Estimating carbon stock in secondary forests: Decisions and uncertainties associated with allometric biomass models

Michiel van Breugel [a,*], Johannes Ransijn [a,b,c], Dylan Craven [a,d], Frans Bongers [b], Jefferson S. Hall [a]

[a] Centre for Tropical Forest Science, Smithsonian Tropical Research Institute, Av. Roosevelt 401, Balboa, Ancón, Panama
[b] Forest Ecology and Forest Management Group, Centre for Ecosystem Studies, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands
[c] Forest & Landscape, University of Copenhagen, Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark
[d] Yale University, School of Forestry and Environmental Studies, 205 Prospect Street, New Haven, CT 06511, USA

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ABSTRACT

Secondary forests are a major terrestrial carbon sink and reliable estimates of their carbon stocks are pivotal for understanding the global carbon balance and initiatives to mitigate CO_2 emissions through forest management and reforestation. A common method to quantify carbon stocks in forests is the use of allometric regression models to convert forest inventory data to estimates of aboveground biomass (AGB). The use of allometric models implies decisions on the selection of extant models or the development of a local model, the predictor variables included in the selected model, and the number of trees and species for destructive biomass measurements. We assess uncertainties associated with these decisions using data from 94 secondary forest plots in central Panama and 244 harvested trees belonging to 26 locally abundant species. AGB estimates from species-specific models were used to assess relative errors of estimates from multispecies models. To reduce uncertainty in the estimation of plot AGB, including wood specific gravity (WSG) in the model was more important than the number of trees used for model fitting. However, decreasing the number of trees increased uncertainty of landscape-level AGB estimates substantially, while including WSG had limited effects on the accuracy of the landscape-level estimates. Predictions of stand and landscape AGB varied strongly among models, making model choice an important source of uncertainty. Local models provided more accurate AGB estimates than foreign models, but high variability in carbon stocks across the landscape implies that developing local models is only justified when landscape sampling is sufficiently intensive.

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1. Introduction

Reliable data on carbon loss and sequestration associated with land-use dynamics is pivotal to initiatives that aim at managing forested landscapes for reducing and mitigating CO_2 emissions (Ramankutty et al., 2007; Putz et al., 2008; Herold and Skutsch, 2011; Pelletier et al., 2011) and to models that link vegetation dynamics to global climate change (Cramer et al., 2004; Poulter et al., 2010). The introduction of carbon credits through programs such as the United Nation's programs for Global Reforestation and Reducing Emissions from Deforestation and Forest Degradation links important financial implications to the accuracy of carbon stock estimates of tropical landscapes (Gibbs et al., 2007; Canadell and Raupach, 2008). The most common methods to determine aboveground biomass (AGB) of forests include the combination of forest inventories with allometric tree biomass regression models and airborne or satellite-based remote-sensing techniques (Houghton et al., 2001; Brown, 2002; Houghton, 2005). Recent remote-sensing techniques such as LiDAR enable increasingly detailed assessments of spatial variation in AGB over large spatial scales, but ultimately their accuracy depends on calibration with field data (Lefsky et al., 2002; Asner et al., 2010; Mascaro et al., 2010). Thus, allometric models are a crucial link in the estimation of forest AGB stocks (Asner et al., Submitted for publication; Houghton et al., 2001; Chave et al., 2004).

The estimation of forest- and landscape-level AGB based on plot inventories involves three steps (Brown et al., 1989; Houghton et al., 2001; Chave et al., 2005): (1) the selection and application of an allometric biomass model for the estimation of individual tree biomass, (2) the summation of individual tree AGB to estimate plot AGB, and (3) the calculation of an across-plot average to yield a forest or landscape-level estimate. For the first step, either a previously published allometric must be selected or a new, local allometric must be developed. An important corollary to model selection is which and how many predictor variables to include in the selected model. While diameter at breast height can be obtained readily, other ecologically important variables, such as wood specific gravity (WSG) and tree height, can greatly improve accuracy of tree AGB, yet are logistically more difficult to obtain.

When developing a local allometric model, the number and size distribution of trees for destructive sampling must be determined. Locally developed allometric models are assumed to provide more accurate AGB estimates, but they are usually fitted using a limited number of trees and species (e.g., Chave et al., 2005; Basuki et al., 2009; Kenzo et al., 2009), which might not be representative of the regional species pool. Therefore, it has been argued that pan-tropical models for broadly defined forest types based on large, compiled datasets may encompass more of the community-level allometric variability of a given forest than a local model (Brown et al., 1989; Chave et al., 2004, 2005; Djomo et al., 2010).

Currently there are many multispecies models developed for tropical forests, but most of them differ substantially from each other (Alves et al., 1997; Jepsen, 2006; Kenzo et al., 2009). This makes the selection of an allometric AGB model an important source of uncertainty in the estimation of AGB in tropical forests (Chave et al., 2004). Although the use of multispecies models is predicated on the premise that tree-level errors will average out on plot- and landscape scales, this uncertainty is rarely assessed for forest stands and forests across landscapes. The spatial variation in AGB across forests represents another important source of uncertainty and determines the intensity of landscape sampling required to obtain confidence in stand- and landscape-level AGB estimates (Laurance et al., 1999; Clark and Clark, 2000; Sierra et al., 2007; Laumonier et al., 2010).

Young secondary forests are an increasingly important component of tropical landscapes and constitute a mayor global carbon sink (Silver et al., 2000; Grau et al., 2003; Chazdon, 2008; Myster et al., 2008; Kauffman et al., 2009). There are good reasons to develop local allometric biomass models for these secondary forests. Recent pan-tropical consensus models are based on unprecedented large datasets that are, however, largely compiled from mature forest trees (Chave et al., 2005), while existing local models developed for secondary forests vary greatly in their AGB estimates (Nelson et al., 1999; Kenzo et al., 2009). Moreover, these forests are dominated by fewer species and the largest proportion of stand basal area is constituted by smaller-sized trees (Finegan, 1992; van Breugel, 2007), making it more feasible to develop robust local models.

In this study we evaluate the uncertainties in the estimation of AGB densities across young secondary forests associated with the selection of allometric regression models for tree biomass estimation. We developed local multispecies models using 244 trees from 26 locally abundant species and assessed four sources of uncertainties in AGB estimates: (i) uncertainty in AGB estimates bound to the number of trees to build allometric models (ii) the bias introduced when aggregating species in a single multispecies allometric model; and (iii) the uncertainty on the choice of the allometric model, and in particular whether locally developed models AGB estimates are more accurate than estimates of 'foreign' models. Finally, we assessed (iv) sampling variability when estimating the AGB at landscape level, using different numbers of plots and allometric models.

2. Methodology

2.1. Study site

The study was carried out in the Agua Salud Project site, within the Panama Canal Watershed (9°13′ N, 79°47′ W, 330 m amsl) and adjacent to the National Park Soberania. The landscape consists of a small-scale mosaic of active pastures, small agricultural fields, secondary forests on abandoned lands and old-growth forest fragments. The topography is characterized by short and steep slopes (Hassler et al., 2010) and the soils are silt clay to clay with pH values ranging from 4.4 to 5.8 (Hall & van Breugel, unpublished

data). Mean annual rainfall between 1998 and 2007 was 2300 mm, with a dry season from mid-December through April (http://striweb.si.edu/esp/meta_data/details_acp_rain15.htm). Mean daily maximum and minimum temperatures are 32 and 23 °C, respectively (http://striweb.si.edu/esp/physical_monitoring/descrip_bci.htm).

2.2. Field data

In 2008 and 2009 108 20 × 50 m (0.1 ha) plots were established in an area of approximately 15 km^2 which was largely covered by secondary forests of different ages. Time since abandonment of the secondary forest patches ranged from 0 to 25 years for all but 14 plots, which are estimated to be older than 40 years. In each plot, all stems with a diameter at breast height (DBH) ⩾5 cm were identified, labeled and measured. In one half of each plot (0.05 ha), all stems ⩾1 cm DBH were measured in the same manner.

A total of 385 tree and shrub species were found in the study plots. For this study, 26 of the most abundant species in terms of basal area across the 1–25 year old sites were selected for destructive sampling (Table 1, please contact the first author when interested in the raw data). In 41 plots, these species constituted ⩾75% of stand basal area and maximum DBH values were similar or lower than the maximum DBH values of the trees sampled destructively. Subsequently, these 41 plots were used to assess the first three sources of uncertainty (see last paragraph of the Section 1).

A total of 244 trees were selected in the areas adjacent to the study plots. Trees were cut and divided into stems, small -, medium - and large branches (diameter ⩽1 cm, >1 and ⩽3 cm, >3 cm diameter, respectively), petioles, leaves and fruits. Fresh weights were measured for all components using field scales with 1 and 20 kg capacity (10 and 50 g accuracy, respectively). Samples of each component were transported to the field station in sealed plastic bags, weighed the same day on an electronic balance (accuracy 0.1 g), dried at 70 °Celsius until achieving a stable weight and re-weighed. The fresh-to-dry weight ratios of these samples were used to calculate total dry weight of each tree component. Tree weights and measurements were subsequently used to fit allometric AGB models.

2.3. Analysis

2.3.1. Fitting and evaluating local allometric AGB models

We fitted the species-specific allometric regression equation $\ln(AGB) = a + b \times \ln(DBH)$ for each of the 26 species (SSM, Table 1). Multispecies models were developed based on either DBH (multispecies model 1, M1) and DBH and wood specific gravity (WSG, g cm^{-3}) (multispecies model 2, M2), using the regression equation: $\ln(AGB) = a + b_1 \times \ln(DBH) + b_2 \times \ln(WSG)$ (Table 2). Average WSG values for the studied species were obtained from a regional dataset (Muller-Landau, 2004; Wright et al., 2010). Back-transformed AGB estimates were multiplied by the correction factor CF = $e^{0.5 \times MSE}$, where MSE is the mean squared error of the model regression (Sprugel, 1983).

To evaluate the regression models, we used (i) the proportion of variance explained by the model (R^2 adjusted for the number of predictor variables); (ii) the mean squared error (MSE); and (iii) the mean of the absolute relative differences between the model AGB estimates and the observed AGB values (%). Lastly, (iv) the Akaike information criterion (AIC) (Johnson and Omland, 2004) was used in model assessments.

2.3.2. Bias due to aggregating species in multispecies allometric models

We evaluated the bias introduced when aggregating species in a single multispecies allometric model by comparing the plot AGB estimate of the multispecies model with the estimate based on

Table 1
Species information for the 26 species used to construct allometric regression models. Species: DBH_{max}, the maximum DBH in the combined datasets of this project and the CTFS sample plot database (cm) (http://www.ctfs.si.edu/group/General%20Information/Datasets); WSG, wood specific gravity (g cm^{-3}). Harvest: #, number of weighted trees; DBH_{max}, the maximum DBH among the sampled trees (cm). Census:%BA, cumulative percentage of the basal area in 94 secondary forest plots (1–25 years old). Allometric model: 'a' and 'b', coefficients for the species-specific allometric regression models ln(AGB) = a + b × ln(DBH); R^2_{adj}, the adjusted R^2; MSE, mean squared error; CF, correction factor (CF).

Species			Harvest		Census	Allometric model				
	DBH_{max}	WSG	#	DBH_{max}	% BA	a	b	R^2_{adj}	MSE	CF
Xylopia frutescens	31	0.590	13	18.1	6.4	−1.769	2.269	0.984	0.127	1.066
Miconia argentea	62	0.697	14	22	5.8	−2.054	2.389	0.995	0.046	1.023
Inga cocleensis	96	0.667	12	25.8	4.8	−1.865	2.408	0.998	0.021	1.011
Vismia macrophylla	53	0.518	12	24.5	4.6	−1.926	2.379	0.995	0.023	1.012
Trichospermum galeottii	65	0.296	9	25.9	4.5	−2.943	2.43	0.974	0.078	1.04
Byrsonima crassifolia	54	0.575	12	23	4.4	−1.696	2.226	0.992	0.06	1.03
Schefflera morototoni	85	0.388	10	21.5	4.0	−2.59	2.426	0.988	0.086	1.044
Pachira sessilis	290	0.475	9	29	3.4	−2.514	2.295	0.991	0.055	1.028
Vismia baccifera	24	0.531	7	12.4	2.9	−2.485	2.509	0.972	0.098	1.05
Terminalia amazonia	196	0.665	14	15.9	2.8	−1.675	2.326	0.981	0.085	1.043
Annona spraguei	60	0.426	11	26.5	2.7	−2.772	2.562	0.981	0.075	1.038
Conostegia xalapensis	23	0.576	17	7.2	2.6	−1.354	1.952	0.966	0.103	1.053
Apeiba tibourbou	93	0.343	9	24.3	2.2	−2.788	2.27	0.992	0.036	1.018
Inga thibaudiana	60	0.494	11	20.6	1.9	−1.791	2.334	0.991	0.062	1.032
Cordia bicolor	75	0.373	8	17	1.6	−2.41	2.327	0.992	0.031	1.015
Cochlospermum vitifolium	45	0.258	7	20.2	1.5	−2.23	2.034	0.992	0.02	1.01
Banara guianensis	46	0.486	7	16.5	1.4	−1.782	2.218	0.994	0.018	1.009
Thevetia ahouai	18	0.457	6	11.9	1.4	−2.332	2.288	0.991	0.045	1.023
Casearia sylvestris	33	0.662	8	15.1	1.3	−1.939	2.437	0.995	0.025	1.013
Cupania cinerea	32	0.495	9	15.4	1.2	−1.969	2.386	0.996	0.012	1.006
Cupania scrobiculata	31	0.558	8	6.7	1.0	−2.189	2.427	0.981	0.055	1.028
Miconia affinis	24	0.570	7	9.2	0.9	−1.748	2.304	0.997	0.014	1.007
Lacistema aggregatum	26	0.558	6	11.5	0.9	−1.685	2.114	0.989	0.035	1.018
Ryania speciosa	14	0.493	7	3.8	0.6	−1.828	2.185	0.973	0.038	1.019
Vernonanthura patens	12	0.346	7	7.3	0.4	−1.78	1.76	0.983	0.035	1.018
Trema micrantha	83	0.386	6	18.6	0.2	−2.305	2.351	0.992	0.065	1.033
		Mean: 0.496	Sum:		65.8					

Table 2
Local multispecies allometric regression models for estimation of individual tree aboveground biomass (AGB). Models are based on linear regression of AGB for 244 harvested trees (26 species). Predictor variables are diameter at breast height (DBH) and wood specific gravity (WSG). The table shows coefficient values, R^2 adjusted; mean relative difference (MRD, the average deviation in% of the model estimate from the observed value), mean squared error (MSE, residual variance), Akaike information criterion (AIC) and the correction factor for back-transformed AGB values (CF) for each multispecies model. All regression coefficients used were statistically significant ($p < 0.001$). In the text we refer to model 1 (M1) and model 2 (M2).

Regression models	Model	Coefficient		R^2_{adj}	MRD	AIC	MSE	CF
ln(AGB) = $a + b_1 \times$ ln(DBH)	M1	a	−1.863	0.967	42%	288	0.191	1.100
		b1	2.208					
ln(AGB) = $a + b_1 \times$ ln(DBH) + $b_2 \times$ ln(WSG)	M2	a	−1.130	0.982	30%	145	0.106	1.054
		b1	2.267					
		b2	1.186					

the 26 species-specific allometric models. This analysis included multispecies models M1 and M2 and six previously published multispecies models (Table 3). Henceforth we will refer to each individual model by the name of the first author of the paper in which they were published (e.g. *the Chave model*) and we will refer to them collectively as 'foreign models'. For the purpose of this analysis, stems of species not belonging to the studied species were excluded from the 41 plots we used for this analysis (see Section 2.1), leaving filtered plots with 83.1% (±1.0 s.e.) of the original basal area. This enabled us to directly compare plot-level AGB estimates of multispecies allometric biomass models (AGB_{ms}) with estimates generated by the species-specific models (AGB_{ss}). The relative error of multispecies allometric model ms for plot i was computed as:

$$100 \times (AGB_{ms,i} - AGB_{ss,i})/AGB_{ss,i}$$

Table 3
Foreign multispecies allometric models. The models predict aboveground tree biomass (AGB) based on diameter at breast height (DBH) and wood specific gravity (WSG). Models are based on either mature forest (M) or young secondary forest (S). N is the number of trees on which the models are based. DBH provides the DBH-ranges of the sampled trees. References: (1) Chave et al. (2005); (2) Brown et al. (1989); (3) Ketterings et al. (2001); (4) Kenzo et al. (2009); (5) Nelson et al. (1999); (6) Sierra et al. (2007).

Model		Model: AGB =	FT	Region	N	DBH (cm)	Ref.
Chave	C	1.066 × exp(−1.864 + 2.608 × ln(DBH) + ln(WSG))	M	Global	1589	5–156	1
Brown	B	exp(−2.134 + 2.530 × ln(DBH))	M	Global	269	5–130	2
Kenzo	K1	exp(−2.489 + 2.43 × ln(DBH))	S	Malaysia	136	0.11–28.7	4
Ketterings[a]	K2	exp(−2.207 + 2.62 × ln(DBH) + ln(WSG))	S	Indonesia	29	7.6–48.1	3
Nelson	N	exp(−1.997 + 2.413 × ln(DBH))	S	C. Amazonia	132	1.2–28.6	5
Sierra	S	1.087 × exp(−2.232 + 2.422 × ln(DBH))	S	Colombia	152	0.9–40	6

[a] Coefficients were estimated from the DBH-height relationship of the 244 harvested trees as detailed in Ketterings et al. (2001).

the mean relative error of plot-level AGB estimates as:

$$\frac{100}{41}\sum_{i=1}^{41}(|\mathrm{AGB}_{\mathrm{ms},i} - \mathrm{AGB}_{\mathrm{ss},i}|/\mathrm{AGB}_{\mathrm{ss},i})$$

and the mean relative error of the across-plot average of AGB estimates as:

$$100 \times \left| \left(\frac{1}{41}\sum_{i=1}^{41}\mathrm{AGB}_{\mathrm{ms},i} \right) - \left(\frac{1}{41}\sum_{i=1}^{41}\mathrm{AGB}_{\mathrm{ss},i} \right) \right| \Big/ \frac{1}{41}\sum_{i=1}^{41}\mathrm{AGB}_{\mathrm{ss},i}$$

All three error terms are thus expressed in percentages.

Confidence intervals of plot level AGB estimates obtained by the combined species-specific models were calculated as follows: First, we calculated the relative standard error of each species-specific models (RSE_i) as $\sqrt{(\exp(\mathrm{MSE}/(n-k))-1)}$, where MSE is the mean squared error from the regression, n the number of individuals, and k the number of parameters in the model. Second, the standard error for the AGB estimate for a specific species (SE_i) was then calculated as $\mathrm{SE}_i = \mathrm{RSE}_i \times \mathrm{AGB}_i$. $\mathrm{SE}_{\mathrm{plot}}$ was then calculated for combinations of uncorrelated variables with different variances: $\mathrm{SE}_{\mathrm{plot}} = \sqrt{(\sum(\mathrm{SE}_1^2 \ldots \mathrm{SE}_n^2))}$. Finally, the 95% confidence intervals for the AGB estimate by species-specific allometric models were calculated as the estimated plot AGB ± 1.96 × $\mathrm{SE}_{\mathrm{plot}}$. AGB estimates of the multispecies models that fell outside the 95% confidence interval were considered significantly different.

2.3.3. Uncertainty in AGB estimates associated to the number of trees used to fit the allometric models

Uncertainty in AGB estimates associated with the number of trees for constructing allometric models was evaluated using rarefaction. The full database of 244 trees was stratified by DBH class and subsets of 80%, 60%, 40% and 20% (195, 146, 98 and 49 trees, respectively) were randomly drawn from each DBH class, maintaining the same relative abundance per class as in the full database (⩽5 cm: 43%, 5–10 cm: 24%, 10–20 cm: 24%, 20–29 cm: 9%). These trees were used to construct allometric regression models for each sampling intensity. The AGB of the 41 study plots was estimated using these models and the procedure was repeated 1000 times to quantify the variance among estimates of different sampling intensities. For each run, the mean relative error of plot-level AGB estimates and the mean relative error of the across-plot average of AGB estimates were calculated as indicated above.

2.3.4. Variation in the estimation of landscape-scale AGB stocks

To assess the uncertainty in estimation of AGB at landscape level and how this uncertainty is affected by sampling intensity (number of plots) and model choice, we used the inventory data of the 94 plots that were abandoned for less than 25 years. We calculated the AGB of these plots using a combination of M2 or foreign secondary forest models (Table 3) for trees ⩽25 cm DBH and the Chave model for trees >25 cm DBH. The latter was done to avoid using the secondary forest allometric models beyond the size range of the trees that were used to fit them. For comparison, we included AGB estimates based on the Chave model only. We calculated across-plot means of plot AGB and tested for significant differences between models using an ANOVA and a Tukey post-hoc test.

Next, we evaluated the contribution of foreign model choice to uncertainty in landscape-level AGB estimates across decreasing levels of sampling intensity (5, 10, 15, 20, 30, ..., 80 plots). This was done as follows: First, we calculated the means of plot AGB estimates ($\mathrm{mAGB}_{\mathrm{X},n}$) computed from the different allometric models (X), but using different numbers of randomly selected plots (n). Then we calculated the relative deviation (RD) of these means from the mean plot AGB of the full database (94 plots), which was calculated using M2 (trees ⩽25 cm) and the Chave model (trees >25 cm), as follows: $\mathrm{RD} = 100 \times (|\mathrm{mAGB}_{\mathrm{X},n} - \mathrm{mAGB}_{\mathrm{M2},94}|)/\mathrm{mAGB}_{\mathrm{M2},94}$. For each combination of model (X) and sample size (n), 1000 random draws were performed, which were used to generate a mean relative deviation ($\mathrm{MRD}_{\mathrm{X},n}$). Finally, we estimated the relative contribution of the choice of the foreign models to $\mathrm{MRD}_{\mathrm{X},n}$, at sample size n, as $100 \times (|\mathrm{MRD}_{\mathrm{X},n} - \mathrm{MRD}_{\mathrm{M2},n}|)/\mathrm{MRD}_{\mathrm{X},n}$.

3. Results

3.1. Local allometric models

The 26 individual species allometric models explained 97.2–99.8% of the variance in tree AGB (Table 1). The coefficients of the DBH–AGB relationships varied substantially among the 26 study species, resulting in four to sixfold differences in AGB estimates at similar DBH values (Fig. 1). Species-specific WSG accounted for a substantial proportion of these differences. Linear regressions of predicted AGB at 5, 10 and 15 cm DBH of the 26 species against their species-specific average WSG yielded R^2 of 0.74, 0.73 and 0.70, respectively.

The multispecies model including only DBH accounted for 97% of the variance in tree AGB (Table 2). Including wood specific gravity slightly increased R^2_{adjusted} (98%), substantially improved model fit in terms of AIC, and resulted in decreased MRD and MSE values, which indicates improved precision of the estimates (Table 2).

3.2. Bias due to aggregating species in multispecies allometric models

3.2.1. Local allometric models

The mean of the relative errors of M1 was 13.7% (±1.9 SE)(black dot, Fig. 2) and the estimated $\mathrm{AGB}_{\mathrm{M1}}$ of 51% of the 41 plots fell outside the confidence intervals of the corresponding estimations based on the species-specific models (white dots, Fig. 3a). Adding wood specific gravity as a predictor variable improved plot-level predictions substantially (i.e., decreased the bias of the multispecies model): AGB estimates based on M2 ($\mathrm{AGB}_{\mathrm{M2}}$) were significantly different from AGB estimates based on species-specific models ($\mathrm{AGB}_{\mathrm{ss}}$) in only 22% of the plots (white dots, Fig. 3b) and the mean of the relative errors decreased to 7.9% (±1.0 SE)(black dot, Fig. 2). Across plots, the negative and positive relative errors
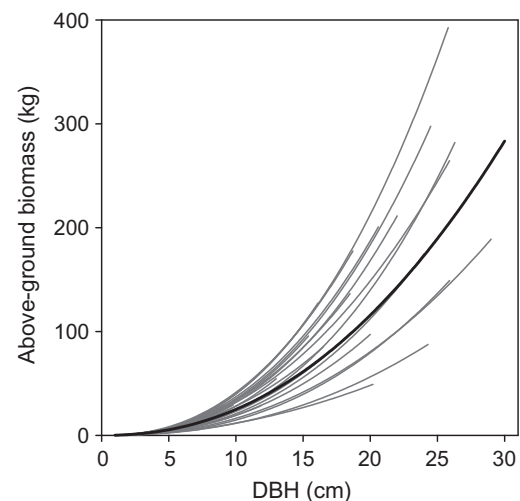

Fig. 1. Allometric relationships between DBH and above-ground biomass (AGB) of the 26 studied species. Thin lines are species-specific allometric regression models (Table 1). Bold line corresponds to mixed-species allometric regression model 1 (Table 3). Back-transformed data are presented.
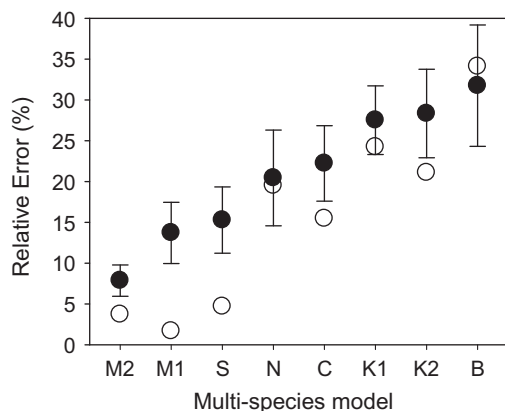
Fig. 2. Mean bias in plot – and landscape level AGB estimates resulting from the aggregation of species in multispecies models. Black dots give the mean relative error of plot-level AGB estimates and open dots the relative error of the across-plot average of AGB estimates. Relative errors are computed as the absolute relative differences between AGB estimates from the multispecies models and from the AGB estimates of the combined species-specific models, as a percentage of the latter. Error bars indicate 95% confidence intervals. Model abbreviations on the x-axis follow Tables 2 and 3.

of AGB_{M1} and AGB_{M2} largely balanced out, resulting in relative errors of the average plot AGB of 3.7% and 1.7%, respectively (white dots, Fig. 2). The relative error of M2 was positively correlated with plot AGB (Pearson correlation coefficient 0.45, $p < 0.001$).

3.2.2. Foreign allometric models

The relative errors of plot-level AGB estimations varied strongly among plots and among the foreign models (Fig. 3b–h). The mean relative error of plot AGB estimates of the foreign models varied between 15% and 32%, which was substantially higher than the mean relative error of the two local models M1 and M2 (Fig. 2, black dots). The Brown and Nelson models overestimated plot AGB in all but 6 plots with low biomass (Fig. 3c and g) while, in contrast, the Kenzo and Ketterings models underestimated AGB in nearly all plots (Fig. 3e and f). The Chave and Sierra models tended to underestimate AGB in plots with low biomass and significantly overestimated AGB in plots with high basal area (Fig. 3d and h). The relative errors of all models were positively correlated with plot AGB, with Pearson correlation coefficients ranging from 0.46 to 0.63 ($p < 0.05$).

The relative error of the across-plot mean AGB was significantly below the mean relative error of plot AGB estimates in case of the Chave, Ketterings and Sierra models (Fig. 2, open dots), i.e. positive and negative plot-level errors partially averaged out across plots.

3.2.3. Uncertainty in AGB estimates associated to the number of trees used to fit the allometric models

Using allometric models based on a smaller number of trees increased variation in the mean relative error (MRE) of plot-level AGB estimates (Fig. 4a). The standard deviation of the average MRE increased from 0.5 to 1.2 (M1) and from 0.7 to 1.9 (M2), when sampling intensity decreased from 80% to 20%. Consequently, lower sampling intensities increased probabilities of substantially higher relative errors. Using M2, the proportion of AGB estimates with a MRE of more than 10% increased from 0.02 to 0.26 when sampling intensity decreased from 80% to 20%. Similarly, the proportion of MREs >15% increased from 4% to 21% when the sampling intensity for M1 went from 80% to 20%.

Variation in the relative errors of the landscape-level AGB estimates increased strongly with decreasing sample size (Fig. 4b). The standard deviations of the average of the relative errors increased from 1.1 to 3.6 when sampling intensity decreased from 80% to 20%

(M1 and M2). The probability of a relative error twice the relative error of the models based on the full dataset went up from 0.10 to 0.56 (M1) and from less than 0.01 to 0.24 (M2).

The development of an allometric model that includes DBH and WSG as predictor variables would require a much lower sampling intensity than a model that includes only DBH as predictor variable. Even when based on a sample five times larger (244 versus 49 trees), the probability that M1 yielded a lower MRE of plot-level AGB estimates than M2 was only 2.8%. However, on a landscape scale, both models yielded similar relative errors and similar relationships between uncertainty and sampling intensity.

3.3. Sampling variability when estimating landscape level AGB

The use of different allometric models for trees <25 cm DBH, which constituted on average 90.8% (±1.1 s.e., $n = 94$) of total plot basal area, yielded landscape-level AGB estimates that varied between 50.5 Mg/ha (±3.5 s.e.) and 69.6 Mg/ha (±4.3 s.e.) (Fig. 5a). Large spatial variation in AGB stocks resulted in wide confidence intervals around these estimates. Thus, differences were only significant between estimates using the Nelson and Chave models and the Kenzo and Ketterings models ($p < 0.05$, Tukey post hoc test).

The mean relative deviations (MRD) of the landscape-level AGB estimates based on M2 increased rapidly with decreasing sample size (Fig. 5b), from 2% when sample size was 80 plots to more than 10% when sample size was less than 20 plots. The AGB estimates of the Sierra model were very similar to the M2 estimates (Fig. 5a) and consequently a very similar pattern of decreasing MRD with sample size (Fig. 5b). Because the AGB estimates of the other models differed substantially more from the M2 estimates, their MRD leveled off quickly at stayed at 12–17% even at larger sample sizes.

As a consequence, the proportion of the variation associated with the choice of a foreign model, relative to the uncertainty associated with sample size, was in four of the five foreign models approximately 20% when sample size was only five plots, and was greater than 80% when sample size was at least 80 (Fig. 5c). For example, the MRD at a sample size of 40 plots was 5.9% and 17.4% for estimates computed with M2 and the Kenzo model, respectively. The proportion of the MRD due to the choice of the Kenzo model was thus estimated as 66% (($17.4 - 5.9$)/17.4 = 0.66).

4. Discussion

Multispecies allometric regression models for the estimation of tree AGB are a pivotal link – and a major source of uncertainty – in the estimation of plot and landscape level carbon stocks and accumulation rates in the Tropics. The use of allometric models involves several decisions on the employment of limited funds and labor that influence the uncertainty in the estimation of AGB on both plot and landscape-level, yet these decisions have often not been explicitly addressed. This study evaluated uncertainties associated with decisions on the choice for extant models vs. the development of a local model, on the sample size for destructive tree biomass measurements, and on the use of WSG as a predictor variable.

4.1. Uncertainty associated with the number of trees used to build an allometric model

To evaluate different variants of locally developed and foreign allometric models, we utilized 'model communities' consisting of inventory data of the studied 26 species in 41 plots where they represented over 75% of stand basal area. This means that the local multispecies models represented the entire species pool of the
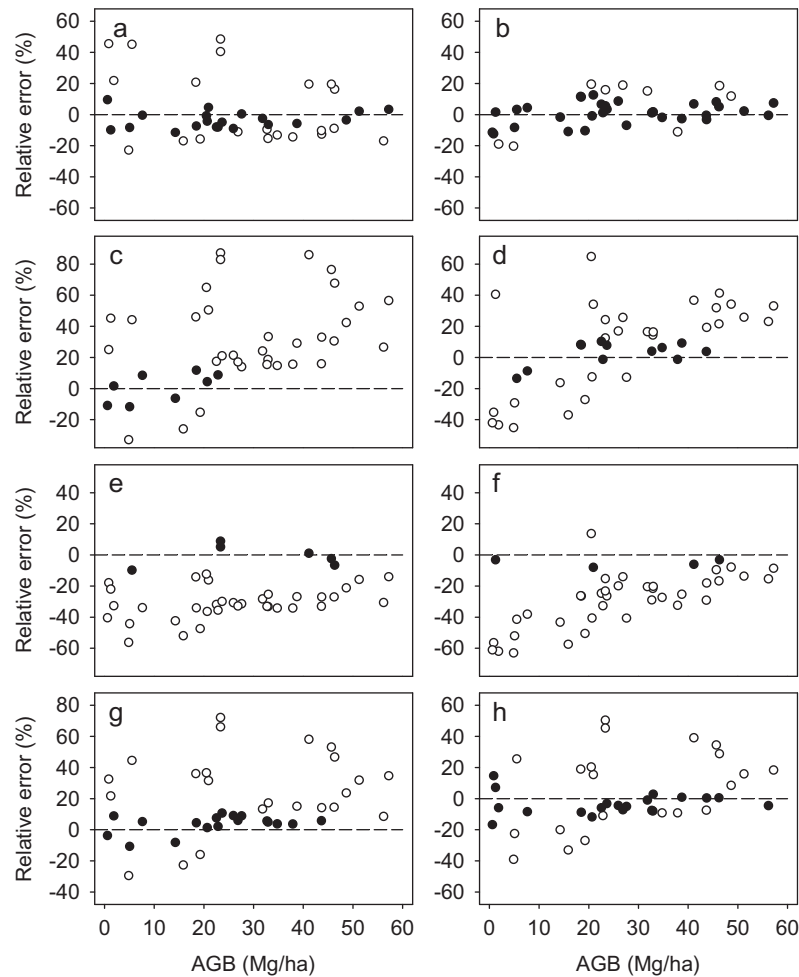
Fig. 3. Bias in the AGB estimates of individual plots resulting from the aggregation of species in multispecies models. The relative errors of plot-level AGB estimates are plotted against plot AGB. AGB estimates of the multispecies models that fell within the 95% confidence intervals of the AGB estimates based in the species-specific models are indicated by black dots. (A) local model 1 (M1), (B) local model 2 (M2), (C) Brown, (D) Chave, (E) Kenzo, (F) Ketterings, (G) Nelson, (H) Sierra. References and model equations are provided in Tables 2 and 3. The length of the y-axis is always 140%.
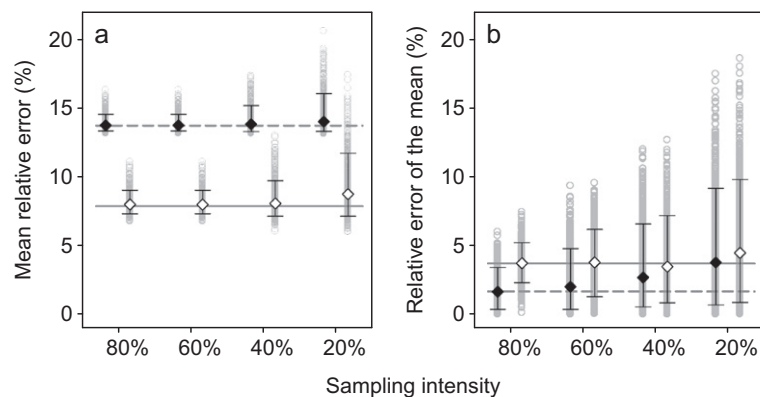
Fig. 4. Sampling variability in the estimation of landscape level AGB. Distribution of (A) means of the relative errors of plot-level AGB estimates and (B) the relative errors of the across-plot averages of AGB estimates. Open grey dots give data points, diamonds the median of M1 (black) and M2 (white), error bards the 10th and 90th percentiles and the grey lines in both graphs indicate relative errors of M1 (dashed line) and M2 (continuous line) based on the full dataset. Sampling intensity refers to the size of the subsamples, as a percentage of the original dataset of 244 trees (percentages correspond to (195, 146, 98 and 49 trees, respectively).

'model communities' and that the relative errors of plot-level AGB estimates largely reflected differences in the relative abundances of these species. At lower sampling intensities, multispecies allometric models utilized allometric information of an increasingly smaller proportion of the model community. Our smallest random subsamples (20% of our harvest dataset, 49 trees) included on

average 43% of the species in each DBH class, which led to substantial uncertainty in the estimation of plot and landscape-level AGB (Fig. 4).

Locally developed models are, often implicitly, assumed to better represent the variation in allometric relationships among the species of the local community. However, in highly diverse tropical
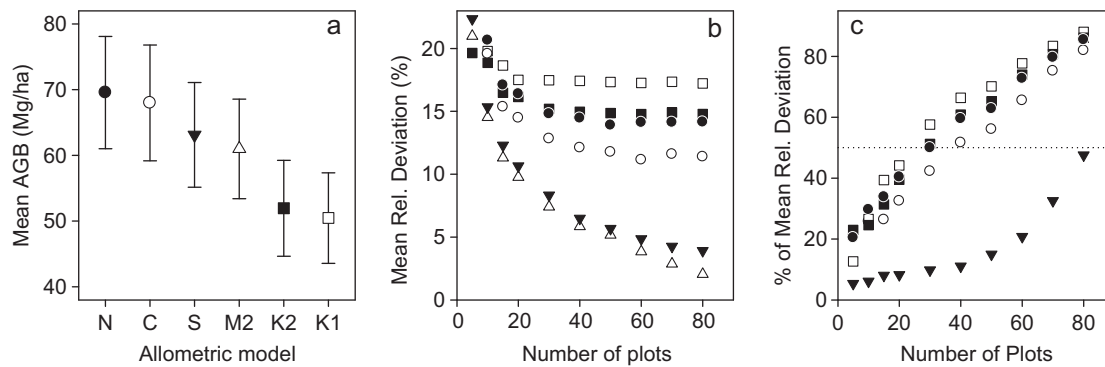
Fig. 5. Variation in landscape-level estimation of secondary forest AGB stocks during early secondary succession associated with allometric model choice and sampling intensity. (A) Across-plot means and 95% confidence intervals of AGB estimates for 94 plots using the Chave model for trees with a >25 cm DBH and different allometric regression models for trees ⩽25 cm DBH. The latter models are represented by different symbols; M2 is local model 2 and other model abbreviations follow Fig. 2. (B) Mean relative deviation of landscape-level AGB estimates from the best available landscape-level AGB estimate (MRD, see Section 2), as a function of sampling intensity. (C) Relative contribution of allometric model choice to uncertainty of landscape-level AGB estimates as a function of sample intensity, computed as the difference between the MRD of each of the five foreign models and the MRD of M2, as a proportion of the former (see Section 2).

forests, even relatively large samples normally represent much less than 43% of the local species pool, and uncertainties in AGB estimates associated with the 'representativeness' of a multispecies model will be substantial. It is, therefore, an important challenge to find ways of selecting a representative sample of the total community.

One approach to achieving representativeness of multispecies allometric models is to focus on dominant species (Alves et al., 1997; Cairns et al., 2003; e.g., Segura and Kanninen, 2005; Alamgir and Al-Amin, 2008), especially since relatively small samples may represent relatively large proportions of the AGB stocks in secondary forests (Read and Lawrence, 2003; van Breugel et al., 2006). In the present study, this approach did not result in a biased and limited variation in species characteristics. The 26 selected species represented on average 68.9 ± 1.8% (mean ± s.e.) of the basal area in the 94 young secondary forests plots, covered a wide variation in size-AGB allometries, WSG and maximum size and their mean WSG (0.496) was close to the mean basal area-weighted WSG across the young secondary forest plots (0.507 ± 0.01 s.e.) (Fig. 1, Table 1). However, most studies provide scant information on how and why trees and species were selected (e.g., Nelson et al., 1999; Ketterings et al., 2001; Sierra et al., 2007; Kenzo et al., 2009; Overman et al., 2009), making it difficult to assess how representative selected species are for the community at large.

4.2. Including wood specific gravity in allometric biomass models

Species-specific averages of wood specific gravity (WSG) accounted for a large proportion of the marked variation in DBH–AGB relationships among species, even while intraspecific variations in WSG can be substantial (e.g., Nock et al., 2009; Henry et al., 2010). As a consequence, adding WSG as a predictor variable significantly improved the fit of multispecies DBH–AGB regression models (Table 2) (Chave et al., 2004).

While it has been often emphasized that ignoring interspecific variation in average WSG may result in significant errors in plot and landscape-level AGB estimates (Fearnside, 1997; Clark and Clark, 2000; Baker et al., 2004; Chave et al., 2006; Djomo et al., 2010), few allometric models for secondary forests actually include WSG (but see Saldarriaga et al., 1988). Moreover, as average WSG may differ considerably among tropical regions, the applicability of locally developed models elsewhere may be limited when WSG is not included in the model (Baker et al., 2004; Muller-Landau, 2004; Chave et al., 2006, 2009). For example, average wood specific gravity of the species included in the Kenzo model

was 0.354 g cm^{-3}, compared to 0.496 g cm^{-3} across the species included in our model (Table 1), which probably accounts for the consistently low AGB estimates of the Kenzo model (Fig. 3).

Recently, large data sets of species-specific wood specific gravity have become available, facilitating the use of WSG data in the estimation of AGB (Fearnside, 1997; Chave et al., 2009; Zanne et al., 2009). However, in many regions these data sets will cover only a small fraction of the tree community. The collection of community-wide WSG values is not a trivial task, especially when botanical expertise is limited or proper processing of wood samples is logistically difficult and, thus, begs the question if and when such efforts are justified.

Our results confirmed that including data on wood specific gravity in allometric models improves plot-level AGB estimates significantly. Allometric model with WSG as a predictor variable yielded more accurate predictions, even when based on considerably lower sample sizes (# of trees) than the model that did not include WSG (Fig. 4a). However, our results also indicated that the decision to include WSG becomes more ambiguous when it comes to landscape-level AGB estimates. Plot-level errors in the estimation of AGB stocks mostly balanced out across plots and, as a result, M1 and M2 produced similar errors in the estimation of landscape-level AGB stocks (Fig. 4b). This suggests that, ultimately, the decision to prioritize different aspects of developing allometric models depends on the specific research questions and, more particularly, whether they concern plot-level or landscape-level AGB stocks and dynamics.

4.3. Local allometric models or extant foreign models?

The principal limitation for developing robust local multispecies models is logistical – sampling a sufficient quantity of trees >25 cm DBH. Extant allometric models based on large pan-tropical compilations seem to be the best available choice for such trees, as they include a range of variation in tree allometry that is unattainable for individual studies (Chave et al., 2005). However, our results indicate that models that focus on large diameter classes, such as the Chave and Brown models, consistently overestimate AGB for smaller diameter classes (Figs. 2 and 3). In the present study, trees ⩽25 cm DBH constituted on average 90.8% of stand basal area (Fig. 6), indicating that the development of allometric models for smaller size classes is particularly important in young secondary forests.

Local model 2 (M2) yielded significantly lower plot-level mean relative errors than 6 foreign allometric models (Figs. 2 and 3).
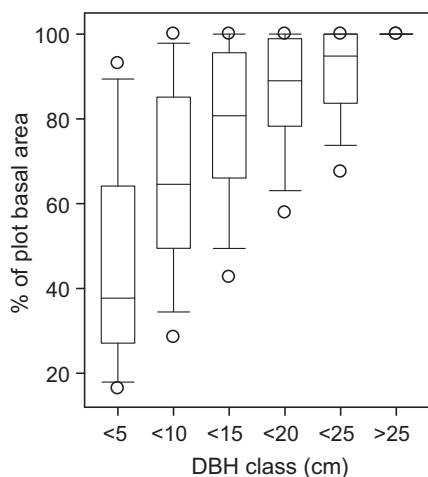
Fig. 6. The accumulative proportion of stand basal in DBH size classes. Box plots statistics are calculated from 94 plots in secondary forests that were abandoned between 1 and 25 years ago. Box plots give the median, and the 25th, 75th (box), 10th and 90th (whiskers) and 5th and 95th percentile (open dots).

Even when based on sample sizes of 49 trees only, the probability of less accurate landscape-level AGB estimates than any of the foreign models was less than 1% for the local model that included DBH and WSG as predictor variables (M2) and 18% for the model that included only DBH as predictor variable (M1). These results suggest that local allometric models likely produce more accurate AGB estimates, especially when species-specific wood specific gravity is included.

We expected that models developed for secondary forest would yield consistently more accurate AGB estimates than the two mature forest models, as early successional species generally have different ecological characteristics than those from mature forest, such as lower wood specific gravity, tree height and trunk taper (van Gelder et al., 2006; Poorter et al., 2006; Keeling et al., 2008). However, the results did not substantiate expectations. AGB estimates were inconsistent among these models, with two models estimating 15–17% lower and two models estimating 3.5–14.0% higher landscape-level AGB than M2. Similarly, the two models that included wood specific gravity did not perform consistently better than the models that did not include WSG (Figs. 2 and 5).

Currently, clear guidelines are missing for the selection of extant models for local carbon studies. The development of criteria for selecting the most appropriate allometric regression models for a specific site is, therefore, an important task and requires continuous efforts in the development of local models and collection of corresponding data on site and species characteristics. A promising analytical approach for future work could be Bayesian model averaging, which combines multiple competing models into a single predictive model. Although it has rarely been used in forestry (but see Li et al., 2008), it is quite common in other fields (e.g., Fraley et al., 2010). Until better criteria are developed, we recommend that the uncertainty in model choice is explicitly accounted for by providing estimates computed from different models (e.g., Alves et al., 1997; Jepsen, 2006).

4.4. Uncertainty associated with model choice vs. spatial variability in AGB stocks

Clark and Clark (2000) and Chave et al. (2004) have proposed the use of sample plots of >0.25 ha for carbon stock estimates. However, when landscapes are complex mosaics of secondary forests of different ages, many small plots rather than a few large plots will best reflect the spatial variability of AGB stocks in these landscapes and also may reduce the uncertainty in the estimation of landscape-level AGB (Sierra et al., 2007; Kauffman et al., 2009). In our study, mean relative deviation of landscape-level AGB estimates from the most accurate landscape-level AGB estimate (61 Mg/ha, using all 94 plots, M2) increased strongly with decreasing number of sample plots (Fig. 5c). This trend reflects large variation in AGB stocks across secondary forests of different ages (Sierra et al., 2007).

The mean deviation of the AGB estimates of most foreign models from the estimates of our local model varied little at different levels of landscape sampling intensities. Consequently, the relative contribution of the choice of these models to uncertainty in landscape-level AGB estimates declined with decreasing levels of landscape sampling intensity. In other words, when landscape-level AGB estimates are based on few sample plots, the uncertainty associated with sample size is much higher than the uncertainty associated with model choice. In practical terms, this implies that the development of a local allometric model is justified when it is part of a program of extensive landscape-level inventories of AGB. In our landscape, the development of a local model is justified at a sampling intensity of at least 30–40 plots – the threshold at which more than half of the relative deviation of the best AGB estimate was associated with the choice of four of the five foreign models.

5. Conclusions

Allometric models vary strongly in their prediction of stand and landscape AGB, making model choice an important source of uncertainty. Local models may provide more accurate AGB estimates than foreign models, but because carbon stocks are highly variable across rural landscapes, developing local models is only justified when landscape sampling is sufficiently intensive. When a local model is developed, the inclusion of wood specific gravity (WSG) as a predictor variable may decrease the uncertainty in the estimation of plot AGB substantially, but will have a more limited effect on the accuracy of landscape-level estimates. Conversely, the number of trees used for model fitting may have a very strong effect on the uncertainty of landscape-level AGB estimates, while the effect may be more limited on plot level. This suggests that, when the focus is on plot-level research questions, part of available funds and labor should be used for the collection of community-wide WSG data at the cost of the sample size for model fitting. When the focus is on the estimation of landscape-level AGB, though, efforts are best concentrated on increasing the sample size (number of plots) for model fitting.

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