Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia

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ABSTRACT

In this study, we analyzed the above-ground biomass data for 631 trees with a diameter $\geqslant 10$ cm from different biogeographical regions in Colombia. The aims of this research were (1) to evaluate the accuracy of the most commonly employed pantropical allometric models for the estimation of above-ground biomass of natural forests in different sites located along a complex environmental gradient, (2) to develop new models that enable more precise estimations of current carbon stores in the above-ground biomass of natural forest ecosystems in Colombia, and (3) to evaluate the effect on allometric models of forest type classifications as determinants of above-ground biomass variation. The Brown et al. (1989) model for moist forests, which includes diameter, height, and wood density, showed the overall best performance in Colombian sites. The Type II models of Chave et al. (2005; hereafter Chave II), which include diameter and wood density but not height, tended to strikingly overestimate the above-ground biomass (54.7 ± 135.7%) in the studied Colombian sites. The use of forest classification based on the life zone system systematically led to better statistical models to estimate AGB at the individual scale and site scale than the use of Chave's classification. Our results propose that Chave II models should be evaluated prior to their use for a given ecosystem. For Colombia, the new allometric models developed, which employed diameter, wood density, and height, could help improving our understanding of the carbon cycle. Forest type classification was found to be an important determinant of the above-ground biomass estimation when altitudinal and other complex environmental gradients are included. The new models presented here can be considered as an alternative option for assessing carbon stocks in the above-ground biomass of natural forests in neotropical countries.

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1. Introduction

Allometric equations are an essential tool for understanding the storage and flux of carbon in tropical forests (Brown, 1997; Chave et al., 2005; IPCC, 2007). A large number of allometric models for estimating above-ground biomass (AGB) have been published during the last decades (Brown et al., 1989; Brown, 1997; West et al., 1999; Baker et al., 2004; Chave et al., 2004, 2005; Sierra et al., 2007; Zianis, 2008; Navar, 2009). However, the pantropical models developed by Chave et al. (2005) are widely considered to be the best current approximation for sites for which local equations are not available (Clark, 2007). Chave et al. (2005) showed that the predictive power of their global model differs among sites;

for some regions, the relative error could be low, while for others, it could be high. For this reason, the evaluation of the accuracy of these models with new data and in different geographic locations is needed.

At a local scale, the simplest models are based only upon tree diameter at breast height (D). When these models exist, they are the most practical options for assessing AGB (Sierra et al., 2007; Litton and Kauffman, 2008; Basuki et al., 2009). At regional or global scales, models based only upon D (West et al., 1999; Zianis, 2008) may have a greater associated uncertainty than more complex models, a finding that could negatively affect project developers interested in assessing carbon and biomass contents in sites and regions for which local equations are not available (IPCC, 2007). In fact, tree biomass estimation can be significantly improved by including wood density (Brown et al., 1989; Baker et al., 2004; Chave et al., 2006; Ter Steege et al., 2006; Patiño et al., 2009) and tree height (Brown, 1997; Wang et al., 2006;

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Nogueira et al., 2008) in the allometric models in addition to tree diameter. For example, in the Amazonian watershed, the inclusion of wood density (Baker et al., 2004) and tree height (Nogueira et al., 2008) has revealed spatial biomass patterns and carbon contents in these forests that were not previously reported. However, measuring height (H) and wood density (ρ) requires additional work, increasing project time and costs.

Pantropical models based only upon D can be divided into two types: theoretical and empirical. Metabolic ecology theory has proposed theoretical allometric models derived from metabolic principles (West et al., 1999; Brown et al., 2004). According to metabolic theory, AGB should be proportional to $D^{8/3}$. However, studies based on compilations of both empirical data and models have shown a systematic AGB overestimation when this idealized exponent is employed (Zianis and Mencuccini, 2004; Muller-Landau et al., 2006). In fact, mature trees can be shorter than predicted from diameter alone due to climatic and environmental variation along with other factors. Architectural differences in branches, roots or crowns along with tree damage could also explain the failure of the idealized predictions using either theoretical or empirical universal scaling exponent models.

To solve this inconvenience, Chave et al. (2005) included wood density and H (or its equivalent allometric model based on D) within their models and proposed a global forest classification system that contains three climatic categories (dry, moist, and wet) to account for climatic constraints determining the AGB variation. However, this climatic classification, currently accepted at a global scale (e.g., Feldpausch et al., 2010), could lead to a very weak differentiation of forest types at both regional and local scales. In altitudinal gradients, for example, variations in temperature and solar radiation are expected to cause changes in the degree of humidity, affecting both productivity rates and AGB distribution patterns (Aiba and Kitayama, 1999; Girardin et al., 2010). Thus, other forest classifications that include a greater number of forest types, at a regional scale, could provide additional information to improve our knowledge of biomass distribution in the presence of complex environmental gradients.

In this study, we analyzed new AGB data for 631 trees ($D \geqslant 10$ cm) representing different biogeographical regions in Colombia to evaluate the accuracy and usefulness of the most popular pantropical AGB models for these regions (Brown et al., 1989; Chave et al., 2005; Zianis, 2008). Colombia, a tropical country with a continental surface area of 1.1 million km^2 and which still contains a good portion of forests in climatically and geological diverse regions (IDEAM et al., 2007), provides a test bed for the applicability of pantropical allometric models. Therefore, the aims of this research are the following: (1) to evaluate the accuracy of the most commonly employed pantropical allometric models to estimate AGB in different sites located along a complex environmental gradient; (2) to develop new models that enable more precise estimations of the current carbon stores in the AGB of natural forest ecosystems in Colombia; and (3) to evaluate the effect on allometric models of forest type classifications as determinants of AGB variation. This study is expected to contribute to the implementation of efficient conservation mechanisms and policies based on a better quantification of the environmental services provided by forests in the carbon cycle at national and regional scales (e.g., REDD).

2. Materials and methods

2.1. Study sites

This study took place in Colombia in natural forests located along a complex environmental gradient that includes different geological, biogeographical and climatic regions (Table 1; Figure S1). The AGB information used for the study was obtained from published and unpublished works, including data from 15 sites (14 in Colombia and one in Puerto Rico), one of which (Overman et al., 1994) was included in the Chave et al. (2005) dataset. The Puerto Rico site corresponds to a subtropical dry forest (STd) of the Caribbean region (Brandeis et al., 2006) and was included due to the low number of individuals available for the tropical dry forest region, the ecosystem type considered to be the most threatened in Colombia (Chaves and Santamaría 2006). Although it would have been desirable to include them, no tree biomass data were found for other neotropical high mountain forests (>2000 masl) from regions other than Colombia. From this point onwards, we will refer to the AGB in Colombia, even though this study includes the one site outside of the country.

All of the sites where trees were harvested were selected *in situ* on the principle of being in a mature and well-preserved forest, except for the SCRion site, which included trees from fallows between 10 and 35 years old. However, in Colombia, some regions have been strongly deforested, and we cannot be sure that forest degradation has not occurred in the past. In particular, dry forests covers are currently represented by only 5% of the original cover, making it difficult to expect a completely undisturbed patch of forest, at least in the sampled regions. Likewise, deforestation in the Andean mountains has already destroyed approximately 75% of the original forest cover (Armenteras et al. 2003). Further, approximately 80% of the 45 million people inhabiting the country live in the Colombian Andean region, and this anthropogenic influence has left its fingerprint on the current stage of the natural forests, again making it difficult to be sure that the studied sites have not been disturbed in the past. Therefore, it is expected that the likely degradation to which these forests may have been submitted must in principle have reduced the average wood density compared to completely undisturbed forests. However, it is important to realize that the studied sites are a very representative sample of the forests existing in Colombia today.

2.2. Tree harvesting

A total of 631 trees with $D \geqslant 10$ cm, measured at 1.3 m or above buttresses (FAO, 2004), harvested from Colombian forests were included in this study. A total of 185 of the trees were already included in other publications (Saldarriaga et al., 1988; Overman et al., 1994; Brandeis et al., 2006; Sierra et al., 2007), while data from 446 of the trees are newly presented in this study (Table 1). In most cases, the selected harvest trees came from a previous plot census, in which the dominant species and number of sample trees were selected according to the diameter distribution in each location (see details in Electronic Supplementary Material S1). After being felled, the total height (H) of the trees was measured on the ground using a measuring tape from the base towards the apex of the crown. The majority of trees (69%; $D \leqslant 30$ cm) were felled, and all of their components were separated into pools (trunk, branches and foliage) that were directly weighed in the field using scales with a 200-kg capacity. The remaining trees (31%; $D \geqslant 30$ cm) were felled, and the branches and foliage were weighed in the field as before, but the trunks were cut into sections (logs) to estimate their volume. The volume (V) of each section was estimated employing the Smalian approach, which is defined by $V = (\pi/8) * L * (d_1^2 + d_2^2)$, where d_1 and d_2 are the diameter of the log at each extreme. The total volume of the trunk was calculated as the sum of the volume of all of the sections or logs. Two to six samples of wood from the transverse section of the trunk and branches were taken from each tree to determine the moisture content (CH%) and specific wood density (ρ = dry weight/green volume in g cm^{-3}) of each pool. Likewise, three foliage samples of each tree were taken to determine their moisture content (CH%).

Table 1
Descriptions of the sites where harvested trees were sampled for assessing AGB in this study. Life zones sensu Holdridge et al. (1971): Tm = Tropical moist, Tw = Tropical wet, STd = Subtropical dry, Td = Tropical dry, LMm = Lower montane moist, PMw = Premontane wet, LMw = Lower montane wet, PMm = Premontane moist and Mw = Montane wet. n = number of trees harvested in each site.

Site	Region	Latitude	Longitude	Life Zone	Altitude (masl)	Rainfall (mm yr^{-1})	n	D (cm)	ρ (g cm^{-3})	H (m)	AGB-tree (kg)
CariS[a]	Caribe coast	10°37′45″N	75°13′55″O	Td	30	1030	20	27.2 ± 11.8 (10.4–51.0)	0.53 ± 0.19 (0.31–0.84)	13.2 ± 3.5 (8.2–18.4)	304.9 ± 294.0 (21.6–933.7)
BPRico[b]	Puerto Rico	17°58′37″N	66°40′18″O	STd	100	800	17	20.9 ± 8.5 (10.3–45.0)	0.54 ± 0.25 (0.31–0.79)	10.5 ± 2.9 (5.9–15.3)	238.1 ± 282.2 (20.3–1104.6)
AraL[a]	Amazonia	0°37′28″S	72°6′24″O	Tm	100	3060	84	30.6 ± 25.2 (10.0–130.0)	0.70 ± 0.15 (0.38–0.97)	20.0 ± 8.6 (7.5–44.3)	1612.6 ± 3128.6 (17.9–17994.9)
AraP[a]	Amazonia	0°34′17″S	72°6′21″O	Tm	100	3060	22	22.6 ± 13.3 (10.2–55.0)	0.78 ± 0.04 (0.71–0.85)	20.8 ± 4.7 (12.4–31.5)	644.6 ± 946.2 (43.1–3668.7)
AraT[c]	Amazonia	0°38′01″S	72°22′7″O	Tm	100	3060	53	43.4 ± 24.3 (10.2–97.9)	0.63 ± 0.14 (0.32–0.89)	27.2 ± 6.4 (14.9–39.3)	2638.0 ± 3129.9 (26.9–12643.4)
CarOp[a]	Magdalena valley	6°35′2″N	73°55′28″O	Tm	300	3000	22	37.1 ± 25.6 (10.0–84.3)	0.54 ± 0.11 (0.35–0.75)	18.6 ± 8.6 (6.7–36.2)	1538.9 ± 2159.9 (43.1–7125.3)
Rmelc[c]	Magdalena valley	6°27′41″N	75°10′58″O	Tm	500	3000	161	25.0 ± 12.8 (10.1–84.4)	0.57 ± 0.12 (0.22–0.86)	18.2 ± 5.1 (8.9–39.0)	590.8 ± 905.9 (34.2–8181.0)
SCRion[d]	Amazonia	1°52′11″N	67°3′55″O	Tm	100	3565	28	39.0 ± 32.7 (11.6–136.8)	0.61 ± 0.12 (0.30–0.77)	25.2 ± 5.0 (17.4–37.9)	1447.7 ± 2233.3 (61.5–9816.2)
Capiro[a]	Choco		67°	Tw	100	7000	53	51.7 ± 28.9 (10.7–126.7)	0.51 ± 0.14 (0.27–0.78)	29.7 ± 8.4 (15.0–48.0)	3015.8 ± 3052.1 (42.4–12006.0)
Bcal[a]	Choco	3°59′55″N	76°57′31″O	Tw	97	8000	14	15.4 ± 8.1 (10.5–37.5)	0.60 ± 0.09 (0.51–0.78)	13.3 ± 6.8 (6.0–30.0)	188.3 ± 413.5 (15.3–1597.2)
Porce[e]	Central Andes C	6°46′51″N	75°6′46″O	PMm	1000	3050	87	41.9 ± 38.8 (10.1–198.9)	0.52 ± 0.15 (0.23–0.80)	22.0 ± 9.9 (7.0–46.7)	2597.8 ± 4984.2 (13.1–27504.8)
Svic[a]	East Andes	6°54′5″N	73°18′4″O	PMm	1300	2000	14	30.7 ± 13.8 (14.3–59.5)	0.64 ± 0.13 (0.40–0.84)	16.8 ± 4.7 (9.2–26.7)	693.6 ± 793.4 (60.2–2487.3)
Pied[a]	East Andes	7°2′48″N	73°0′9″O	LMw	2350	2100	13	27.7 ± 19.6 (10.4–62.7)	0.65 ± 0.10 (0.50–0.84)	15.5 ± 6.2 (9.3–26.7)	949.9 ± 1334.0 (40.6–3948.3)
Shel[a]	Central Andes	6°16′52″N	75°30′10″O	LMw	2500	2500	31	18.1 ± 6.3 (10.4–38.3)	0.57 ± 0.07 (0.43–0.68)	11.2 ± 3.2 (6.0–17.8)	201.6 ± 203.2 (39.7–1115.0)
Tona[a]	East Andes	7°4′51″N	2°55′58″O	Mw	3100	1069	12	17.7 ± 4.1 (10.9–26.5)	0.48 ± 0.05 (0.39–0.62)	8.5 ± 2.4 (5.2–13)	68.7 ± 48.0 (27.6–194.1)

[a] This study.
[b] Brandeis et al. (2006).
[c] Overman et al. (1994).
[d] Saldarriaga et al. (1988).
[e] Sierra et al. (2007).

The fresh volume of the wood samples collected in the field was determined using geometrical methods. The height of the sample was calculated as the average of 4–6 measurements of different parts of the sample, while its area was obtained after tracing the exact shape of the sample on a piece of paper. All of the samples were dried at temperatures between 102–105 °C until they reached a constant weight and were subsequently weighed using precision scales to 0.001 g. In this way, the dry weight of the trees with $D \leqslant 30$ cm was obtained by multiplying the fresh weight of each pool (obtained in the field) by 1 – CH% of the samples. In the case of trees with $D > 30$ cm, the biomass was obtained by multiplying the trunk volume by the wood density of the trunk and subsequently adding the dry weight of the branches and foliage. However, for trees collected in the Bcal and Rmelc locations, there were not wood density measurements, but there were botanical identifications. For these trees from South and Central America humid forests, a wood density value was assigned to each individual at the species, genus or family level according to Chave et al. (2009) and Zanne et al. (2009). In contrast, for the AraT site, trees did not have vouchers or botanical identifications, but the wood density for each individual was available from field observations (i.e., Overman et al., 1994). Bearing these restrictions in mind, a database was created with botanical identification information, D (cm), H (m), ρ (gr cm^{-3}), and dry weight or biomass (dry mass; kg).

2.3. Evaluation of existing models

We evaluated the accuracy of the pantropical allometric models developed by Brown et al. (1989), Chave et al. (2005), and Zianis

(2008) (Table 2) by calculating the relative error in the total biomass for each site. The relative error (RE) was calculated using the following equation:

$$RE = (AGB_{predicted} - AGB_{measured})/AGB_{measured}.$$

Following Chave et al. (2005), the overall biases were evaluated by examining the mean relative error (%), and the accuracy was evaluated by examining the standard deviation of relative error (%) across sites, which represented the overall predictive power of the regression (Chave et al., 2005).

2.4. Allometric models for the estimation of above-ground biomass in Colombia

To develop new allometric models for Colombia, the methodology and nomenclature of Chave et al. (2005) were applied. Six regression models based on D, H, and ρ (Type I models) as well as six models that only consider D and ρ (Type II models) (see Chave et al. 2005 for details) were generated and tested. This analysis was performed using two forest type classifications:

1. The forest type classification proposed by Chave et al. (2005), which delineates wet, moist, and dry forests. Wet forests are defined as aseasonal forests in which evapotranspiration exceeds precipitation for less than one month of the year. This forest category corresponds to aseasonal lowland forests with a mean annual precipitation >3500 mm and cloud forests. Moist forests are defined as those in which evapotranspiration exceeds precipitation between one and five months, according

Table 2
Evaluated pantropical models for estimating the above-ground biomass (dry mass) of tropical trees from their diameter (cm), height (m), and wood density (g cm^{-3}).

Model code	Climate	Model – Tree biomass (kg)	Source
Chave Type I	Dry	$\exp(-2.187 + 0.916 \ln(\rho\, D^2 H)) = 0.112\,(\rho\, D^2 H)^{0.916}$	Chave et al. (2005)
Chave Type I	Moist	$\exp(-2.977 + 0.916 \times \ln(\rho\, D^2 H)) = 0.0509\,(\rho\, D^2 H)$	Chave et al. (2005)
Chave Type I	Wet	$\exp(-2.557 + 0.940 \ln(\rho\, D^2 H))) = 0.0776\,(\rho\, D^2 H)^{0.940}$	Chave et al. (2005)
Chave Type II	Dry	$\rho \exp(-0.667 + 1.784 \ln(D) + 0.207\,(\ln(D))^2 - 0.0281\,(\ln(D))^3)$	Chave et al. (2005)
Chave Type II	Moist	$\rho \exp(-1.499 + 2.148 \ln(D) + 0.207\,(\ln(D))^2 - 0.0281\,(\ln(D))^3)$	Chave et al. (2005)
Chave Type II	Wet	$\rho \exp(-1.239 + 1.980 \ln(D) + 0.207\,(\ln(D))^2 - 0.0281\,(\ln(D))^3)$	Chave et al. (2005)
Brown	All	$\exp(-2.4090 + 0.9522 \ln(\rho\, D^2 H))$	Brown et al. (1989)
Zianis	All	$0.1424\, D^{2.3679}$	Zianis (2008)

to climate averages over several years. This forest type corresponds to semi-deciduous lowland forests, which have a precipitation of approximately 1550–3500 mm yr^{-1}. Finally, dry forests are defined as those for which evapotranspiration exceeds precipitation for more than 5 months and overall precipitation is less than 1500 mm yr^{-1}.

2. The life zones system of Holdridge et al. (1971), which describes forest types based on altitudinal ranges (0–1000, 1000–2000, 2000–2500, and 2500–3000 masl) according to their potential evapotranspiration. This classification was used in another similar study but in a wider context (Brown et al. 1989). The tree data comes from the following life zones: tropical and subtropical dry forest (Td & STd, both considered as dry), tropical moist forest (Tm), tropical wet forest (Tw), premontane moist forest (PMm), lower mountain wet forest (LMw), and montane wet forest (Mw).

For the selection of the best statistical model to estimate the individual tree AGB, the Akaike information criterion (AIC) was used, which penalizes according to the number of parameters (Burnham and Anderson, 2002; Chave et al., 2005). Better models have lower AIC values. For each of the models, the residual standard error (RSE) was presented as an alternative criterion. Finally, for the selection of the overall best model according to the lowest bias and accuracy in each site, the estimated relative error was used (Chave et al., 2005). A correction factor required for the back logarithmic transformations was applied to generate predictions using all of the models, defined by the following equation: correction factor = $\exp(\text{RSE}^2/2)$ (Chave et al., 2005). All of the analyses were performed using the program R 2.13.1 (R Development Core Team, 2011).

3. Results

3.1. Wood specific gravity and size patterns

The wood specific gravity (ρ in g cm^{-3}), or wood density distribution, followed a bimodal pattern with maxima approximately 5.5 g cm^{-3} and 7.5 g cm^{-3} (Fig. 1). The humped shape with an average ρ of 7.5 g cm^{-3} was largely determined by the sampled trees in the Araracuara region, Colombian Amazon, which were mainly located on nutrient-poor sandy soils (one of them on a white sands transition zone). These three sites contained 51% of all of the individuals with a $\rho \geqslant 0.7$. The SCRion site had the lowest mean ρ (0.61) in the Colombian Amazon. This site included a large portion of secondary species (S1). The lowest average ρ (0.48) was found in the Tona site, located at the highest elevation (Table 1). Categorized by forest type, the ρ distribution under the Chave's forest type classification remained bimodal in the three forest categories, but showed a striking decrease of mean ρ in the dry forest. Under the life zones classification, the ρ distribution in Tw, LMw, and Mw
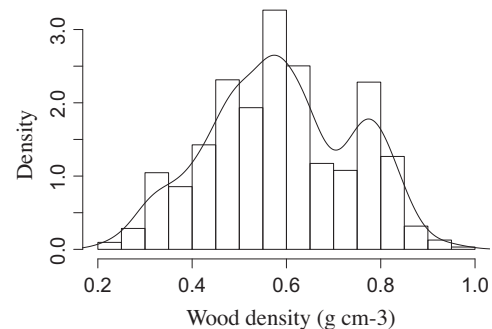

Fig. 1. Wood density distribution for 631 trees ($D \geqslant 10$ cm) sampled in different forest types in Colombia.

were skewed but unimodal in shape, while the distribution in Td, Tm and PMm remained bimodal (Figure S2).

There were significant differences in the average ρ among forest types using both the Chave's forest type (one-way ANOVA; $P < 0.001$, DF = 628) and life zones classifications ($P < 0.001$, DF = 625) (Fig. 2). According to the Tukey honestly significant difference test, under the Chave's forest type, the average ρ was significantly higher in wet (0.604 g cm^{-3}) than in moist (0.535 g cm^{-3}) and dry (0.534 g cm^{-3}) forest types. According to the life zones, Tw forests had a higher average ρ (0.622 g cm^{-3}) than all of the other forest types (mean 0.519 g cm^{-3}) except for LMw (0.592 g cm^{-3}).

Diameter (D) showed an inverse J-shaped distribution for both all of the data and the data arranged by forest type. There were significant differences in the arithmetic mean D among forest types under both Chave's forest type ($P \leqslant 0.001$, DF = 628) and life zones ($P \leqslant 0.001$, DF = 625) (Fig. 3). According to the life zones, Tw and PMm forests had a higher mean D (44.2 and 40.3 cm, respectively) than the other forest types. The lowest mean D was found in the Mw forest (17.7 cm) (Table 1). Regarding mean height (H), there were significant differences among forest types (life zones, $P < 0.001$ ∗∗∗, DF = 625). H showed an inverse pattern with altitude, except in Td and STd forests (Table 1).

3.2. Estimation of the AGB of trees in Colombia using pantropical models

Overall, the Zianis (2008) model had the lowest bias for estimating the total average AGB in different Colombian sites (-5.9%). However, this model was quite unstable at the site scale (39.1%). The Type I models of Chave et al. (2005; hereafter Chave I) at the site scale underestimated the average AGB of the forests within acceptable limits (−10.6%) and had the lowest uncertainty (22.1%). The model of Brown et al. (1989; hereafter Brown) had a similar but positive bias in magnitude at the site scale (10.7%) when compared to the Chave I but a slightly higher uncertainty (25.6%). However, except for the higher overestimation of the
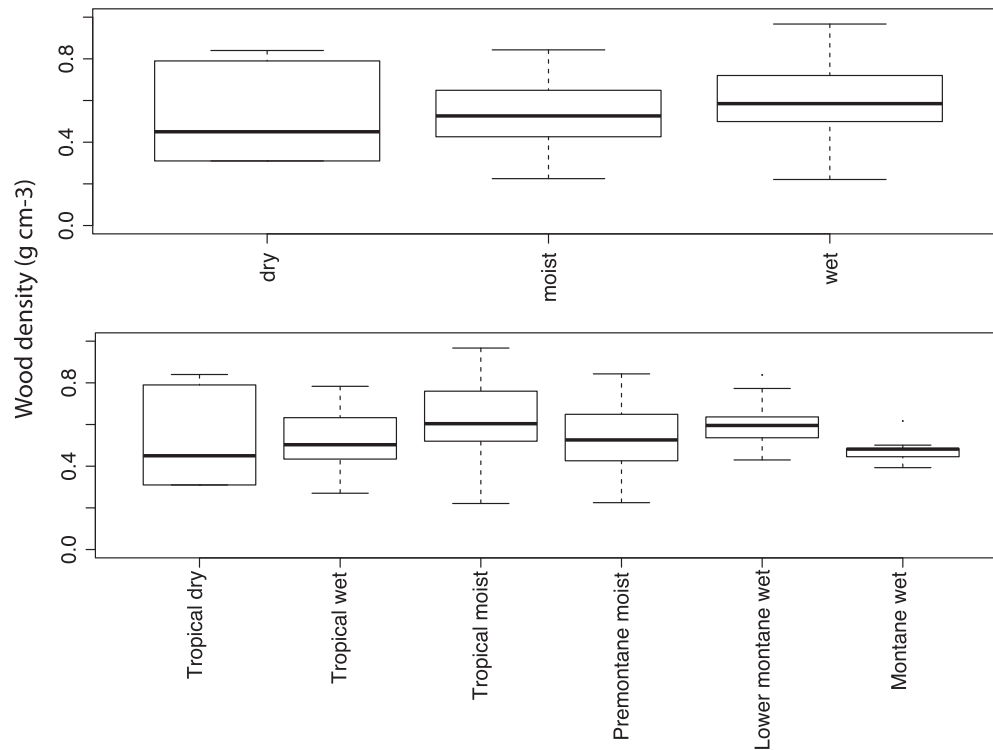
Fig. 2. Wood density among forest types. In the upper panel, the variation is based on the Chave's forest type classification. In the lower panel, the variation is based on the life zones classification.

Brown model at the CariS, SCRion, and Tona locations, it performed equally as well as or better than Chave I at all of other sites (Table 3). In contrast, Chave II overestimated by three- to fourfold the AGB in dry forests but underestimated the AGB in three of the four Amazonian sites (−13.9% to 31.1%) and had a tendency to overestimate the AGB in the high mountain ecosystems (−10.3% to 83.9%). All of the pantropical models evaluated overestimated the AGB in the SCRion (12.9% to 90.9%) and CariS sites (15.1% to 414%). Likewise, all of the pantropical models underestimated the AGB in the two highland (>2000 masl) sites of Pied (−10.7% to −32.3%) and Shel (−10.3% to 36.2%) (Table 3).

3.3. Models for estimating the above-ground biomass of forests in Colombia

Of the Type I models at the individual scale, the Type I.1 model that used the life zones classification system was statistically the best of all of the models evaluated (AIC = 369) (Table 4). Model Type I.1 also showed the best performance at the individual site scale (Table 5). Model Type II.1 using the life zones classification was in turn the best statistical model of all of those evaluated at the individual scale that did not include *H* (Table 4). Furthermore, at the site level, this model also had the best performance of all of the evaluated models in terms of both bias and accuracy (6 ± 19.6%) (Fig. 4).

The Chave's forest type classification systematically led to models for estimating individual tree AGB with higher AIC values (Table S1) and higher bias and accuracy than those employing the life zones at the site scale. According to the AIC values of the Type I models employing Chave's forest type classification, the best model was again Type I.1 (Table S1). However, the model with the lowest individual site-level error and uncertainty (8.3 ± 24.0%) was model I.3 (Table 5); from a statistical point of view, this is a simpler model and would be preferred. The inclusion of the three forest types defined by the Chave's forest type classification as factors into

the general models did not substantially improve the model fit at either individual or site scales (Table S1; Table 6). Similarly, the Type II models incorporating the Chave's forest type classification generally developed into individual tree AGB models with higher AIC values (Table 4), greater bias and lower accuracy at the site scale (Table 6) than the models that used life zones as the forest classification system. Equally, for Type II models, the inclusion of Chave's forest type classification slightly improved the statistical performance (Table S1) and bias rather than accuracy (Table 6) in comparison with general Type II models that did not include it.

4. Discussion

4.1. Evaluation and accuracy of pantropical models

The allometric model developed by Zianis (2008), which only included *D* as explanatory variable, had the lowest net bias for estimating AGB in Colombia at the national scale. This model outperformed other empirical models, such as those that included *H*, ρ and forest type (Brown et al., 1989; Chave et al., 2005). However, due to the high uncertainty associated with the Zianis model (Zianis, 2008), one could also expect a high average deviation stemming from chance, which would reduce its reliability for indiscriminate application at national or regional scales. To obtain reliable and precise estimations of C and AGB based upon simple dendrometric variables, such as *D* or basal area, model validation and construction using regional or local data are required (Chambers et al., 2001; Baker et al., 2004; Sierra et al., 2007; Litton and Kauffman, 2008; Basuki et al., 2009). In contrast, the generalized allometric models that included *D*, *H*, and ρ (Brown et al., 1989; Chave et al., 2005), which had a slightly higher bias than the Zianis model, presented more stability and less uncertainty, confirming their usefulness for the estimation of stored C in tropical forests on regional and global scales. Of all of the pantropical models evaluated
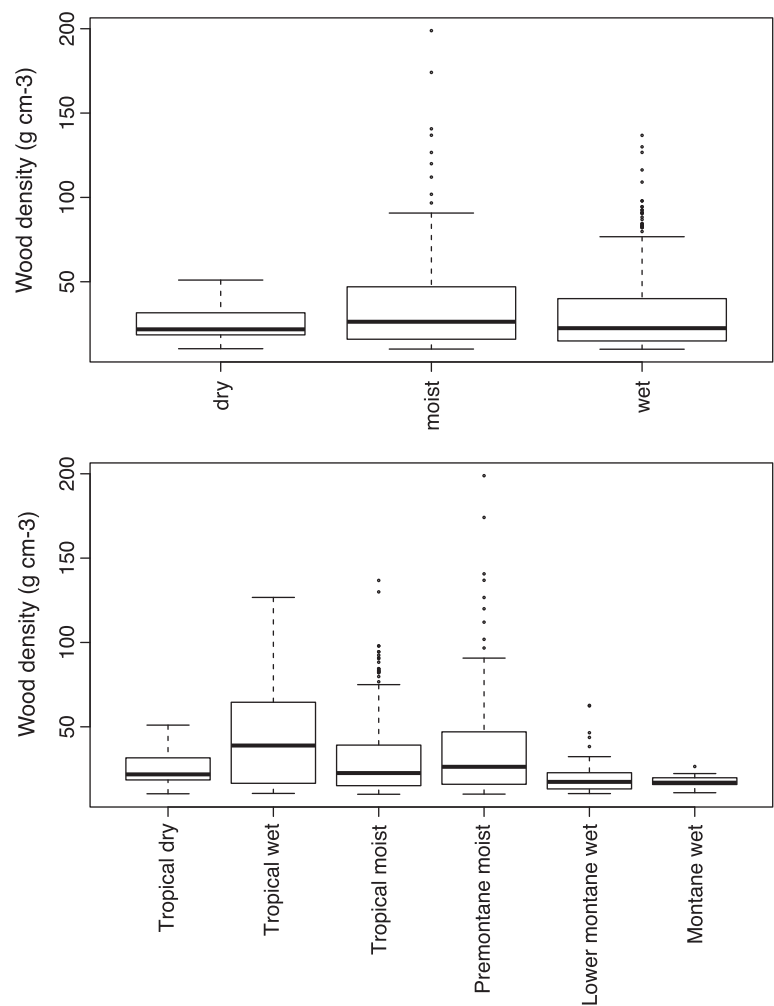
Fig. 3. Diameter among forest types. In the upper panel, it is the Chave's forest type classification. In the lower panel, it is the life zones classification.

Table 3
Relative percent error of the total biomass (assessed as the sum of all trees weighed in each site) across 15 sites in Colombia for the allometric models commonly employed to assess AGB in tropical forests. The relative percent error was calculated as $(AGB_{predicted} - AGB_{measured})/AGB_{measured} \times 100\%$. Chave's forest type: forest type defined by Chave et al. (2005). SD: Standard deviation. The sites are as defined in Tables 1 and S1.

Site	Total AGB (Mg)	Chave's forest type	Relative error (%)			
			Chave I	Chave II	Brown	Zianis
CariS	6.10	Dry	15.1	414	28.6	50.7
BPRico	4.05	Dry	−10.4	335.8	−0.8	1.1
AraL	135.46	Wet	−30.7	−31.1	−7.9	−35.1
AraP	14.18	Wet	−12.1	−13.9	15.4	−44.2
AraT	139.82	Wet	−22.3	−22.8	3.6	−38.5
CarOp	33.86	Wet	−24.5	−11.9	0.3	−15.0
Rmelc	95.12	Wet	−27.8	−21.3	−5.5	−28.4
SCRion	40.54	Wet	42.4	53.9	90.9	27.4
Capiro	159.84	Wet	−18.2	−23.9	9.3	−18.6
Bcal	2.64	Wet	−15.8	−18.6	9.0	−28.5
Porce	226.01	Moist	21.7	47.5	18.9	−1.7
Svic	9.71	Moist	−4.2	52.8	5.3	−10.2
Pied	12.35	Wet	−32.3	−13.9	−10.7	−30.1
Shel	6.25	Wet	−36.2	−10.3	−18.1	−19.0
Tona	0.82	Wet	−4.0	83.9	21.7	102
Mean (%)			−10.6	54.7	10.7	−5.9
SD (%)			22.1	135.7	25.6	39.1

at the site scale, both the Chave I and Brown allometric models for mixed species (Brown et al. 1989; Chave et al., 2005) appear as the most appropriate for estimating AGB in Colombian natural forests when either regional or local allometric equations do not exist. Nonetheless, when the SCRion data taken mostly from secondary forests were not taken into account for assessing the performance

Table 4
Tree biomass allometric models for Colombian forests following the life zones forest type classification of Holdridge et al. (1971) and according to Chave et al. (2005) approach but based on life zones. Model coefficients: a, b_1, b_2, b_3, c, and d. DF: degrees of freedom. RSE: Residual Standard Error. R^2: Squared R. Life zones as in Table 1. AIC: Akaike's Information Criterion.

	Forest type	a	b_1	b_2	b_3	c	d	DF	RSE	R^2	AIC
Models type I											
$\ln(AGB) = a + b_1\ln(D) + c\ln(H) + d\ln(\rho)$											
I.1	Mw	−2.294	2.081			0.587	1.016				
	LMw	−3.670	2.081			0.587	−0.360				
	PMm	−2.221	2.081			0.587	1.089	617	0.320	0.961	369
	Tm	−2.919	2.081			0.587	0.391				
	Tw	−2.857	2.081			0.587	0.453				
	Td & Std	−2.217	2.081			0.587	1.092				
I.2	All types	−2.277	2.017			0.715	0.718	627	0.347	0.954	462
$\ln(AGB) = a + c\ln(D^2\,H\,\rho)$											
I.3	Mw	−2.485	–			0.937	–				
	LMw	−2.032	–			0.937	–				
	PMm	−2.332	–			0.937	–	624	0.353	0.953	485
	Tm	−2.261	–			0.937	–				
	Tw	−2.289	–			0.937	–				
	Td & Std	−2.328	–			0.937	–				
I.4	All types	−2.231	–			0.933	–	629	0.359	0.945	503
$\ln(AGB) = a + \ln(D^2\,H\,\rho)$											
I.5	Mw	−2.927	–			–	–				
	LMw	−2.520	–			–	–				
	PMm	−2.904	–			–	–	625	0.367	0.954	533
	Tm	−2.820	–			–	–				
	Tw	−2.889	–			–	–				
	Td & Std	−2.825	–			–	–				
I.6	All types	−2.818	–			–	–	630	0.376	–	561
Models type II											
$\ln(AGB) = a + b_1\ln(D)+b_2(\ln(D))^2 + b_3(\ln(D))^3 + d\ln(\rho)$											
II.1	Mw	3.130	−1.536	1.169	−0.122		1.767				
	LMw	1.836	−1.255	1.169	−0.122		−0.222				
	PMm	1.960	−1.098	1.169	−0.122		1.061	611	0.336	0.958	436
	Tm	2.406	−1.289	1.169	−0.122		0.445				
	Tw	1.662	−1.114	1.169	−0.122		0.331				
	Td & Std	3.652	−1.697	1.169	−0.122		1.285				
II.2	All types	3.103	−1.794	1.290	−0.128		0.819	626	0.393	0.941	619
$\ln(AGB) = a + b_1\ln(D)+b_2(\ln(D))^2 + b_3(\ln(D))^3 + \ln(\rho)$											
II.3	Mw	1.665	−0.633	0.892	−0.097		1				
	LMw	1.442	−0.295	0.892	−0.097		1				
	PMm	0.780	−0.108	0.892	−0.097		1	617	0.360	0.952	515
	Tm	1.516	−0.289	0.892	−0.097		1				
	Tw	0.921	−0.108	0.892	−0.097		1				
	Td & Std	2.183	−0.665	0.892	−0.097		1				
II.4	All types	2.789	−1.414	1.178	−0.118		1	627	0.396	0.940	626
$\ln(AGB) = a + b_1\ln(D)+\ln(\rho)$											
II.5	Mw	−1.053	2.079				1				
	LMw	−1.200	2.391				1				
	PMm	−1.410	2.431				1	619	0.364	0.951	530
	Tm	−0.983	2.350				1				
	Tw	−1.482	2.499				1				
	Td & Std	−0.496	2.036				1				
II.6	All types	−1.218	2.404				1	629	0.399	0.939	634

of all of the AGB pantropical models at the site scale (see details below), the Brown model's bias decreased and accuracy increased to 4.9 + 13.3%, while the Chave I model's bias increased to −14.4% and accuracy increased to 17.2%. Therefore, in this particular case for Colombian forests, the Brown model might be recommended over the most commonly employed Chave I. This finding is a striking result, considering that most of data sources in Brown et al. (1989) came from other continents rather than America (Table 1, page 884) and that the model tested was developed only for moist forests (Brown et al. 1989).

The Chave I model underestimated the AGB in 12 out of the 15 sites studied. This result contrasts with other studies that have found a systematic AGB overestimation using these models (Litton and Kauffman, 2008; Basuki et al., 2009). In these studies, the Chave I AGB overestimation was mainly explained by the inclusion of very large trees from Asia. Asian trees have been shown to have a greater $H{:}D$ rate of change than Amazonian trees (Feldpausch et al., 2010), i.e., trees in Asia are taller at the same diameter than those in the Amazon. For this reason, and opposite to the results of this study, we might also expect an overestimation of the AGB of trees from northwest Amazonia when employing the Chave I model. Therefore, it can be concluded that $H{:}D$ relationships across different forest types in Colombia were well-captured and well-modeled using Chave I, except in the SCRion site, suggesting that model underestimation may be explained by changes in other factors, such as wood density. This tendency of the Chave I model to underestimate the AGB was confirmed at the stand level employing plot data from the 25-ha Amacayacu plot in the Colombian Amazon. In this forest, we tested the AGB estimations using the Chave I model against the Overman et al. (1994) model and a local bole biomass model under construction that does not include either branches or leaves. In the first case, we found that the Overman model yielded 22% more AGB than that estimated by the Chave I model. In the second case, we did not find significant

Table 5
Evaluation of the Type I models developed for assessing above-ground biomass in Colombian forests with forest type according to the life zones classification. The values are percentages (%) of the total error, as explained in the methods section. The bias and uncertainty for the same models but excluding the SCRion site from the mean and SD calculations are shown. The details at the site scale for the evaluation of the Type I models developed following the Chave's forest type classification are presented in Table S2.

Site	AGB (Mg)	Total relative error per site (%)					
		I.1	I.2	I.3	I.4	I.5	I.6
CariS	6.1	21.2	41.3	20.8	28.5	31.8	32.7
BPRico	4.0	−0.9	4.4	−6.5	−0.4	0.6	1.3
AraL	135.5	−6.4	−10.6	−10.3	−11.5	4.8	5.0
AraP	14.2	−4.1	2.8	14.2	13.2	24.5	24.7
AraT	139.8	−4.2	−3.4	0.5	−0.9	18.9	19.0
CarOp	33.9	10.5	2.1	−2.2	−3.4	13.1	13.3
Rmelc	95.1	−1.4	−6.6	−6.1	−6.8	0.7	0.8
SCRion	40.5	84.8	83.7	84.0	81.0	123.9	124.2
Capiro	159.8	3.9	7.6	2.9	4.2	17.9	26.6
Bcal	2.6	−2.8	4.6	6.8	9.3	3.8	11.4
Porce	226.0	11.4	19.7	6.0	11.8	31.0	42.6
Svic	9.7	5.2	7.7	−2.5	3.9	3.1	12.3
Pied	12.3	−3.0	−10.7	10.5	−13.0	32.1	−2.0
Shel	6.2	7.2	−12.9	4.9	−16.7	9.0	−19.1
Tona	0.8	0.0	46.3	0.7	26.1	2.9	14.6
Mean (%)		8.1	11.7	8.3	8.3	21.2	20.5
SD (%)		22.5	26.5	22.5	24.0	24.0	32.5
Models Type I life zones classification excluding the SCRion site							
Mean (%)		2.6	6.6	2.8	3.1	13.9	13.1
SD (%)		7.8	18.1	8.5	13.7	12.1	15.8
Models Type I Chave's forest type classification							
Mean (%)		10.6	11.7	8.3	8.3	20.5	20.5
SD (%)		26.8	26.5	24.0	24.0	24.0	32.5

differences between the bole biomass local model and the AGB estimated using the Chave I model (A. Duque *personal observation*). These values are in line with the observed AGB differences (%) in the Colombian sites assessed with the Chave I model.

Some fundamental differences in the way ρ was assessed and included in either the present study or the study by Chave et al. (2005) could explain the observed AGB underestimation using the Chave I model for the Colombian sites. First, the harvested tree sampling schemes could affect comparisons among studies. In most of the study sites, we followed a sampling scheme for harvesting trees based on the local species dominance, and this scheme could drive the sampling to bias the typical average ρ of each forest as a whole. For example, the four sites from the Amazon basin (AraL, AraP, AraT, and SCRion) had a higher average ρ (0.61 to 0.78 g cm^{-3}) than the 0.58 g cm^{-3} reported for the whole Amazon basin (Ter Steege et al., 2006). These Colombian Amazon sites were located on poor, sandy soils largely dominated by the Leguminosae, Lecythidaceae, and Sapotaceae families, which usually have a high wood density. This trend could have led to higher average values in this dataset than in those obtained under a random sampling scheme. Because dominant species usually represent approximately 70% of the total individuals (Pitman et al., 2001), this assertion may be considered as a hypothesis that would need to be tested. Second, measured versus inferred wood density values could create different model outcomes. The inferred ρ values from the literature have several disadvantages in comparison to field measurement values because they add an additional amount of uncertainty to the models. For example, when a comparison was made between observed and inferred ρ values, according to the Pearson correlation coefficient, the inferred data explained 79% ($n = 266$; $P \leqslant 0.001$) of the variation at the species level, 67% ($n = 456$; $P \leqslant 0.001$) at the genus level, and 51% ($n = 456$; $P \leqslant 0.001$) at the family level. Furthermore, the inferred ρ data assumed a unique value for each species even under different environmental conditions, in contrast to what would be found in

nature (Patiño et al. 2009). Third, the use of datasets constructed by different research teams at different times brings to the models (both the models used by Chave and in this study) an unknown amount of uncertainty due to the impossibility of ensuring standard procedures in both field and laboratory conditions. This challenge is particularly true for the Chave et al. (2005) study, which incorporated a significant amount of raw information from figures in the literature. Therefore, additional studies following standard tree-harvesting sampling methods at large scales and using standardized procedures will help to improve the estimation of the AGB in natural tropical ecosystems.

The Chave II model (without H) showed very high bias and uncertainty in estimating the AGB figures for the Colombian forests. In addition to the concerns related to ρ measurement discussed above, the results showed that changes in the $H:D$ relationship determined by the environmental variation included in this study were not detected by this model; this lack of detection appears to be the most likely explanation for the observed 55% mean overestimation. A similar result was found at the stand level along an altitudinal gradient in Peru, where the Chave II model overestimated the AGB by 52% (±10%) (Girardin et al., 2010). These authors claimed that the trees become more squat and stunted with increasing elevation. The lack of fit using the Chave II model for the $H:D$ relationship caused a systematic AGB overestimation. However, the average ρ of all of the sites located over 2000 masl was 28% (±36%), a finding that did not support the hypothesis of a systematic overestimation caused only by the variation in tree form with increasing elevation. The AGB overestimation in the Tona site (83%) by the Chave II model likely did not result only from the effect of tree form variation. The overestimation may rather be a combined effect of tree form and a lower mean ρ, which was found in this site. Indeed, the high bias and accuracy associated with the Chave II model was largely based on the AGB overestimation by approximately 300% to 400% of the two dry forests included in this work. A high portion of pioneer species representing dry forests and the Tona site, as shown by the average ρ, seems to promote a systematic AGB overestimation of the Chave II model. Typical secondary species could also alter the $H:D$ relationship because they are expected to be taller at a given diameter than slow-growing or shade-tolerant species. This allometric change does not seem to be properly assessed by the Chave II model. Indeed, the Chave II model developed for dry forests (Chave et al., 2005) appears to have been built based on dry forests different from those existing in Colombia, which correspond to one of the most threatened ecosystems in this country that is currently represented by only 5% of its original cover (Chaves and Santamaría, 2006). In spite of the fact that the Chave II model is the most widely used model for estimating AGB data coming from forestry inventories (see Chave et al., 2008), this study suggests that the use of that model will require an assessment with external data prior to implementation.

4.2. Allometric models for the estimation of AGB in Colombia

The Type I.1 models developed in this study using the life zones classification was the best model for assessing the AGB of individual trees, yet this model showed an overall higher bias (8.1%) and lower accuracy (22.5%) at the site scale than that obtained employing the Type II.1 model (6.0 and 19.6%, respectively). Such a result is quite controversial because it means that $H:D$ allometry is better modeled by a D cubic log-transformed polynomial than by H itself. However, when analyzing the goodness-of-fit test employed at the site scale (Table 5), it is clear that the SCRion site data were systematically and significantly overestimated using all of the models (including the Type II, see Table 6). It seems that the SCRion site does not belong to the same population of individual trees as the
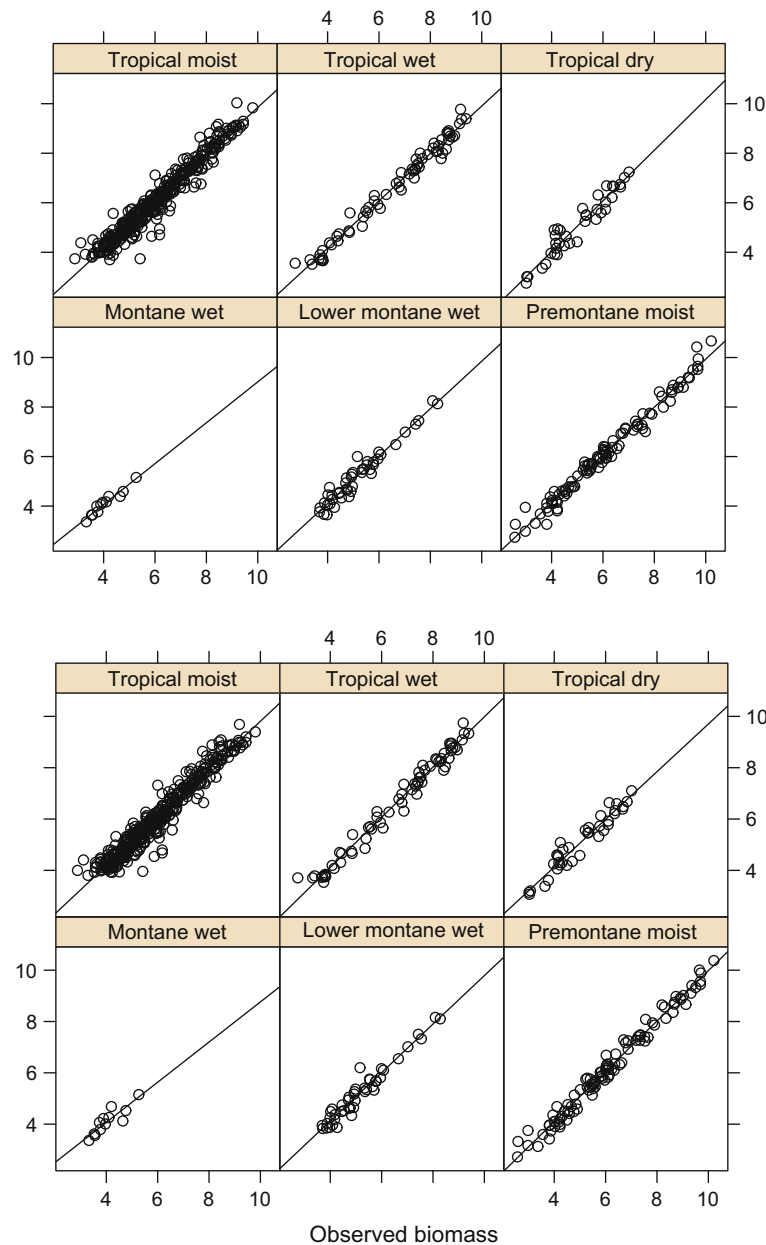
Fig. 4. Observed versus predicted values of above-ground biomass for 631 trees in different forest types, according to the life zones classification. The values are based on the Type I.1 (upper panel) or Type II.1 model (lower panel) developed for Colombian forests. Each dot represents an individually weighed tree.

other remaining sites because 78% of the harvested trees at the SCRion site came from fallows with ages between 10 to 35 years (Saldarriaga et al., 1988). However, the main differences of the SCRion site may come from particular $H:D$ relationships in this site, supported by the fact that the mean ρ (0.61 g cm^{-3}) was similar to that expected in mature forests. This high mean ρ for forests including pioneer species is due to in very poor sandy soils, the mean ρ of mature forest may be higher than 0.7 g cm^{-3} as was shown in the AraP site. Indeed, Type I models were shown to be sensitive to the inclusion of secondary forests, such as those sampled in the SCRion site, leading the general performance of the models to a higher bias and inaccuracy than that found in other studies also carried out at large scales (Chave et al., 2005).

In fact, when we evaluated the overall bias by examining the mean relative error and the accuracy by examining the standard deviation of relative error across all of the sites excluding the

SCRion site, the Type I.1 model reached an overall performance of 2.6 ± 7.8% in the remaining sites (Table 5). The accuracy of these findings was even better than that obtained with model Type II.1, which still showed the lowest bias of all of the tested models (1.8 ± 11.3%), after excluding the SCRion site (Table 6). We also developed alternative (A) new models and selected the best ones, Type IA and Type IIA, following the same criteria as before but without including the 28 trees from the SCRion site (Table S4). However, these models did not perform better at the site scale than the two models selected above (Table S5). Therefore, the two best models already presented here both with and without including H (Type I.3 and Type II.1), based on all 631 trees instead of 603 (not including the SCRion site), appear to be the best option for estimating the carbon stored in the AGB of individual trees and forest stands in Colombian natural forests. This assertion will remain true only if there are not local AGB equations.

Table 6
Evaluation of the Type II models developed for assessing AGB in Colombian forests with forest type according to the life zones classification. The values are percentages of the total error, as explained in the methods section. The bias and uncertainty for the same models but excluding the SCRion site from the mean and SD calculations are shown. The details at the site scale for the evaluation of the Type II models developed following the Chave's forest type classification are presented in Table S3.

Site	AGB (Mg)	Total relative error per site (%)					
		I.1	I.2	I.3	I.4	I.5	I.6
CariS	6.1	3.6	92.7	2.7	90.5	2.9	84.0
BPRico	4.0	−3.3	49.5	−10.2	54.7	−10.0	51.4
AraL	135.5	−15.4	−12.8	−15.3	−11.9	−9.6	−10.5
AraP	14.2	−4.5	2.0	11.9	8.2	8.7	4.5
AraT	139.8	−10.6	−3.4	−4.3	−0.1	−0.1	−0.8
CarOp	33.9	13.8	14.4	9.5	14.2	13.8	12.8
Rmelc	95.1	3.8	−1.5	1.7	−1.3	−0.3	−3.9
SCRion	40.5	65.0	87.2	79.5	94.9	109.9	111.3
Capiro	159.8	7.6	−1.2	10.3	−2.3	17.4	1.1
Bcal	2.6	−5.5	−0.9	5.1	0.1	2.2	−1.5
Porce	226.0	2.1	3.4	3.2	5.0	22.4	30.5
Svic	9.7	30.0	32.1	29.0	33.8	17.5	28.7
Pied	12.3	−6.1	8.6	0.2	10.8	2.7	6.1
Shel	6.2	8.5	7.7	6.8	8.3	6.0	8.3
Tona	0.8	1.2	125.7	0.5	119.5	0.6	123.0
Mean (%)		6.0	26.9	8.7	28.3	12.3	29.7
SD (%)		19.6	42.4	22.0	41.6	41.6	43.3
Models Type II life zones classification excluding the SCRion site							
Mean (%)		1.8	22.6	3.7	23.5	5.3	23.8
SD (%)		11.3	40.4	10.5	38.7	9.7	38.3
Models Type II Chave's forest type classification							
Mean (%)		19.2	26.9	20.2	28.3	23.1	29.7
SD (%)		42.4	42.4	39.2	41.6	41.6	43.3

4.3. Forest type classification as a determinant of the AGB distribution

At the site scale, the use of Type I models based on the Chave's forest type classification did not result in a significant reduction in the bias or uncertainty of the AGB estimation in Colombia. These results demonstrate that the Chave's forest type classification was not able to differentiate the expected variation in tree form among forest types along the altitudinal gradient, which largely causes the variation in AGB (Aiba and Kitayama, 1999; Girardin et al., 2010). In the case of Type II models, the models constructed using the Chave's forest type classification produced more imprecise and uncertain estimations than when the life zones classification was employed. For example, the Type II.1 model resulted in a bias of 6.0% to 19.2%% and an accuracy of 19.2% to 42.4% when the life zones and Chave's forest type classifications were employed, respectively. These results emphasize that the forest categories used by Chave et al. (2005) on a global scale (see also Feldpausch et al., 2010) would not be ideal for measurement studies of C at national or subnational scales in highly environmentally heterogeneous countries, such as the Andean regions.

4.4. Sampling and model representativeness

Despite the fact that this work has possibly the best dataset ever published of harvested trees for AGB studies from any neotropical mountainous country, all of the models based on a small dataset of sampled trees need to be considered as preliminary. For the particular case of Colombia, a better understanding of the AGB variation in high lands as well as in dry forests will require additional data from newly harvested trees. However, we may consider that the Chave models could also bring some unaccounted source of uncertainty from secondary information. Likewise, the basic information included by Brown et al. (1989) also lacks ρ data from wet forests, has a lower sample size than this study, and is primarily based on data from Asia, India, and Africa. Therefore, the new models presented here can be considered as an alternative option for

assessing carbon stocks in the AGB of natural forests in neotropical countries.

The mean ρ found in this study (0.58 ± 0.15 g cm^{-3}) was similar to the one reported as expected for mature tropical forests (0.58 or 0.6 g cm^{-3}) in other studies (Chave et al., 2005; Ter Steege et al., 2006). However, we found a high variation in the mean ρ among the sites, which has surely been caused by forest degradation. In Colombia, an assumption of an idealized mean ρ of 0.58 or 0.6 g cm^{-3} in regions other than the Amazon basin is not supported by empirical results and could result in a systematic overestimation of the AGB. The lower true mean ρ is due to significant ecosystem degradation caused by an annual deforestation rate of approximately 330,000 ha (IDEAM, 2010). As shown in this study, most of the sites from the Choco and Andean region had a lower mean ρ than the expected value for pristine forests. In high lands, however, many of the forest remnants in Colombia are dominated by *Quercus humboldtii* (Fagaceae), a species with a mean ρ close to 0.7 g cm^{-3} that can reach up to 35 m in height. This species, which can in many cases be considered as a pioneer species, shares its natural habitat with other families also with high ρ values (Lecythidaceae, Juglandaceae, Lauraceae, and others). This species composition explains why in high mountains, carbon stocks can in many cases equal or surpass those reported for low lands (Phillips et al., 2011). Unfortunately, the site features where the data for this study was taken may be considered as representative of a high portion of actual Colombian forests.

Thus, an additional question about the representativeness of our ρ sample for each forest type cannot be resolved yet. It is impossible, with a sample of 631 individuals, to attempt to represent all of the forest types of a country with thousands of species. In an ideal distribution of ρ, we would expect a symmetrical unimodal distribution of ρ in very diverse forests if the sample were large enough to capture it. However, we may not expect such a distribution in forests dominated by very few species, such as the case in high lands, where skewed or bimodal distributions might arise as well. To assess the ρ representativeness of our dataset, we

compared our ρ dataset to an external dataset composed of 65,535 tree individuals to which we assigned a ρ value from the literature. The trees were sampled in 121 plots ranging in size from 0.25 to 1 ha that were each assigned to the life zones available for our data. First, we found that the ρ distribution of the whole plot dataset was bimodal (Figure S3), similar to the main dataset used in this study. Second, there were significant differences in the mean ρ between the plot data and our data in the montane wet (0.63 vs. 0.48, respectively), premontane moist (0.57 vs. 0.54), and tropical wet zones (0.60 vs. 0.62). Thus, assuming that the 121 1-ha plots represent Colombian forests, the dataset of ρ collected in this study would be representative of only 50% of all of the mature forest types expected to occur in Colombia. According to this result, the models developed in this study could be underestimating tree AGB in montane wet and premontane moist forests, but overestimating it in tropical wet forests. In the remaining three forest types evaluated, we do not expect to have introduced any bias in the allometric models by differences in ρ between collected and plot-based datasets.

5. Conclusions

After the seminal work published by Chave et al. (2005), this study appears as the first attempt to evaluate the overall performance of these widely employed models for estimating the AGB of tropical forests. The way we assess AGB has major implications for understanding terrestrial carbon cycling and its role on climate change. Our results mainly emphasized that Chave II models, which are the most widely employed models to estimate tree AGB in sites where local models do not exist, should be evaluated before their use. Finally, forest type classification was shown to be an important determinant of AGB estimation when altitudinal and complex environmental gradients were included. The development and improvement of the existing models, perhaps by pooling existing data, may help to foster new strategies to diminish forests loss and degradation along with their expected negative effects on climate change.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2011.12.013.

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