Tree allometry in Central Africa: Testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks

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ABSTRACT

There is a lot of uncertainty in the amount and spatial variations of above-ground biomass in Africa, partly because very few allometric equations are available. The aim of this study was to assess the validity of using pan-tropical multispecies allometric equations developed by Chave et al. (2005) for estimating the above-ground biomass of trees in Central Africa and/or to develop site-specific equations. The study was conducted in lowland tropical forests of South-eastern Cameroon, at the edge between evergreen and semi-evergreen forests. Data of above-ground woody biomass were obtained from destructive sampling of 138 trees belonging to 47 taxa across a huge range of diameter (5.30–192.50 cm) and wood specific gravity (0.284–1.152 g cm^{-3}). A set of local site-specific multi- and single-species models relating above-ground biomass to tree diameter and wood specific gravity were fitted to the data. The best model was selected using information criterion. Both tree diameter and wood specific gravity were important predictor to consider for the estimation of above-ground biomass at tree scale. Single-species models were not necessarily better than multi-species models including wood specific gravity as a predictor. The best local multi-species model had the same structure and parameters as the pan-tropical equation developed by Chave et al. (2005) for moist forests. The estimates from the pan-tropical multi-species equation were nearly as good as those of the local multi-species equation. Using wood specific gravity from the global data base only slightly increased the estimation errors, because for the study taxa wood specific gravity was highly correlated to wood specific gravity from the global data base. In this study, we showed that the pantropical multi-species allometric equation developed for moist forests can be used to produce accurate estimates of biomass and carbon stocks from diameter measurement in forest inventory and wood specific gravity from global data base at species level. These findings are especially timely given the urgent need to quantify biomass and carbon stocks in the tropics, and given the spatial extent of moist forests in Central Africa.

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1. Introduction

Tropical forests are a key component of the global carbon cycle (Cramer et al., 2004; Malhi and Grace, 2000). While the Congo basin is the second largest block of continuous tropical forest after the Amazonian basin, there is still a lot of uncertainty about the amount and spatial variations in above-ground biomass (biomass hereafter) and carbon stocks (Baccini et al., 2008; Mitchard et al., 2011; Zhang et al., 2002).

Many techniques exist to estimate forest biomass at different spatial scales, but they all ultimately rely on ground and destruc-tive measurements of individual tree biomass to calibrate allometric equations (Gibbs et al., 2007). An allometric equation is a statistical model relating tree biomass to a set of predictors such as tree diameter and/or height, wood specific gravity, or forest type (Chave et al., 2005). Allometric equations are used to convert forest inventory data into biomass estimates at tree-level, and the sum of all data for the trees allows a biomass estimate to be obtained at plot level (Chave et al., 2004; Wharton and Cunia, 1987). Since existing allometric equations for tropical trees in African moist forests are restricted to a few specific species or sites (Deans et al., 1996; Djomo et al., 2010; Henry et al., 2010, 2011), pantropical multi-species equations are being used instead to estimate biomass from inventory data (Gourlet-Fleury et al., 2011; Lewis et al., 2009; Maniatis et al., 2011a). The pantropical multi-species equations developed by Chave et al. (2005) were calibrated on an extensive dataset of 2410 trees ⩾5 cm diameter from 27 study

sites across the tropics, but excluding Africa. Although widely used to estimate biomass from forest inventory data, the validity of these pantropical equations has been tested only rarely in Africa, i.e. for a small number of species and trees in Ghana (Henry et al., 2010), in the Democratic Republic of Congo (Ebuy et al., 2011) and in Madagascar (Vieilledent et al., 2012). Since the choice of allometric model is an important source of error in biomass estimation at landscape scale (Chave et al., 2004; Molto et al., 2012; Van Breugel et al., 2011), there is an urgent need to test the validity of pantropical equations in Africa in order to obtain accurate estimates of biomass and carbon stocks.

The allometry of tropical trees varies greatly with forest type, and specific allometric equations have been developed separately for wet, moist, and dry forests (Brown et al., 1989; Chave et al., 2005). Global analyses have recently shown that allometric relationships between height and diameter for tropical trees vary with geographic location (Feldpausch et al., 2011). In addition, location within a specific continent has been found to explain almost 50% of variations in tree allometry (Banin et al., 2012). These studies both demonstrated that mean and maximum height tend to be greater for Asian, than for African, and American tropical trees, respectively. These results are in agreement with existing empirical knowledge. The geographic variations found in tree allometry have been mostly attributable to environmental and structural variations between forests rather than to floristic variations (Banin et al., 2012; Feldpausch et al., 2011). This finding suggests that the high rate of endemism in tropical Africa (White, 1983) may be less important for tree allometry than particular environmental conditions. The same environmental or structural conditions that have been found to influence diameter:height allometry could also influence biomass allometric equations.

The most important predictors of tree biomass have been shown to be, in order of decreasing importance, its trunk diameter, wood specific gravity, and total height (Chave et al., 2005). Although it is important to consider tree height in biomass estimation (Feldpausch et al., 2012), it is extremely difficult to measure this variable accurately within the structurally complex tropical forests, and this measurement is only rarely available in forest inventory data. A proper test of the pantropical multi-species equations and/or the development of site-specific equations require a large sampling effort in terms of individuals (at least 100, Chave et al., 2004), diameters and species, but also rigorous measurements of wood specific gravity (Chave et al., 2005; Ebuy et al., 2011; Woodcock and Shier, 2002). It has been shown in Central Panama that wood specific gravity is even more important than the number of trees used for fitting the multi-species equation (Van Breugel et al., 2011). To the best of our knowledge, there are only a small number of published studies reporting tree biomass data in the Congo basin. Biomass data have been reported for Eucalypt hybrid trees in plantations in the Republic of Congo (Saint-André et al., 2005), three forest species in plantations in the Democratic Republic of Congo (Ebuy et al., 2011), five pioneer species in plantations and/or previously logged secondary forests in Cameroon (Deans et al., 1996) and a total of 31 forest species in old-growth forest in Cameroon (Djomo et al., 2010). In all cases, available biomass data concerned only a small number of trees, diameters and species. In addition, in natural forests of Central Africa, it is quite common to find trees with a diameter far beyond the validity threshold of pantropical equations (i.e. 150 cm), and these trees store the greatest proportion of biomass (Feldpausch et al., 2012). The classical approach to obtaining biomass estimates is to combine diameter measurements from forest inventories and information on species wood specific gravity from external sources (Gourlet-Fleury et al., 2011; Maniatis et al., 2011a). This is possible because between-species variations in wood specific gravity are more important than within-species variations (Molto et al.,

2012), and because huge efforts have been made to gather information on species wood specific gravity at a global scale (Zanne et al., 2009). The validity of pantropical equations thus needs to be tested across a huge diameter range and using wood specific gravity information from external sources.

The aim of this study was to assess the validity of using pantropical multi-species allometric equations developed by Chave et al. (2005) to estimate the above-ground biomass of trees in Central Africa and/or to develop site-specific equations. In this study, we focused on above-ground woody biomass rather than on total above-ground biomass. This is because woody organs (stump, stem and branches) contain the majority of the biomass, 96.7% and 98.1%, respectively, for 12 and 42 trees in the Democratic Republic of Congo (Ebuy et al., 2011) and Ghana (Henry et al., 2010). In addition, the biomass contained in leaves, flowers, and fruits, varies greatly both within and between years. Based on an extensive dataset of 138 trees destructively sampled in South-eastern Cameroon across a huge range of diameter (5.30–192.50 cm) and wood specific gravity (0.284–1.152 g cm^{-3}), we tested the null hypothesis that the allometry of African tree species does not differ from common allometric patterns that have been reported across the tropics. Because tree height measurements are rarely available in forest inventory data, we focused solely on diameter and wood specific gravity as explanatory variables of tree biomass, and assumed that the particular allometric relationship between tree height and diameter was modeled in the biomass equation. We addressed the following specific questions: (1) Do pantropical equations differ from and perform worse than local site-specific equations? (2) Does using wood specific gravity from the global data base significantly impact biomass estimates? (3) Are single-species models better than multi-species models?

2. Materials and methods

2.1. Study area

The study area is located in South-eastern Cameroon, in the Haut-Nyong Department, close to the city of Mindourou, about 450 km east of Yaoundé. The study was conducted in the logging concessions sustainably managed by the Pallisco company. The extremes encompassed by the study were 3°01′N and 3°44′N (southern and northern); and 13°20′E and 14°31′E (western and eastern). Average annual rainfall in the area varies between 1500 and 2000 mm with a 3 to 4-months dry season (November/December–February). The annual average monthly temperature varies at around 24 °C. Altitude varies between 600 and 760 m. The study site lies on a Precambrian substrate. Soils are deep ferralitic red or yellow soils. The vegetation belongs to the dense forest of the Guineo–Congolian region (White, 1983). The study site is located at the edge between evergreen and semi-evergreen forests (Letouzey, 1985).

2.2. Data collection

Above-ground biomass data were obtained from the destructive sampling of 138 trees across a huge range of diameter (5.30–192.50 cm, Table 1). The trees belonged to 23 families, and 47 identified taxa, of which 42 were determined to species level and five to genus level. Two individuals remained undetermined. In order to comply with national legislation, for trees with a diameter at breast height (dbh) larger than the minimum diameter for exploitation (MDE), we focused on three timber species harvested by the logging company (Entandrophragma cylindricum, Erythrophleum suaveolens and Pericopsis elata, Table 1). Smaller trees were

Table 1
Description of the 47 taxa (42 determined to species level and 5 to genus level) for which destructive above-ground woody biomass data were obtained in this study. Number of individual (n), wood specific gravity in the global data base (σ_{global}), mean and range of wood specific gravity calculated in this study (σ_{local}), and range of diameter at breast height (dbh) are given for each taxon.

Taxon	Family	Wood specific gravity (g cm^{-3})				dbh (cm)
		n	σ_{global}	σ_{local} Mean	Range	
Afzelia bipindensis	Caesalpiniaceae	3	0.731	0.666	0.595–0.739	31.2–57.9
Alstonia boonei	Apocynaceae	2	0.324	0.407	0.392–0.422	24.2–61.1
Angylocalyx pynaertii	Fabaceae	1	0.611	0.700		47.8
Annickia chlorantha	Annonaceae	3	0.437	0.482	0.451–0.520	27.9–47.3
Anopyxis klaineana	Rhizophoraceae	2	0.800	0.648	0.622–0.674	35.3–46.8
Baillonella toxisperma	Sapotaceae	3	0.697	0.693	0.670–0.728	112.5–153.5
Beilschmiedia congolana	Lauraceae	1	0.613	0.572		16.0
Blighia welwitschii	Sapindaceae	1	0.786	0.717		49.8
Cassipourea spp.	Rhizophoraceae	1	0.684	0.524		35.4
Celtis adolfi-friderici	Ulmaceae	5	0.581	0.670	0.617–0.747	23.1–50.3
Celtis mildbraedii	Ulmaceae	1	0.594	0.640		36.0
Cleistopholis glauca	Annonaceae	1	0.309	0.443		48.9
Cleistopholis patens	Annonaceae	2	0.335	0.297	0.284–0.309	26.9–29.7
Discoglypremna caloneura	Euphorbiaceae	1	0.340	0.412		38.0
Drypetes gossweileri	Euphorbiaceae	1	0.669	0.668		19.5
Drypetes spp.	euphorbiaceae	3	0.715	0.643	0.630–0.655	8.4–15.2
Duguetia confinis	Annonaceae	2	0.621	0.625	0.613–0.637	22.8–57.6
Entandrophragma cylindricum	Meliaceae	16	0.572	0.613	0.480–0.686	5.3–192.5
Eribroma oblongum	Sterculiaceae	4	0.638	0.461	0.439–0.494	20–35.6
Erythrophleum suaveolens	Caesalpiniaceae	14	0.872	0.994	0.851–1.152	50.3–137.5
Fernandoa adolfi-friderici	Bignoniaceae	1	0.449	0.502		48.4
Funtumia africana	Apocynaceae	2	0.424	0.413	0.404–0.423	32–38.5
Guarea thompsonii	Meliaceae	2	0.552	0.452	0.408–0.497	22.3–31.7
Keayodendron bridelioides	Phyllanthaceae	4	0.622	0.628	0.611–0.648	17.7–47.1
Lecaniodiscus cupanioides	Sapindaceae	1	0.636	0.533		29.9–29.9
Mansonia altissima	Sterculiaceae	7	0.564	0.551	0.530–0.596	21.6–70
Markhamia tomentosa	Bignoniaceae	1	0.473	0.461		22.4
Millettia spp.	Fabaceae	1	0.714	0.797		29.4
Ongokea gore	Olacaceae	1	0.749	0.749		13.6
Pericopsis elata	Fabaceae	16	0.639	0.610	0.428–0.686	22.3–121.4
Phyllocosmus africanus	Ixonanthaceae	1	0.780	0.729		28.4
Piptadeniastrum africanum	Mimosaceae	1	0.605	0.632		55.2
Polyalthia suaveolens	Annonaceae	8	0.695	0.560	0.532–0.618	13.2–44.4
Rauvolfia caffra	Apocynaceae	1	0.465	0.410		48.4
Sorindeia spp.	Anacardiaceae	1	0.501	0.679		9.9
Spathodea campanulata	Bignoniaceae	1	0.232	0.500		46.8
Strombosia pustulata	Olacaceae	1	0.830	0.657		27.3
Syzygium staudtii	Myrtaceae	1	0.632	0.557		21.1
Terminalia superba	Combretaceae	6	0.459	0.596	0.356–0.804	22.4–75.2
Tessmannia africana	Caesalpiniaceae	1	0.824	0.824		11.0
Tricalysia spp.	Rubiaceae	1	0.642	0.537		7.8
Trichilia monadelpha	Meliaceae	1	0.460	0.485		41.1
Triplochiton scleroxylon	Malvaceae	1	0.335	0.359		55.8
Undetermined		2	0.622	0.640	0.630–0.649	11.2–51
Xylopia chrysophylla	Annonaceae	1	0.597	0.540		24.6
Xylopia cupularis	Annonaceae	1	0.738	0.738		16.6
Xylopia hypolampra	Annonaceae	3	0.640	0.659	0.653–0.666	19.8–30.6
Xylopia phloiodora	Annonaceae	2	0.597	0.527	0.509–0.545	33.6–37.3

randomly selected and harvested during the construction of logging roads, 5 m apart on both sides of the road. The allometry of these trees was not influenced by any particular growth conditions. All the trees that were felled for this study were destined to be destroyed, either because they were harvestable (trees from commercial species larger than the *MDE*) or because they were located on future logging roads (small trees).

Indirect and direct measurements were used to gather biomass data and a method based on photogrammetry was developed to estimate the stump area of irregularly shaped trunks. Before felling, diameter at breast height or 30 cm above buttresses was measured according to international standards (Cailliez, 1980). After felling, flowers, fruits, leaves, and epiphytes were removed from all branches. A voucher specimen was collected for each individual to ensure later botanic determination. Trees were divided into three compartments: the stem (including the stump and the log), the branches and the crotches. All regularly shaped elements were cubed, while all other elements such as crotches and broken or irregularly shaped branches were weighed. Wood samples were collected in each compartment for the laboratory measurements needed for the calculation of wood specific gravity (ratio of the oven-dried dry mass per unit green volume) and moisture content (ratio between the mass of water and the green mass). The shape of the samples was either a disk or a disk portion so that the radial variations in wood specific gravity were taken into account. The green volume of cubed elements and the green biomass of weighed elements were converted into dry biomass using the wood specific gravity and moisture content, respectively. The above-ground woody biomass (*AGB*, in kg) of the whole tree was calculated as the sum of the dry biomass of all woody compartments (stem, branches and crotches). We identified only slight variations in wood specific gravity from the stump to the branches. The mean wood specific gravity was thus calculated across compartments at the tree level.

2.3. Data analysis

Firstly, we developed a set of local site-specific allometric equations. Following Chave et al. (2005), we fitted the following general allometric model to the observed data:

$$\ln AGB = a + b \times \ln(D) + c \times (\ln(D)^2) + d \times (\ln(D)^3) + e \times \ln(\rho) \quad \text{(model1)}$$

where AGB, D and ρ are tree above-ground biomass (in kg), diameter (in cm) and wood specific gravity (in g cm^{-3}), respectively, and a, b, c, d, and e, the model parameters. Three alternative models were derived from model 1. Model 2 was similar to model 1 but assumed that e = 1; model 3 assumed that c = d = 0 and e = 1, and model 4 assumed that c = d = e = 0 (Table 2). Model 4, which depended solely on diameter, was fitted to the multi-species dataset and to three species separately (single-species models 4.1, 4.2 and 4.3 for E. cylindricum, E. suaveolens and P. elata, respectively). In order to test the effect of including species identity, we also performed a covariance analysis including the species factor to the multi-species model 4. The four types of model were fitted to the log-transformed data by the method of ordinary least squares. The value, significance and 95% confidence interval were reported for all estimated parameters (a, b, c, d and e). The goodness of fit was measured by the residual standard error (RSE) of the fit, by the coefficient of determination (R^2) and by the Akaike Information Criterion (AIC). In order to correct for the systematic bias induced by the log-transformation, when back-transforming the data, we applied a first order correction factor (CF), which was calculated as follows (Baskerville, 1972; Sprugel, 1983).

$$CF = e^{\left(\frac{RSE^2}{2}\right)} \quad (1)$$

We then estimated the above-ground biomass (AGB_{est}, in kg) of each individual tree from the diameter (D, in cm) and wood specific gravity (ρ, in g cm^{-3}) using the pantropical equation developed by Chave et al. (2005) for moist forests (corresponding to forests with a marked dry season and between 1500 and 3500 mm annual rainfall), as follows:

$$AGB = \rho \times e^{-1.499 + 2.148 \times \ln(D) + 0.207 \times (\ln(D))^2 - 0.0281 \times (\ln(D))^3} \quad (2)$$

and the local multi- and single-species equations developed in this study, using both the wood specific gravity of individual trees calculated in this study and the mean values at species level in the global wood specific gravity data base (Zanne et al., 2009), available from the dryad repository (http://datadryad.org/). There were thus twelve estimated values of above-ground biomass for each tree, derived from the pantropical equation and the three multi-species local equations (models 1, 2 and 3) using values of wood specific gravity from this study and from the global data base, and using only diameter for predictions (multi-species model 4 and the three single-species models 4.1, 4.2, and 4.3). Values of wood specific gravity were not always available at the species level in the global wood specific gravity data base. We therefore used the mean at the genus level for Beilschmiedia congolana, Syzygium staudtii, Xylopia chrysophylla and Xylopia phloiodora, the mean at the family level for Angylocalyx pynaertii, Fernandoa adolfi-friderici, Lecaniodiscus cupanioides, Sorindeia sp., Tricalysia sp., and the mean at the site level for Keayodendron bridelioides and the two undetermined trees. In order to compare the estimates, we calculated the root mean

Table 2
Local site-specific allometric equations. Four types of multi-species allometric model and three single-species models were fitted to the data. The estimate and 95% confidence interval (2.5 and 97.5% lower and upper limits, respectively) are given for each parameter. Significance of the parameter estimate is indicated with *** for P < 0.001, ** for P < 0.01, and * for P < 0.05. Pantropical estimates for the first three multi-species models are given for comparison, and significantly different parameters (i.e. those not included in the confidence interval of the local parameter) are italicized.

Model		a	b	c	D	e	df	RSE	R^2	AIC
Model 1: ln AGB = a + b ln D + c (ln D)^2 + d(ln D)^3 + e ln ρ										
Local	Estimate	−1.170	1.907*	0.247	−0.0291	0.979***	132	0.189	0.989	−60.71
	2.5%	−3.33	−0.03	−0.31	−0.08	0.84				
	97.5%	0.99	3.85	0.81	0.02	1.12				
Pantropical	Estimate	−1.576	2.179	0.198	−0.0272	1.036				
Model 2: ln AGB = a + b ln D + c (ln D)^2 + d (ln D)^3 + ln ρ										
Local	Estimate	−1.201	1.940*	0.239	−0.0285		133	0.188	0.989	−62.63
	2.5%	−3.34	0.02	−0.32	−0.08					
	97.5%	0.94	3.86	0.79	0.02					
Pantropical	Estimate	−1.562	2.148	0.207	−0.0281					
Model 3: ln AGB = a + b ln D + ln ρ										
Local	Estimate	−1.497***	2.506***				135	0.192	0.988	−58.32
	2.5%	−1.68	2.46							
	97.5%	−1.32	2.55							
Pantropical	Estimate	*−1.864*	*2.608*							
Model 4: ln AGB = a + b ln D multi-species										
Local	Estimate	−2.331***	2.596***				135	0.295	0.974	58.26
	2.5%	−2.60	−2.06							
	97.5%	2.52	2.66							
Model 4.1: ln AGB = a + b ln D Entandrophragma cylindricum										
Local	Estimate	−2.246***	2.552***				14	0.203	0.992	−1.83
	2.5%	−2.80	2.42							
	97.5%	−1.69	2.68							
Model 4.2: ln AGB = a + b ln D Erythrophleum suaveolens										
Local	Estimate	−0.394	2.257***				12	0.195	0.936	−2.19
	2.5%	−1.98	1.90							
	97.5%	1.19	2.61							
Model 4.3: ln AGB = a + b ln D Pericopsis elata										
Local	Estimate	−1.583***	2.401***				14	0.162	0.982	−8.99
	2.5%	−2.34	2.22							
	97.5%	−0.83	2.58							

squared error (RMSE), which quantifies the difference between the observed values and estimates.

$$RSME = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(AGB_{est,i} - AGB_{obs,i})^2} \qquad (3)$$

where $AGB_{est,i}$ and $AGB_{obs,i}$ are the estimated and observed above-ground biomass for a tree i, respectively, and n is the total number of trees. We used the paired t-test between observed values and estimates to identify significant biases in the estimations. We calculated the relative error as the ratio between the absolute error (difference between the observed value and estimates) and the observed value for each tree. We plotted the relative error (in%) against tree diameter and smoothed the plot using a lowess procedure (locally weighted scatter plot smoothing).

Statistical analyses (regressions and tests) were all performed within the R environment (R Development Core Team, 2011).

3. Results

3.1. Development of site-specific equations

Four multi-species and three single-species allometric models were fitted to the dataset composed of 138 trees destructively sampled in South-eastern Cameroon (Table 1). Mean above-ground biomass was 6359 kg, and varied between 8 and 70,380 kg for the largest tree, an *E. cylindricum* with a diameter greater than 190 cm (Fig. 1). Mean wood specific gravity was 0.627 g cm^{-3}, and varied between 0.284 and 1.152 g cm^{-3} for the tree with the slightest and densest wood, a *Cleistopholis patens* with a diameter of 27 cm and an *E. suaveolens* with a diameter of 121 cm, respectively.

Models 1, 2 and 3 relating above-ground biomass to both tree diameter and wood specific gravity all explained more than 98% of variance and provided a good fit of the data, with a low residual

Fig. 1. Relationship between above-ground woody biomass (*AGB*) and tree diameter (*D*). Each dot corresponds to an individually weighed tree. The size of symbols is proportional to wood specific gravity and the colored symbols indicate three particular species: red circles for *Entandrophragma cylindricum*, green circles for *Erythrophleum suaveolens*, and blue circles for *Pericopis elata*. Solid lines correspond to the fit of the multi- and single-species models relating biomass to diameter (back transformed models 4, 4.1, 4.2 and 4.3). Black, red, green and blue lines correspond to all species, *Entandrophragma cylindricum*, *Erythrophleum suaveolens*, and *Pericopis elata*, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

standard error (*RSE* < 0.192, Table 2). The parameter estimates of pantropical models 1 and 2 developed by Chave et al. (2005) were all included in the 95% confidence interval of the local parameter estimates, but the parameters of model 3 were significantly different from the local parameters. Similarly to Chave et al. (2005), we found model 2 to be the best model (lowest AIC). The back-transformed equation including the correction factor is given below.

$$AGB = \rho \times e^{-1.183+1.940\times\ln(D)+0.239\times(\ln(D))^2-0.0285\times(\ln(D))^3} \qquad (4)$$

Both tree diameter and wood specific gravity were important predictors of tree above-ground biomass, since the simple model 4 (which did not include wood specific gravity as a predictor) provided a weaker fit of the data (*RSE* = 0.295), obviously because of the overestimation of above-ground biomass for slight-wooded species and the underestimation of dense-wooded species (Fig. 1).
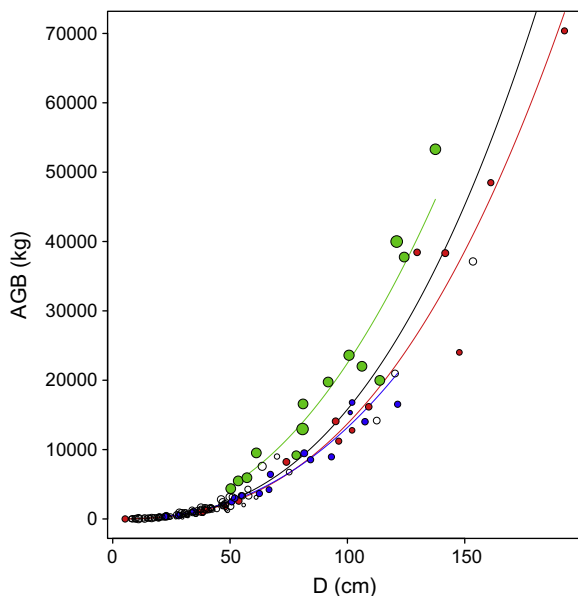
Simple model 4 relating above-ground biomass to the tree diameter was additionally fitted to three species separately, single-species models 4.1, 4.2 and 4.3 for *E. cylindricum*, *E. suaveolens* and *P. elata*, respectively. Differences in the intercept estimate across species were associated with wood specific gravity (Fig. 1, Tables 1 and 2). The intercept was lower for *E. cylindricum* (0.572 g cm^{-3}), than for *P. elata* (0.639 g cm^{-3}), and for *E. suaveolens* (0.872 g cm^{-3}). The goodness of fit of single-species models was not necessarily better than that of the multi-species models that included wood specific gravity as a predictor (Table 2). Indeed, the AIC of the covariance analysis including the species factor within model 4 (−27.47) was higher than that of the tree multi-species model including wood specific gravity within the set of predictors (−60.72, −62.63, and −58.32, respectively, for models 1, 2 and 3).

3.2. Above-ground biomass estimates

Neither the estimates of the pantropical equation developed by Chave et al. (2005) for moist forests, nor those of the local multi- and single-species equations developed in this study, tended to show a significant bias, i.e. a significant trend toward over or underestimation (non-significant P-value of the paired t-tests, Table 3). This holds true when using wood specific gravity from the global data base.

The differences between the observed values and the pantropical estimates (RMSE = 2462 kg) were only slightly bigger than that of local multi-species equations including wood specific gravity as a predictor (RMSE < 2389 kg for local models 1, 2 and 3, Table 3). The differences substantially increased when using wood specific gravity from the global data base, and even more so when using the local multi-species equations that did not include wood specific gravity as a predictor (RMSE = 3783 kg for local model 4). Within species, the differences between the observed values and estimates were extremely high for *E. cylindricum* and *E. suaveolens* (RMSE > 4027 kg, higher than the worst multi-species model, model 4).

For both the pantropical and local equations, the errors in the estimates of above-ground biomass from tree diameter and wood specific gravity were well distributed across the whole range of diameter (around 0 in Fig. 2a–d). Using wood specific gravity from the global data base tended to increase slightly the range of errors (increase point dispersal around 0 in Fig. 2e–h), and in agreement with previous results, this was even worse when wood specific gravity was not included as a predictor (Fig. 2i). Overestimations (points below 0 in Fig. 2i) corresponded to slight-wooded species (small circles) while underestimations (points above 0) corresponded to dense-wooded species (big circles). Within species, the errors in the estimates from single-species equations were low and well distributed across the range of diameter (Fig. 2j–l), except for one *E. cylindricum* tree and two *E. suaveolens* trees, for

Table 3
Error and bias in the estimates of above-ground woody biomass. The root mean squared error (*RMSE*) and results (degree of freedom, statistics and *P*-value) of paired *t*-tests between estimated and observed values are given for all estimates. Estimates were obtained using wood specific gravity from this study and (a) the pantropical equation developed by Chave et al. (2005) for moist forests, (b) local model 1 developed in this study, (c) local model 2, (d) local model 3; and using wood specific gravity from the global data base, and (e) the pantropical equation, (f) local model 1, (g) local model 2, (h) local model 3; and using only diameter for predictions, (i) local multi-species model 4, and the three local single-species models 4.1, 4.2, and 4.3 developed for (j) *Entandrophragma cylindricum*, (k) *Erythrophleum suaveolens*, and (l) *Pericopsis elata*, respectively.

	Model	RMSE (kg)	Paired *t*-test		
			df	Statistic	P-value
Using wood specific gravity from this study (σ_{local})					
(a)	Pantropical model for moist forests	2 462	136	0.247	0.805
(b)	Local model 1	2 308	136	0.003	0.998
(c)	Local model 2	2 323	136	−0.027	0.978
(d)	Local model 3	2 389	136	−1.824	0.070
Using wood specific gravity from the global data base (σ_{global})					
(e)	Pantropical model for moist forests	3 179	136	1.653	0.101
(f)	Local model 1	2 984	136	1.543	0.125
(g)	Local model 2	2 996	136	1.550	0.123
(h)	Local model 3	2 634	136	0.261	0.794
Using only diameter for predictions					
(i)	Local model 4 (multi-species)	3 783	136	−0.315	0.753
(j)	Local model 4.1 (*Entandrophragma cylindricum*)	4 743	15	0.113	0.912
(k)	Local model 4.2 (*Erythrophleum suaveolens*)	4 027	13	0.093	0.927
(l)	Local model 4.3 (*Pericopsis elata*)	1 663	15	−0.287	0.778
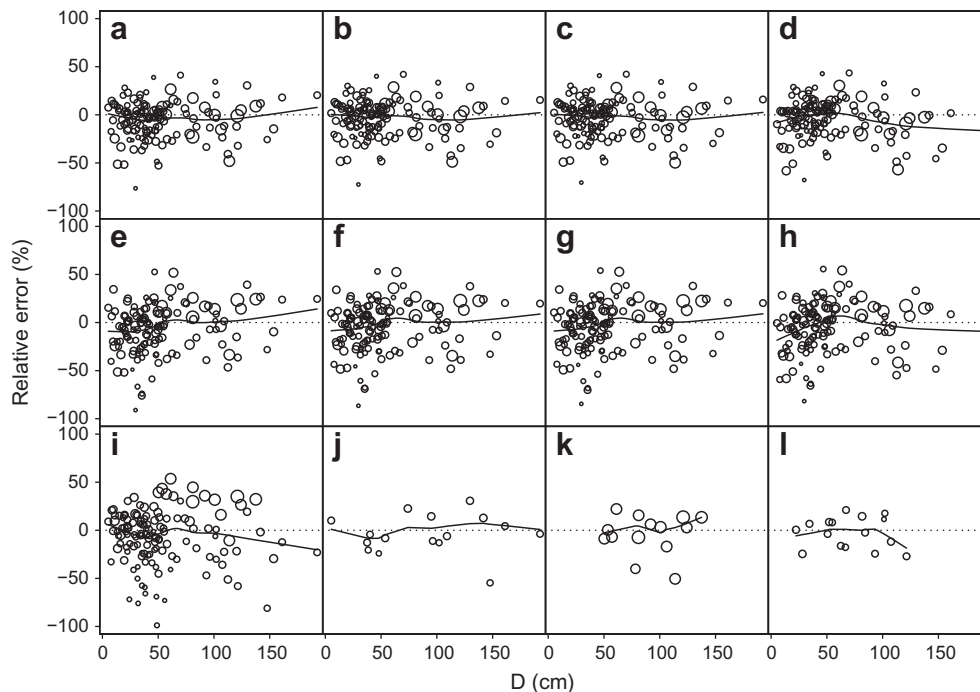
Fig. 2. Relationships between the relative error in the estimation of above-ground woody biomass and tree diameter (*D*). Estimations were obtained using wood specific gravity from this study and (a) the pantropical equation developed by Chave et al. (2005) for moist forests, (b) local model 1 developed in this study, (c) local model 2, (d) local model 3; and using wood specific gravity from the global data base, and (e) the pantropical equation, (f) local model 1, (g) local model 2, (h) local model 3; and using only diameter for predictions, (i) local multi-species model 4, and the three local single-species models 4.1, 4.2, and 4.3 developed for (j) *Entandrophragma cylindricum*, (k) *Erythrophleum suaveolens*, and (l) *Pericopsis elata*, respectively. The solid lines correspond to the smoothing made by a lowess method. Each dot corresponds to the error made on an individually weighed tree. The size of symbols is proportional to wood specific gravity.

which above-ground biomass was highly overestimated. This explains the high values of *RMSE* for the corresponding single-species models 4.1 and 4.2 (Table 3).

4. Discussion

### 4.1. The specific equation for South-eastern Cameroon

In this paper, we have provided a rigorous test of the validity of the pantropical equation developed by Chave et al. (2005) for moist forests in South-eastern Cameroon. With probably no or few spe-

cies in common with the data set used to fit the set of pantropical equations due to the high rate of endemism in tropical Africa (White, 1983), we showed that the pantropical equation developed for moist forests was valid in South-eastern Cameroon. This finding thus confirmed the early results obtained across a small range of diameters in Southern Cameroon (Djomo et al., 2010) and in the Democratic Republic of Congo for only 12 trees of three forest species in plantations (Ebuy et al., 2011). The number of trees used for fitting, the representativeness of species, the range of diameter and wood specific gravity, and the within-tree variations of wood specific gravity have all been previously identified as potential sources

of error in developing allometric equations (Basuki et al., 2009; Chave et al., 2005, 2004; Van Breugel et al., 2011). In this study, the potential sources of error were minimized since the analyses were based on 138 trees destructively sampled, belonging to 47 taxa representative of the area, across a huge range of diameter (5.30–192.50 cm) and wood specific gravity (0.284–1.152 g cm^{-3}), and integrating within-tree variations of wood specific gravity for the calculation of the biomass of the cubed elements. Based on this extensive dataset for a single site, we were able to develop a set of local site-specific multi- and single-species equations. The best local model had the same structure as the best pantropical model (model 2) with no parameter estimate for wood specific gravity. This result confirms that the above-ground biomass of a tree could be considered as a product of wood specific gravity and tree volume (Djomo et al., 2010). In addition, the parameter estimates of the best local multi-species model were not significantly different from the pantropical parameter estimates. These findings thus suggest that the pantropical equation is not significantly different from the local site-specific equation. Forest inventory data gathered over large spatial scale (>100,000 hectares) by logging companies in the process of management planning combined with pantropical allometric equations could thus be used to estimate the spatial variations in above-ground biomass in Central Africa (Gourlet-Fleury et al., 2011; Maniatis et al., 2011a). It has, however, been shown that allometric models that focus on large trees tend to overestimate biomass for small trees (Deans et al., 1996; Van Breugel et al., 2011). In this study, we showed that above-ground biomass estimates at tree scale were moreover highly concordant with observed values across the whole range of above-ground biomass and diameter. We also confirmed that wood specific gravity is an important predictor of above-ground biomass (Baker et al., 2004; Chave et al., 2005; Deans et al., 1996; Vieilledent et al., 2012). This suggests the need for a revision of the IPCC guidelines (Aalde et al., 2006). These guidelines recommend the general allometric equations developed by Brown et al. (1989), which depend only on tree diameter.

4.2. Using wood specific gravity from global data bases

In this study, we showed that the pantropical equation developed by Chave et al. (2005) for moist forests relating above-ground biomass to tree diameter and wood specific gravity was valid in South-eastern Cameroon, even when using the wood specific gravity from the global data base (Zanne et al., 2009). Using wood specific gravity extracted from the global data base increased only slightly the errors in the estimation because wood specific gravity observed in this study was highly correlated to wood specific gravity extracted from the global data base for the studied taxa (Fig. 3). This result is of great importance, since the classical approach for estimating above-ground biomass (Gourlet-Fleury et al., 2011; Maniatis et al., 2011a) and/or carbon stocks (Lewis et al., 2009) at plot, forest, landscape, and even regional scale, is to combine diameter measurements from forest inventory and species wood specific gravity from external sources. Huge efforts have been made to gather information on wood specific gravity at a global scale, and the global data base includes information for 540 species, 291 genera and 68 families in tropical Africa (Zanne et al., 2009). In this study, because we focused on abundant and timber species, wood specific gravity information was available at species level for most species ($n = 34$ out of the 42 taxa determined at species level, 81%) in the global data base. When wood specific gravity is not available at species level, the common approach is to use the mean value at higher taxonomical level (genus, family or order). This is possible because wood specific gravity has been shown to be mainly explained by the wood specific gravity at genus level (Baker et al., 2004; Slik, 2006), and even to be conserved across
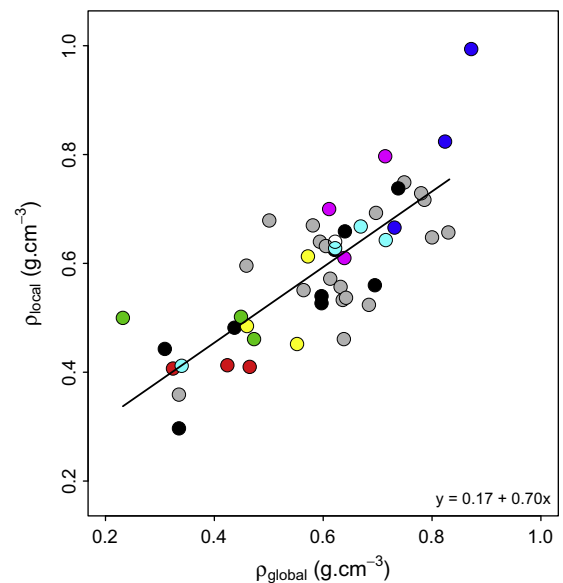
Fig. 3. Relationships between wood specific gravity calculated in this study (σ_{local}) and the mean value in the global data base (σ_{global}). Each dot corresponds to a single taxon (species or genus). Colored symbols indicate families represented by more than three taxa, black circles for *Annonaceae*, red circles for *Apocynaceae*, green circles for *Bignoniaceae*, blue circles for *Caesalpiniaceae*, cyan circles for *Euphorbiaceae*, pink circles for *Fabaceae*, and yellow circles for *Meliaceae*, grey circles for the other families (*Anacardiaceae, Combretaceae, Ixonanthaceae, Lauraceae, Malvaceae, Mimosaceae, Myrtaceae, Olacaceae, Rhizophoraceae, Rubiaceae, Sapindaceae, Sapotaceae, Sterculiaceae,* and *Ulmaceae*), and a white circle for the undetermined family. The black line corresponds to the linear regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the entire seed plant phylogeny (Swenson and Enquist, 2007). In this study we assigned wood specific gravity at higher taxonomical level for only a small proportion of taxa and there was only one species *Keayodendron bridelioides* for which no information was available at either taxonomical level. In comparison, using the CIRAD data base on wood technical properties, Gourlet-Fleury et al. (2011) had access to information for only 99 species out the 208 taxa determined at species level (47.6%) in the forest inventory data in the Central African Republic. In order to be able to make accurate estimates of the carbon stocks present in the world's tropical forests, there is thus a growing need to gather information on wood specific gravity for the missing species, genera and possibly families in international data bases. This implies rigorous laboratory measurements for the calculation of wood specific gravity (Williamson and Wiemann, 2010; Woodcock and Shier, 2002). In this context, the potential for using xylarium wood samples has recently been acknowledged (Maniatis et al., 2011b).

4.3. The need for general or specific allometric equations

There is a growing body of evidence on the validity of the pantropical equations developed by Chave et al. (2005) throughout the tropics (Djomo et al., 2010; Van Breugel et al., 2011; Vieilledent et al., 2012), although a significant bias has also been reported by Henry et al. (2010) in Ghana, by Alvarez et al. (2012) in Columbia, and by Nogueira Lima et al. (2012) in Brazil. The question currently under discussion among scientists is whether, elsewhere in the tropics where no species- or site-specific allometric model is available, it would be better to use the general pantropical equations or to develop local equations. Although model choice is an important source of uncertainty in biomass estimations (Chave et al., 2004; Molto et al., 2012; Van Breugel et al., 2011; Wharton and Cunia,

1987), there is an overall lack of clear guidelines for the selection of existing models. On the one hand, Basuki et al. (2009) concluded that the generalized equations are not sufficient to estimate the biomass for certain types of forest, such as the lowland Dipterocarp forests of Indonesia. These authors discussed the applicability of pantropical equations for the diverse structure and composition of tropical forests. On the other hand, in their review of methods to estimate biomass of tropical forests, Gibbs et al. (2007) argued that the effort required to develop species- or site-specific allometric equations would not typically improve accuracy in biomass estimations. In this study, we showed that single-species models were not necessarily better than multi-species models including wood specific gravity as a predictor. Contrary to the results of Basuki et al. (2009), our results argue for the use of general or site-specific allometric models rather than the development of taxon-specific models. In addition, Chave et al. (2005) showed that a single equation including trunk diameter, wood specific gravity and total tree height already provides an accurate estimate of above-ground biomass, and that including site, successional status, continent or forest type only slightly improves the quality of the fit. This is due to the fact that site differences in tree allometry are almost entirely driven by differences in height:diameter allometry (Banin et al., 2012; Feldpausch et al., 2011), and thus tree height is an important allometric factor that needs to be considered in order to improve forest biomass estimates (Feldpausch et al., 2012). In the present study, however, we showed that using the pantropical equation relating above-ground biomass to tree diameter and wood specific gravity is already able to provide accurate estimates of above-ground biomass at tree scale in South-eastern Cameroon. This may be due to the fact that African trees tend to show an intermediate height:diameter allometry between the small statured Amazonian and the tall Asian trees (Banin et al., 2012; Feldpausch et al., 2011), and that above-ground biomass data for both Amazonian and Asian trees have been used to fit the pantropical equations (Chave et al., 2005). The validity of pantropical equations, however, remains to be tested in particular environmental conditions, e.g. swamps or temporarily flooded forest, that may constrain the allometric relationship between height and diameter (Banin et al., 2012; Feldpausch et al., 2011). For instance, the pantropical multi-species allometric equations are valid in the highly diverse and endemic moist and dry forests of Madagascar but tree height would need to be integrated into the set of predictors (Vieilledent et al., 2012). A possible alternative to integrating tree height into biomass estimations based on diameter measurements in forest inventory would be to construct site-specific height:diameter relationships (Chave et al., 2005; Feldpausch et al., 2011; Vieilledent et al., 2012).

5. Conclusion

The present study showed that the pantropical multi-species allometric equation developed for moist forests can be used to produce accurate estimates of biomass and carbon stocks from diameter measurements in forest inventory data and from external information on wood specific gravity at species level. These findings are especially timely given the urgent need to quantify biomass and carbon stocks in the tropics, and given the spatial extent of moist forests in Central Africa, i.e. almost all lowland terra firme forests.

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