6	16	179	5.66	0.58	2	Tgo	2394	137
7	638 144	1 012 886	60	1	381	26.9	21	219	6.86	0.56	2	Tgo	2438	136
8	637 732	1 013 699	50	1	560	29.9	11	229	3.38	0.52	3	pT	2456	136
9	638 365	1 013 754	410	1	503	32.1	11	265	3.57	0.52	3	pT	2889	136
10	625 402	1 011 039	90	1	403	27.2	16.5	223	5.19	0.55	3	Tcm	2529	135
11	623 291	1 011 065	60	1	449	33.5	9.3	254	3.31	0.46	3	Tcm	2516	135
12	628 587	1 014 891	10	1	521	24.3	17.7	181	6.33	0.57	1	Tbo	2497	134
13	629 529	1 015 836	55	1	647	27.9	9.3	194	3.37	0.48	1	Tcm	2576	133
14	625 125	1 012 545	60	1	381	22.5	12.9	195	4.44	0.58	3	Tcm	2535	134
15	637 861	1 012 976	70	1	457	26.9	18.8	181	6.99	0.47	2	Tgo	2455	136
16	641 464	1 011 328	160	1	467	28.7	11	235	4.01	0.52	3	pT	2502	138
17	641 108	1 011 888	120	1	464	31.8	10.4	231	3.36	0.45	3	pT	2471	138
18	622 785	1 010 903	58	1	431	29.3	11.3	215	3.99	0.46	1	Tcm	2511	135

(*Continued*)

plot number	UTMx	UTMy	elevation (m)	size (ha)	number of trees ≥10 cm	basal area (m² ha⁻¹)	% BA < 10 cm	AGB (Mg ha⁻¹)	% AGB < 10 cm	ρ_{av}	age category	geology type	rainfall (mm yr⁻¹)	dry season (days)
19	634 683	1 017 102	160	1	520	26.1	17.4	199	6.09	0.56	2	pT	2688	134
20	635 754	1 016 123	160	1	539	26.4	23.3	175	9.13	0.51	2	pT	2658	134
21	643 560	1 010 755	110	1	405	35.2	8.2	226	3.66	0.36	2	Tgo	2411	139
22	643 599	1 011 461	180	1	508	32.1	8.6	209	4.03	0.38	2	Tb	2514	138
23	645 805	1 008 575	30	1	590	29.4	14.5	184	7.1	0.44	1	Tlc	2248	140
24	645 416	1 008 797	50	1	568	35.3	13.3	217	6.69	0.39	1	Tlc	2280	140
25	632 003	1 003 751	110	1	600	27.3	24.7	178	9.52	0.56	1	pT	2334	140
26	633 322	1 003 529	50	1	490	26.8	22.2	218	7.38	0.61	1	pT	2252	140
27	648 907	1 004 027	180	1	395	34.6	5	258	1.68	0.42	2	Tl	2305	143
28	649 196	1 004 697	160	1	410	31.1	6.6	226	2.72	0.42	2	Tl	2294	143
29	649 678	993 573	100	1	357	36.3	6.4	265	2.22	0.4	2	Tb	1969	149
30	649 221	994 670	180	1	306	28	12.2	205	5	0.43	2	Tb	2096	148
31	637 474	1 034 700	343	1	498	30.3	15.1	254	4.7	0.58	3	pT	3292	125
32	639 832	1 034 475	340	1	537	26.7	n.a.	240	n.a.	0.54	3	pT	3293	126
33	647 620	1 038 364	600	0.32	222	38.4	n.a.	329	n.a.	0.51	3	pT	3615	125
34	660 393	1 041 453	210	0.32	174	39.2	n.a.	362	n.a.	0.51	3	pT	3107	126
35	656 577	1 045 987	830	0.32	188	36.2	n.a.	332	n.a.	0.54	3	pT	4002	123
36	661 790	1 039 037	200	0.32	256	34	n.a.	318	n.a.	0.61	3	pT	3029	127
37	688 165	1 030 609	600	0.32	260	33.8	n.a.	276	n.a.	0.55	3	pT	3134	137
38	600 714	962 862	810	0.32	277	37.8	n.a.	314	n.a.	0.53	2	pT	2517	155
39	601 167	966 019	660	0.32	204	56.2	n.a.	464	n.a.	0.49	2	pT	2401	154
40	670 204	1 026 675	160	0.32	135	33.3	n.a.	324	n.a.	0.52	3	pT	2623	135
41	674 032	1 027 111	280	0.32	223	35.7	n.a.	370	n.a.	0.61	3	pT	2743	136
C1	651 916	993 636	50	1	281	37.3	5.1	232	2.08	0.32	2	pT	1888	149
C2	651 916	993 736	50	1	255	33.1	5.6	233	2.06	0.37	2	pT	1890	149
C3	651 916	993 836	50	1	249	29.2	5.9	219	1.99	0.4	2	pT	1892	149
C4	652 016	993 636	50	1	294	35.8	4.3	221	1.77	0.32	2	Tb	1887	149
G1	625 935	1 006 017	55	1	424	21.4	20.9	169	7.56	0.6	2	Tb	2374	138
G2	625 975	1 006 497	60	1	390	22.5	15.3	183	5.31	0.54	2	Tb	2389	137
P1	620 342	1 008 821	80	1	441	26.4	10.2	202	3.3	0.49	1	Tue*	2531	135
P2	622 483	1 008 890	40	1	473	29.5	9.8	226	3.4	0.49	1	Tcm	2468	136
S0	612 610	1 026 067	140	1	464	30.4	9.7	246	2.93	0.51	1	Tc	3026	125
S1	612 710	1 026 067	140	1	531	30.4	11.2	266	3.15	0.58	1	Tc	3026	125
S2	612 710	1 026 167	140	1	500	29.5	14.2	263	4.09	0.61	1	Tc	3028	125
S3	612 710	1 026 267	140	1	516	32	10.5	277	3.06	0.55	1	Tc	3030	125
S4	612 710	1 026 367	140	1	849	31.2	14.7	187	5.92	0.49	2	Tc	3032	125
SH	612 647	1 026 097	140	0.96	503	32.4	11.9	292	3.46	0.58	1	Tc	3030	125

APPENDIX C

Oven-dry wood specific gravity for selected Amazonian tree species. Here, we only report the species for which more than six different bibliographical sources were available (Détienne *et al.* 1982; Chudnoff 1984; for other partial lists, see Chave *et al.* 2003; Baker *et al.* 2004a). All of these species have either a pan-neotropical or a pan-Amazonian distribution.

family	species name	specific gravity (g cm⁻³)	number of estimates	s.e.m. (g cm⁻³)	relative error (%)
Anacardiaceae	*Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels	0.39	8	0.04	11.07
Anacardiaceae	*Astronium graveolens* Jacq.	0.86	7	0.17	19.68
Anacardiaceae	*Spondias mombin* L.	0.37	13	0.04	10.78
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	0.43	14	0.07	15.83
					(Continued)

family	species name	specific gravity (g cm^{-3})	number of estimates	s.e.m. (g cm^{-3})	relative error (%)
Bignoniaceae	*Jacaranda copaia* (Aubl.) D. Don	0.35	18	0.04	10.87
Bignoniaceae	*Tabebuia serratifolia* (Vahl) G. Nicholson	0.92	9	0.04	4.49
Bombacaceae	*Ceiba pentandra* (L.) Gaertn.	0.31	14	0.10	30.97
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	0.50	8	0.11	22.25
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	0.73	8	0.03	4.62
Celastraceae	*Goupia glabra* Aubl.	0.72	15	0.05	6.39
Clusiaceae	*Calophyllum brasiliense* Cambess.	0.55	9	0.06	10.46
Clusiaceae	*Symphonia globulifera* L. f.	0.60	15	0.06	9.51
Combretaceae	*Terminalia amazonia* (J. F. Gmel.) Exell	0.68	13	0.06	8.65
Euphorbiaceae	*Hieronyma alchorneoides* Allemao	0.63	10	0.06	8.83
Euphorbiaceae	*Hura crepitans* L.	0.38	10	0.04	9.77
Fabaceae	*Cedrelinga cateniformis* (Ducke) Ducke	0.49	12	0.08	15.38
Fabaceae	*Dialium guianense* (Aubl.) Sandwith	0.87	10	0.14	16.07
Fabaceae	*Dinizia excelsa* Ducke	0.89	7	0.05	5.90
Fabaceae	*Dipteryx odorata* (Aubl.) Willd.	0.93	13	0.04	4.38
Fabaceae	*Enterolobium schomburgkii* (Benth.) Benth.	0.71	15	0.11	15.66
Fabaceae	*Hymenaea courbaril* L.	0.76	12	0.06	8.15
Fabaceae	*Inga alba* (Sw.) Willd.	0.61	7	0.05	8.00
Fabaceae	*Parkia pendula* (Willd.) Benth. ex Walp.	0.54	10	0.15	28.02
Fabaceae	*Pentaclethra macroloba* (Willd.) Kuntze	0.54	8	0.09	16.67
Fabaceae	*Pseudopiptadenia suaveolens* (Miq.) J. W. Grimes	0.69	9	0.11	16.02
Flacourtiaceae	*Laetia procera* (Poepp.) Eichler	0.64	11	0.06	9.02
Lauraceae	*Mezilaurus itauba* (Meisn.) Taub. ex Mez	0.73	9	0.04	5.15
Lauraceae	*Sextonia rubra* (Mez) van der Werff	0.55	11	0.07	12.46
Lecythidaceae	*Bertholletia excelsa* Bonpl.	0.63	8	0.05	8.12
Lecythidaceae	*Couratari guianensis* Aubl.	0.53	8	0.04	7.84
Lecythidaceae	*Eschweilera coriacea* (DC.) S. A. Mori	0.83	9	0.06	7.23
Lecythidaceae	*Lecythis zabucajo* Aubl.	0.86	7	0.04	4.35
Meliaceae	*Carapa guianensis* Aubl.	0.53	13	0.07	13.14
Meliaceae	*Cedrela odorata* L.	0.42	8	0.04	9.99
Meliaceae	*Guarea guidonia* (L.) Sleumer	0.62	8	0.09	14.30
Moraceae	*Bagassa guianensis* Aubl.	0.69	7	0.05	7.19
Moraceae	*Brosimum guianense* (Aubl.) Huber	0.89	7	0.14	15.58
Moraceae	*Brosimum parinarioides* Ducke ssp. *parinarioides*	0.60	7	0.13	21.69
Moraceae	*Brosimum rubescens* Taub.	0.88	10	0.08	9.53
Moraceae	*Brosimum utile* (Kunth) Pittier ssp. *ovatifolium* (Ducke) C. C. Berg	0.49	10	0.08	16.78
Moraceae	*Clarisia racemosa* Ruiz & Pav.	0.58	17	0.07	11.97
Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	0.78	8	0.09	11.59
Myristicaceae	*Virola sebifera* Aubl.	0.45	7	0.06	12.92
Olacaceae	*Minquartia guianensis* Aubl.	0.75	8	0.08	10.89
Sapotaceae	*Manilkara bidentata* (A. DC.) A. Chev.	0.87	9	0.04	4.70
Sapotaceae	*Manilkara huberi* (Ducke) A. Chev.	0.92	9	0.04	3.86
Simaroubaceae	*Simarouba amara* Aubl.	0.38	19	0.04	10.65
Tiliaceae	*Apeiba petoumo* Aubl.	0.31	9	0.06	19.90
Vochysiaceae	*Erisma uncinatum* Warm.	0.51	12	0.05	8.98

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GLOSSARY

AGB: above-ground biomass
BA: basal area
BCI: Barro Colorado Island
BGB: below-ground biomass