Tree Allometry and Improved Estimation of Carbon Stocks and Balance in Tropical Forests

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Abstract Tropical forests hold large stores of carbon, yet uncertainty remains regarding their quantitative contribution to the global carbon cycle. One approach to quantifying carbon biomass stores consists in inferring changes from long-term forest inventory plots. Regression models are used to convert inventory data into an estimate of aboveground biomass (AGB). We provide a critical reassessment of the quality and the robustness of these models across tropical forest types, using a large dataset of 2,410 trees ≥ 5 cm diameter, directly harvested in 27 study sites across the tropics. Proportional relationships between aboveground biomass and the product of wood density, trunk cross-sectional area, and total height are constructed. We also develop a regression model involving wood density and stem diameter only. Our models were tested for secondary and old-growth forests, for dry, moist and wet forests, for lowland and montane forests, and for mangrove forests. The most important predictors of AGB of a tree were, in decreasing order of importance, its trunk diameter, wood specific gravity, total height, and forest type (dry, moist, or wet). Overestimates prevailed, giving a bias of 0.5–6.5% when errors were averaged across all stands. Our regression models can be used reliably to predict aboveground tree biomass across a broad range of tropical forests. Because they are based on an unprecedented dataset, these models should improve the quality

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of tropical biomass estimates, and bring consensus about the contribution of the tropical forest biome and tropical deforestation to the global carbon cycle.

Introduction

The response of tropical forest ecosystems to natural or anthropogenic environmental changes is a central topic in ecology (Lugo and Brown 1986; Phillips et al. 1998; Houghton et al. 2001; Chambers et al. 2001a; Grace 2004). Long-term forest inventories are most useful in order to evaluate the magnitude of carbon fluxes between aboveground forest ecosystems and the atmosphere (Houghton 2003; Grace 2004). Guidelines have been published for setting up permanent plots, censusing trees correctly (Sheil 1995; Condit 1998), and for estimating aboveground biomass (AGB) stocks and changes from these datasets (Brown 1997; Clark et al. 2001; Phillips et al. 2002; Chave et al. 2004). However, one of the large sources of uncertainty in all estimates of carbon stocks in tropical forests is the lack of standard models for converting tree measurements to aboveground biomass estimates. Here, we directly appraise a critical step in the plot-based biomass estimation procedure, namely the conversion of plot census data into estimates of AGB.

The use of allometric regression models is a crucial step in estimating AGB, yet it is seldom directly tested (Crow 1978; Cunia 1987; Brown et al. 1989; Houghton et al. 2001; Chave et al. 2001). Because 1 ha of tropical forest may shelter as many as 300 different tree species (Oliveira and Mori 1999), one cannot use species-specific regression models, as in the temperate zone (Ter-Mikaelian and Korzukhin 1997; Shepashenko et al. 1998; Brown and Schroeder 1999). Instead, mixed species tree biomass regression models must be used. Moreover, published regression models are usually based on a small number of directly harvested trees and include very few large diameter trees, thus not well representing the forest at large. This explains why two models constructed for the same forest may yield different AGB estimates, a difference exacerbated for large trees, which imposes a great uncertainty on stand-level biomass estimates (Brown 1997; Nelson et al. 1999; Clark and Clark 2000; Houghton et al. 2001; Chave et al. 2004). Direct tree harvest data are difficult to acquire in the field, and few published studies are available. Therefore, it is often impossible to independently assess the model's quality.

A simple geometrical argument suggests that the total aboveground biomass (AGB, in kg) of a tree with diameter D should be proportional to the product of wood specific gravity (ρ, oven-dry wood over green volume), times trunk basal area (BA = $\pi D^2/4$), times total tree height (H). Hence, the following relationship should hold across forests:

$$\text{AGB} = F \times \rho \times \left(\frac{\pi D^2}{4}\right) \times H \tag{1}$$

This model assumes taper does not change as trees get larger. The multiplicative coefficient F depends on tree taper only. In our measurement units (AGB, D in cm, ρ g/cm^3, H in m), Dawkins (1961) and Gray (1966) predicted a constant form factor F across broadleaf species, with $F = 0.06$ (Cannell 1984). If trees were assumed to be poles with no taper and uniform wood specific gravity, the form factor of Eq. 1 should be $F = 0.1$. If instead trees had a perfect conical shape (uniform taper), it should be $F = 0.0333$. This formula, originally developed by foresters, has seldom been used in the recent literature on the tropical carbon cycle. The first reason is that a comparison with available data shows that a relationship of the form

$$\text{AGB} = F \times \left(\rho \times \left(\frac{\pi D^2}{4}\right) \times H\right)^{\beta} \tag{2}$$

with $\beta < 1$, may actually be a better model than Eq. 1 (Brown et al. 1989). The second reason is that formula 1 requires that total height be available on each tree, a variable difficult to measure in closed-canopy forests. Hence, models involving only trunk diameter are usually preferred. The most popular such models are constructed by assuming a power-law relationship between tree height and trunk diameter: $H \sim D^B$, where the symbol $\sim$ means that the two terms are proportional. Then, a model for the tree AGB may be obtained by substituting equation $H \sim D^B$ into Eq. 1:

$$\text{AGB} = c\rho D^{2+B} \tag{3}$$

where c measures the taper of a mean tree. The exponent B can be derived from engineering considerations (McMahon and Kronauer 1976), and c measures the taper of a mean tree. In reality a power-law is not the best relationship for predicting height from diameter. Trees of large diameter show negative residuals, suggesting there are mechanical and/or physiological limits to height increase in large diameter trees (Niklas 1995; Midgley 2003). Hence, models slightly more complex than Eq. 2 should be used. We propose below a number of regression models constructed along the same lines, and we test their quality.

The predictive power of these models depends on how well they are validated using tree biomass data obtained directly from destructive harvest experiments. In the present work, we carry out the first among-site validation of biomass regression models with a large dataset collected at sites ranging from dry woodlands to hyperhumid closed-canopy forests, from highly seasonal to aseasonal climates, lowland to high-elevation forests, and secondary to old-growth forests. We also included two mangrove forest studies (e.g. Sherman et al. 2003).

This dataset considerably expands previous studies by including new data from Australia, Brazil, French Guiana, Guadeloupe, India, Indonesia, Malaysia, Mexico, and Venezuela. We use this database to test the generality of simple models, and ask whether common allometric patterns can be found for trees grown in different environments. We test the assumption that a single pan-tropical allometry can be used in AGB estimation procedures. Specifically, we ask to what extent the observed differences among site-derived allometries are due to the limited sample size used to construct the allometry. Our approach relies on model selection based on penalized likelihood. This enables us to construct a general procedure for estimating the AGB held in tropical forest trees.

Materials and methods

Study sites

Our analysis relies upon a compilation of tree harvest studies carried out since the 1950s. Our compilation comprises 27 published and unpublished datasets, from tropical forests in three continents: America, Asia, and Oceania (Fig. 1), for a total of 2,410 trees ≥5 cm in dbh (Table 1). Details on site geographical location, climate, altitude, successional status, and forest type, are provided in Table 1. These sites encompass a broad array of environmental conditions. We restricted ourselves to forests growing in tropical climates, and that regenerate naturally, thus excluding plantations or managed forests. Further details on these sites and datasets are available as Electronic Supplementary Materials. We further partitioned forests into young, or 'successional' (S) and 'old-growth' (OG) forests. Forests where evapotranspiration exceeds rainfall during less than a month were classified as 'wet forests'. Practically, this corresponds to high-rainfall lowland forests (rainfall greater than 3,500 mm/year and no seasonality), and montane cloud forests. Forests where evapotranspiration exceeds rainfall during more than a month (climatological average over many years), but less than 5 month were classified as 'moist forests'. These are forests with a marked dry season (one to 4 months), sometimes with a semi-deciduous canopy, and corresponding to ca. 1,500–3,500 mm/year in rainfall for lowland forests. Finally, forests with a pronounced dry

season, during which the plants suffer serious water stresses, are classified as 'dry forests' (below 1,500 mm/year, over 5 months dry season).

For each harvested tree, our dataset reports biometric variables (trunk diameter at 130 cm aboveground or above buttresses, total tree height), and wood specific gravity (oven-dry weight over green volume). For identified trees that lacked a direct measurement of specific gravity, species-level, or genus-level averages were used wherever possible (see details in "Electronic Supplementary Material"). In a few cases a site-averaged value of wood specific gravity had to be used. It was deduced from available floristic censuses in nearby plots.

Regression models

We compared a number of statistical models commonly used to estimate AGB in the forestry literature. A large number of regression models have already been published, and we only selected a limited subset of these, based on their mathematical simplicity and their applied relevance.

Biomass-diameter-height regression (model I)

Biomass regression models may include information on trunk diameter D (in cm), total tree height H (in m) and wood specific gravity ρ (in g/cm^3). Dawkins' regression model (Eq. 1) is a simple version of a more general model, first proposed by Schumacher and Hall (1933), and henceforth referred to as our *model I*:

$$\ln(\mathrm{AGB}) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho) \qquad (4)$$

Indeed, if $\beta_1 = 2$, $\beta_2 = 1$, $\beta_3 = 1$, the above formula is equivalent to $\mathrm{AGB} = \exp(\alpha) \times \rho D^2 H$. We now define six versions of this model, based on additional assumptions on the parameters. Model I.1 is the full model, with all four parameter independently fitted for the different forest types. Model I.2 is like model I.1, but it assumes that the four parameters do not vary across forest types. In the remaining four models, the compound variable $\rho D^2 H$ is the only predictor of AGB, like in Eqs. 1 and 2 above. The model described in Eq. 2, henceforth our model I.3, is rewritten as $\ln(\mathrm{AGB}) = \alpha + \beta_2 \ln(D^2 H \rho)$. Here, again, model I.4 is like model I.3, but it assumes that the two parameters α and β_2 do not vary across forest types. Finally, the

Fig. 1 Location of the study sites. All of the experiments were carried out in the Neotropics and in South-East Asia or Oceania. Notice the absence of study sites in Africa
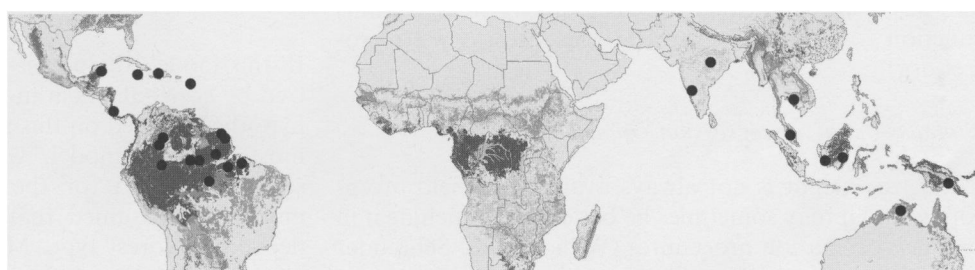
Table 1 Description of the study sites included in this study. The first column provides the site label used in the text. Successional status was categorized into old growth forests (OG) and secondary forests (S). Three forest types (dry, moist, and wet) were based on potential evapotranspiration, function of rainfall and elevation. Supplementary information on the sites and on the data is provided in the Appendix

Label	Country	Site	Latitude, longitude	Max dbh	Trees, ≥5 cm	Trees, ≥10 cm	Rainfall	Altitude	Dry months	Succ status	Forest type
Australia	Australia	Darwin	12°30′S,132°00′E	52.4	133	82	1,700	20	8	OG	Dry
BraMan1	Brazil	Manaus	2°57′S, 60°12′W	120.0	315	161	2,200	100	3	OG	Moist
BraMan2	Brazil	Manaus	2°30′S, 60°00′W	38.2	123	83	2,700	100	3	S	Moist
BraMatoG	Brazil	Mato Grosso	9°52′S, 56°06′W	93.0	34	34	2,300	100	5	OG	Moist
BraPara1	Brazil	Tomé Acu, Para	2°30′S, 48°08′W	138.0	127	127	2,200	100	4	OG	Moist
BraPara2	Brazil	Jari, Para	NA	38.0	15	15	2,200	100	4	OG	Moist
BraPara3	Brazil	Belem	1°30′S, 48°30′W	55.0	21	20	3,000	20	0	S	Moist
BraRond	Brazil	Rondônia	8°45′S, 63°23′W	89.0	8	8	2,300	110	4	OG	Moist
Cambodia	Cambodia	Cheko	10°56′N, 103°2′E	133.2	72	20	3,726	20	3	OG	Wet
Colombia	Colombia	Araracuara	0°38′S, 72°22′W	98.2	52	51	3,000	200	0	OG	Wet
CostaRica	Costa Rica	La Selva	10°43′N, 83°98′W	116.0	96	92	3,824	42	0	OG	Wet
FrenchGu	French Guiana	Piste St Elie	5°20′N, 53°00′W	117.8	363	187	3,125	50	2	OG	Moist
IndiaCha	India	Uttar Pradesh	25°20′N, 83°00′E	34.7	23	23	1,200	350	7	S	Dry
IndiaKarna	India	Karnataka	12°50′N, 75°20′E	61.2	188	182	6,000	500	5	OG	Moist
Jamaica	Jamaica	J Crow Ridge	18°08′N, 76°65′W	52.4	86	55	2,335	1,572	1	OG	Wet
Kaliman1	Indonesia	Kalimantan, Balikpapan	0°40′S, 116°45′E	77.6	23	23	2,200	250	2	OG	Moist
Kaliman2	Indonesia	Kalimantan, Sebulu	1°50′S, 116°58′E	130.5	69	38	1,862	50	1	OG	Moist
Llanosec	Venezuela	Llanos secondary	7°26′N, 70°55′W	23.3	24	18	1,800	100	4	S	Moist
Llanosold	Venezuela	Llanos old-growth	7°26′N, 70°55′W	156.0	27	27	1,800	100	4	OG	Moist
Malaysia	Malaysia	Pasoh	2°98′N, 102°31′E	101.6	139	78	2,054	100	1	OG	Moist
MfrenchG	French Guiana	Cayenne	4°52′N, 52°19′W								
		Sinnamary	5°28′N, 53°00′W	42.0	29	11	3,200	0	2	OG	Moist-Mangrove
		Iracoubo	5°30′N, 53°10′W								
Mguadel	Guadeloupe	Grand Cul-De-Sac Marin	16°19′N, 61°32′W	40.7	55	41	1,800	0	4	OG	Moist-Mangrove
NewGuinea	New Guinea	Marafunga	6°00′S, 145°18′E	110.1	42	42	3,936	2,450	0	OG	Wet
PuertoRi	Puerto Rico	El Verde	18°32′N, 65°82′W	45.7	30	16	3,500	510	1	OG	Wet
Sumatra	Indonesia	Sumatra	1°29′S, 102°14′E	48.1	29	24	3,000	100	2	S	Moist
Venezuela	Venezuela	San Carlos	1°93′N, 67°05′W	67.5	41	30	3,500	120	0	OG	Wet
Yucatan	Mexico	La Pantera	20°00′N, 88°00′W	63.4	248	177	1,200	20	5	OG	Dry

model described in Eq. 1: $\ln(\text{AGB}) = \alpha + \ln(D^2 H \rho)$ is our model I.5 if α varies across forest types, and I.6 if it does not. This last model provides a null hypothesis: $\beta_1 = 2$, $\beta_2 = 1$, $\beta_3 = 1$, with just one parameter (cf. Eq. 1). An alternative hypothesis, namely that AGB does not depend on wood specific gravity, was also tested ($\beta_3 = 0$). These models are written down explicitly in Table 2. Roughly, this suite of models defines a decreasing sequence of complexity, and they are compared following the approach of the model selection procedure (e.g. Burnham and Anderson 2002, Johnson and Omland 2004, Wirth et al. 2004). Both regressions and tests are implemented using linear models (lm() function of the R software, see http://www.r-project.org).

Biomass-diameter regression (model II)

Total tree height is not always available in field inventories, and it may sometimes be better not to include it in biomass estimation procedures (Williams and Schreuder 2000). A concave shaped relationship is observed when the logarithm of height, $\ln(H)$, is plotted against the logarithm of diameter, $\ln(D)$. This indicates a progressive departure from the ideal allometry during the tree's ontogeny. A polynomial model relating $\ln(H)$ and $\ln(D)$ provides a reasonable generalization of the power-law model (Niklas 1995, 1997). Assuming such a polynomial relationship between $\ln(H)$ and $\ln(D)$ together with Eq. 4, it is easy to deduce the following equation, which is our *model II*:

$$\ln(\text{AGB}) = a + b\ln(D) + c(\ln(D))^2 + d(\ln(D))^3 + \beta_3 \ln(\rho) \tag{5}$$

In this model, the power-law relationship is parameterized by $c = d = 0$. As in model I, we tested six alternative hypotheses based on this model. Our model II.1 was the most complex model, with all the parameters being separately fitted for the different forest types, while model II.2 assumed that the five parameters did not depend on forest type. Model II.3 was like model II.1,

Table 2 Results of the regression analyses with model I, assuming that all four parameters depend on the type of forest, or that some of them are fixed. Only six alternative models are reported, corresponding to the most parsimonious ones

Model	Forest type	α	β_1	β_2	β_3	df	RSE	r^2	AIC
$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho)$									
I.1	Dry	−2.680	1.805	1.038	0.377	312			
	Moist	−2.994	2.135	0.824	0.809	1344	0.302	0.996	818
	Wet	−2.408	2.040	0.659	0.746	139			
I.2	All types	−2.801	2.115	0.780	0.809	1,804	0.316	0.969	971
$\ln(AGB) = \alpha + \beta_2 \ln(D^2 H\rho)$									
I.3	Dry	−2.235	–	0.916	–	314			
	Moist	−3.080	–	1.007	–	1,346	0.311	0.996	913
	Wet	−2.605	–	0.940	–	141			
I.4	All types	−2.922	–	0.990	–	1,806	0.323	0.967	1,050
$\ln(AGB) = \alpha + \ln(D^2 H\rho)$									
I.5	Dry	−2.843	–	–	–	316			
	Moist	−3.027	–	–	–	1,349	0.316	0.989	972
	Wet	−3.024	–	–	–	143			
I.6	All types	−2.994	–	–	–	1,808	0.324	–	1,053

Parameters α, β_1, β_2, and β_3 are the model's fitted parameters. The best-fit parameters are reported for each model, together with the degrees of freedom (df), residual standard error (RSE), squared coefficient of regression, and Akaike Information Criterion (AIC)

and model II.4 like model II.2, but they both assumed $\beta_3 = 1$. Finally, model II.5 was like model II.3 and model II.6 like model II.4, but they both assumed no quadratic and cubic terms in Eq. 5, that is: $c = d = 0$. In all models II.1, II.3, and II.5, the parameters were independently fitted for different forest types, while in models II.2, II.4, and II.6 they were assumed constant. These models are written down explicitly in Table 4.

Model selection

To select the best statistical model we used a penalized likelihood criterion (Burnham and Anderson 2002; Johnson and Omland 2004). Specifically, we used a penalization on the number of parameters, the Akaike information criterion (AIC):

$$AIC = -2\ln(L) + 2p \qquad (6)$$

In this formula, L is the likelihood of the fitted model, p is the total number of parameters in the model. The best statistical model minimizes the value of AIC. As an alternative statistic, we also reported residual standard error (RSE), the standard error of the residuals. All statistical analyses were carried out with the R software package (http://www.r-project.org/). More complex regression procedures, such as weighted regression, have been proposed but they do not conclusively provide much better fits than classical regressions (Cormier et al. 1992). Various statistics for evaluating goodness-of-fit have also been advocated in the literature (reviewed in Parresol 1999), but AIC and RSE reported together provide sufficient information on the quality of a statistical fit for a mixed-species regression model. Besides goodness of fit measures, we evaluate a posteriori the performance of the regression model by measuring the deviation of the predicted versus measured total AGB at each site: Error = 100×(AGB_predict − AGB_measured)/ AGB_measured. The mean across all sites was called the

mean error (or bias, in %), and the standard deviation of *Error* across sites was the standard error (also expressed in %), and represented the overall predictive power of the regression.

Model prediction

Models I and II can, in principle, be used to estimate plant AGB, so long as their residuals are normally distributed. The log-transformation of the data entails a bias in the final biomass estimation (Baskerville 1972; Duan 1983; Parresol 1999), and uncorrected biomass estimates are theoretically expected to underestimate the real value. A simple, first order, correction for this effect consists of multiplying the estimate by the correction factor:

$$CF = \exp\left(\frac{RSE^2}{2}\right) \qquad (7)$$

which is always a number greater than 1, and where, here again, RSE is obtained from the model regression procedure. The larger RSE is, the poorer the regression model, and the larger the correction factor. To show the tendency of the final regression model, we plotted the model's relative error against AGB, and we smoothed this plot using a lowess procedure (locally weighted scatterplot smoothing, Cleveland 1979; Nelson et al. 1999).

Results

Biomass-diameter-height regression (model I)

We tested model I for 20 sites, and 1,808 trees (Fig. 2). We tested the following explanatory variables: D, H, and ρ, forest type, successional status, and regional location. The most important predictive variables were D, H, ρ,
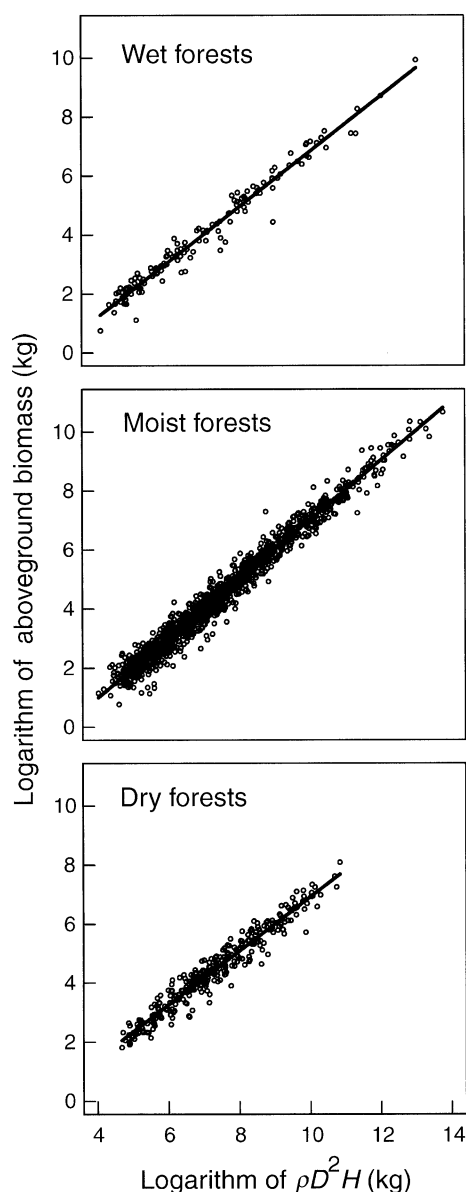
Fig. 2 Regression between the logarithm of $\rho D^2 H$ and the logarithm of aboveground biomass (AGB) for the three forest types (wet, moist and dry forests). Each dot corresponds to an individually weighed tree. The corresponding regression models are summarized in Table 2

and forest type. Including site, successional status, continent, or forest type did not improve the quality of the fit. Results for the six variants of model I are summarized in Table 2. The model including all four predictive variables performed best in all cases, but the simpler models $\ln(AGB) = \alpha + \beta_2 \ln(D^2H\rho)$, and $\ln(AGB) = \alpha + \ln(D^2H\rho)$ gave good fits. Wood specific gravity was an important predictive variable in all regressions.

To test the consistency of our model, we compared the summed AGB as measured at each site and as estimated by our regression models (Table 3). All models tended to overestimate the true biomass by 0.5–6.5% when averaged across sites. The models' predictions made an error over ±20% at five sites out of 21:

BraRond, Kaliman1, Llanosol, NewGuinea, and PuertoRi. Small sample size and the presence of a few very large trees may help explain some of this overall poor performance at these sites. The model that best predicted the stand level AGB was model I.3, similar to that of Brown et al. (1989). In the case of moist forests, the predicted value for β was very close to 1, and model I.5 was chosen instead. The standard deviation of all divergences between observed and predicted stand biomass, was within 11.8–15.6%, and complex models did not produce better results than simpler ones. For trees ≥20 cm only, the models were also correct to within 15% with a bias of −1–6.2% (results not shown).

Biomass-diameter regression (model II)

Model II was tested for 27 sites, and 2,410 trees (Fig. 3). The most important predictive variables were D, ρ, and forest type. In this case, the model's predictive power was improved if mangrove forests were considered as a fourth group. Forest type was an important predictive variable, as it contributed to significantly reduce both RSE and AIC. The most parsimonious model was obtained when the parameters a and b varied with forest type, but not c and d. As for models of type I, we provided a comparison with simpler models (Table 4). Averaged across sites, the models all overestimated the true AGB by 5.5–16.4%, and the standard deviation of error was 19–30.7%, substantially larger than for models of type I (Table 5). The six models predicted site-level AGB with an error of over ±20% for 8–14 sites out of 27, depending on the model. Models that did not include forest type as a predictive variable (models II.2, II.4, and II.6) systematically overestimated the AGB of wet forest sites, sometimes by over 50%. Models that did not include higher order polynomial terms in D (models II.5 and II.6) led to the most serious overestimation in AGB, due to an overestimation of the biomass of the largest trees (results not shown).

Choice of the best predictive models

The overall best model, depending on whether total tree height H is available, was: Dry forest stands:

$$\langle AGB \rangle_{est} = \exp\left(-2.187 + 0.916 \times \ln\left(\rho D^2 H\right)\right)$$
$$\equiv 0.112 \times \left(\rho D^2 H\right)^{0.916}$$

$$\langle AGB \rangle_{est} = \rho \times \exp(-0.667 + 1.784\ln(D)$$
$$+ 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

Moist forest stands:

$$\langle AGB \rangle_{est} = \exp\left(-2.977 + \ln\left(\rho D^2 H\right)\right) \equiv 0.0509 \times \rho D^2 H$$

$$\langle AGB \rangle_{est} = \rho \times \exp(-1.499 + 2.148\ln(D)$$
$$+ 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

Table 3 Validation of model I. Total aboveground biomass (AGB) was estimated for each of the six models summarized in Table 2 (model I.1–I.6), and the departure between estimated and measured was reported (in %)

Site	Nb trees	Total biomass	I.1	I.2	I.3	I.4	I.5	I.6
Australia	46	3240	9.66	0.76	8.81	−3.63	12.30	−3.20
BraMan1	315	147,928	10.16	6.76	9.75	7.35	7.44	11.33
BraMan2	123	13,004	−0.56	1.11	−8.70	−6.28	−8.82	−5.52
BraPara1	127	105,147	5.07	0.77	3.29	0.09	0.73	4.38
BraPara3	21	15,982	0.27	−1.96	0.42	−0.70	−1.24	2.33
BraRond	8	20,117	−25.58	−28.78	−27.18	−29.60	−29.05	−26.48
Cambodia	71	25,739	−17.20	18.10	−18.04	9.89	11.90	15.61
FrenchGu	360	138,029	−0.50	−3.63	−2.75	−4.71	−4.72	−1.27
IndiaCha	23	5,954	−4.01	6.94	−0.39	−3.69	13.56	−2.10
Kaliman1	23	44,376	27.73	21.50	26.56	22.56	23.39	27.86
Kaliman2	69	99,027	13.17	5.81	16.00	9.77	12.03	16.08
Llanosec	24	1,040	16.99	19.78	−6.11	−1.83	−5.52	−2.10
Llanosol	27	119,886	−9.84	−14.99	−22.08	−25.76	−24.54	−21.80
Malaysia	139	121,488	4.43	−0.40	5.21	1.93	2.60	6.31
MfrenchG	29	5,495	7.28	7.03	9.15	9.35	7.92	11.83
MGuadel	55	9,110	11.05	12.99	10.27	12.12	9.70	13.67
NewGuinea	42	27,640	12.84	49.21	9.46	36.67	37.11	41.65
PuertoRi	30	3,506	2.41	21.02	−0.81	12.79	11.05	14.73
Sumatra	29	9,477	6.41	5.37	−1.85	−1.72	−2.98	0.53
Yucatan	247	51,438	1.99	4.34	0.49	−0.09	18.29	1.98
Mean error			3.59	6.59	0.57	2.23	4.56	5.29
Standard error			11.85	15.63	12.82	14.58	15.21	15.26

Moist mangrove forest stands:

$$\langle AGB \rangle_{est} = \exp\left(-2.977 + \ln\left(\rho D^2 H\right)\right) \equiv 0.0509 \times \rho D^2 H$$

$$\langle AGB \rangle_{est} = \rho \times \exp(-1.349 + 1.980\ln(D)$$
$$+ 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

Wet forest stands:

$$\langle AGB \rangle_{est} = \exp\left(-2.557 + 0.940 \times \ln\left(\rho D^2 H\right)\right)$$
$$\equiv 0.0776 \times \left(\rho D^2 H\right)^{0.940}$$

$$\langle AGB \rangle_{est} = \rho \times \exp(-1.239 + 1.980\ln(D)$$
$$+ 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

These equations already include the correction factor (Eq. 7). The symbol $\equiv$ means a mathematical identity: both formulas can be used in the biomass estimation procedure. The standard error in estimating stand biomass was 12.5% if H is available, and 19.5% if H is not available. For these two models, smoothed residuals with the lowess method were plotted in Fig. 4. We found that locally, the error on the estimation of a tree's biomass was on the order of ±5%.

Discussion

AGB regression models with tree height

A number of previous studies have attempted to produce general biomass regression models for the tropics. Dawkins (1961) collected data from forests in Trinidad, Puerto Rico, and Honduras. He used 38 trees from 8 different species. He predicted that a single biomass equation, $\langle AGB \rangle_{est} \approx 0.0694$ $(\rho D^2 H)$, should hold across these species. Later, Ogawa et al. (1965), contrasted results from four forests stands in Thailand, a dry monsoon forest, a mixed savanna-monsoon forest, a savanna forest, and a tropical rain forest. They found that the variable $D^2 H$ was a suitable predictor of total tree AGB across this gradient and proposed the general equation $\langle AGB \rangle_{est} = 0.0430 \ (D^2 H)^{0.950}$ $(n = 119)$. More recently, Brown et al. (1989) constructed two different models including dbh and height as predictive variables, one for moist forests ($n = 168$, RSE = 0.341), and one for wet forests ($n = 69$, RSE = 0.459). They also proposed an equation including wood specific gravity, only for moist forests ($n = 94$, RSE = 0.247). This last model had a much smaller RSE. This suggests, that including wood specific gravity leads to an important improvement for AGB estimation models, as confirmed in the present study. We should also mention Cannell's (1984) model relating stand level basal area and maximal tree height to stand level AGB. This model was validated with a large compilation of studies published across broadly variable vegetation types. Malhi et al. (2004) recently followed a strategy similar to Cannell's and developed a stand-level regression model. This approach is potentially very useful, but it also needs to be calibrated across regions with tree-level studies.

The present work generalizes these previous results in several ways. We assessed the validity of the regression model $\ln(\mathrm{AGB}) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho)$ across a number of different forests, and asked whether a single model could be used across all sites. Based on criteria of goodness of fit and of parsimony, we selected a regression model using the compound variable $\rho D^2 H$

Fig. 3 Regression between the logarithm of *D* and the logarithm AGB for the four forest types (wet, moist, dry, and mangrove forests). *Each dot* corresponds to an individually weighed tree. The corresponding regression models are summarized in Table 4

Logarithm of stem diameter (cm)
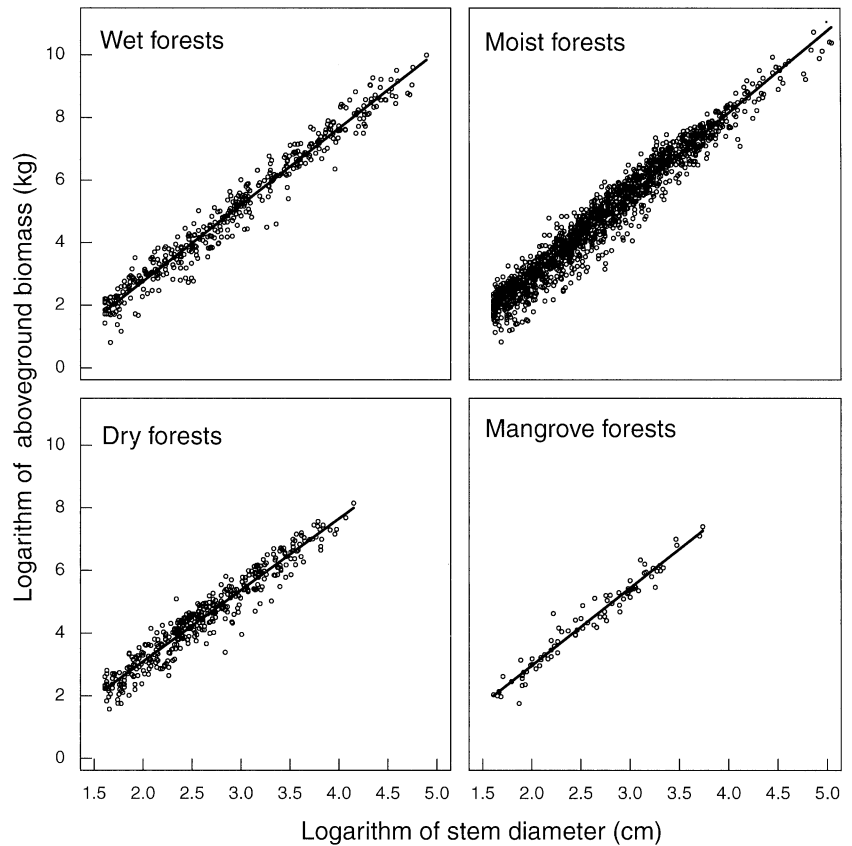
as a single predictor. The goodness of fit of our model was measured by the residual standard error of the fit (RSE), and by a penalized likelihood criterion (AIC). This model estimated accurately the AGB at most sites, although they encompassed dry, moist, and wet forests, lowland and montane forests, and secondary and old-growth forests. Hence, provided that diameter, total height and wood specific gravity of a tree are available, its AGB is easily estimated, irrespective of the tree species and of the stand location. We emphasize that the site name was not a significant factor in the linear model. This shows that there was no detectable investigator's effect in our dataset (see Wirth et al. 2004 for a related discussion).

Table 4 Results of the regression analyses with model II, assuming that all five parameters depend on the type of forest, or that some of them are fixed

Model	Forest type	a	b	c	d	β_3	df	RSE	r^2	AIC
$\ln(\text{AGB}) = a + b \ln (D) + c(\ln (D))^2 + d(\ln (D))^3 + \beta_3 \ln(\rho)$										
II.1	Dry	−1.023	1.821	0.198	−0.0272	0.388	401			
	Moist	−1.576	2.179			1.036	1,501	0.353	0.995	1,837
	Wet	−1.362	2.013			0.956	415			
	Mangrove	−1.265	2.009			1.700	81			
II.2	All types	−1.602	2.266	0.136	−0.0206	0.809	2,405	0.377	0.958	2,145
$\ln(\text{AGB}) = a + b \ln(D) + c(\ln(D))^2 + d(\ln(D))^3 + \ln(\rho)$										
II.3	Dry	−0.730	1.784	0.207	−0.0281	−	402			
	Moist	−1.562	2.148			−	1,502	0.356	0.996	1,869
	Wet	−1.302	1.980			−	416			
	Mangrove	−1.412	1.980			−	82			
II.4	All types	−1.589	2.284	0.129	−0.0197	−	2,408	0.377	0.958	2,146
$\ln(\text{AGB}) = a + b\ln(D) + \ln(\rho)$										
II.5	Dry	−1.083	2.266	−	−	−	402			
	Moist	−1.864	2.608	−	−	−	1,502	0.357	0.996	1,883
	Wet	−1.554	2.420	−	−	−	416			
	Mangrove	−1.786	2.471	−	−	−	82			
II.6	All types	−1.667	2.510	−	−	−	2,408	0.378	0.957	2,159

Parameters *a*, *b*, *c*, *d*, and β_3 are the model's fitted parameters. The best fit parameters are reported for each model, together with the degrees of freedom (df), residual standard error (RSE), squared coefficient of regression, and Akaike Information Criterion (AIC)

Table 5 Validation of model II. Total AGB was estimated for each of the six models summarized in Table 4 (model II.1 to II.6), and the departure between estimated and measured was reported (in %)

Site	Nb trees	Total biomass	II.1	II.2	II.3	II.4	II.5	II.6
Australia	133	26847	0.57	1.41	1.58	33.61	2.81	34.69
BraMan1	315	147928	18.39	22.99	17.26	−1.43	25.10	5.96
BraMan2	123	13004	20.70	17.63	21.37	10.83	18.88	12.62
BraMatoG	34	26158	34.89	38.38	34.23	13.46	40.49	20.70
BraPara1	127	105147	4.98	14.64	4.10	−13.19	16.55	−2.77
BraPara2	15	5741	−18.41	−21.11	−18.67	−28.20	−19.97	−27.48
BraPara3	21	15982	5.15	2.25	4.45	−10.24	3.88	−8.80
BraRond	8	20117	−23.94	−18.18	−24.55	−37.94	−16.83	−31.01
Cambodia	71	25739	−24.37	−10.56	−25.30	−0.39	−10.70	24.66
Colombia	52	136122	−28.18	−25.52	−28.76	−8.81	−25.52	0.61
CostaRica	96	177466	17.33	24.18	16.32	50.17	24.18	69.06
FrenchGu	362	138048	1.78	6.25	1.25	−14.57	7.87	−7.69
IndiaCha	23	5954	32.62	31.67	34.66	72.51	34.21	71.31
IndiaKarna	188	125855	14.67	10.22	13.44	−1.31	12.17	−0.95
Jamaica	86	6109	52.89	48.35	51.58	78.94	47.94	82.24
Kaliman1	23	44376	8.48	13.24	8.24	−10.61	14.85	−2.97
Kaliman2	69	99027	−5.55	11.80	−6.81	−24.76	13.90	−9.30
Llanosec	24	1040	21.05	22.03	24.48	16.22	22.14	22.02
Llanosol	27	119886	−11.89	14.27	−11.73	−29.38	15.60	−7.52
Malaysia	139	121488	−7.81	−3.36	−8.36	−23.87	−1.84	−17.28
MfrenchG	29	5495	−12.34	26.48	−12.74	16.23	−11.60	15.65
MGuadel	55	9110	9.88	51.80	9.21	43.39	9.46	41.94
NewGuinea	42	27640	8.67	12.06	6.70	35.25	11.08	50.35
PuertoRi	30	3506	17.72	13.67	16.81	39.60	13.47	42.00
Sumatra	29	9477	21.80	19.21	22.22	6.36	20.60	8.81
Venezuela	41	27379	−0.90	−2.65	−0.92	22.46	−2.11	26.44
Yucatan	248	51937	−1.26	−0.28	−1.17	29.42	0.11	30.72
Mean error			5.81	11.88	5.51	9.77	9.88	16.44
Standard error			19.28	19.05	19.48	30.67	17.66	29.46

Fig. 4 Structure of the residuals (percent difference between real and predicted biomass for individual trees) plotted against the logarithm of predicted AGB, smoothed by a lowess method. *Left panel* shows results of the best type I model including ρ, D, and H as predictors and coefficients tailored to four forest types; *right panel* corresponds to the best type II model, which includes ρ, and D as predictors and coefficients by forest type
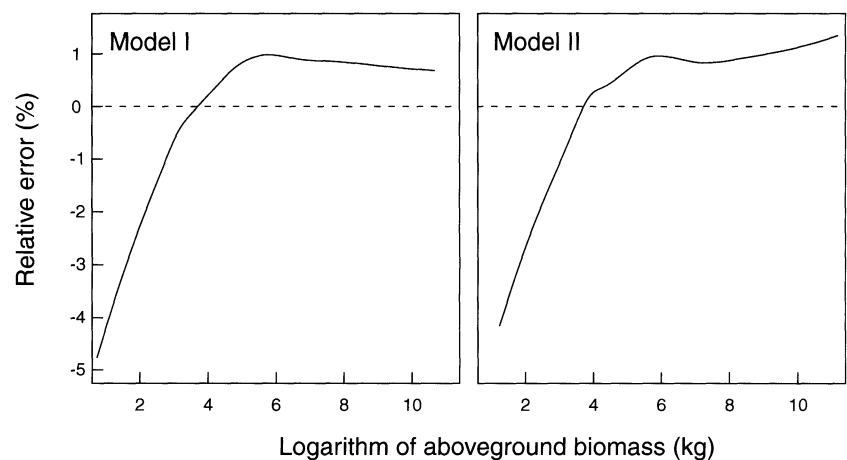
The simplest predictive model was: $\langle AGB\rangle_{est} = 0.0509 \times \rho\, D^2\, H$ (model I.6). We did not select this model because our statistical analyses showed that this model should depend on forest type. Yet, it is interesting to discuss this very simple model in detail. According to our result, the form factor F in Eq. 1 should be equal to 0.0648, close to the predictions of Dawkins (1961) and Gray (1966) for broadleaf tree species. Engineering arguments (MacMahon and Kronauer 1976) suggest that trees taper as a power law along the main stem: that is, trunk diameter at height z

should be $D_z = D_0\,(1-z/H)^{\gamma}$. The exponent γ characterizes the stem shape, being 0 in the case of a pole, and 1 in the case of a perfectly conical stem. It is a simple matter of calculus to show that F and γ are related through $F = 0.1/(2\gamma + 1)$, and that for our model, $\gamma = 0.271$. This result should be compared to the area-preserving branching hypothesis of West et al. (1999), which would amount to setting $\gamma = 0$ (no taper), and to ignoring structural considerations. Our regressions were not improved by the inclusion of a cross-continent variation. Thus, we have shown that tree allometry is

conserved across sites on different continents. These sites typically contained no species in common, thus this character is highly conserved across the phylogeny of self-supporting woody plants. Plant form is strongly selected, as photosynthetic production should be allocated optimally into construction features. It would be important to further test this model for temperate broadleaf trees. Published single-species regression models suggest that this is indeed the case (Tritton and Hornbeck 1982).

AGB regression models without tree height

Tree height measurements are often difficult to make because treetops are hidden by the canopy layer. Also, historical tree inventories are very valuable in ecological research, but they may not have recorded tree height. For these various reasons, it has often been claimed that it was better to simply use the trunk diameter as a predictive variable for the AGB (cf. for instance Ter-Mikaelian and Khozurkhin 1997, and references therein, however see Wirth et al. 2004 for different conclusions). Here, we show that the situation is more complex for the tropical forest biome, where mixed-species regression models should be used, than the temperate forest biome, where single species models are used. The best predictive models were forest type-dependent. Also, as previously noted by Chambers et al. (2001b), AGB does not follow a simple power-law scaling relation with stem diameter alone. The 'universal' power-law allometry proposed by West et al. (1999) considerably overestimates the mass of the largest trees. The polynomial terms in our model II, although yielding only small improvements in the goodness of fit measures (RSE and AIC), enable us to offset the overestimation observed with West et al.'s (1999) power-law model.

This departure from ideal power-law allometry can be interpreted as follows. The largest trees in an old-growth moist tropical forest can be older than 100–200 years (indeed some trees have been ^{14}C dated over 1,000 years, Chambers et al. 1998). These trees tend to be smaller and lighter than predicted by the ideal model because throughout life span they have been subject to the 'forces of nature', that often cause them to develop hollow trunks and/or lose large branches. Further, contrary to understory trees, canopy trees have no incentive to outgrow but continue to increase their crown size to maximize light interception.

On finding the 'best' statistical model

A considerable amount of literature has sought to find the 'best' biomass regression model for mixed-species forests (c.f. Brown et al. 1989; Shepashenko et al. 1998), or for single-species forests (c.f. Wirth et al. 2004). Most of these studies constructed complex models, with many fitted parameters, in order to minimize the goodness of fit measures. However, the principle of parsimony stipulates that the quality of a fit should depend on the model complexity, as measured by the number of parameters in the models (Burnham and Anderson 2002). To account for this principle, we selected only two sets of nested models (I and II) based on their mathematical simplicity, and discussed the performance of these models using the AIC as a selection criterion. However, it is important to realize that no simple statistical procedure permits to unambiguously decide which model is the best in the case of complex, inhomogeneous datasets (Burnham and Anderson 2002). Our dataset is almost certainly not free of measurement error, and it is not homogeneous either, being a collection of independent studies led by different investigators, and collected during a time span of over 40 years. These limitations usually tend to favor complex models over simple ones: simple model may be incorrectly rejected. Therefore, we do not exclude that more parsimonious models than the ones we recommend here, may in fact predict correctly the AGB of tropical trees. Our models represent a consensus among many studies, and the current state of knowledge; further field work should be carried out for improving their quality and their regional coverage.

Among type II models, the simplest relationship is II.6: $\ln(\text{AGB}) = a + \ln(\rho) + b \ln(D)$, with a and b constant across forest types. However, not only was this model a poor fit of the data (RSE = 0.378), it also poorly estimated the aboveground stand biomass of over 50% of the sites. That the model parameters should vary across forests is easily interpretable, because forest types with similar diametric structure may vary considerably in canopy height.

During the validation procedure, the predicted total aboveground stand biomass differed by over 20% from the measured value in several sites. Most of these sites had less than 30 trees, and in such small samples, only a few trees may bias the overall prediction. Our models tend to overestimate the AGB by 0–5%. Several authors have already noticed that such models tend to overestimate aboveground biomass (Magdewick and Satoo 1975). We believe that this overestimation cannot be offset without explicitly accounting for the log-transform correction factor $\text{CF} = \exp(\text{RSE}^2/2)$ (Saldarriaga et al. 1988). Indeed, a regression model should account for as many known sources of bias as possible, even if they result in a slightly worse fit. We therefore included this correction term in our final statistical model. Duan (1983) suggested an even better correction procedure for back-transforming the data (see Wirth et al. 2004). This could be another way of improving the models reported here.

Recommendations for measuring AGB in tropical forest stands

The motivation for this study was to provide consensus mixed-species AGB regression models for a broad range
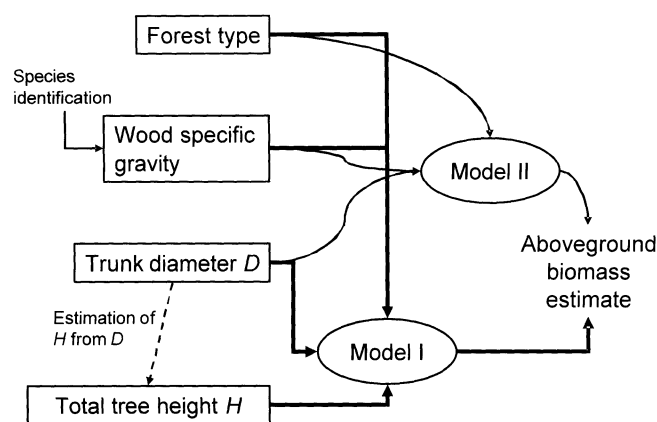
Fig. 5 Estimation of the AGB of tropical trees. Predicting variables are forest type, wood specific gravity, trunk diameter and total tree height. Models I and II differ in that Model II does not assume any knowledge of total tree height. Wood specific gravity may be estimated from species-specific literature values

of forest types, and to reduce the likelihood of estimation errors due to the use of improper models. Here, we focused only on total AGB. Models for belowground biomass estimation can be found in Cairns et al. (1997). It should also be mentioned that most studies are concerned with evaluating forest carbon pools, not biomass pools. It has traditionally been assumed that the carbon content of dry biomass of a tree was 50% (Brown and Lugo 1982; Roy et al. 2001; Malhi et al. 2004), however it should be emphasized that wood carbon fraction may exhibit some small across species variation (Elias and Potvin 2003).

The general method for estimating AGB from tropical forest stands and for assessing error in these protocols is described in Chave et al. (2004), and Fig. 5 summarizes the necessary information for this procedure. We assume here that the forest plots have been correctly designed, are large enough, and the tree diameters are measured accurately (above buttresses, if necessary). Depending on the data available, one of the two models presented above should be used. If D, H, and ρ are available for each tree, then the model using $\rho D^2 H$ as a predictive compound variable should be used (three different models for dry, moist, or wet forest types). If total tree height is missing, then a model using ρ and D as predictive variables should be used instead, with four different models for dry, moist, mangrove, or wet forest types. The AGB estimate should be accompanied by an estimation of the error due to both data measurement and model uncertainty (Cunia 1987; Chave et al. 2004). The error due to the measurement of dbh, height, or wood density can be factored in just one error term (Chave et al. 2004, Appendix A). The standard deviation measuring the error due to the regression model is given by $\sqrt{CF^2 - 1} \times \langle AGB \rangle$, where CF is the correction factor and $\langle AGB \rangle$ is the AGB estimate (Parresol 1999; Chave et al. 2004).

Wood specific gravity is an important predictive variable in all of these models. Its importance may not be obvious if one is interested in estimating the biomass in an old-growth forest dominated by hardwood species, spanning a narrow range of wood densities. However, Baker et al. (2004) have shown that ignoring variations in wood density should result in poor overall prediction of the stand AGB. Direct wood density measurements are seldom available for the trees in permanent forest stands. It is recommended to use a species-level average (Brown et al. 1989; Nelson et al. 1999; Chave et al. 2003), or, if detailed floristic information is unavailable, a stand-level average (Baker et al. 2004). Compilations of species-specific wood specific gravity are being made available to facilitate this procedure (Reyes et al. 1992; Wood Density database http://www.worldagroforestry.org/sea/Products/AFDbases/WD; J. Chave et al. in preparation).

The use of tree height as a predictive variable also improved the quality of the model. However, this variable is usually not available for censused trees. While models ignoring total tree height should be applicable in most forests, caution should be exerted when using them. For instance, the wet forest equation II.3 predicted a very large AGB stock for the montane forest at Blue Mountains, Jamaica (see Table 5). This forest is regularly impacted by hurricanes and is dominated by short trees. In this case, height is a crucial variable, and ignoring it would result in an overestimation of the forest AGB. The alternative solution is to construct a stand-specific diameter-height allometry between dbh and total height to estimate the total height of each tree in permanent plots (Ogawa et al. 1965; Brown et al 1989). The estimated tree height could in turn be used in the biomass regression model I.3 (cf. Fig. 5) although this of course will increase the regression error in the biomass estimate.

Regression models should not be used beyond their range of validity. The models proposed here are valid in the range 5–156 cm for D, and 50–1,000,000 for $\rho\, D^2\, H$. We stress that in the models presented here, D should be measured in centimeter, H in meter, and ρ in grams per cubic meter. The resulting AGB estimated from the equation is then in kilograms. Moreover, ρ should represent an oven dry mass (103°C) divided by green volume, not an air-dry wood density. Finally, these equations should in principle only be used for broadleaf tree species, and different models should hold for conifers, palms, and lianas. We are hoping that these will improve the quality of tropical biomass estimates, and bring consensus regarding the contribution of this biome to the global carbon cycle.

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