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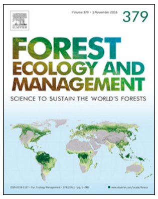

A regional allometry for the Congo basin forests based on the largest ever destructive sampling

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ABSTRACT

The estimation and monitoring of the huge amount of carbon contained in tropical forests, and specifically in the above-ground biomass (AGB) of trees, is needed for the successful implementation of climate change mitigation strategies. Its accuracy depends on the availability of reliable allometric equations to convert forest inventory data into AGB estimates. In this study, we tested whether central African forests are really different from other tropical forests with respect to biomass allometry, and further examined the regional variation in tropical tree allometry across the Congo basin forests. Following the same standardized protocol, trees were destructively sampled for AGB in six sites representative of terra firme forests. We fitted regional and local allometric models, including tree diameter, wood specific gravity, tree height, and crown radius in the AGB predictors. We also evaluated the AGB predictions at the tree level across the six sites of our new models and of existing allometric models, including the pantropical equations developed by Chave et al. (2014, 2005) and the local equations developed by Ngomanda et al. (2014) in Gabon. With a total of 845 tropical trees belonging to 55 African species and covering a large range of diameters (up to 200 cm), the original data presented here can be considered as the largest ever destructive sampling for a tropical region. Regional allometric models were established and including tree height and crown radius had a small but significant effect on AGB predictions. In contrast to our expectations, tree height and crown radius did not explain much between-site variation. Examining the performance of general models (pantropical or regional) *versus* local models (site-specific), we found little advantage of using local equations. Earlier pantropical equations developed for moist forests were found to provide reasonable predictions of tree AGB in most sites, though the wettest sites, *i.e.*, evergreen forests in Equatorial Guinea and, to a lesser extent in Gabon, tended to show a wet forest allometry. For the Congo basin forests, except in Equatorial Guinea where local models might be preferred, we recommend using our regional models, and otherwise the most recent pantropical models, that were validated here. These results constitute a critical step for the estimation and monitoring of biomass/carbon stocks

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contained in the second largest contiguous block of tropical forests worldwide, and the successful implementation of climate change mitigation strategies, such as REDD+.

1. Introduction

The increase in greenhouse gas concentrations has, had, and will have, strong impacts on the global climate (IPCC fifth report on climate change, Pachauri et al., 2014). Deforestation and forest degradation was a major source of greenhouse emissions in the 1990s contributing to ~20% of total greenhouse gas emissions (Malhi and Grace, 2000) but decreasing in the 2000s to 10–12% of total emissions (Van der Werf et al., 2009) due to the acceleration of fossil energy emissions. Forest losses are still widely reported and deforestation has been estimated to 129 million of hectares between 1990 and 2015, mostly in the tropics (FAO, 2015; Keenan et al., 2015). To limit the emissions due to deforestation and forest degradation, but also to conserve tropical forest biodiversity and ecosystem services, the mechanism for the Reduction of the Emissions from Deforestation and Degradation (REDD+) is under negotiation. Though the implementation of REDD+ is still being discussed, specifically the financial incentives, strong efforts have been made by the scientific community to standardise methods for monitoring biomass/carbon stocks in tropical forests, a key component for making REDD+ a reality (Gibbs et al., 2007).

Forest biomass/carbon stocks are not directly measured in the field, but estimated following a three-step approach (Chave et al., 2004; Clark and Kellner, 2012). (1) The estimation of individual tree biomass is obtained by converting forest inventory data using an allometric equation. (2) The estimation of plot biomass is then computed from the sum of individual tree biomasses, for all trees inventoried in the plot. At the tree or plot levels, carbon stocks are deduced from biomass estimates by multiplying by carbon content (Thomas and Martin, 2012). (3) For the mapping of forest biomass/carbon stocks at a larger scale, remote-sensing data are used to expand the plot-level estimates over larger areas.

Allometry is the relationship between a tree measurement (typically its biomass) and another measurement, more easily measurable in the field, *i.e.*, tree diameter and/or height (Picard et al., 2012). An allometric equation is a mathematical expression which formalizes this relationship in a quantitative way. In forest sciences, allometric relationships have been classically established to estimate the stem volume or the tree biomass (see Henry et al., 2011 for a catalogue of available equations for sub-Saharan Africa). While volume estimation is of extreme importance for forest management and timber commercialization, a renewed interest in biomass estimation has been observed for approximately one decade (Zianis and Mencuccini, 2004). The implementation of climate change mitigation strategies, and specifically REDD+, will need accurate and repeatable estimations of forest biomass/carbons stocks (Gibbs et al., 2007) and the choice of an appropriate allometric model has been demonstrated to be a critical step (Chave et al., 2004; Molto et al., 2013).

The first tree allometry work for species-rich and structurally complex tropical rainforests goes back to 1989 by Brown et al. (1989). In this seminal paper, pantropical multi-species allometric equations predicting AGB of individual trees as a function of diameter at breast height, total tree height, and wood specific gravity (the oven-dry mass of a wood sample divided by its green volume) were proposed for the first time, and different equations were provided according to the forest type. Chambers et al. (2001) then developed an unbiased model for the relationship between tree diameter and biomass from 315 trees harvested in the central Amazon, and showed major differences for large trees when compared to existing models. Chave et al. (2005) updated the pantropical multi-species allometric equations and proposed allometric equations for wet, moist, dry and mangrove forests. The most important predictors of tree AGB were, in order of importance, tree diameter, wood specific gravity and tree height, and the inclusion of tree height in the model predictors obviated the differences between forest types. The pantropical models of Chave et al. (2005) were used in a variety of contexts (cited more than 2050 times on 24th of April 2018) though their application in tropical Africa was questioned because the calibration dataset, though impressive (with 2410 trees with a diameter ≥ 5 cm destructively sampled, from 27 study sites), did not include any data from Africa. The predictions of the pantropical model for moist forests was, however, found unbiased and accurate in Cameroon (Fayolle et al., 2013) but showed 40% overestimation in Gabon (Ngomanda et al., 2014), though in the latter site the wet forest equation was appropriate. The selection of the appropriate allometric model among a set of existing models is thus not straightforward, as also shown in Colombia (Alvarez et al., 2012). The pantropical allometric equations have been recently revised (Chave et al., 2014), including this time destructive data from Africa in the calibration dataset (4004 trees ≥ 5 cm destructively sampled, from 38 study sites). The general model (Eq. (4) from Chave et al., 2014) solely depending on a synthetic variable composed of tree diameter (D in cm), total height (H, in m), and species wood specific gravity (WSG, in g cm^{-3}), is relatively simple in its form:

$$AGB_{est} = 0.0673 \times (WSG \times D^2 \times H)^{0.976}$$

When height data are not available, a model including an environmental stress variable (E) was proposed (Eq. (7) from Chave et al., 2014):

$$AGB_{est} = \exp[-1.803 - 0.976 \times E + 0.976 \times \ln(WSG) + 2.673 \times \ln(D) - 0.299 \times [\ln(D)]^2]$$

The E variable models the H-D relationship, and it is clearly imperfect locally as shown in Cameroon (Fayolle et al., 2016), and already acknowledged in Chave et al. (2014).

Given the information provided by the multi-site analyses of published data and the proposed pantropical equations (Brown et al., 1989; Chave et al., 2014, 2005), improving our understanding of tropical tree allometry will require new data in under-sampled areas such as the Congo basin forests (Verbeeck et al., 2011). This newly collected data should follow a comparable protocol and an appropriate sampling: at least 100 trees covering a large range of diameter, as suggested by Chave et al. (2004), and including extremely large trees given their contribution to plot-level AGB (Slik et al., 2013) and their strong variability (Chambers et al., 2001; Picard et al., 2012). The destructive sampling should target species with contrasted wood specific gravity, which is a key functional trait (Chave et al., 2009) and the second most important predictors of tree AGB (Chave et al., 2014, 2005). Other tree dimensions have been demonstrated to additionally improve the performance of multi-specific allometric models, specifically tree height (Feldpausch et al., 2012) and crown characteristics (Goodman et al., 2013; Ploton et al., 2016).

In this study, we tested whether central African forests are really different from other tropical forests with respect to biomass allometry, and examined the regional variation in tree allometry across the Congo basin forests. Despite the strong between-site variation in tree allometry reported by Fayolle et al. (2013) in Cameroon and Ngomanda et al. (2014) in Gabon, only little information is available for the Congo basin forests (Loubota Panzou et al., 2016), especially when considering the appropriate sampling needed for an allometric model. A dataset of destructive AGB measurements (n = 845 trees, over a large range of diameters, *i.e.*, 10–208 cm) was assembled to provide a basis for the validation of existing models and to develop allometric models for the Congo basin forests, thanks to the support of the Global Environmental Fund dedicated to the regional REDD+ project (PREREDD+). Following the same standardized protocol, destructive AGB data were collected in six sites representative of terra firme forests in the Congo basin. We first ask how the measured tree dimensions co-vary in the dataset and then assessed the performance of allometric models, including new regional and local models, and previously published ones. According to the previous findings, and mostly from Chave et al. (2014, 2005), we hypothesized that, after tree diameter, (i) wood specific gravity is an important AGB predictor, and explains most of between-species variation, (ii) tree height is also an important AGB predictor, and explains most between-site variation. The importance of crown characteristics on tree AGB recently evidenced by Goodman et al. (2013) and Ploton et al. (2016) was additionally examined. Because the selection of the appropriate allometric model among a set of existing models is not straightforward (e.g. Alvarez et al., 2012; Ngomanda et al., 2014), we also evaluated a set of existing models, including the most recent pantropical equations, and addressed a more applied research question for future biomass/carbon stocks estimation, asking whether general or local models should be preferred for the estimation of tree AGB.

2. Material and methods

2.1. Study sites

A total of six study sites, from evergreen to semi-deciduous lowland terra firme forests, were selected for the destructive sampling of tree AGB (Table 1). The evergreen forests sampled encompass coastal (in Equatorial Guinea) and inland (in northern Gabon) forests. Semi-deciduous forests were sampled in eastern Cameroon and northern Republic of Congo. Transition forests between the evergreen and semi-deciduous types were sampled in Central African Republic (CAR) and in Democratic Republic of Congo (DRC), with contrasting determinants, including substrate and soils in CAR (Fayolle et al., 2014), and climate and continentality in DRC. Monodominant *Gilbertiodendron* stands were also sampled in Congo and DRC to test for a specific allometry. Given the forest types sampled and the spatial extent covered, these sites were representative of the terra firme forests of the Congo basin (White, 1983). The country name will hereafter be used to refer to the site with mention of the forest type only when relevant.

The variation in environmental conditions across the Congo basin forests is relatively well represented by the six study sites, with mean annual rainfall varying from 1400 in the driest site (Cameroun, semi-deciduous forest) up to 2700 mm in the wettest site (Equatorial Guinea, coastal evergreen forest). Most sites, except Equatorial Guinea, were above 400 m a.s.l., and the semi-deciduous forest in Cameroon showed the highest altitude (> 600 m). The measure of environmental stress developed by Chave et al. (2014), compounding indices of temperature seasonality, drought intensity and precipitation seasonality varies from -0.15 for the evergreen forests (in Equatorial Guinea and Gabon) to ~ 0 for the other sites further inland. The variation across the six study sites was, however, restricted, compared with the pantropical variation, *i.e.*, between -0.2 and 1, and which encompassed wet, moist and dry forests, and woodlands.

2.2. Species and tree sampling

The development of allometric equations requires a large sampling effort in terms of individuals (at least 100 trees, Chave et al., 2004), diameters and species, but also rigorous measurements of wood specific gravity (Woodcock and Shier, 2002). The unpublished destructive data presented here followed a standardized protocol adapted from Fayolle et al. (2013) and Ngomanda et al. (2014), and suitable for extremely large trees. In each of the six study sites, a partnership was established with a logging company (Table 1) for both logistic support and compliance with national forest laws. Based on forest inventory data (specifically management inventories) but also on field expertise, a set of 15 species, locally abundant and characteristic of the forest type, but also with contrasting wood specific gravities, was selected in each site. At this stage, average values for tropical Africa were computed at the species or genus level (Table 2) from the global database (Chave et al., 2009; Zanne et al., 2009). In each site, we aimed to sample between 120 and 130 trees belonging to the 15 targeted species and covering a large diameter range, to fulfil the recommendations of Chave et al.

Table 1

Characteristics of the study sites, including country and name of the logging company, geographical coordinates, forest type, environmental conditions, specifically: mean annual temperature (MAT), mean annual rainfall (MAR), altitude and E-value *sensu* Chave et al. (2014), and sampling effort in terms of the number of trees (n_{tree}) and species (n_{spe}), and diameter range (D in cm). Sites are ordered from West to East.

Site (logging company)	Coordinates	Forest type	Environment	Sampling
1. EqG Equatorial Guinea (COMALI)	Lon = 9.537° Lat = 1.316°	Coastal evergreen forest	MAT = 25.2 °C MAR = 2699 mm alt = 52 m E = −0.1509	$n_{tree} = 109$ $n_{spe} = 14$ D [11–172]
2. Gab Gabon (Rougier Haut-Abanga)	Lon = 11.131° Lat = 0.505°	Evergreen forest inland	MAT = 23.7 °C MAR = 1905 mm alt = 496 m E = −0.1203	$n_{tree} = 178$ $n_{spe} = 16$ D [12.3–169.3]
3. Cam Cameroon (GRUMCAM)	Lon = 14.809° Lat = 3.952°	Semi-deciduous forest	MAT = 23.6 °C MAR = 1396 mm alt = 663 m E = −0.0131	$n_{tree} = 132$ $n_{spe} = 15$ D [11.5–180]
4. CAR Central African Republic (SEFCA)	Lon = 16.896° Lat = 3.919°	Transition forest between the evergreen and semi-deciduous types on sandstone plateau	MAT = 24.0 °C MAR = 1570 mm alt = 565 m E = −0.0023	$n_{tree} = 143$ $n_{spe} = 16$ D [10.5–173]
5. Cgo Republic of Congo (CIB-OLAM)	Lon = 16.970° Lat = 2.484°	Semi-deciduous forest	MAT = 24.4 °C MAR = 1704 mm alt = 442 m E = −0.0314	$n_{tree} = 141$ $n_{spe} = 16$ D [10.3–208]
6. DRC Democratic Republic of Congo (CFT)	Lon = 25.206° Lat = 0.348°	Transition forest between the evergreen and semi-deciduous types	MAT = 25.2 °C MAR = 1772 mm alt = 423 m E = −0.0355	$n_{tree} = 142$ $n_{spe} = 16$ D [11.7–160.5]

Table 2

Characteristics of the species destructively sampled, including scientific and commercial names, number (n) of trees sampled, range of diameters (D in cm) and mean wood specific gravity (in g cm^{-3}) from our local measurements (WSG$_L$), and from the global database (WSG$_G$), are given for each sampled species. The taxonomic level (Lev., species or genus) and the number of individuals (n$_G$) used to compute WSG$_G$ are also given. Species are ordered by botanical family.

Genus	Species	Com. name	n	D	WSG$_L$	WSG$_G$	Lev.	n$_G$
Anisophylleaceae								
Poga	*oleosa*	Ovoga	7	[24–130]	0.421	0.393	sp	9
Annonaceae								
Annickia	*affinis*	Moambe jaune	5	[11.3–51]	0.449	0.468	ge	2
Anonidium	*mannii*	Ebom	13	[18.7–71.8]	0.329	0.291	sp	2
Greenwayodendron	*suaveolens*	Otungui	13	[14.5–51]	0.622	0.695	sp	1
Xylopia	*aethiopica*	Okala	26	[15–76.7]	0.529	0.442	sp	2
Apocynaceae								
Alstonia	*boonei*	Emien	9	[16–128.75]	0.374	0.321	sp	5
Burseraceae								
Aucoumea	*klaineana*	Okoumé	36	[14–169.3]	0.384	0.378	sp	26
Canarium	*schweinfurthii*	Aiélé	8	[20.8–160.5]	0.411	0.409	sp	16
Santiria	*trimera*	Ebo (Ebap)	9	[12.3–52.5]	0.548	0.546	sp	3
Cannabaceae								
Celtis	*adolfi-friderici*	Diana	9	[17.7–70.5]	0.594	0.581	sp	3
Combretaceae								
Terminalia	*superba*	Fraké	28	[13–113.5]	0.47	0.459	sp	57
Euphorbiaceae								
Macaranga	*spp*		12	[14.8–53.5]	0.347	0.380	ge	3
Plagiostyles	*africana*	Essoula	12	[17.1–51.5]	0.575	0.741	sp	3
Ricinodendron	*heudelotii*	Essessang	23	[14.5–126]	0.269	0.211	sp	5
Fabaceae								
Baphia	*spp*	Baphia	6	[14.5–67]	0.801	0.772	ge	2
Brachystegia	*laurentii*	Bomanga	9	[11.7–146.5]	0.438	0.500	sp	15
Calpocalyx	*heitzii*	Miama	7	[18–88]	0.684	0.727	sp	15
Cylicodiscus	*gabunensis*	Okan	19	[13.5–159.5]	0.749	0.790	sp	18
Cynometra	*hankei*		12	[17.8–112]	0.693	0.841	sp	2
Dialium	*pachyphyllum*	Omvgong	13	[16–129]	0.74	0.923	sp	2
Erythrophleum	*ivorense*	Tali	10	[17.5–172]	0.704	0.774	sp	19
Erythrophleum	*suaveolens*	Tali Yaoundé	22	[16.6–120.5]	0.74	0.873	sp	5
Gilbertiodendron	*dewevrei*	Limbali	39	[11.7–158]	0.668	0.707	sp	4
Julbernardia	*pellegriniana*	Beli	3	[80–108.6]	0.698	0.675	sp	9
Pentaclethra	*macrophylla*	Mubala	13	[11.5–112]	0.744	0.841	sp	9
Pericopsis	*elata*	Afrormosia	9	[14.8–158.5]	0.649	0.639	sp	12
Prioria	*balsamifera*	Agba	1	[133.3–133.3]	0.442	0.407	sp	9
Prioria	*oxyphylla*	Tchitola	10	[14.8–110]	0.534	0.570	sp	4
Pterocarpus	*soyauxii*	Padouk	51	[11.6–144]	0.594	0.658	sp	14
Scorodophloeus	*zenkeri*	Divida	7	[15.8–97.5]	0.66	0.724	sp	4
Irvingiaceae								
Desbordesia	*glaucescens*	Alep	12	[14.5–170]	0.807	0.915	sp	7
Irvingia	*grandifolia*	Olen	8	[10.3–134]	0.756	0.801	sp	4
Klainedoxa	*gabonensis*	Eveuss	5	[52–102]	0.781	0.926	sp	12
Lecythidaceae								
Petersianthus	*macrocarpus*	Essia (Abalé)	50	[12.5–115]	0.588	0.677	sp	10
Malvaceae								
Duboscia	*macrocarpa*	Akak	8	[26.5–120.3]	0.55			
Eribroma	*oblongum*	Eyong	9	[17.8–100.8]	0.547	0.638	sp	11
Mansonia	*altissima*	Bété	7	[19–74.56]	0.519	0.564	sp	24
Triplochiton	*scleroxylon*	Ayous	21	[13.5–208]	0.378	0.335	sp	24
Meliaceae								
Entandrophragma	candollei	Kossipo	9	[15–173]	0.547	0.574	sp	10
Entandrophragma	cylindricum	Sapelli	41	[15.2–169.42]	0.551	0.572	sp	16
Guarea	*cedrata*	Bossé clair	8	[16.5–70.5]	0.562	0.527	ge	1
Khaya	*anthotheca*	Acajou	8	[12.1–113]	0.52	0.491	sp	11
Lovoa	*trichilioides*	Dibétou	6	[45.5–107.6]	0.599	0.455	sp	19
Moraceae								
Milicia	*excelsa*	Iroko	21	[18.5–116]	0.516	0.575	sp	24
Myristicaceae								
Pycnanthus	*angolensis*	Ilomba	59	[13–130]	0.41	0.409	sp	20
Scyphocephalium	*mannii*	Sorro	12	[36.8–109.8]	0.446	0.507	sp	9
Staudtia	*kamerunensis*	Niové	44	[12.6–119.3]	0.675	0.797	sp	17
Ochnaceae								
Lophira	*alata*	Azobé	35	[11–152]	0.833	0.897	sp	30

(*continued on next page*)

Table 2 (*continued*)

Genus	Species	Com. name	n	D	WSG_L	WSG_G	Lev.	n_G
Olacaceae								
Ongokea	*gore*	Angueuk	7	[36.1–72.5]	0.692	0.749	sp	10
Strombosia	*grandifolia*	Booko	8	[14.5–54.7]	0.647	0.825	sp	6
Sapotaceae								
Autranella	*congolensis*	Mukulungu	12	[10.5–200]	0.732	0.777	sp	8
Manilkara	*mabokeënsis*		14	[14.5–106]	0.738	0.879	ge	4

(2004). Trees, sought to be representative of the sampled forest, were selected during a prospecting phase. Specific authorizations were obtained from national authorities for the destructive sampling of trees of timber species with a diameter below the minimum cutting diameter limit. Finally, a total of 55 species were sampled belonging to 49 genera and 17 families (Table 2) including the Fabaceae (specifically the Caesalpinioideae subfamily) characteristic of the evergreen forests, and the Malvaceae, Sapotaceae and Meliaceae families, characteristic of the semi-deciduous forests (White, 1983).

2.3. Biomass measurements

Prior to felling, tree location was recorded with a global positioning system (GPS) and dendrometric measurements were performed on standing trees. Tree diameter was measured with a tape at breast height or 30 cm above the stem deformations. Total tree height was measured with a VERTEX IV rangefinder from two different positions located at a minimum distance of tree height (Larjavaara and Muller-Landau, 2013). Crown was defined as everything above the first major branch and four different measurements of crown radius were performed according to cardinal points (Rondeux, 1999).

After felling, the tree length (including the bole and crown) and stump height were measured with a tape. The felled trees were then divided into compartments, *i.e.*, the stump, the bole, the large branches (with a diameter ≥ 20 cm), the medium branches (between 20 and 5 cm) and the small branches (< 5 cm), and a last compartment composed of twigs, leaves, and flowers and fruits, when present. When possible, tree compartments were directly weighed in the field, except the stump of all trees, and the stem of commercial trees, which were cubed and later converted into dry biomass (Fayolle et al., 2013). The stem volume of commercial trees was estimated from consecutive measurements of 1–2 m logs. The stump basal area was computed from georeferenced photographs, on which the stump edge was manually digitised in QGIS (version 2.8). The stump volume was estimated from the stump area and height. Several samples were collected on each compartment for laboratory measurements. Woody samples (including bark) corresponded to disks or disk portions to respect radial variation. Two opposite disk portions were sampled on the stump, and at both end of the bole, and three disks were sampled in the branches (one in the large, one in the medium and one in the small branches). Three random samples were collected on the last compartment composed of twigs, leaves, and flowers and fruits.

In the laboratory, the green volume of woody samples, and the fresh mass and oven-dried mass of all samples, were measured in order to compute the wood specific gravity (ratio of the dry mass over the green volume) and the dry matter content (ratio of the dry mass over the fresh mass). The water displacement method was used for the green volume measurements (Rondeux, 1999). Dry mass of all samples was obtained after several days drying at 105 °C until constant mass, *i.e.*, < 1% difference between two measurements at 6 h interval.

2.4. Allometric modelling

We first used the destructively sampled trees from six sites across the Congo basin forests as a calibration dataset to develop regional (and local) allometric equations. Tree diameter and height, and species wood specific gravity, have long been recognized as important predictors of tree AGB and the pantropical allometric model developed by Chave et al. (2014) relied on the general equation:

$$\mathrm{AGB} = \mathrm{a}\times \mathrm{WSG}^{\mathrm{b}} \times \mathrm{D}^{\mathrm{c}} \times \mathrm{H}^{\mathrm{d}} \tag{1}$$

Once the total tree height (H, in m) is known, we assumed that the site effect becomes negligible. When the height, H, is unknown, it is replaced by a function of the diameter (D, in cm) and the environmental stress variable (E, dimensionless). It was also assumed that the model has a multiplicative error distributed according to a log-normal distribution. In this study, we followed the same modelling strategy that (i) generalizes all biomass models built upon the mechanistic mass of a cylinder (Molto et al., 2013), (ii) respects the proportionality principle between the total biomass of a plant and its size (West et al., 1999, 1997) and, (iii) has been demonstrated to be very efficient regarding the recent studies (e.g. Goodman et al., 2013; Ngomanda et al., 2014). In addition, Eq. (1) becomes a simple linear model after log-transformation (Eq. (2) which is recommended for allometric modelling (Kerkhoff and Enquist, 2009):

$$\log(\mathrm{AGB}) = \log(\mathrm{a}) + \mathrm{b}\times \log(\mathrm{WSG}) + \mathrm{c}\times \log(\mathrm{D}) + \mathrm{d}\times \log(\mathrm{H}) \tag{2}$$

The log-transformation, however, introduces a bias when back-transforming the data (Sprugel, 1983) and the bias was corrected using a correction factor, $\mathrm{CF} = \exp(\mathrm{RSE}^2/2)$, where RSE is the residual standard error.

Additional models derived from this general modelling approach were also examined, with fixed coefficients, with and without total tree height in the predictors, substituting local height-diameter allometry by the environmental stress of the site (Chave et al., 2014), and including the crown radius as an AGB predictor (Goodman et al., 2013). Here, we used the mean wood specific gravity of the stem samples at the tree level. Missing values due to laboratory problems were replaced by species average (n = 13 trees belonging to 8 species). For total tree height, we used the mean of the two non-destructive measurements, and crown radius corresponded to the mean of the four measurements. To evaluate the relative importance of crown radius, in comparison with the more classical AGB predictors (*i.e.*, tree diameter, wood specific gravity and total tree height), we computed the proportion of type III sum of squares explained by the variable in the most complete model:

$$\log(\mathrm{AGB}) = \log(\mathrm{a}) + \mathrm{b}\times \log(\mathrm{WSG}) + \mathrm{c}\times \log(\mathrm{D}) + \mathrm{d}\times \log(\mathrm{H}) + \mathrm{e}\times \log(\mathrm{CR}) \tag{3}$$

2.5. Evaluating new and existing models

To assess the performance of the new models tested we used the variance explained (R^2), Akaike and Bayesian Information Criteria (AIC and BIC, respectively), and the RMSE computed on back-transformed AGB estimates (AGB_{est}, including the correction factor) and AGB observations (AGB_{obs}) as follows.

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(AGB_{est,i} - AGB_{obs,i})^2} \qquad (4)$$

The distribution of model residuals was examined visually, and the departure from a normal distribution was tested according to the Anderson-Darling normality test. A Box-Cox transformation was also applied on the residuals.

We then evaluated the performance of regional allometric models at the site level. Because general models are calibrated on large datasets, the model coefficients are expected to be more precisely estimated, but general models can be locally biased. We computed the performance of the regional models for each site separately, in terms of RMSE (in kg) and mean relative bias (in %).

$$bias\,(\%) = \frac{1}{n}\sum_{i=1}^{n}(AGB_{est,i} - AGB_{obs,i})/AGB_{obs,i} \qquad (5)$$

Bias significance was also tested using *t*-tests.

To get a broader view of the regional variation in tree allometry, the performance of local models was also tested in all other sites, as a calibration validation procedure, in order to identify which site-specific model is valid where. In the pairwise validation, the allometric model was calibrated in one site (calibration dataset) and then applied to all other sites independently (validation dataset). For this approach, two models were retained, a model including WSG, D, and H in the AGB predictors derived from the most recent pantropical model (Chave et al., 2014), and a model only including WSG and D in the AGB predictors that was close to the earlier pantropical models (Chave et al., 2005).

Finally, we also used the trees destructively sampled in six sites across the Congo basin forests as a validation dataset to evaluate existing models. We specifically tested the predictions of the general pantropical models developed by Chave et al. (2014, 2005) and of the local models established by Ngomanda et al. (2014) in the Zadié site in Gabon. We did not test the predictions of the model developed by Fayolle et al. (2013) in the Mindourou site in Cameroon, because this model was found to be quite close to the moist forest model of Chave et al. (2005), and of the other local models established on a restricted dataset (e.g. Djomo et al., 2010 in Cameroon; Ebuy et al., 2011 in DRC). To evaluate AGB predictions of existing models, we used several statistical criteria. We computed the root mean square error (RMSE in kg) between estimations and observations and we tested for the presence of a significant bias using t-tests on the relative bias (in %). We also fitted a linear model between the individual error (estimation - observation) and diameter at the site level, and examined the value and significance of coefficients. The same analyses were replicated for large trees, using a diameter threshold of 70 cm according to Slik et al. (2013).

The R environment was used for the whole data analyses and modelling (R Development Core Team, 2017).

3. Results

3.1. Covariations between tree dimensions and AGB

We first asked how the measured tree dimensions co-vary in the combined dataset including 845 trees from 55 species (14–16 in each site), among which wood specific gravity varied between 0.269 g cm^{-3} for *Ricinodendron heudelotii* (Euphorbiaceae) and 0.833 g cm^{-3} for *Lophira alata* (Ochnaceae), with a mean of 0.582 g cm^{-3} across species. The most massive tree was a *Autranella congolensis* (Sapotaceae) of 66 Mg sampled in northern Congo, and was therefore slighter than the heaviest tropical tree ever weighed (76 Mg in southwestern Amazonia, Goodman et al., 2012) and in central Africa (72 Mg in southeastern Cameroon, Fayolle et al., 2013). However, it has to be noted that attention was paid to sampling extremely large trees in all sites (Fig. 1) confirming the great interest of using this dataset for the calibration of new allometric models and for the evaluation of existing equations. For instance, among the 845 trees sampled, a total of 225 trees had a diameter > 70 cm, *i.e.*, large trees according to Slik et al. (2013), and 132 trees showed AGB > 10 Mg, *i.e.*, large trees according to Ploton et al. (2016). In comparison, among the 4004 trees of the pantropical dataset of Chave et al. (2014), a total of 252 trees had a diameter > 70 cm and 108 trees showed AGB > 10 Mg. Obviously, large trees were tall and had large crowns, and power-law relationships provided good fit to the data for both height-diameter and crown-diameter allometries (Fig. S1) with significant between-site variation (Table S1). The highest tree, a

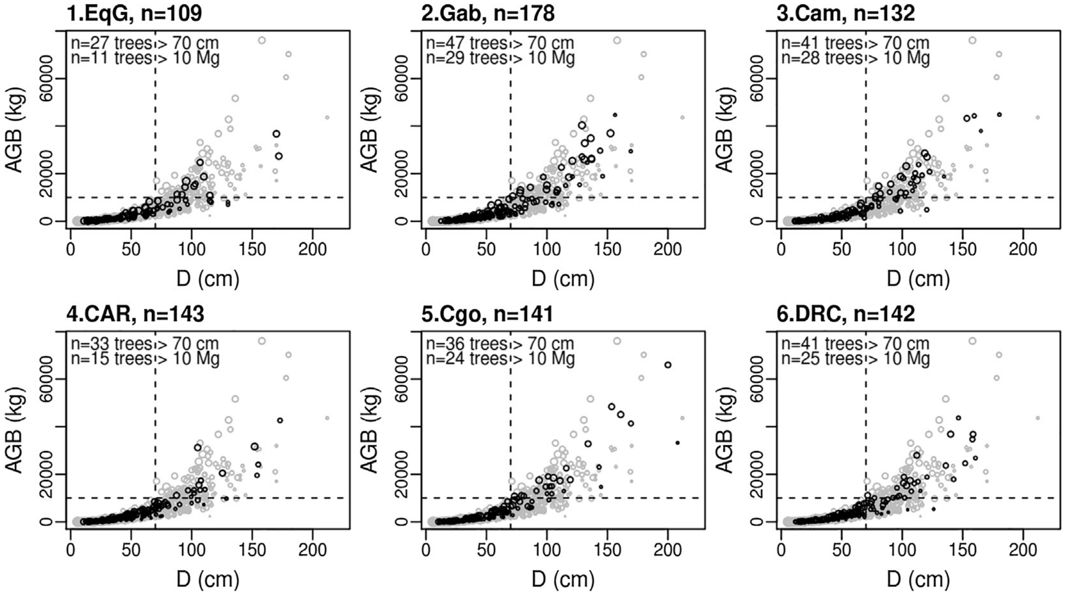

Fig. 1. Trees destructively sampled in six sites across the Congo basin forests (in black) overlaying the 4004 trees of the pantropical dataset assembled by Chave et al. (2014, in grey). Circles represent the aboveground biomass (AGB, in kg) of all sampled trees plotted according to diameter (D in cm) with size proportional to wood specific gravity (in g cm^{-3}). The dashed lines corresponds to the diameter and biomass thresholds for large trees according to Slik et al. (2013, D > 70 cm) and to Ploton et al. (2016, AGB > 10 Mg). Sites are ordered from West to East.

Terminalia superba (Combretaceae) of 67 m height was sampled in Cameroon (semi-deciduous forest). The tree with the largest crown, a *Brachystegia laurentii* (Fabaceae) with a mean crown radius of 22 m, for only 31 m height, was sampled in DRC (transition forest).

We then examined how the measured tree dimensions relate to AGB in the combined dataset. We first fitted the general allometric model including tree diameter, mean stem wood specific gravity, and total tree height in the AGB predictors, and two parameters in the model, *i.e.*, an intercept and a single scaling coefficient for the term WSG × D^2 × H (model 1, Table 3). We found that this model, relatively simple in its form, provided a relatively good fit to the data. Including specific scaling coefficients for each predictor provided lowest values of AIC, BIC, among the tested models including these three predictors (model 3, Table 3), though such models do not take into account the co-variation between H and D. However, constraining the covariation of D and H through the use of the compound variable $D^2 \times H$ (models 5–7) provided higher AIC and BIC. Fitting a set of derivative models, we found that including tree height as a predictor strongly improved AGB estimates and that models with unconstrained coefficients generally provided better fits, though estimated coefficients were close to 1 for wood specific gravity and close to 2 for tree diameter (Table 3). The RMSE comparing back-transformed AGB estimates to observations confirmed the good performance of model 3. The RMSE was, however, the lowest for the derivative model including a scaling coefficient constrained to 2 for tree diameter (model 4). Following the approach developed by Chave et al. (2014), we further examined whether tree height could be advantageously replaced by the environmental stress variable fitting the same relatively complex model (model 13). Including the environmental stress did not improve the model, since the AIC and BIC values remained higher than previously obtained. Extending the same modelling approach and including crown radius in the predictors, we found that crown size significantly improved AGB estimates (Table 3) reducing model AIC, BIC and RMSE. Substituting total tree height by crown size in the full model showed that crown radius was less effective than total tree height to estimate AGB (model 16 indeed showed higher AIC, BIC and RMSE values than model 3). Computing type III sum of squares of the full model including tree diameter, wood specific gravity, total tree height and crown radius, and with unconstrained coefficients (model 14), further confirmed the more limited role of crown radius (0.87%, proportion of type III sum of squares explained), and tree height (2.05%), with respect to wood specific gravity (15.5%) and diameter (65.5%) to explain AGB variation. However, despite the only marginal variation explained by crown radius, the model including crown radius was significantly better than the model not including crown radius among the AGB predictors ($P < 0.001$, likelihood ratio tests). For all tested models, the residual distribution generally departed from a normal distribution according to the Anderson-Darling normality test but the graphical analysis did not reveal any particular structure. Residuals were thus considered acceptable, which was confirmed by the Box-Cox transformation (scaling coefficients close to 1).

3.2. Evaluation of model performance at the tree level across sites

We then assessed the performance of allometric models, including the new regional models fitted on the combined dataset, and previously published ones, at the tree level, across all sites. We first examined for each site separately, the performance of all regional models (Table 4) and we found, surprisingly, that including tree height in the predictors did not necessarily improve AGB estimates, since site-level RMSE and bias were comparable between model 8–12 (only including tree diameter and wood specific gravity in the predictors) and model 1–7 (also including tree height). The sites in Cameroon, Congo, and to a lesser extent in CAR showed an intermediate allometry, and regional models provided unbiased AGB estimates, while the DRC site and the sites in Gabon and Equatorial Guinea showed contrasted biomass allometry, and significantly biased AGB estimates.

To further examine the regional variation in biomass allometry across the Congo basin forests, we evaluated the performance of all local models tested in all other sites, in a pairwise validation procedure. We restricted the analysis to two model forms that showed a good performance for regional models (models 3 and 12, Table 3). We found a highly specific allometry in Equatorial Guinea (Table 5) since using the local models fitted in Equatorial Guinea to estimate tree AGB in any of the other sites across the Congo basin forests lead to high site-level RMSE values and strong negative bias. Conversely testing all other local models in Equatorial Guinea also showed high site-level RMSE values and strong positive biases that tended to increase with the distance from East to West. In contrast, local models fitted and tested in the five other sites seemed to provide reliable AGB estimates in the other sites, with, however, a tendency for greater allometric differences (higher site-level RMSE) between the most distant sites, e.g. Gabon and DRC.

The same results were found for the different models tested, with, however, less difference reported with model 12 (not including tree height in the AGB predictors) contrary to our expectation that total tree height captures most between-site variation in tree allometry. Again, including tree height in the predictors did not necessarily improve AGB estimates, since site-level RMSE of local model 12 was not systematically higher or more biased than that of local model 3. As expected, site-level RMSE (in kg) and bias (in %) of the regional models both tended to be more important (Table 4) than that of local models of the same form (Table 5).

Finally, to test whether central African tropical forests are really different from other tropical forests with respect to biomass allometry we tested the performance of pantropical models, which tended to provide significantly biased AGB estimates at the tree level for most sites (Fig. 2). The performance of pantropical models was, however, found only slightly lower than that of regional models, with comparable site-level RMSE, but larger and highly significant bias for pantropical models (Fig. 2 and Table S2) and smaller but significant bias for regional models (Table 4). The moist forest equations of Chave et al. (2005, Ch05mD and Ch05mDH) significantly overestimated tree AGB in Equatorial Guinea (23.3 and 26.1%), in Gabon (13.4 and 16.4%), in Cameroon (19.9 and 22.1%) and CAR (14.4 and 9.3%), but provided unbiased estimates in Congo, and variable results in DRC, with significant AGB overestimation for the model not including height (Ch05mD, 10.4%), and significant underestimation for the model including height (Ch05mDH, −9.8%). The wet forest equations (Ch05wD and Ch05wDH) and the local equations developed by Ngomanda et al. (2014, Ng14D and Ng14DH) in Gabon provided reliable estimates in Equatorial Guinea, and to a lesser extent in the new site sampled in Gabon, but significantly underestimated tree AGB in all other sites (up to −28.9%). These results argue for a wet forest allometry in Equatorial Guinea, a moist forest allometry in Cameroon, Congo, and to a lesser extent in CAR and DRC, and an intermediate allometry in Gabon. The most recent pantropical equations of Chave et al. (2014, Ch14DH and Ch14DE) provided almost unbiased AGB estimates in Cameroon (25.2 and 5.6%), Congo (7.5 and −4.2%), CAR (12.6 and 2.3%) and DRC (−6.7 and −0.6%). In the wettest forests of Equatorial Guinea (28.9 and 23.7%) and Gabon (18.8 and 9.9%), both equations significantly overestimated tree AGB, confirming the specificity of these sites (tendency towards a wet forest allometry). Overall, and in contrast with our expectations, models including tree height did not consistently improve AGB estimates. This can be easily observed when comparing pairs of models, *i.e.*, Ch05mD and Ch05mDH, Ch05wD and Ch05wDH, Ng14D

Table 3

Regional allometric models for the Congo basin forests including tree diameter (D in cm), mean stem wood specific gravity (WSG in g cm^{-3}), total tree height (H in m), crown radius (CR in m), and the environmental stress variable (E), to estimate tree above-ground biomass (AGB in kg). The AIC, BIC, variance explained (R^2), and Root Mean Square Error (RMSE in kg) computed on back-transformed data, and coefficient estimates (a, b, c, d, and e) and confidence interval at 2.5% and 97.5% are reported for all tested models.

		Performance criteria				Coefficient estimates [confidence interval]				
	Model	AIC	BIC	R^2	RMSE	a	b	c	d	e
(1) Fitting the general models of Chave et al. (2014) and including WSG, D and H in the AGB predictors										
1	log(AGB) ~ a + b × log(WSG * D^2 * H)	164.1	178.3	0.973	2986	−2.9313 [−3.05; −2.813]	0.9891 [0.978; 1]	–	–	–
2	log(AGB) ~ a + log(WSG * D^2 * H)	165.8	175.3	–	3063	−3.046 [−3.064; −3.028]	–	–	–	–
3	log(AGB) ~ a + b × log(WSG) + c × log(D) + d × log(H)	43.9	67.5	0.977	2934	−2.1099 [−2.299; −1.921]	1.0788 [1.018; 1.14]	2.21 [2.165; 2.256]	0.5061 [0.423; 0.589]	–
4	log(AGB) ~ a + b × log(WSG) + log(D^2) + c × log(H)	120.5	139.5	0.973	2896	−2.378 [−2.567; −2.189]	1.0515 [0.988; 1.115]	0.8146 [0.763; 0.866]	–	–
5	log(AGB) ~ a + b × log(WSG) + c × log(D^2 * H)	165.6	184.6	0.973	3007	−2.904 [−3.047; −2.762]	1.0109 [0.947; 1.075]	0.9878 [0.976; 1]	–	–
6	log(AGB) ~ a + log(WSG) + b × log(D^2 * H)	163.7	178	0.973	2995	−2.9138 [−3.044; −2.784]	0.9881 [0.977; 1]	–	–	–
7	log(AGB) ~ a + b × log(WSG) + log(D^2 * H)	167.8	182	0.974	3064	−3.0454 [−3.047; −3.003]	1.0011 [0.938; 1.065]	–	–	–
(2) Testing the importance of H, i.e., comparing the performance of models with and without H										
8	log(AGB) ~ a + b × log(WSG) + c × log(D)	175.3	194.3	0.973	3230	−1.1883 [−1.312; −1.064]	1.1559 [1.092; 1.22]	2.4344 [2.405; 2.463]	–	–
9	log(AGB) ~ a + b × log(WSG) + log(D^2)	768.4	782.6	0.926	3484	0.5536 [0.494; 0.613]	1.2731 [1.182; 1.364]	–	–	–
10	log(AGB) ~ a + log(WSG) + c × log(D)	195.8	210	0.972	3014	−1.3143 [−1.428; −1.2]	2.443 [2.414; 2.472]	–	–	–
11	log(AGB) ~ a + log(WSG) + log(D^2)	800.8	810.3	–	3554	0.391 [0.365; 0.417]	–	–	–	–
12	log(AGB) ~ a + b × log(WSG) + c × log(D) + d×(log(D))^2 + e×(log(D))^3	160.4	188.8	0.973	2817	0.0535 [−2.747; 2.854]	1.1523 [1.089; 1.216]	1.0937 [−1.19; 3.377]	0.4418 [−0.167; 1.05]	−0.0456 [−0.099; 0.008]
(3) Substituting H by the environmental stress of the site										
13	log(AGB) ~ a + b × log(WSG) + c × log(D) + d×(log(D))^2 + e × E	159.6	188	0.973	2820	−2.3027 [−2.858; −1.747]	1.1599 [1.096; 1.224]	3.0484 [2.754; 3.343]	−0.0807 [−0.119; −0.042]	0.3197 [−0.01; 0.649]
(4) Including crown dimensions (CR = crown radius) in the AGB predictors										
14	log(AGB) ~ a + b × log(WSG) + c × log(D) + d × log(H) + e × log(CR)	−20.1	8.3	0.979	2743	−1.9129 [−2.101; −1.725]	1.0432 [0.984; 1.102]	2.0583 [2.002; 2.115]	0.5124 [0.433; 0.592]	0.2057 [0.157; 0.255]
15	log(AGB) ~ a + b × llog(WSG) + log(D^2)+ c × log(H) + d × log(CR)	−18	5.7	0.978	2694	−1.9266 [−2.115; −1.739]	1.0332 [0.975; 1.092]	0.5644 [0.503; 0.626]	0.2377 [0.2; 0.275]	–
(5) Substituting H by CR, i.e., comparing the performance of models with H and with CR										
16	log(AGB) ~ a + b × log(WSG) + c × log(D) + e × log(CR)	124.6	148.3	0.974	3054	−0.9858 [−1.118; −0.854]	1.1224 [1.059; 1.185]	2.2898 [2.242; 2.338]	0.1998 [0.146; 0.253]	–

Table 4
Comparison of the regional model performance across sites. RMSE (in kg) and mean relative bias (in brackets, in %, and significance according to *t*-test) were computed for each site separately on back-transformed predictions for the 16 regional models (Table 3). Significance levels correspond to : *** for $P < 0.001$, ** for $P < 0.01$, * for $P < 0.05$, and ns for not significant. Unbiased AGB estimates at site-level are shown in bold. Number of trees and mean AGB are given for each site. Sites are ordered from West to East.

Model	RMSE (bias and significance)					
	1. EqG (n = 109, AGB = 4086 kg)	2. Gab (n = 178, AGB = 5543 kg)	3. Cam (n = 132, AGB = 6124 kg)	4. CAR (n = 143, AGB = 4163 kg)	5. Con (n = 141, AGB = 5707 kg)	6. DRC (n = 142, AGB = 5511 kg)
(1) Fitting the general models of Chave et al. (2014) and including WSG, D and H in the AGB predictors						
1	8260 (39.2***)	6805 (19***)	**3552 (6.3 ns)**	**3506 (4.2 ns)**	**3019 (−4.3 ns)**	6950 (−24.8***)
2	8904 (42.4***)	7165 (21.8***)	**3385 (8.7 ns)**	3660 (6.2*)	**2908 (−2.2 ns)**	6732 (−23.6***)
3	9411 (39.7***)	6587 (17.1***)	**4089 (2.7 ns)**	4338 (7.8*)	**2873 (−1.8 ns)**	4890 (−12.7***)
4	8325 (39.3***)	6887 (19***)	**3612 (6.1 ns)**	**3517 (4ns)**	**3002 (−4.4 ns)**	6959 (−25***)
5	8273 (39.1***)	6837 (18.9***)	**3589 (6.2 ns)**	**3508 (4.1 ns)**	**3016 (−4.4 ns)**	6961 (−25***)
6	8912 (42.4***)	7172 (21.8***)	**3387 (8.7 ns)**	3662 (6.2*)	**2907 (−2.2 ns)**	6731 (−23.6***)
7	7513 (33.3***)	6359 (13.1*)	**4331 (0.2 ns)**	**3484 (0.8 ns)**	3206 (−7.8*)	6742 (−24.5***)
(2) Testing the importance of H, i.e.,comparing the performance of models with and without H						
8	10,540 (40.1***)	6329 (14.8**)	**5054 (−0.7 ns)**	5581 (11.7*)	**4249 (0.7 ns)**	**4762 (2.7 ns)**
9	**3978 (4.9 ns)**	6842 (−13.7***)	8900 (−25.7***)	4446 (−15.5***)	6923 (−25***)	6444 (−24.3***)
10	9800 (38.7***)	5647 (13.9**)	**4663 (−0.7 ns)**	5357 (12.5*)	**4029 (0.4 ns)**	**4664 (4.1 ns)**
11	**3661 (2ns)**	7015 (−15.6***)	8806 (−26.5***)	4592 (−15.2***)	7462 (−26.4***)	6606 (−23.3***)
12	8057 (36.2***)	5832 (12*)	**5910 (−2.9 ns)**	4428 (9.5*)	**2596 (−2.7 ns)**	**4358 (0ns)**
(3) Substituting H by the environmental stress of the site						
13	8183 (32***)	5770 (9.5*)	**5573 (−1.9 ns)**	4734 (10*)	**2806 (−0.8 ns)**	**4424 (0.4 ns)**
(4) Including crown dimensions (CR = crown radius) in the AGB predictors						
14	8974 (41.5***)	5917 (13.3*)	**3683 (5.1 ns)**	4342 (8.8*)	**2915 (−3.6 ns)**	4489 (−11***)
15	8596 (40.6***)	5832 (12.1*)	**3657 (5.1 ns)**	4143 (7.7*)	**2794 (−4.9 ns)**	4723 (−12.9***)
(5) Substituting H by CR, i.e., comparing the performance of models with H and with CR						
16	10,030 (41.6***)	5684 (11.1*)	4610 (1.2 ns)	5602 (12.7**)	**4339 (−0.9 ns)**	**4445 (4.7 ns)**

Table 5
Comparison of the local model performance across sites (pairewise validation). RMSE (in kg) and mean relative bias (in brackets, in %, and significance according to *t*-test) were computed for each site separately on back-transformed predictions for two local site-specific models (3 and 12, Table 3). Significance levels correspond to : *** for $P < 0.001$, ** for $P < 0.01$, * for $P < 0.05$, and ns for not significant. Unbiased AGB estimates at site-level are shown in bold. Number of trees and mean AGB are given for each site. Sites are ordered from West to East.

		RMSE (bias and significance)					
		1. EqG (n = 109, AGB = 4086)	2. Gab (n = 178, AGB = 5543 kg)	3. Cam (n = 132, AGB = 6124 kg)	4. CAR (n = 143, AGB = 4163 kg)	5. Con (n = 141, AGB = 5707 kg)	6. DRC (n = 142, AGB = 5511 kg)
(1) Including WSG, D and H in the predictors of tree AGB							
Model 3 calibrated in	**1. EqG**	–	6669 (−9.9*)	7222 (−20***)	4690 (−20.6***)	7418 (−27.5***)	9453 (−42.5***)
	2. Gab	6775 (27.5***)	–	**4878 (−5.2 ns)**	**3561 (0.1 ns)**	3282 (−10***)	5872 (−19.1***)
	3. Cam	8196 (34.9***)	6622 (15.5**)	–	**3518 (0.7 ns)**	3115 (−7*)	7111 (−27.5***)
	4. CAR	7953 (33.6***)	6324 (12.8*)	**4339 (−0.4 ns)**	–	2873 (−7*)	6147 (−21.5***)
	5. Cgo	11,890 (50.4***)	8104 (25.5***)	4077 (9.2 ns)	5586 (14.8***)	–	**4338 (−6.1 ns)**
	6. DRC	16,797 (74.9***)	12,149 (45.7***)	5459 (25.8**)	8370 (30.5***)	8877 (21.6***)	–
(2) Including WSG and D in the predictors of tree AGB							
Model 12 calibrated in	**1. EqG**	–	7799 (−15.4***)	10,098 (−26.5***)	5415 (−16.6***)	10,227 (−27.4***)	7547 (−25.8***)
	2. Gab	8821 (32.6***)	–	**5176 (−5.3 ns)**	**4742 (7.4 ns)**	**3285 (−4.1 ns)**	**4472 (−1 ns)**
	3. Cam	12,207 (54.3***)	6972 (26.7***)	–	7196 (25.3***)	6451 (11.7**)	5886 (16.9**)
	4. CAR	6009 (29.7***)	**6027 (6.8 ns)**	**7264 (−7.6 ns)**	–	4759 (−8.2*)	**4746 (−6.2 ns)**
	5. Cgo	9614 (44.4***)	6631 (18.5***)	**5755 (2.3 ns)**	5154 (14.8***)	–	**4533 (4.6 ns)**
	6. DRC	8270 (46.9***)	6995 (20.7***)	**6878 (4.2 ns)**	4754 (16.1***)	**3951 (3.4 ns)**	–

and Ng14DH, without and with total tree height in the AGB predictors. Surprisingly, the most recent pantropical model including the stress variable (Ch14DE) provided less biased AGB estimates than the model including tree height in the AGB predictors (Ch14DH). Finally, similar but accentuated results were retrieved when only considering large trees (Figs. 2 and S2), specifically absolute bias and RMSE increased strongly when only considering large trees (Table S2).

4. Discussion

In this study, using the dataset assembled in the PREREDD+ project, we tested whether central African forests are really different from other tropical forests with respect to biomass allometry, and further examined the regional variation in tropical tree allometry across the Congo basin forests that are of extreme importance for forest management and carbon storage.

4.1. A moist forest allometry for most Congo basin forests

Pantropical models should be evaluated prior to their use, since huge deviations were locally reported, e.g. in central Amazon (Chambers et al., 2001) for the earlier pantropical equations developed

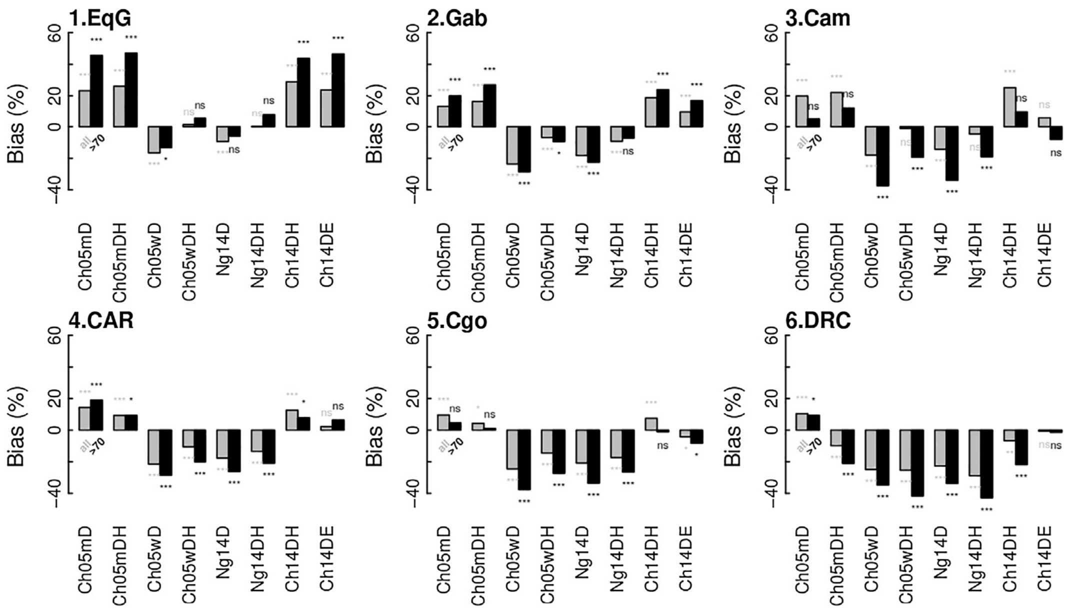

Fig. 2. Mean value and significance of the relative bias (in %) in AGB predictions at the tree level from the pantropical equations developed by Chave et al. (2005) for moist forests (including in the predictors, wood specific gravity and tree diameter, Ch05mD, and additionally total tree height, Ch05mDH) and wet forests (including wood specific gravity and tree diameter, Ch05wD, and additionally height, Ch05wDH), and by Chave et al. (2014) for all tropical forests (including wood specific gravity, tree diameter, and height, Ch14DH, or the environmental stress variable, Ch14DE), and from the local equations developed by Ngomanda et al. (2014) in Gabon (including wood specific gravity and tree diameter, Ng14D, and additionally height, Ng14DH). Prediction tests were performed at the site level for all sampled trees (in grey) and separately for large trees (diameter $>$ 70 cm, in black). Significance levels correspond to : *** for $P < 0.001$, ** for $P < 0.01$, * for $P < 0.05$, and ns for not significant. Sites are ordered from West to East.

by Brown et al. (1989), and in Indonesia (Basuki et al., 2009), in Colombia (Alvarez et al., 2012), in southwestern Amazon (Goodman et al., 2013) and in Gabon (Ngomanda et al., 2014) for the pantropical equations developed by Chave et al. (2005). The most recent pantropical equations (Chave et al., 2014) have not previously been evaluated in central Africa. Here, we found that the pantropical equations developed for moist forests (Chave et al., 2005) provided biased but reasonable estimates of tree AGB in most sites, except in the wettest site, *i.e.*, coastal evergreen forests in Equatorial Guinea, which showed a wet forest allometry, and where pantropical equations developed for wet forests (Chave et al., 2005) provided better estimates. In the evergreen forests further inland, sampled in Gabon, trees tended to present an intermediate allometry between wet and moist forests. However, using the pantropical equations for moist forests (Chave et al., 2005) seemed preferable, and even better than the most recent pantropical equations including H in the AGB predictors (Chave et al., 2014). The good performance of the most recent pantropical equations including E as a proxy of the H-D relationship (Chave et al., 2014) has to be noted, and the use of this model can be recommended in the Congo basin forests.

Despite the significant deviation already observed in Gabon by Ngomanda et al. (2014) and here in Equatorial Guinea, most Congo basin forests showed a moist forest allometry, as previously reported in southeastern Cameroon (Fayolle et al., 2013) and in Yangambi, DRC (Ebuy et al., 2011). When considering the climatic thresholds used by Chave et al. (2005), most of the Congo basin forests can be considered as moist forests, *i.e.*, forests with a marked dry season, from one to 4 months, and sometimes with a semi-deciduous canopy, and corresponding to 1500–3500 mm per year in rainfall (Chave et al., 2005). In contrast, high-rainfall lowland wet forests, with rainfall greater than 3500 mm per year and no seasonality (Chave et al., 2005), are restricted to a small area along the gulf of Guinea, and montane cloud forests are restricted to small areas along the Volcanic Line of Mount Cameroon and along the Albertine rift. In this study, montane forests were not sampled, and have never been destructively sampled for biomass and allometry in tropical Africa (Loubota Panzou et al., 2016). The relatively dry and seasonal climate across the Congo basin forests has been recognized for long and invoked to explain the low species richness in comparison to the Neotropics (Parmentier et al., 2007). However, the huge cloud cover over coastal forests and most Gabonese forests explains forest evergreenness and the tendency for a wet forest allometry, though rainfall is far below the accepted thresholds for wet forests (3500 mm). The link between evergreen- or deciduous-ness and tree allometry is, however, not straightforward.

Since specific and common species were sampled in each site, it might be worth exploring between-site variation for shared species in order to disentangle floristic and environmental control on tree allometry (Fayolle et al., 2016). Specific equations could also be developed for the species/genera well represented in the combined dataset, as done for most commercial species/genera in Dipterocarp forests of East Kalimantan, Indonesia (Basuki et al., 2009). Specifically, the allometry of *Gilbertiodendron dewevrei*, that forms almost pure stands, could be further examined, and compared to the results of Umunay et al. (2017) obtained with a very different approach (randomized branch sampling). However, it should be kept in mind that developing species- or genus-specific biomass allometries across the tropics will not be possible, and that multi-species allometries are needed for forest biomass and carbon monitoring.

Interestingly, the pantropical equation of Chave et al. (2014) substituting height-diameter allometry by the environmental stress of the site provided relatively reliable AGB estimates, for all sites but the one in Equatorial Guinea that, again, appeared divergent. Even on the reduced environmental gradient covered here, *i.e.*, sampling did not include any dry forests or woodlands, the environmental stress variable seemed to satisfyingly determine height-diameter allometry, in contrast with earlier results in Cameroon (Fayolle et al., 2016).

4.2. *A regional allometry for the Congo basin forests*

Using this unique dataset as a calibration dataset, we first fitted the general allometric model form retained by Chave et al. (2014):

$$AGB_{est} = 0.055 \times (WSG \times D^2 \times H)^{0.989} \qquad \text{(regional model 1)}$$

We found that the model, relatively simple in its form, provided a relatively good fit to the data, and more importantly, we found that the estimated coefficients (including the correction factor) for the Congo basin forests were quite close to the pantropical coefficients. This result is a strong argument for a universal approach to estimate biomass and carbon stocks as highlighted by Vieilledent et al. (2012) in Madagascar and in line with the development of pantropical allometric equations (Brown et al., 1989; Chave et al., 2014, 2005). The strong convergence in tropical tree allometry demonstrated in Madagascar (Vieilledent et al., 2012), in Indonesia (Rutishauser et al., 2013), in Cameroon (Fayolle et al., 2013) can be interpreted as strong (and similar) constraints on the architecture of self-supporting plants, as discussed in Chave et al. (2014). Because uncertainty computation is key in the IPCC guidelines, the variance-covariance matrix of the coefficients needed to compute exact confidence intervals around predictions are given for the retained models (Table S3).

Though estimated coefficients were close to 1 for wood specific gravity and close to 2 for tree diameter, including specific scaling coefficients for each predictor significantly improved the model, arguing for a more complex, or flexible, allometry than the simple power-law model proposed by Chave et al. (2014). The biological relevance of complex allometries have been questioned in detail (Sileshi, 2014) though it is generally recognized that complex allometric models outperform simple power models (Picard et al., 2015). For future estimation and monitoring of biomass/carbon stocks in the Congo basin forests, we recommend the following regional model:

$$AGB_{est} = 0.125 \times WSG^{1.079} \times D^{2.210} \times H^{0.506} \qquad \text{(regional model 3)}$$

Including total tree height in the predictors only slightly improved the AGB estimates, in contrast to common sense and previous results (Feldpausch et al., 2012; Vieilledent et al., 2012). More importantly, between-site variation remained in the model residuals, in contrast to our expectation that total tree height captures most between-site variation as proposed by Ketterings et al. (2001) and demonstrated by Chave et al. (2014, 2005) across the tropics. Since tree height is almost never available in large-scale forest inventory data, and extremely difficult to measure in tropical forests (Larjavaara and Muller-Landau, 2013), the following regional model only including tree diameter and wood specific gravity in the AGB predictors is also recommended:

$$\begin{aligned} AGB_{est} = \exp[&0.046 + 1.156 \times \log(WSG) + 1.123 \times \log(D) \\ &+ 0.436 \times (\log(D))^2 - 0.045 \times (\log(D))^3] \qquad \text{(regional model 12)} \end{aligned}$$

Examining the performance of general models (either pantropical or regional) *versus* local site-specific models, we found only little advantage of using local models, except in Equatorial Guinea, were tree allometry deviated from the regional pattern. Inconsistent sites were also reported by Chave et al. (2014), but the relatively old data could not allow tracing back the inconsistencies.

Though the RMSEs were comparable, our regional models showed smaller bias, and should therefore be preferred to pantropical models. With almost an equal number of trees in all diameter size classes and a good representation of size and wood specific gravity in all sites, our sampling is appropriate for establishing allometric equations (Picard et al., 2012), but not representative of forest stands (Goodman et al., 2013). An interesting perspective would be to examine error propagation at plot level, using inventory data (Ploton et al., 2016) or typical diameter distribution (Chave et al., 2014). Indeed, pantropical models provided biased estimates at the tree level though the goal of these models is to make predictions on thousands or millions of trees across large landscapes, so that the errors detected at the site level based on a sample of 100 trees cancelled out based on much larger samples.

4.3. A low contribution of tree height and crown dimensions

Here, for the Congo basin forests, we found that tree height and crown dimensions only had a minor contribution on tree AGB variation, confirming the tremendous importance of tree diameter and wood specific gravity (Chave et al., 2005), while elsewhere, using mean wood specific gravity at the site/plot level has been shown to be acceptable (e.g. Molto et al., 2013 in French Guiana). When wood specific gravity values are missing for some tree species, default value of $0.58\,g\,cm^{-3}$ with an error of 10% is often used (Chave et al., 2004). Here a mean of $0.582\,g\,cm^{-3}$ was reported across species. Despite the efforts made to sample species with contrasted wood specific gravity in each site, the absence of extremely dense-wooded species, e.g. sinkers, can be noted. However, the new information now available for tropical tree species of the Congo basin are valuable, with this new data for 55 African species and including yet unsampled species in the global database (Chave et al., 2009; Zanne et al., 2009), such as *Duboscia macrocarpa*.

Including tree height in the predictors did not necessarily improve AGB estimates, as already reported in southwestern Amazonia, where greater crown mass has been demonstrated to compensate for shorter tree stature (Goodman et al., 2013). In contrast to our expectations, tree height did not capture most between-site variation and crown dimensions were not so important, even for the largest trees. We, however, detected strong and significant between-site variation in both height-diameter and crown-diameter allometries across the Congo basin, in contrast with Antin et al. (2013) who reported little variation in crown allometries. Specifically, in the transition forests of DRC, trees tended to be shorter in height as already reported by Kearsley et al. (2013) in Yangambi, but to develop extremely large crowns, and thus reaching huge AGB though shorter in height, consistent with the moist forest allometry reported by Ebuy et al. (2011). This compensation between tree height and crown size has been well described by Goodman et al. (2013) in southwestern Amazonia. Here, we found that crown radius was only a minor determinant of AGB variation (but significant), and more surprisingly, between-site variation remained when tree height and crown radius were both included in the AGB predictors. Crown radius moreover appeared less effective (0.87%) than total tree height (2.05%) to estimate tree AGB in the Congo basin forests, while in southwestern Amazonia crown radius explained much more variation (10.5%) in AGB than total tree height (6.0%), on a rather limited dataset of 51 trees. The moderate importance of crown for AGB estimation demonstrated here is perhaps related to the lower biomass allocation to the crown (32% ± 1.3% [mean ± SE] in Equatorial Guinea, 33% ± 1.1% in Gabon, 35% ± 1.5% in Cameroon, 27.5% ± 0.9 in CAR, 34.2% ± 1.4% in Congo, and 36.9% ± 1.6% in DRC), much more comparable to the 35.6% reported by Ploton et al. (2016) in comparison to the nearly half of the biomass (44% ± 2%) reported by Goodman et al. (2013). Similar to Ploton et al. (2016), we also retrieved an increase in biomass allocation to crown with tree size with a mean of 27.3% for trees < 30 cm in diameter and up to 46.3% for trees ≥ 120 cm, but the importance of crown characteristics (dimensions or mass) for estimating tree AGB needs further investigations. The difficulties associated with collecting crown dimension data in the field has also to be kept in mind, though emerging techniques, such as high-resolution remote sensing, offer new possibilities to derive crown measurements for emergent and canopy trees, for which biomass estimates and uncertainties are the largest.

5. Conclusion

The choice of the allometric model is still a critical step in the estimation of biomass and carbon stocks contained in tropical forests. Here, we validated the use of pantropical equations in the Congo basin, specifically the model including the E variable as a proxy of the H-D relationship, and developed regional allometric equations for the lowland terra firme forests. Except in Equatorial Guinea were local models should be preferred, we recommend to use our regional models 3 and 12, and otherwise pantropical models, for the estimation and monitoring of biomass/carbon stocks contained in the second largest contiguous block of tropical forests worldwide. The results reported here have strong practical implications for accurate forest biomass/carbon monitoring and the successful implementation of climate change mitigation strategies, such as the REDD + .

Declarations of interest

None.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.030.

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