

A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models

G. VIEILLEDENT,^{1,2,8} R. VAUDRY,³ S. F. D. ANDRIAMANOHISOA,⁴ O. S. RAKOTONARIVO,⁴ H. Z. RANDRIANASOLO,⁴ H. N. RAZAFINDRABE,⁴ C. BIDAUD RAKOTOARIVONY,^{5,6} J. EBELING,⁷ AND M. RASAMOELINA⁷

¹CIRAD, UR 105 Biens et Services des Ecosystèmes Forestiers, TA C-105/D, Campus International de Baillarguet, F-34398 Montpellier Cedex 5 France

²CIRAD-Madagascar, DRP Forêt et Biodiversité, BP 904, Ambatobe, 101-Antananarivo, Madagascar

³Fondation GoodPlanet, Domaine de Longchamp, 1 carrefour de Longchamp, F-75116 Paris, France

⁴ESSA Forêt, BP 175, Campus universitaire d'Ambohitsaina, 101-Antananarivo, Madagascar

⁵IHEID, Graduate Institute of International and Development Studies, Case postale 136, 1211 Genève 21 Switzerland

⁶IRD-Madagascar, Centre d'Economie et d'Ethique pour l'Environnement et le Développement Madagascar (C3EDM), Fac DEGS, Université d'Ankatso, 101-Antananarivo, Madagascar

⁷WWF Madagascar and Western Indian Ocean Programme Office, BP 738, 101-Antananarivo, Madagascar

Abstract. Allometric equations allow aboveground tree biomass and carbon stock to be estimated from tree size. The allometric scaling theory suggests the existence of a universal power-law relationship between tree biomass and tree diameter with a fixed scaling exponent close to 8/3. In addition, generic empirical models, like Chave's or Brown's models, have been proposed for tropical forests in America and Asia. These generic models have been used to estimate forest biomass and carbon worldwide.

However, tree allometry depends on environmental and genetic factors that vary from region to region. Consequently, theoretical models that include too few ecological explicative variables or empirical generic models that have been calibrated at particular sites are unlikely to yield accurate tree biomass estimates at other sites.

In this study, we based our analysis on a destructive sample of 481 trees in Madagascar spiny dry and moist forests characterized by a high rate of endemism (>95%). We show that, among the available generic allometric models, Chave's model including diameter, height, and wood specific gravity as explicative variables for a particular forest type (dry, moist, or wet tropical forest) was the only one that gave accurate tree biomass estimates for Madagascar ($R^2 > 83\%$, bias < 6%), with estimates comparable to those obtained with regional allometric models. When biomass allometric models are not available for a given forest site, this result shows that a simple height–diameter allometry is needed to accurately estimate biomass and carbon stock from plot inventories.

Key words: allometry; bias; biomass; carbon; Madagascar; models; REDD; scaling theory; tropical forest; wood density.

INTRODUCTION

Tropical forests have assumed increasing importance in international efforts to mitigate climate change thanks to their capacity to store carbon and because of the significant emissions caused by their destruction (Malhi and Grace 2000, Gibbs et al. 2007). Reducing emissions from deforestation and forest degradation (REDD) is as a novel mechanism to create financial rewards for countries or projects that prevent forest loss (Ebeling and Yasue 2008). In order to quantify carbon benefits and compensation payments through REDD, carbon stocks in forests have to be estimated. The Intergovernmental Panel on Climate Change (IPCC) provides guidelines to assist countries in developing

carbon accounting methodologies. These guidelines are organized in “tiers,” each tier providing successively higher accuracy and thus potentially higher financial returns for monitoring carbon stocks and reduced emissions. To achieve Tier III levels of accuracy, high resolution methods—including the use of biomass allometric equations—are needed (Aalde et al. 2003, IPCC 2006).

Biomass allometric models enable aboveground tree biomass to be estimated from tree size. Such models are based on theoretical considerations and empirical generic studies. The allometric scaling theory postulates the existence of a universal power-law relationship between tree biomass and tree diameter with a fixed scaling exponent close to 8/3 (Enquist et al. 1998, West et al. 1999, Enquist and Niklas 2001). This value was derived from naturally occurring fractal metabolic networks that branch to supply all parts of living organisms, such as the vascular system and the

Manuscript received 11 January 2011; revised 11 August 2011; accepted 18 August 2011; final version received 8 September 2011. Corresponding Editor: D. S. Schimel.

⁸ E-mail: ghislain.vieilledent@cirad.fr

branching structure in trees (West et al. 1997). Relying on the allometric scaling theory, several authors recently developed regional biomass allometric models assuming a power-law relationship between tree biomass and tree diameter (Ketterings et al. 2001, Chojnacky 2002, Zianis and Mencuccini 2004, Pilli et al. 2006, Navar 2009) while discussing the existence of a truly universal value of 8/3 (2.667) for the scaling exponent. The simple power-law relationship has also been questioned for large trees (Niklas 1995, Chave et al. 2005) because of mechanical and physiological limits to an increase in tree height at large diameters. For this reason, using a power-law relationship might lead to overestimation of biomass for large trees. To overcome this problem, polynomial models of degree two and three on diameter, viewed as a reasonable generalization of the power-law model, have been used (Brown et al. 1989, Niklas 1995, Chave et al. 2005). The hypothesis of a unique explicative variable based on tree size (i.e., tree diameter) to estimate biomass has also been called into question. Including tree height as an additional size covariate has generally been shown to lead to far better biomass estimates (Brown et al. 1989, Chave et al. 2005). Chave et al. (2005) also found that environmental variables such as precipitation and seasonality, which determine forest type (e.g., dry, moist, and wet tropical forest), were significant variables in predicting tree biomass. In addition, the importance of wood density as an intrinsic explicative variable was confirmed in several studies (Baker et al. 2004, Chave et al. 2005, 2009, Henry et al. 2010). Although the value of the allometric scaling theory for reliably estimating biomass in tropical forests seems questionable, the general idea that body size (in this case, tree size) explains much of the structural, functional, and ecological characteristics of an organism (e.g., tree biomass) certainly holds true. This suggests the possibility of developing accurate generic allometric models by using a generalization of the power-law relationship and incorporating a limited number of additional size, species-specific, and environmental covariates (Brown et al. 1989, Niklas 1995, Chave et al. 2005, Pilli et al. 2006).

Two major research efforts sought to establish such generic empirical allometric models for tropical forests by using large pan-continental data sets. Brown et al. (1989) and Brown (1997) used data from Central and South America and south and southeast Asia, and the resulting models were updated by Pearson et al. (2005). These models have particular relevance in the context of REDD because they are formally recommended by the IPCC for estimating carbon stocks in tropical forests (Aalde et al. 2003, IPCC 2006). In the second major study, Chave et al. (2005) used a large data set including 2412 trees from 15 countries in tropical America and tropical Asia to develop generic allometric models. Although data was derived from many different sites throughout the tropical world, the best models led to very high coefficients of determination ($R^2 > 99\%$) and

very low biases ($0 < \text{bias} < 6\%$). This suggests that Chave et al.'s generic models are robust and should yield accurate results for tree biomass throughout the tropics. Indeed, the models developed by Brown et al. and Chave et al. have been widely used to estimate tree biomass and carbon stocks at new sites (Blanc et al. 2009, Fox et al. 2010, Rutishauser et al. 2010). This has even been the case for sites in Africa (Brown et al. 1989, Martin et al. 2004), even though no data from African countries was used to estimate the parameters of either model.

Despite the apparent general validity of allometric equations based on large data sets, trees would be expected to present different allometric relationships from one region to another depending on environmental factors (e.g., soil and climate) and species functional traits (e.g., wood density, crown architecture; Vieilledent et al. 2010). This should prevent the use of generic models calibrated at specific sites to estimate carbon and biomass at other sites. To overcome this challenge, it would be extremely useful to find an accurate universal biomass allometric model (with a high coefficient of determination and a low bias), incorporating a relatively low number of size, species-specific, and environmental covariates. The aim of our study was to identify (or invalidate) such a model among the available generic theoretical and empirical models.

To this end, we compared regional empirical models with theoretical and generic empirical models to estimate tree biomass in several sites in the spiny dry and moist-wet forests of Madagascar. Madagascar forests are a valuable test case for the applicability of generic theoretical and empirical models for two reasons. First, no African data sets have been used to estimate parameters of existing generic allometric models, even though Africa accounts for 30% of tropical forest (FAO 2005). Second, Madagascar has a very high rate of endemism (close to 96%) for tree species (Goodman and Benstead 2005), meaning that tree species may have different functional traits from species in tropical America and Asia. Finally, we demonstrated that Chave's model including height as an additional size covariate to tree diameter and including one synthetic environmental factor (annual precipitation) and one synthetic species functional trait (wood specific gravity) was the only generic model to be particularly robust, leading to accurate estimates of tree biomass at new sites ($R^2 > 83\%$ and bias $< 6\%$). When biomass allometric models are not available for a given forest site, this result shows that a simple height-diameter allometry is needed to accurately estimate biomass and carbon stock from plot inventories.

MATERIAL AND METHODS

Field data

Sites and forest classification.—Data for biomass allometric models were collected in five forest sites in Madagascar (Appendix A and Table 1). Around the central point of each site, we defined a buffer zone with a

TABLE 1. Forest site characteristics: latitude, longitude, altitude, temperature (T), temperature seasonality (T seas.) and precipitation seasonality (P seas.) for the central point of the site.

Forest site, village	Latitude and longitude	Altitude (m)	T (°C; $\times 10$)	Min–max	T seas.	P (mm)
Bealanana, Analila	14.453611° S, 49.046389° E	1214	195	96–287	2156	1502
Ivohibe, Sakaroa	22.439167° S, 46.989722° E	582	213	118–291	2592	1257
Fort Dauphin wet, Beampingaratra	24.475278° S, 46.899722° E	469	214	114–297	2546	1293
Fort Dauphin dry, Manavy	24.954722° S, 45.753889° E	193	237	121–334	2941	538
Fandriana, Fiadanana	20.454444° S, 47.601389° E	1130	181	90–263	2580	1690

Notes: Mean temperature (T) and range (min–max) were computed using the 12 monthly mean temperatures. T seas. was defined as 100 times the standard deviation (SD) of the monthly mean temperatures (°C; $\times 10$). P seas. was defined as the coefficient of variation (SD/mean) of the monthly mean precipitation (in mm). Annual precipitation mean (P) and range (min–max) were computed from the annual precipitation means for the 10 km radius prospecting area around the central point of the site. All bioclimatic variables came from the WorldClim database (Hijmans et al. 2005). Plugge forest categories (very dry, dry, moist, and wet forests) come from a classification based on vegetation image analysis (from MODIS, moderate resolution imaging spectroradiometer), on topographic data (from SRTM, shuttle radar topography mission), and climatic data (Plugge et al. 2010).

10 km radius corresponding to our prospecting area (Appendix A). We used the classification of Plugge et al. (2010) to categorize the five forest sites. This classification was based on vegetation image analysis (from moderate resolution imaging spectroradiometer [MODIS]), on topographic data (from shuttle radar topography mission [SRTM]), and on climatic data. One site (Fort Dauphin dry) was categorized as a tropical spiny dry forest, one site (Fandriana) was categorized as a tropical moist forest, and one site (Fort Dauphin wet) was categorized as a tropical wet forest. Two sites (Bealanana and Ivohibe) were located at the limit of the moist and wet regions and were categorized as moist–wet forests (Appendix A and Table 1). We consequently decided to group the moist and wet forest sites in a single “moist–wet” category for the purpose of our biomass modeling approach.

Species and tree sampling method.—In each of the five forest sites, we identified the dominant tree species. Trees belonging to these species to be cut down were chosen nonrandomly, i.e., in such a way that they spanned a large part of the absolute species diameter range at our sites. Trees up to 54 cm D (D , tree diameter at 1.30 m height) were cut in the moist–wet forest and trees up to 32 cm D were cut in the spiny dry forest. For each tree i , we measured the diameter (D_i , in cm) with a 1-mm precision tape and the total height (H_i , in cm) with a 1-cm precision tape. We chain-sawed the trees into smaller segments and used a 0.25-kg precision scale to weigh the total fresh aboveground biomass of the tree including trunk, branches, and leaves (fAGB $_i$, in kg).

Wood sampling method.—To account for the within-tree variability of the wood physical characteristics, we collected samples of wood at four heights in the tree. One sample was taken at the base, one at the middle, and one at the top of the trunk and one at the crown. As samples of the trunk, using a chainsaw, we removed a rectangular wood core extending from the bark to the

wood heart. As the crown sample, after selecting a branch at random, we took a disk of wood. The green mass of each sample s ($m_{gr,s}$, in g) was measured in the field using a 0.1-g precision scale. Wood samples were stored in hermetically sealed plastic bags until water content and wood specific gravity could be measured at the laboratory.

Water content and wood specific gravity measurement

The green volume (in cm³) of the wood samples was measured using the water displacement method. A container capable of holding the samples was filled with water and placed on a digital 0.01-g precision scale. Each wood sample s was entirely submerged in the water using a thin wire of negligible volume. The measured mass of displaced water (in g) was equal to the volume of the sample (V_s , in cm³) as water density was assumed to be 1 g/cm³ at the ambient temperature in the lab (close to 20°C).

Each sample was oven-dried at 75°C until a constant mass $m_{ov,s}$ was obtained. Using a hygrometric and thermal balance at 103°C, we measured the mean residual water content after drying (RWC $_j$, in %) of 10 wood samples chosen at random for each site j . We then computed the anhydrous mass m_s of sample s from site j , $m_s = m_{ov,s}(1 - \text{RWC}_j/100)$.

With the green volume V_s , the anhydrous mass m_s , and the water density (ρ_{wa} , in g/cm³), we computed the wood specific gravity of sample s (ρ_s , unitless), $\rho_s = m_s/V_s/\rho_{wa}$. The water content of sample s (WC $_s$, in %), was computed using the green mass $m_{gr,s}$ and the anhydrous mass m_s , $\text{WC}_s = 100(m_{gr,s} - m_s)/m_{gr,s}$. We then computed ρ_i and WC $_i$ the mean wood specific gravity and water content of each tree i , respectively (Williamson and Wiemann 2010). We also computed the mean wood specific gravity at the species and genus level to complete the world wood density data base (Appendix B). Using the tree water content (WC $_i$) and the fresh aboveground biomass

TABLE 1. Extended.

Min–max	<i>P</i> seas.	Plugge category	Allometry category	No. trees	dbh range (cm)
1457–1548	92	moist–wet	moist–wet	76	10–54
1096–1414	84	moist–wet	moist–wet	90	6–36
1084–1780	67	wet	moist–wet	90	9–37
524–554	75	very dry	spiny dry	135	3–32
1550–2013	74	moist	moist–wet	90	6–35

(fAGB_{*i*}), we computed the dry aboveground biomass of tree *i* (AGB_{*i*}, in kg), $AGB_i = fAGB_i(1 - WC_i/100)$.

Estimating the parameters of regional allometric models

Allometric models including a measure of tree height.—As a follow-up of the work of Chave et al. (2005), the first kind of model (Mada.I) assumed that tree height is available in forest inventories. Model Mada.I linked the tree dry biomass AGB_{*i*} to the tree diameter *D_i*, the tree total height *H_i*, and the tree-wood specific gravity ρ_{*i*}. This model is the result of a dimensional approach: mass (in kg) = volume (m³) × density (kg/m³). As trees have no regular shape (e.g., conic or cylindrical) volume has to be derived from *D*, *H*, and associated statistical parameters. In the same way, because real tree density is not known (as it depends on many factors including the distribution of leaves, hardwood, and softwood), real tree density was estimated from wood specific gravity ρ and associated statistical parameters. Two different parameterizations were tested for this first kind of model. The first (denoted Mada.I.1, Eq. 1) included the three predictive variables in a Gaussian linear model. Variables were log-transformed to avoid heteroscedasticity in the data:

$$\log(AGB_i) = \beta_0 + \beta_1 \log(D_i) + \beta_2 \log(H_i) + \beta_3 \log(\rho_i) + \varepsilon_i, \varepsilon_i \sim \mathcal{N}(0, \sigma^2) \tag{1}$$

where β₀, β₁, β₂, and β₃ are linear model parameters, ε is the residual error term, *N* is the normal distribution, and σ² is the variance of the residuals.

In the second model parameterization (denoted Mada.I.2, Eq. 2), the compound variable ρ*D*²*H* was the only predictive variable:

$$\log(AGB_i) = \beta_0 + \beta_1 \log(\rho_i D_i^2 H_i) + \varepsilon_i, \varepsilon_i \sim \mathcal{N}(0, \sigma^2). \tag{2}$$

Allometric models including an estimation of tree height.—When tree height is not available in forest inventories, it can be estimated from tree diameter (Brown et al. 1989, Vieilledent et al. 2010). The estimated height can then be used with biomass allometric models that include height as a covariate,

like model Mada.I (Brown et al. 1989, Chave et al. 2005). To test if this approach gives an accurate estimation of tree biomass, we developed height–diameter allometric models for the spiny dry and the moist–wet forest in Madagascar. We supplemented data on height and diameter obtained from felled trees with additional data on standing trees selected at random in each forest type. We used the Vertex-III instrument (Haglöf Company Group, Långsele, Sweden), which uses an ultrasonic method to measure tree height. We collected data for 250 trees with *D* ≤ 128 cm in moist–wet forests and data for 369 trees with *D* ≤ 48 cm in spiny dry forests.

Due to the low competition for light and the fact that scarce water resource is a key limiting factor for an increase in tree height in the spiny dry forest, we estimated the parameters of a biologically consistent monomolecular model (Eq. 3) with an asymptote denoted β₀ and a constraint fixing the intercept β₁ to 1.3 (*H* = 1.3 m when *D* = 0 cm). Since only information on the diameter class of the standing trees was available for the additional height–diameter data in the spiny dry forest, we estimated the asymptote β₀ by computing the 95% quantile of the tree heights (Fig. 1). The free shape parameter β₂ was estimated using the height–diameter data from the felled trees (Fig. 1):

$$H_i = \beta_0 - (\beta_0 - \beta_1)\exp(-\beta_2 D_i) + \varepsilon_i, \varepsilon_i \sim \mathcal{N}(0, \sigma^2). \tag{3}$$

For the moist–wet forest, prior knowledge of the level of resources (strong competition for light and adequate water resources) and field data (Fig. 1) did not support the existence of an asymptote for the height–diameter relationship. We thus compared polynomial models on diameters including linear, squared, and cubic models using Student’s *t* test (results not shown). Parameters for *D*² and *D*³ in polynomial models were not significantly different from zero. The best model for the height–diameter relationship in the moist–wet forest was a simple power model (Eq. 4), indicating that for large diameter trees, an increase in height was not limited by mechanical or physiological constraints, as was the case in other forest types (Niklas 1995, Chave et al. 2005):

$$\log(H_i) = \beta_0 + \beta_1 \log(D_i) + \varepsilon_i, \varepsilon_i \sim \mathcal{N}(0, \sigma^2). \tag{4}$$

We then used height–diameter allometric models to estimate the log-height of each tree *i* from its diameter *D_i* ($[\log(H_i)]_{\text{est}} = \log[\beta_0 - (\beta_0 - \beta_1)\exp(-\beta_2 D_i)]$ in the spiny dry forest and $[\log(H_i)]_{\text{est}} = \beta_0 + \beta_1 \log(D_i)$ in the moist–wet forest). The estimated log-height was then used to estimate the log-AGB of each tree *i* using model Mada.I.1. The overall regional empirical modeling approach to estimate tree biomass from wood specific gravity, diameter, and estimated height was denoted Mada.I.1-wHD (i.e., Mada.I.1 with *H*–*D* relationship):

$$[\log(AGB_i)]_{\text{est}} = \beta_0 + \beta_1 \log(D_i) + \beta_2 [\log(H_i)]_{\text{est}} + \beta_3 \log(\rho_i). \tag{5}$$

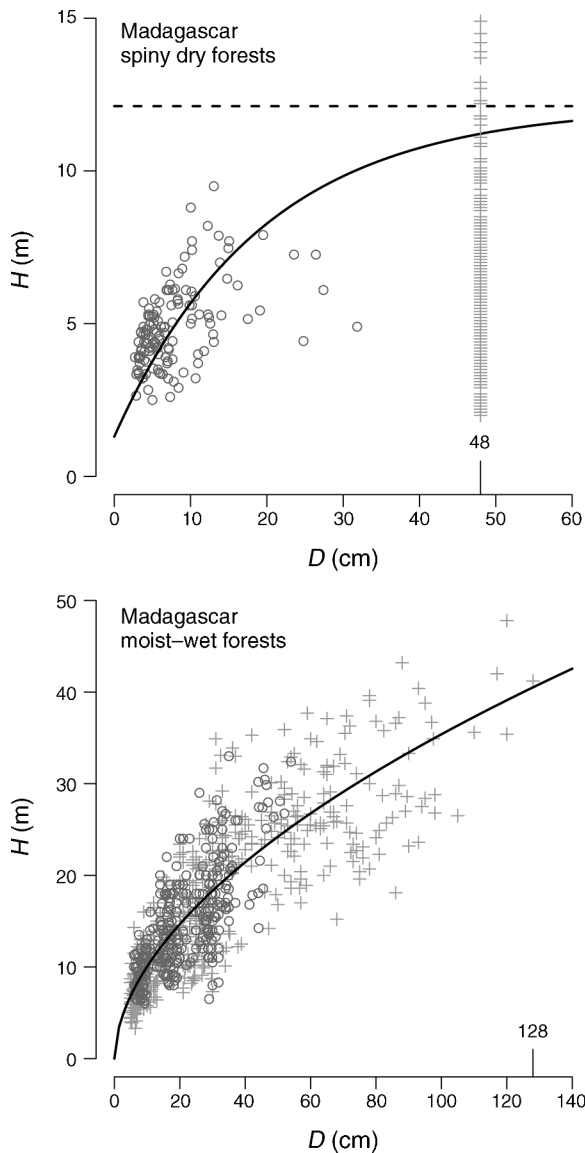


FIG. 1. Height–diameter (H , D) relationship in spiny dry and moist–wet forests. For spiny dry forests, we assumed a monomolecular model with a maximum height (dashed line) due to low competition for light and scarce water resources that limit growth in height in this forest type. For moist–wet forests, we tested a monomolecular model and polynomial models on diameter (up to degree 3). For the second forest type, the simple power model, without asymptote for height, was identified as the best model. For each forest type, the data set combined height–diameter data from felled trees from the biomass protocol (circles) and height–diameter data from independent inventories in each forest type (crosses). The vertical bar on the diameter axis indicates the maximum diameter measured in independent inventories.

Allometric models including only diameter and wood specific gravity.—When tree height is not available in field inventories and a height–diameter allometric model does not exist, it is possible to use a second type of model that defines tree dry biomass AGB_i solely as a

function of tree diameter D_i and tree wood specific gravity ρ_i . We denoted this model as Mada.II in analogy with Chave et al. (2005). We tested a simple parameterization for this second type of model (Mada.II.1), assuming a power-law relationship between tree biomass and diameter as postulated by the scaling theory:

$$\log(AGB_i) = \beta_0 + \beta_1 \log(D_i) + \beta_2 \log(\rho_i) + \varepsilon_i, \varepsilon_i \sim \mathcal{N}(0, \sigma^2). \quad (6)$$

The allometric scaling theory also suggests that tree biomass is proportional to tree size with a 8/3 scaling exponent: $fAGB_i = \alpha D_i^{8/3}$, with α being a normalization constant that varies with the kind of organism concerned (West et al. 1997, Enquist et al. 1998). We then tested a second parameterization for model Mada.II using a fixed scaling exponent equal to 8/3 for D and a normalization constant depending on ρ , the wood specific gravity (Eq. 7). We denoted this model Mada.II.2-WBE in reference to the West, Brown, and Enquist (WBE) model:

$$\log(AGB_i) = \beta_0 + (8/3)\log(D_i) + \log(\rho_i) + \varepsilon_i, \varepsilon_i \sim \mathcal{N}(0, \sigma^2). \quad (7)$$

We estimated the free parameters of the statistical models (Eq. 1–4, 6, 7) for the spiny dry and moist–wet forest data using the maximum likelihood approach using the `lm()` function available in R software (Ihaka and Gentleman 1996).

Comparison of regional allometric models with generic models

We estimated tree biomass using two major existing generic models. First, we used biomass allometric models initially developed by Brown (Brown et al. 1989, Brown 1997) and updated in Pearson et al. (2005) to estimate biomass from our data set. In the remainder of the article, we refer to these models as “Brown” models. The equations from Pearson et al. (2005) included only D as an explicative size variable. One equation was given by forest type with the classification based on annual precipitation (P , in mm). We used the equation defined for the dry forest ($P < 900$) to estimate tree biomass from data on spiny dry forests in Madagascar where $524 \leq P \leq 554$: $[AGB_i]_{\text{est}} = 10^{[-0.535 + \log_{10}(BA_i)]}$, where BA_i is the basal area of tree i ($BA_i = \pi D_i^2/4$) and $[AGB_i]_{\text{est}}$ is the estimated tree biomass. After log-transforming the variables, we obtained the following model:

$$[\log(AGB_i)]_{\text{est}} = -0.535 \log(10) + \log(\pi/4) + 2 \log(D_i). \quad (8)$$

We used the equation defined for the moist forest ($1500 \leq P \leq 4000$) to estimate tree biomass from data on moist–wet forests in Madagascar, where $1096 \leq P \leq 2013$:

$$[\log(\text{AGB}_i)]_{\text{est}} = -2.289 + 2.649 \log(D_i) - 0.021[\log(D_i)]^2. \quad (9)$$

Second, we used biomass allometric models developed by Chave et al. (2005) hereafter denoted “Chave” models. Models including only D and ρ as explicative variables are denoted Chave.D whereas models including H as an additional size covariate are denoted Chave.H. Chave et al. (2005) suggest one equation per model and forest type. The forest type definition was based on annual precipitation and seasonality. We used the two equations defined for the dry forest ($P < 1500$ and more than five months of dry season) to estimate tree biomass from data on spiny dry forests in Madagascar (Eq. 10). In Chave.D models, the authors assume a cubic polynomial relationship between tree height and tree diameter:

$$[\log(\text{AGB}_i)]_{\text{est}} = -0.667 + 1.784 \log(D_i) + 0.207[\log(D_i)]^2 - 0.0281[\log(D_i)]^3 + \log(\rho_i)$$

$$[\log(\text{AGB}_i)]_{\text{est}} = -2.187 + 0.916 \log(\rho_i D_i^2 H_i). \quad (10)$$

We used the two equations defined for the moist forest ($1500 \leq P \leq 3500$ and a one-to-five-month dry season) to estimate tree biomass from the data on moist-wet forests in Madagascar:

$$[\log(\text{AGB}_i)]_{\text{est}} = -1.499 + 2.148 \log(D_i) + 0.207[\log(D_i)]^2 - 0.0281[\log(D_i)]^3 + \log(\rho_i)$$

$$[\log(\text{AGB}_i)]_{\text{est}} = -2.977 + \log(\rho_i D_i^2 H_i). \quad (11)$$

Different indices were used to compare the eight models for each forest type. First, we computed the residual standard error RSE, which was defined as the standard deviation of the residual errors ε_i (with $\varepsilon_i = \log(\text{AGB}_i) - [\log(\text{AGB}_i)]_{\text{est}}$). The smaller the RSE, the smaller the unexplained part of the observed biomass. Second, we computed the coefficient of determination of the model

$$R^2 = 1 - \left[\frac{\sum_i \varepsilon_i^2}{\sum_i (\log(\text{AGB}_i) - [\log(\text{AGB})]_{\text{mean}})^2} \right]$$

with $[\log(\text{AGB})]_{\text{mean}}$ being the mean of the observed log-transformed biomass. The coefficient of determination is an indication of the goodness of fit of the model. R^2 should be interpreted considering the degrees of freedom of the model $df = n_{\text{obs}} - n_{\text{par}}$, with n_{obs} the number of observations and n_{par} the number of parameters, as a model with a higher number of parameters should fit the data better and should have a higher R^2 . Third, we computed the Akaike information criterion for each model, $\text{AIC} = -2 \log(\mathcal{L}) + 2n_{\text{par}}$, \mathcal{L} being the model likelihood. The AIC is a penalized estimation of the

goodness of fit of the model given the number of parameters. As the fourth and last index, we computed the model bias for each tree i , $\text{bias}_i = 100(1/\exp(\varepsilon_i) - 1)$, as a percentage of the tree biomass. The bias can be positive or negative, indicating over- or underestimation of tree biomass. We plotted the bias as a function of the tree diameter and computed the mean bias of the model for each forest type:

$$\text{Bias} = \left(\sum_i \text{bias}_i \right) / n_{\text{obs}}.$$

For each regional empirical model, the estimated value of the intercept β_0 (Table 2) included the correction factor $\text{CF} = \sigma^2/2$ imposed by the inverse log-transformation of the response variable (Chave et al. 2005).

RESULTS

Performance of generic and theoretical biomass allometric models

The Brown models not including WSG as an explicative variable explained 33% and 88% of the biomass variability of the spiny dry and the moist-wet forest, respectively. These were the lowest values of the coefficient of determination of all the models tested in this study (see R^2 in Table 2). In the spiny dry forest of Madagascar, species have highly variable WSG and frequently low WSG (Fig. 3). For this forest type, the Brown model was the most biased and significantly overestimated tree biomass (mean bias equal to 91.1%; Table 2, Figs. 2 and 4).

Chave.D models not including tree height as an explicative variable also yielded relatively poor results. They explained only 70% and 88% of biomass variability in the spiny dry and the moist-wet forest, respectively (Table 2). The cubic polynomial relationship between tree height and diameter was not adapted to Madagascar forests and led to significant overestimation of tree biomass with a mean bias of 63.3% in the spiny dry forest and of 36.9% in the moist-wet forest (Table 2, Fig. 2). One reason for this poor predictive ability is almost certainly the fact that the shape of the Chave.D models does not assume an asymptotic tree height-diameter relationship, which we found to apply to trees in Madagascar spiny-dry forests (Fig. 1). In addition, the models included a significant positive effect of the $(\log(D))^2$ covariate ($\beta_2 = 0.207$ for Chave.D models, Table 2), which we found to be nonsignificant in Madagascar moist-wet forests (Fig. 1).

The Mada.II.2-WEB model, which assumes a power-law relationship between tree biomass and diameter with a fixed scaling exponent of 8/3, performed better than the two previous models in both forest types (R^2 equal to 70% and 91% in spiny dry and moist-wet forests, respectively; Table 2). Nevertheless, the model significantly overestimated tree biomass in the spiny dry forest (mean bias of 22.4%; Table 2, Fig. 2) mainly because it

TABLE 2. We compared regional allometric models (Mada.I.1, Mada.I.1-wHD, Mada.I.2, and Mada.II.1) with generic allometric models (Brown, Chave.H, and Chave.D; see Brown 1997, Chave et al. 2005) and with the WEB theoretical model (Mada.II.2-WEB; see West et al. 1997).

Model	β_0	β_1	β_2	β_3	df	RSE	R^2	AIC	Bias	Eq.
Madagascar spiny dry forests										
Brown	-1.473	2			130	0.84	0.33	335	91.1	A
Chave.H	-2.187	0.916			130	0.42	0.83	156	-2.7	B
Chave.D	-0.667	1.784	0.207	-0.028	128	0.43	0.70	262	63.3	C
Mada.I.1	-1.103	1.994	0.317	1.303	128	0.33	0.90	90	5.3	D
Mada.I.1-wHD	12.120	1.300	0.052		128	0.34	0.89	99	3.9	E
Mada.I.2	-1.778	0.870			130	0.39	0.86	128	7.9	B
Mada.II.1	-0.791	2.118	1.372		129	0.34	0.90	92	5.6	F
Mada.II.2-WEB	-1.999	8/3			131	0.57	0.70	226	22.4	G
Madagascar moist-wet forests										
Brown	-2.289	2.649	-0.021		333	0.39	0.88	438	35.5	H
Chave.H	-2.977				335	0.33	0.93	234	-4.2	I
Chave.D	-1.499	2.148	0.207	-0.028	332	0.38	0.88	444	36.9	C
Mada.I.1	-1.948	1.969	0.660	0.828	332	0.29	0.95	122	4.3	D
Mada.I.1-wHD	1.010	0.547	0.071		332	0.33	0.94	218	4.7	J
Mada.I.2	-2.108	0.908			334	0.29	0.95	135	4.5	B
Mada.II.1	-1.159	2.297	0.830		333	0.33	0.94	215	5.8	G
Mada.II.2-WEB	-2.122	8/3			335	0.39	0.91	320	8.0	H

Notes: RSE is the residual standard error, R^2 is the coefficient of determination, and AIC is the Akaike information criterion. Bias (in %) is the model relative error (see *Material and methods* for details on the index computation). Models selected for each forest type are in boldface type.

Equations (Eq.) are:

- A) $[AGB]_{est} = \exp[\beta_0 + \beta_1 \log(D)]$
- B) $[AGB]_{est} = \exp[\beta_0 + \beta_1 \log(\rho D^2 H)]$
- C) $[AGB]_{est} = \exp\{\beta_0 + \beta_1 \log(D) + \beta_2 [\log(D)]^2 + \beta_3 [\log(D)]^3 + \log(\rho)\}$
- D) $[AGB]_{est} = \exp[\beta_0 + \beta_1 \log(D) + \beta_2 \log(H) + \beta_3 \log(\rho)]$
- E) $[H]_{est} = \beta_0 - (\beta_0 - \beta_1) \exp(-\beta_2 D)$
- F) $[AGB]_{est} = \exp[\beta_0 + \beta_1 \log(D) + \beta_2 \log(\rho)]$
- G) $[AGB]_{est} = \exp[\beta_0 + \beta_1 \log(D) + \log(\rho)]$
- H) $[AGB]_{est} = \exp\{\beta_0 + \beta_1 \log(D) + \beta_2 [\log(D)]^2\}$
- I) $[AGB]_{est} = \exp[\beta_0 + \log(\rho D^2 H)]$
- J) $\log(H) = \beta_0 + \beta_1 \log(D) + \varepsilon$, $\varepsilon \sim \mathcal{N}(0, \text{var} = \beta_2)$

where $[AGB]_{est}$ is estimated aboveground biovolume; β_0 , β_1 , β_2 , and β_3 are linear model parameters; D is tree diameter; H is tree height; ρ is tree-wood specific gravity; ε is the residual error term; and \mathcal{N} refers to the normal distribution.

did not assume an asymptotic height-diameter relationship. However, for the moist-wet forests, the model fitted the data much better and was much less biased than the Brown and Chave.D models (bias < 10%) on the diameter range of our data set. However, due to the high value of the scale parameter for the Mada.II.2-WEB model ($\beta_1 = 8/3 \approx 2.667$), which was higher than the estimated scale in model Mada.II.1 ($\beta_1 = 2.297$), the Mada.II.2-WEB model predicted unrealistically high biomass values for trees with $D \geq 40$ cm (Fig. 4).

The Chave.H model was thus the best model of all the generic and theoretical models for the two types of forest considered in this study (R^2 equal to 83% in the spiny dry forests and 93% in the moist-wet forests). Chave.H models had a low mean bias (-2.7% and -4.2% in the spiny dry and moist-wet forests respectively, Table 2) and performed as well as empirical regional models when considering bias as a function of tree diameter (Fig. 2).

Performance of regional empirical models

The regional empirical models fitted the data better than the theoretical or generic models for both forest types ($R_2 \geq 86\%$ and $R^2 \geq 94\%$ in spiny dry and moist-

wet forests, respectively, Table 2). With the exception of the Chave.H model, regional empirical models were much less biased than the theoretical and generic models (bias $\leq 7.9\%$ and bias $\leq 5.8\%$ in spiny dry and moist-wet forests respectively, Table 2). For both forest types, the first parameterization for model Mada.I, with a linear additive combination of the three explicative variables (D , H , and ρ) fitted the data better (see R^2 and AIC values in Table 2) than the second parameterization, which included a compound variable ($\rho D^2 H$).

For spiny dry forests, models Mada.I.1, Mada.I.1-wHD and Mada.II.1 were equivalent both in terms of goodness of fit ($89\% \leq R^2 \leq 90\%$ and $90 \leq \text{AIC} \leq 99$ Table 2) and in terms of bias ($3.9\% \leq \text{bias} \leq 5.6\%$, Table 2) for the diameter range of our data set ($D \leq 32$ cm). However, field observations and ecological considerations regarding the availability of light and water resources in the spiny dry forest suggest an asymptotic relationship between tree height and diameter (Fig. 1). Therefore, model Mada.I.1 appears to be the best model for spiny dry forests when tree height is known from field inventories whereas model Mada.I.1-wHD is best when tree height is not known, to avoid overestimating biomass for trees with a large diameter ($D > 32$ cm).

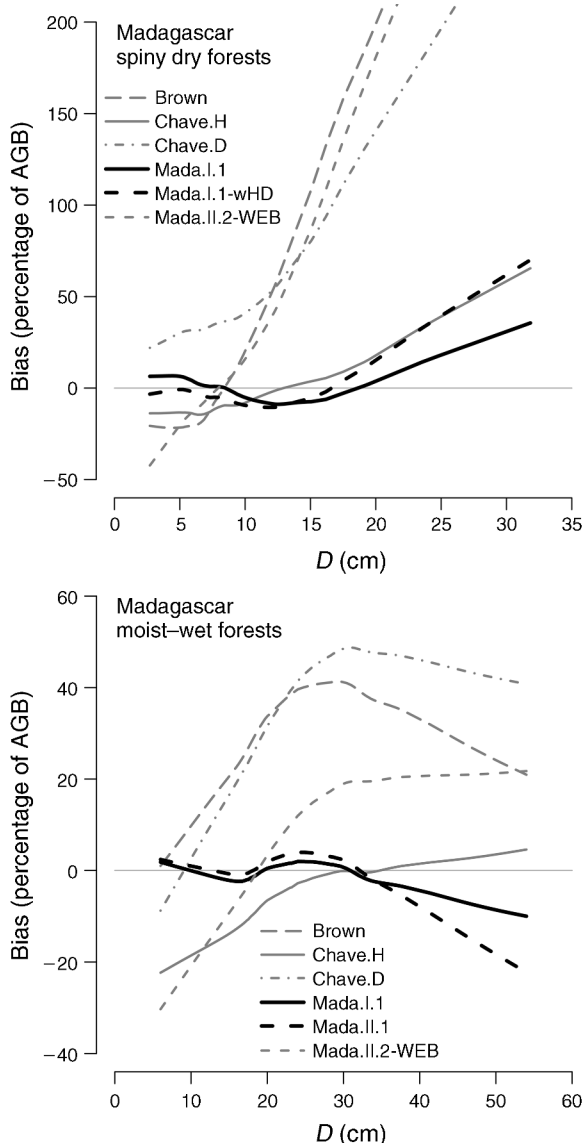


FIG. 2. Model bias as a function of tree diameter. For the theoretical model (Mada.II.2-WBE), the generic models (Brown, Chave.H, and Chave.D) and the best empirical regional models (Mada.I.1 and Mada.I.1-wHD for spiny dry forests, Mada.I.1 and Mada.II.1 for moist-wet forests), we computed the bias (as a percentage of aboveground biomass [AGB]) associated with the prediction for each tree i ($bias_i = 100[1/\exp(\epsilon_i) - 1]$ with $\epsilon_i = \log(AGB_i) - [\log(AGB_i)]_{est}$; see *Material and methods: Comparison of regional allometric models with generic models* for more details on the notation). Models may underestimate tree biomass (model curve under the thin gray zero bias line) or overestimate tree biomass (model curve above the zero bias line). The empirical regional models (black lines) were much less biased than the theoretical model and the generic models (gray lines).

For moist-wet forests, the Mada.I.1 model, which included tree height as an explicative variable, was the best model for any of the statistical criteria examined (see RSE, R^2 , AIC, or bias in Table 2). Models

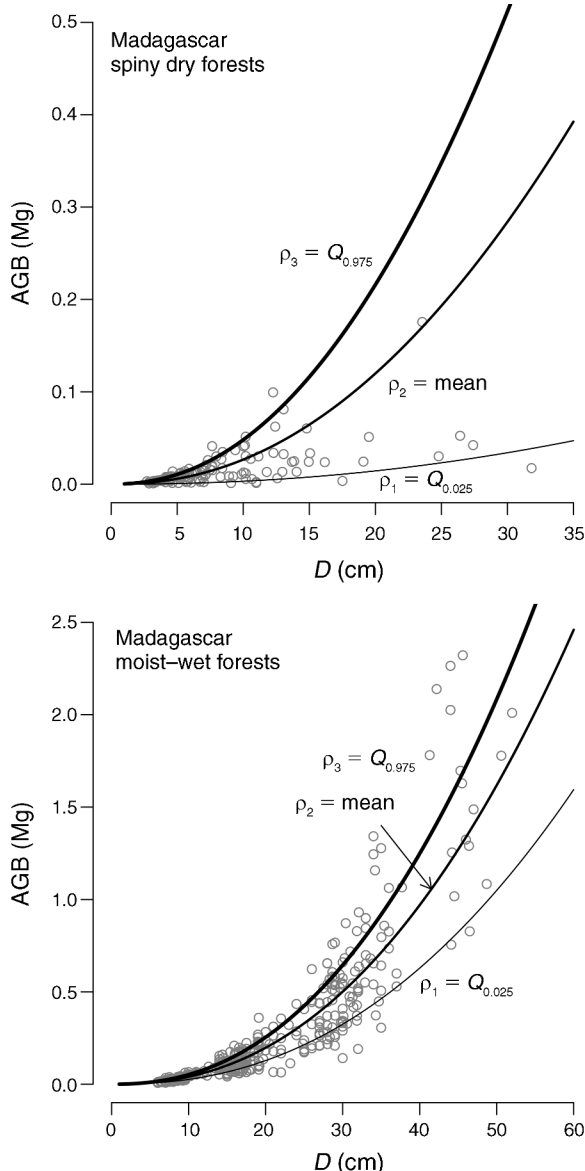


FIG. 3. Biomass prediction as a function of tree diameter and wood specific gravity. To predict biomass, we used the best regional empirical models that included tree diameter and wood specific gravity (WSG) as covariates (Model.I.1-wHD for the spiny dry forests and Model.II.1 for the moist-wet forests). Each gray dot corresponds to an individually weighed tree. We plotted the biomass-diameter predicted relationship for three levels of wood specific gravity: the mean of the WSG for the forest type ($\rho_2 = \text{mean}$), the 0.025 quantile ($\rho_1 = Q_{0.025}$), and the 0.975 quantile ($\rho_3 = Q_{0.975}$). For the spiny dry forests, WSG was highly variable (in comparison with the moist-wet forests), and WSG explained a high percentage of the variability of tree biomass.

Mada.I.1-wHD and Mada.II.1 were largely equivalent both in terms of goodness of fit ($94\% \leq R^2 \leq 95\%$ and $215 \leq AIC \leq 218$; Table 2) and in terms of bias $4.7\% \leq \text{bias} \leq 5.8\%$, Table 2) with model Mada.II.1 performing

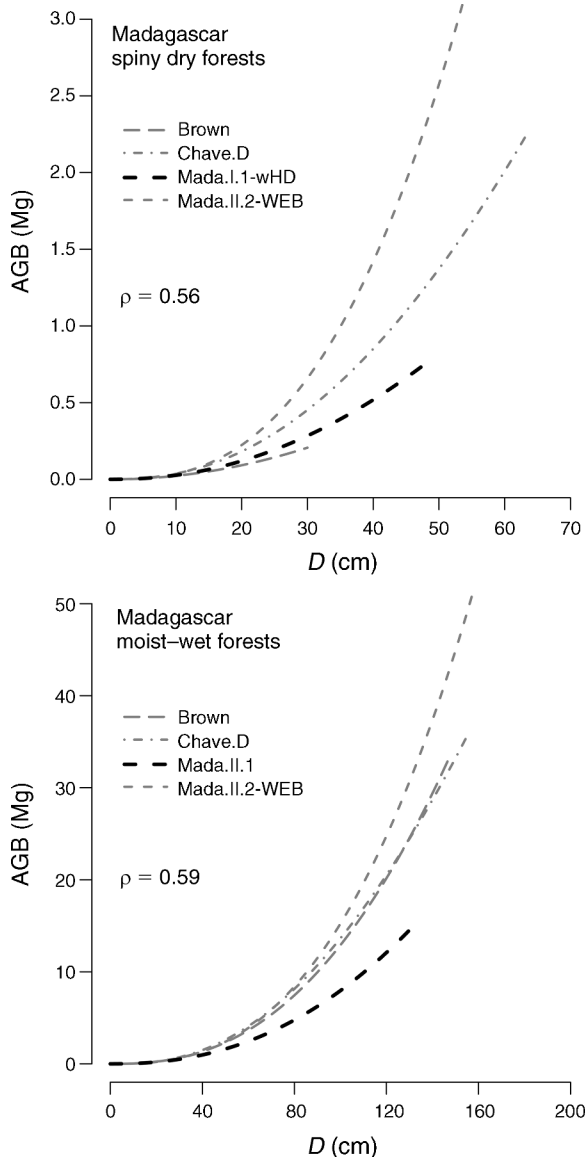


FIG. 4. Comparing model biomass predictions for large diameter trees. From the diameter and wood specific gravity, we compared the biomass predictions of the best regional empirical models (Mada.I.1-wHD for spiny dry forests and Mada.II.1 for moist-wet forests) with the predictions of the theoretical and generic models. The diameter values used for predictions were limited to the validity domain of each model, which depended on the maximum diameter of the data used to estimate the parameters of each model. The wood specific gravity (ρ) was set at the mean for each forest type. For large trees ($D \geq 20$ cm for spiny dry forests and $D \geq 40$ cm for moist-wet forests), the theoretical and generic models (gray lines) considerably overestimated biomass compared to the best models we identified (black lines).

slightly better. This can be explained by the fact that the Mada.I.1-wHD model uses a power-law relationship between tree height and diameter (Fig. 1) to estimate tree height in the first step and tree biomass in the second step compared to model Mada.I.1, which already

includes height and diameter. This approach increases the regression error in the estimation of biomass compared to direct estimation of biomass from a unique power-law relationship based on diameter, which is the case in the Mada.II.1 model. Therefore, the Mada.II.1 model appears to be the best approach for estimating biomass in moist-wet forests when tree height is not available in forest inventories.

DISCUSSION

Using regional biomass allometric models for conservation purposes in Madagascar

High-resolution methods and biomass allometric equations are needed to achieve Tier III level of accuracy for the application of REDD (Aalde et al. 2003, IPCC 2006). Here, we demonstrate that regional allometric models performed better than generic or theoretical models in Madagascar forests, with the best regional models explaining 89% and 94% of the variation in tree AGB for spiny dry and moist-wet forests, respectively. Chave et al. (2004) recommend pan-tropical models rather than local allometric models that may be based on less than 100 destructively sampled trees to estimate forest biomass. In Madagascar, we sampled 135 trees in the spiny dry forest and 346 trees in the moist-wet forest. As an indication of sampling intensity and representativeness, we sampled 3.75 trees/km² of tropical forest in Madagascar. In contrast, allometries in Chave et al. (2005) are based on 0.23 trees/km² of forest in other countries (Appendix C).

Aalde et al. (2003) underlined that allometric models should not be used out of their domain of validity. In our case, the maximum tree diameter in the samples used to estimate biomass allometric models was relatively low (32 cm in the spiny dry forests and 54 cm in the moist-wet forests) compared to the maximum diameter of the randomly sampled trees we used to estimate height-diameter allometric models (48 cm and 128 cm, respectively). However, the main pitfall of biomass allometric models of type II (that do not use tree height as an explicative variable), when they are extrapolated beyond the maximum tree diameter, is that the limited increase in tree height at large diameters due to mechanical or physiological constraints (Niklas 1995, Midgley 2003, Vieilledent et al. 2010) is not included in the model. This leads to considerable overestimation of the tree biomass at large diameters (Zianis and Mencuccini 2004, Chave et al. 2005). In our study, we measured and modeled the change in the height-diameter relationship up to tree diameters of 48 cm and 128 cm for spiny dry and moist-wet forests, respectively, and we used the results to choose between model Mada.I.1-wHD and Mada.II.1 for tree biomass estimation in cases when height is not available in forest inventories. Therefore, we can confidently state that the domain of validity of our models is $D \in [5, 48$ cm] in the spiny dry forest and $D \in [5, 128$ cm] in the moist-wet forest of Madagascar.

Our results show that generic biomass allometric models that include WSG as an explicative variable are preferable to models that do not, especially in dry forest ecosystems where species mean wood specific gravity is highly variable and can be very low (as low as 0.10 for *Pachypodium lamerei* Drake in the Madagascar spiny dry forest; Appendix B). In the present study, we provided WSG estimations for the most abundant species and genera in the spiny dry forest (21 identified species and 40 genera) and in the moist-wet forest (31 identified species and 15 genera) of Madagascar (Appendix B). The mean WSG by taxonomic level took into account intra-individual, inter-individual and, in the case of the WSG at the genus level, interspecific WSG variability. We supplemented these data with WSG for commercial species and genera from the work of Rakotovo et al. (2011) and built a large WSG data base containing 265 species and genera (Appendix B) that can be used to estimate biomass and carbon stock in the tropical forests of Madagascar.

As part of the REDD+ pilot project called “Holistic Conservation Programme for Forests” (PHCF) in Madagascar (for more details see the Acknowledgements), the specific biomass allometric models and the large WSG data base we obtained for Madagascar were used to compute the aboveground carbon density (ACD, in Mg C/ha) at 83 sites in the spiny dry and moist-wet forests (G. P. Asner et al., *unpublished manuscript*; Asner et al., *in press*). Field plot carbon measurements were used to calibrate the airborne light detection and ranging (lidar) data used to derive carbon maps of a 3 670 081-ha region covering both spiny dry and moist-wet forests in Madagascar (G. P. Asner et al., *unpublished manuscript*; Asner et al., *in press*).

Identifying a universal biomass allometric model

Although several authors found WSG to be a key explicative variable for estimating tree biomass (Baker et al. 2004, Chave et al. 2005, 2009), Brown et al.’s models which do not include WSG are those suggested by the IPCC (Aalde et al. 2003) and by Pearson et al. (2005). This represents a significant caveat to developing sound carbon estimates for REDD. Brown et al.’s models were published in 1989 and 1997 and aimed at providing generic allometric models at a time when information on wood density was scarce. Today, reliable world data sets on wood densities exist (Reyes et al. 1992, IPCC 2006, Chave et al. 2009, WAC 2010) and methods have been proposed to estimate species wood density from phylogeny for use when information is not available at the species level (Baker et al. 2004, Slik 2006).

Our results show that the use of the power-law relationship between biomass and diameter, advocated by the WBE allometric scaling theory, does not always lead to accurate biomass estimates (R^2 equal to 70% and bias of 22.4% for the spiny dry forest of Madagascar). Although the first aim of the WBE theoretical model was not to accurately estimate tree biomass but rather to

demonstrate that “size affects rates of all biological structures and processes from cellular metabolism to population dynamics” (West et al. 1997), several authors whose aim was to develop biomass allometric model referred to the work of West et al. (1997) to explain the choice of the power-law relationship (Ketterings et al. 2001, Chojnacky 2002, Zianis and Mencuccini 2004). Through our study, we show that the power-law is only adapted to forests where tree height-diameter allometry can also be modeled with a power-law relationship (such as in the moist-wet forest of Madagascar).

Among Chave’s models, the Chave.H model was the only one to be particularly robust. The model satisfactorily fitted the data for both spiny dry and moist-wet forests (R^2 of 83% and 93%, respectively) with a very low bias (−2.7% and −4.2%, respectively). Although Chave et al. (2005) demonstrated that this model produces a very high coefficient of determination ($R^2 \geq 99\%$) for many different forest types across various tropical countries, its robustness for forests in Madagascar was not a priori obvious because no African data were used to estimate the Chave.H model parameters and because Madagascar has a very high rate of endemism, close to 96% for tree species (Goodman and Benstead 2005). In the evergreen forests of Ghana, Henry et al. (2010) also found that the Chave.H model provided accurate estimates of tree biomass ($R^2 = 97\%$ and mean bias = 3.74%). Considering that constructing allometric models specific to each country is destructive, time-consuming, and expensive, we suggest using the Chave.H model as a first approximation to estimate tree biomass when country-specific allometric models are not available. The Chave.H model should be especially valuable in Africa, considering that the continent’s tropical forests represent 30% of the global total (FAO 2005) and that almost no allometric models are available for Africa (but see Henry et al. 2010 and Kaonga and Bayliss-Smith 2010).

Utility of developing tree height-diameter allometry to estimate forest biomass

Because height is often not measured in forest inventories, tree diameter is usually the only size covariate available to estimate tree biomass and consequently, the Chave.H model cannot be used directly. Thus, when regional biomass allometric models are not available, the results of our study suggest that regional height-diameter allometries in conjunction with Chave.H biomass allometric models should be used to obtain accurate estimates of tropical forest biomass and carbon stock. When the height-diameter relationship is asymptotic, as is the case in the spiny dry forest of Madagascar, tree height can be modeled as a function of diameter using an asymptotic nonlinear model such as the monomolecular model used in this study. The estimated height can then be used as an input variable for the Chave.H biomass allometric model that includes

height as a covariate. This approach was used in the PHCF REDD+ pilot-project to estimate ACD at cloud forest sites in the mountainous Tsaratanana region (northern Madagascar). These sites were characterized by higher altitude (> 2000 m), higher precipitation (> 3000 mm/yr), and smaller trees compared to the sample sites used in the present study. For these cloud forest sites, a local height–diameter relationship was estimated based on a sample of trees and used in conjunction with the Chave.H wet forest model to estimate ACD (see Appendix 1 in G. P. Asner et al., *unpublished manuscript*). Measuring tree height and diameter in a forest is not destructive and has become relatively easy and affordable thanks to new instruments and technologies, such as the ultrasonic instrument used in this study, even in closed tropical forest canopies. The height measurement error using such instruments has been estimated to be close to 10%, which is sufficiently accurate to estimate reliable height–diameter allometry (Vieilledent et al. 2010). This approach should be advocated by international organizations for the application of REDD in poor countries that cannot afford to develop country-specific biomass allometric models.

ACKNOWLEDGMENTS

The authors are very grateful for the help of the many people in Madagascar and in foreign institutes who participated in the research project. They personally thank all the Directeurs Régionaux de l'Environnement et des Forêts de Madagascar (MEF-Madagascar), Matthieu Tiberghien (GoodPlanet), Greg P. Asner (Carnegie Institution for Science), Alain Albrecht (IRD), Herintsitohaina Razakamanarivo (IRD), Matieu Henry (IRD), Philippe Collas de Chatelperron (Satob company), Barry Ferguson (University of East Anglia), Christian Camara (MBG), Chris Birkinshaw (MBG), Pascal Danthu (Cirad), Sylvain Mahazotahy (WWF), Théodule Tovosaona (lumberjack), Ludg Ratobiarisaona (lumberjack), and all assistant botanists, workers, and people from local communities who welcomed us. This study is part of the Holistic Conservation Programme for Forests (PHCF) in Madagascar. The PHCF is a REDD+ pilot-project funded by the GoodPlanet Foundation with Air France as sole sponsor and is jointly implemented on the ground by WWF and Good Planet. The main goal of the project is to increase knowledge on forest carbon using complementary approaches: field inventories, allometry, analysis of high-resolution Spot and lidar images, soil organic carbon assessment, and so on.

LITERATURE CITED

- Aalde, H., A. Abdelgadir, J. Penman, M. Gytarsky, and T. Hiraishi. 2003. Forest land. Good practice guidance for land use, land-use change and forestry. Institute for Global Environmental Strategies (IGES) for the IPCC, Kanagawa, Japan.
- Asner, G. P., J. Mascaro, H. C. Muller-Landau, G. Vieilledent, R. Vaudry, M. Rasamolina, J. Hall, and M. van Breguel. *In press*. A universal airborne LiDAR approach for tropical forest carbon mapping. *Oecologia*. <http://dx.doi.org/10.1007/s00442-011-2165-z>
- Baker, T. R., et al. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology* 10:545–562.
- Blanc, L., M. Echard, B. Herault, D. Bonal, E. Marcon, J. Chave, and C. Baraloto. 2009. Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecological Applications* 19:1397–1404.
- Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. Technical report, FAO Forestry Paper 134. FAO, Rome, Italy.
- Brown, S., A. J. R. Gillespie, and A. E. Lugo. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science* 35:881–902.
- Chave, J., et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99.
- Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao, and R. Perez. 2004. Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society B* 359:409–420.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Chojnacky, D. C. 2002. Allometric scaling theory applied to FIA biomass estimation. Pages 96–102 in R. E. McRoberts, G. A. Reams, P. C. Van Deusen, and J. W. Moser, editors. Proceedings of the Third Annual Forest Inventory and Analysis Symposium. General Technical Report NC-230. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, Minnesota, USA.
- Ebeling, J., and M. Yasue. 2008. Generating carbon finance through avoided deforestation and its potential to create climatic, conservation and human development benefits. *Philosophical Transactions of the Royal Society B* 363:1917–1924.
- Enquist, B. J., J. H. Brown, and G. B. West. 1998. Allometric scaling of plant energetics and population density. *Nature* 395:163–165.
- Enquist, B. J., and K. J. Niklas. 2001. Invariant scaling relations across tree-dominated communities. *Nature* 410:655–660.
- FAO. 2005. Global forest resources assessment 2005. Technical report. Food and Agriculture Organization of the United Nations, Rome Italy.
- Fox, J. C., C. K. Yosi, P. Nimiago, F. Oavika, J. N. Pokana, K. Lavong, and R. J. Keenan. 2010. Assessment of aboveground carbon in primary and selectively harvested tropical forest in Papua New Guinea. *Biotropica* 42:410–419.
- Gibbs, H., S. Brown, J. Niles, and J. Foley. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters* 2:045023.
- Goodman, S. M., and J. P. Benstead. 2005. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39:73–77.
- Henry, M., A. Besnard, W. A. Asante, J. Eshun, S. Adu-Bredu, R. Valentini, M. Bernoux, and L. Saint-Andre. 2010. Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. *Forest Ecology and Management* 260:1375–1388.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Ihaka, R., and R. Gentleman. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5:299–314.
- IPCC. 2006. Guidelines for national greenhouse gas inventories. Prepared by the National Greenhouse Gas Inventories Programme. Technical report. The Intergovernmental Panel on Climate Change, IPCC/IGES, Kanagawa, Japan.
- Kaonga, M. L., and T. P. Bayliss-Smith. 2010. Allometric models for estimation of aboveground carbon stocks in improved fallows in eastern Zambia. *Agroforestry Systems* 78:217–232.
- Ketterings, Q. M., R. Coe, M. van Noordwijk, Y. Ambagau, and C. A. Palm. 2001. Reducing uncertainty in the use of

- allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management* 146:199–209.
- Malhi, Y., and J. Grace. 2000. Tropical forests and atmospheric carbon dioxide. *Trends in Ecology and Evolution* 15:332–337.
- Martin, N., D. Shoch, T. Pearson, A. Dushku, and S. Brown. 2004. Feasibility study for an avoided deforestation project in the Makira Region of Madagascar. Technical report. Winrock International, Little Rock, Arkansas, USA.
- Midgley, J. J. 2003. Is bigger better in plants? The hydraulic costs of increasing size in trees. *Trends in Ecology and Evolution* 18:5–6.
- Navar, J. 2009. Allometric equations for tree species and carbon stocks for forests of northwestern Mexico. *Forest Ecology and Management* 257:427–434.
- Niklas, K. J. 1995. Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of Botany* 75:217–227.
- Pearson, T., S. Walker, and S. Brown. 2005. Sourcebook for land use, land-use change and forestry projects. Technical report. Winrock International, Little Rock, Arkansas, USA.
- Pilli, R., T. Anfodillo, and M. Carrer. 2006. Towards a functional and simplified allometry for estimating forest biomass. *Forest Ecology and Management* 237:583–593.
- Plugge, D. I., T. I. Baldauf, H. R. Ratsimba, G. Rajoelison, and M. Kohl. 2010. Combined biomass inventory in the scope of REDD (Reducing Emissions from Deforestation and Forest Degradation). Madagascar Conservation and Development 5:23–34.
- Rakotovo, G., A. Rabevohitra, J. Gerad, and P. Collas de Chatelperron. 2011. Atlas des Bois de Madagascar. Technical report. Cirad and Fofifa, Montpellier, France.
- Reyes, G., S. Brown, J. Chapman, and A. E. Lugo. 1992. Wood densities of tropical tree species. General technical report SO-88. USDA Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, USA.
- Rutishauser, E., F. Wagner, B. Hérault, E. A. Nicolini, and L. Blanc. 2010. Contrasting above-ground biomass balance in a Neotropical rain forest. *Journal of Vegetation Science* 21:672–682.
- Slik, J. W. F. 2006. Estimating species-specific wood density from the genus average in Indonesian trees. *Journal of Tropical Ecology* 22:481–482.
- Veilleux, G., B. Courbaud, G. Kunstler, J.-F. Dhote, and J. S. Clark. 2010. Individual variability in tree allometry determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach. *Oecologia* 163:759–773.
- WAC. 2010. Wood density database. World Agroforestry Center, Nairobi, Kenya. <http://www.worldagroforestrycentre.org/sea/Products/AFDbases/WD/>
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.
- West, G. B., J. H. Brown, and B. J. Enquist. 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400:664–667.
- Williamson, G. B., and M. C. Wiemann. 2010. Measuring wood specific gravity correctly. *American Journal of Botany* 97:519–524.
- Zianis, D., and M. Mencuccini. 2004. On simplifying allometric analyses of forest biomass. *Forest Ecology and Management* 187:311–332.

SUPPLEMENTAL MATERIAL

Appendix A

Location of study sites and forest categories (*Ecological Archives* A022-035-A1).

Appendix B

Wood characteristics of tree species and genera in the tropical forests of Madagascar (*Ecological Archives* A022-035-A2).

Appendix C

Number of destructively sampled trees per country used to develop generic biomass allometric models (*Ecological Archives* A022-035-A3).