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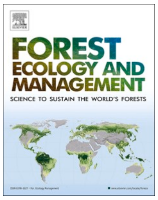

Tropical tree allometry and crown allocation, and their relationship with species traits in central Africa

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ABSTRACT

Common allometric patterns have been reported across the tropics and good performance on independent data was retrieved for the most recent pantropical model predicting tree aboveground biomass (AGB) from stem diameter, wood density and total height. General models are undoubtedly useful for the estimation and monitoring of biomass and carbon stocks in tropical forests, however specific allometry, allocation, and traits, are at the core of many models of vegetation dynamics, and there is lack of such information for some regions and species. In this study, we specifically evaluated how size-dependent changes in above-ground biomass and biomass allocation to crown relate to other allometric and life-history traits for tropical tree species. We gathered destructive data available in eight terra firme forest sites across central Africa and the combined dataset consisted of 1,023 trees belonging to 54 tropical tree species phylogenetically dispersed, with only two congeneric species. A huge body of field and laboratory measurements was used for computing AGB and crown mass ratio (CMR) at the tree level, and to derive key allometric traits at the species level. For the latter, species-specific relationships between tree diameter and total height, crown exposure to light, wood density, and bark thickness were fitted for 50 species. Our results show interspecific variation in the relationships relating tree diameter to both AGB and CMR, and including species traits in a multi-specific AGB model confirmed that interspecific variation in biomass allometry is primarily determined by species wood density. We also showed that the allocation of biomass to crown increases linearly with tree diameter for most species, and that interspecific variation in the CMR model is associated with the species dispersal mode and maximum height. Trait covariations among our set of tropical tree species widespread and/or locally abundant in central Africa, revealed a continuum between large-statured species, which tended to be light-demanding, deciduous and wind-dispersed, and species with opposite attributes. Information on allometry, allocation, and traits provided here could further be used in comparative ecology and for parameterizing dynamic and succession models. Also importantly, the species-specific AGB models fitted for major tree species, including most timber species of central Africa, will help improve biomass estimates.

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1. Introduction

Accurate assessments of biomass and carbon stocks in tropical forests underpin policies that aim to mitigate carbon dioxide emissions such as the UN-REDD + program and the recommendations of the Intergovernmental Panel on Climate Change (Gibbs et al., 2007) and using allometric equations to predict the aboveground biomass (AGB) of tropical trees is a cost-effective and accurate approach (Chave et al., 2004, 2014). In the last decades, general multi-specific allometric models have been updated, with the pantropical model of Chave et al. (2014) refining the previously developed models (Brown et al., 1989; Chave et al., 2005). The most recent pantropical model of Chave et al. (2014) has been shown to perform well at the tree level, on independent dataset of destructive AGB in a peat swamp forest in Indonesia (Manuri et al., 2014) and in six terra firme forest sites distributed across central Africa (Fayolle et al., 2018).

After tree diameter, species wood density and total tree height are both important AGB predictors for tropical trees (Brown et al., 1989; Chave et al., 2014; 2005; Feldpausch et al., 2011; Van Breugel et al., 2011), respectively expected to explain between-species and between-site variations (Ketterings et al., 2001). The inclusion of height has indeed been shown to offset allometric variation across forest types (Chave et al., 2005), and when not available locally, height can possibly be predicted from tree diameter using a local or a regional equation (Feldpausch et al., 2011) or using a general equation including an environmental stress variable (Chave et al., 2014). In addition to the classical AGB predictors, the use of crown information has recently received attention (Goodman et al., 2014; Fayolle et al., 2018), and its importance to predict AGB has been notably explained by ontogenic and/or size-related changes in biomass allocation to crown (Ploton et al., 2016). Besides wood density averaged at species (Molto et al., 2013) or even at genus level (Slik, 2005), interspecific variation in tropical tree allometry and allocation have not been deeply explored. Because it is extremely costly, time-consuming, and difficult to collect and assemble biomass data at the tree and species levels (Picard et al., 2012), many questions about the usefulness of generic models remain unanswered. Still, it is unclear to what extent data on biomass allometry should be pooled or separated according to morphological, phylogenetic and/or phenological characteristics of species (Paul et al., 2016). In the latter study, specific allometric equations have been developed for species grouped into a few plant functional types covering contrasted biomes and ecoregions across Australia. It has also been argued that species-specific models are especially needed when the gains in accuracy at the stand level are high, which is true for high-value monocultures (Paul et al., 2016) or for monodominant species such as *Gilbertiodendron dewevrei* in central Africa, and for which a specific allometry has been developed (Umunay et al., 2017). Specific allometric relationships have been developed for species grouped at genus level in a Dipterocarp forest of south-eastern Asia (Basuki et al., 2009) or by family and wood density in peat swamp forests in Indonesia (Manuri et al., 2014). In the latter study, it has to be noted, however, that the multi-specific pantropical model showed similar performance as the local models.

Interspecific variation in tropical tree allometry has been demonstrated in the early stages (seedlings and saplings) and related to life-history strategy and traits in Panama (King, 1990, 1996). The allometric specialization of light-demanding species was found to be associated with biomass allocation toward efficient height growth, and that of understory species with the maximization of light interception and the persistence in the shaded understory (King, 1990). Light-demanding species are indeed generally more exposed to light at 10 cm diameter (Sheil et al., 2006) because of greater height, as reported in Bolivia (Poorter et al., 2006) and in northern Congo (Loubota Panzou et al., 2018). It is thus important to both consider allometry and allocation in evaluating the adaptive significance of interspecific variation. In addition, grouping tropical tree species into meaningful groups of tree species is not straightforward (Swaine and Whitmore, 1988) and only a few plant functional types are generally recognized in Dynamic Global Vegetation Models (DGVM, Fisher et al., 2018), generally two groups, evergreen *vs* deciduous tropical trees. In the successional model TROLL (Maréchaux and Chave, 2017), up to 12 tropical plant functional types are recognized, and for each of them, the tree geometry is modelled explicitly with specific allometric relationships relating tree diameter, to height, crown radius and depth. Though plant functional types are at the core of many models of vegetation dynamics or of forest succession, the lack of information on allometry, allocation and traits, for some species and regions hampers models predictions and this is particularly true for central Africa which is a largely under-sampled region.

In this study, we evaluated how size-dependent changes in aboveground biomass and biomass allocation to crown relate to other allometric and life-history traits for tropical tree species. We addressed three questions. First, to what extent biomass allometry and allocation vary among a set of tropical tree species? Using published data of destructive biomass in central Africa, we were able to provide new information on biomass allometry and allocation for 54 tropical tree species widespread and/or locally abundant, and covering a variety of genera and families. Second, is interspecific variation in allometry and allocation related to key traits? We notably tested the hypothesis of contrasted biomass allometry and allocation, between evergreen and deciduous species, but besides these two groups, we further investigated interspecific variation in response to life-history traits extracted from literature and to allometric traits newly developed for 50 species, and characterizing species architecture, light requirement, the wood economics spectrum, and adaptation to fire (Table 1). Third, which allometric or life-history traits can be used in multi-specific allometry and allocation models as a surrogate of interspecific variation? We notably tested the hypothesis that wood density explains interspecific variation in biomass allometry (Ketterings et al., 2001) and that light requirement explains interspecific variation in biomass allocation to crown (King, 1990).

2. Material and methods

2.1. Study sites

Destructive biomass data were available for more than 1,000 trees sampled across central Africa in eight sites (Fig. 1) which includes the six sites sampled in the PREREDD+ project (sites #1–2 and #5–8 on the map, Fayolle et al., 2018), and two sites sampled earlier, the Zadié site in Gabon (#3, Ngomanda et al., 2014) and the Mindourou site in Cameroon (#4, Fayolle et al., 2013). In each site, the sampling covered a

Table 1
Characteristics of the life-history and allometric traits selected, description and main references. The abbreviations corresponds to Ani.: Animal, Unas.: Unassisted and Wind: Wind dispersal for the dispersal mode; to Dec.: Deciduous and Ev.: Evergreen species for the leaf phenology; and to P: Pioneer, NPLD: Non-Pioneer Light Demander, and SB: Shade Bearer for the regeneration guild.

Trait	Unit	Function	Reference
Life history traits			
Dispersal mode (Ani., Unas., Wind)		Dispersal	
Leaf phenology (Dec., Ev.)		Drought tolerance	
Regeneration guild (P, NPLD, SB)		Light requirement, succession	Hawthorne (1995)
Allometric traits			
Height at 10 cm and at max. diameter	m	Architecture, structure	Poorter et al. (2006)
Crown Exposure Index at 10 cm diameter		Light requirement	Sheil et al. (2006)
Trunk bark thickness at 10 cm diameter	cm	Defense	Pellegrini et al. (2017)
Wood economics spectrum			
Mean wood density	$g.cm^{-3}$	Transport, structure, defense	Chave et al. (2009)

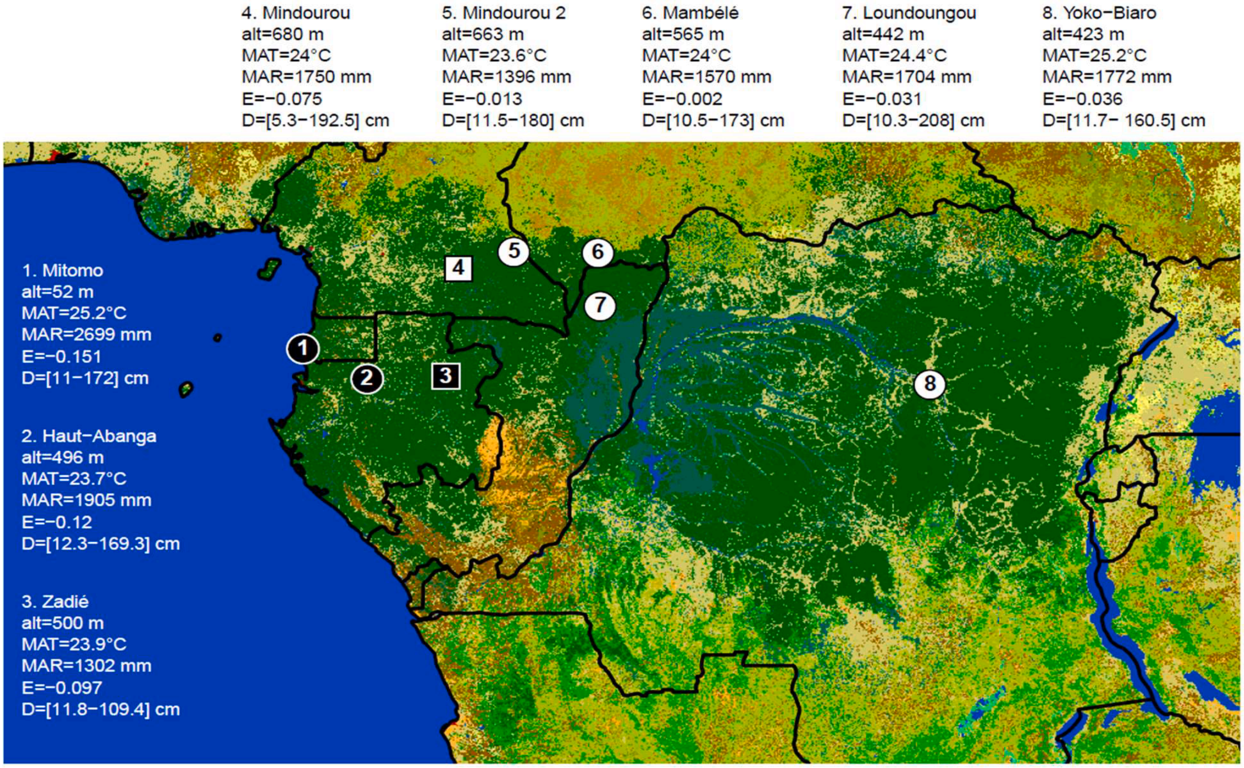

Fig. 1. Location and characteristics of the eight sites in central Africa for which destructive AGB data are available. The base map corresponds to land cover on a spectrum of high (green) to low (orange) tree cover (data downloaded from ESA at 5° x 5° resolution). Altitude (alt, in m) derived from the Shuttle Radar Topography Mission (SRTM, Jarvis et al., 2008), mean annual temperature (MAT, in °C) and mean annual rainfall (MAR, in mm) derived from Worldclim 2 (Fick and Hijmans, 2017), E index of environmental stress derived from Chave et al. (2014), and sampling effort in terms of diameter (D, in cm) range are provided for the eight sites. Symbols distinguish the six sites sampled in the frame of the PREREDD+ project (Fayolle et al., 2018, circles) and the two other sites sampled earlier (Fayolle et al., 2013; Ngomanda et al., 2014, squares). Black and white symbols refer to the color of the text on the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

large number of trees (≥100) and a vast range of diameters and wood density, as recommended by Chave et al. (2004).

We used mean annual rainfall (MAR, in mm.yr^{-1}), mean annual temperature (MAT, in °C), both derived from Worldclim 2 (Fick and Hijmans, 2017), and overall environmental stress of the site (E index proposed by Chave et al., 2014) to determine the range of environmental conditions covered by the eight sites. Except in Mitomo (#1), a coastal site in Equatorial Guinea, at 52 m a.s.l (according to the data from the Shuttle Radar Topography Mission, Jarvis et al., 2008), sites are located between 400 and 700 m a.s.l. Mitomo is also the wettest site with ~ 2700 mm of rainfall and the only site above 2000 mm, the threshold generally recognized for wet evergreen forests (Guan et al., 2015), while the two driest sites, Zadié in Gabon (1,300 mm, #3) and Mindourou 2 in Cameroon (1,400 mm, #5) are just above the 1,000 mm threshold generally recognized for tropical forest. The variation of the E value across the eight sites [-0.15; 0] is restricted compared to the pantropical variation across wet, moist and dry forests, and woodlands [−0.2 and 1], though it has to be noted that the sampled sites covered the wet and moist forests of central Africa (Fayolle et al., 2014).

2.2. Tree measurements

For the computation of AGB, a huge body of measurements is needed in the field on the tree compartments (stump, stem, branches, and a last compartment composed of leaves, flowers and fruits), and also in the laboratory on collected samples. Here, we detailed the measurements of tree diameter (D, over-bark in cm), total tree height (H, in m) and wood density (WD, in g.cm^{-3}), which are classical AGB predictors at the tree level, and also that of the crown exposure index (CEI, dimensionless) and bark thickness (BT, in mm), both used to derive traits at the species level (Table 1).

Prior to tree felling, D at breast height or above deformations was measured with a tape. In the six sites sampled during the PREREDD+ project (sites #1–2 and #5–8), H was measured from two locations at approximately a distance of tree height with a Vertex IV and the CEI was visually estimated based on crown position in the canopy. A CEI value of 1 corresponds to lower understory trees entirely shaded vertically and laterally, of 2 to upper understory trees entirely shaded vertically but with some direct sidelight, of 3 to lower canopy trees partly exposed and partly shaded vertically, of 4 to upper canopy trees exposed vertically but with other crowns laterally, and of 5 to emergent trees. H was measured after felling in Zadié (#3) and not measured at all in Mindourou (#4) and for both sites the CEI data were missing.

After felling, tree compartments were directly weighed (most stems, all branches) in the field and/or estimated from fresh volumes computed from diameter and length measurements (stump, and some stems). For all sites except Zadié (#3), disks or disk portions (including bark) were sampled in all compartments for the conversion of fresh masses and volumes into dry masses, and BT was measured with a caliper at the ends of the inner and outer edges of the bark. In the laboratory, the fresh volume of samples was measured by water displacement, and the dry mass was obtained after several days at 103°C until reaching a constant mass (<1% difference between two measurements with 6 h interval). WD was computed as the ratio of oven-dry mass of the sample on its green volume. For each tree, in order to be comparable with other studies, we computed the average value of WD and BT for the samples collected on the lower part of the trunk, considered to be representative of breast height. For trees for which WD was not available (6% of the dataset, all trees sampled in Zadié (#3) and few other trees due to laboratory problems), we used the species average from the combined dataset, and for the four species for which WD was not available in any other sites, we used the global wood density database (Chave et al., 2009; Zanne et al., 2009) to compute the species average across tropical Africa (Appendix A).

The aboveground biomass (AGB, in kg) of the whole tree was calculated as the sum of the dry biomass of all compartments. For biomass allocation, we used the crown mass ratio (CMR, in %) first proposed by Ploton et al. (2016) and which corresponds to the ratio of biomass in the crown (all branches, leaves, flowers and fruits) over the AGB, multiplied by 100.

2.3. Species selection

Out of the 1,083 trees sampled across the eight sites (Fig. 1), species-level identification was available for 1,074 trees belonging to 86 species. Because we were interested in interspecific variation in biomass allometry and allocation, we retained species with at least five trees sampled for the analyses, resulting in a final dataset of 1,023 trees belonging to 54 species, 52 genera and 19 botanical families (Appendix A), and excluding only 60 trees (5% of the original dataset). The Fabaceae family, which is an important and diverse family in tropical Africa, was largely represented with 318 trees (31%) and 15 species (28%) kept for analyses. So were the Myristicaceae ($n = 145$ trees, $n = 4$ species) and the Meliaceae ($n = 88$ trees, $n = 5$ species) both indicative of moist semi-deciduous forests (White, 1983) that cover vast areas in central Africa (Fayolle et al., 2014).

We extracted information on key life-history traits (Appendix A) from the checklist of Gillet and Doucet (2012) in northern Congo and from the book of Meunier et al. (2015) in Gabon, which were complemented by floras. We specifically gathered information on the dispersal mode with 26 animal-dispersed species, 11 unassisted dispersal, and 17 wind-dispersed; information on leaf phenology with 24 deciduous and 30 evergreen species, and information on species regeneration guild, with 15 pioneer, 21 non-pioneer light demanders and 18 shade bearers (Appendix A).

2.4. Data analyses

All analyses were performed with the R open source environment (R Development Core Team, 2018). For each of the 54 species for which at least five trees were sampled, we regressed the natural logarithm of AGB (in kg) in response to the natural logarithm of tree D (in cm) using Ordinary Least Squares. Response and explanatory variables were log-transformed to linearize the power law relationship. It has indeed been long recognized that power models nicely fit the allometry of a wide range of plants (Niklas, 2006) and the vast majority of biomass equations reviewed for forest species take this simple form, $\log(AGB) = a \log(D) + b$, a being the allometric exponent or scaling coefficient, and b the intercept (see Zianis et al., 2005 for Europe). To ease the use of the species-specific AGB models, the values reported for the coefficients correspond to the back-transformation to the power law model, $AGB = \beta \times D^a$, and estimates of β, the normalization (allometric) constant (Niklas, 2006), include the correction factor which corrects for the bias systematically induced by the log-transformation (Sprugel, 1983). The relationship between biomass allocation to crown and tree D has been less documented (but see Ploton et al., 2016). Based on the visual examination of our observations, we chose to model the CMR (in %) as a linear function of D. The exact same approach using Ordinary Least Squares regressions was applied, without any log-transformation. For both allometry and allocation relationships, t-tests were used to test the difference in model coefficients between evergreen and deciduous species, and Pearson correlation coefficients were used to test for the correlation between the model coefficients.

Next, we fitted models of H, WD, BT, and CEI in response to tree diameter in order to estimate new allometric traits (Table 1) for 50 of the 54 study species due to missing data in some sites, H and CEI were not available in Mindourou (#4) and CEI, WD and BT were not available in Zadié (#3). Ordinary Least Squares regression models were fitted to predict log-transformed H, WD, and BT in response to log-transformed D (Appendix B) whereas ordinal regressions were fitted to predict CEI in response to D following Jucker et al. (2014). The latter was performed using the *ordinal* package (version 2019.4–25). These models were used to extract, for each species, model predictions of H, WD, BT, and CEI at 10 cm diameter (indicating the sapling stage) and predictions of H at the 98th percentile of observed tree diameter (called hereafter maximum diameter, DMAX, and indicating the adult stage). Because the fitted relationships between WD and D were weak (scaling coefficients close to 0 for most species), the average wood density was reported for each species instead of any model prediction. Trait covariations were examined with a Principal Correspondence Analysis (PCA). The latter was performed with the *ade4* package (version 1.7–11) and coefficients of species-specific AGB and CMR models were added as supplementary variables on the correlation circle.

To further explore the variation in biomass allometry and allocation across species and traits, we fitted a set of multi-specific linear mixed models of tree AGB in response to tree D, both log-transformed, and of tree CMR in response to tree D. The traits included in the multi-specific allometry and allocation models (Table 1) corresponds to the height at 10 cm and maximum diameter (*H*10 and HMAX, respectively), the crown exposure index (CEI) and the bark thickness (BT) both estimated at 10 cm diameter, and the qualitative traits from the literature, the dispersal mode (DISP), the leaf phenology (PHENO) and the regeneration guild (RG). The maximum diameter (DMAX) used to compute HMAX was also included in the models. The dataset was restricted to the 981 trees belonging to the 50 species for which all allometric traits could be estimated. The mixed models were fitted using the *lme4* package (version 1.1–21) and random effects were added in the models to account for a species effect. The tested random effect terms were a random intercept and a random slope of the tree D. The best model was selected with a backward elimination of random effects followed by a backward elimination of fixed effects (Zuur et al., 2009) using likelihood ratio tests, AIC and BIC, and performed with the *lmerTest* package (version 3.1–0).

3. Results

3.1. Tree allometry

Benefitting from existing destructive AGB data in eight sites across central Africa, we were able to fit species-specific allometric models for 54 tropical tree species (5–69 trees per species, mean of 19). As expected, we found strong interspecific variation in tree allometry when only considering the bivariate relationships between tree AGB and D (Fig. 2). The coefficients of AGB models varied among the 54 tropical tree species with a mean of 2.45 (± 0.24 standard deviation) found for the scaling coefficient and of 0.31 (± 0.69) for the intercept (Fig. 2B-C). The scaling coefficient tended to be lower in average for evergreen species with a mean scaling coefficient of 2.36 *vs* 2.56 for deciduous, and this difference was significant according to the result of a *t*-test (*P-value* = 0.001). The scaling coefficient also tended to be lower for shade bearers (results not shown), and since the two coefficients are intrinsically related ($r_{Pearson} = -0.71$), the intercept tended to be higher for those species.

3.2. Biomass allocation

We used the crown mass ratio (CMR, %) to depict changes in biomass allocation with tree D. The CMR was highly variable among trees, from 1.2% and up to 84.2%, with a mean of 29.6%, and increased linearly with tree D (Fig. 3). The coefficients of CMR models varied among the 54

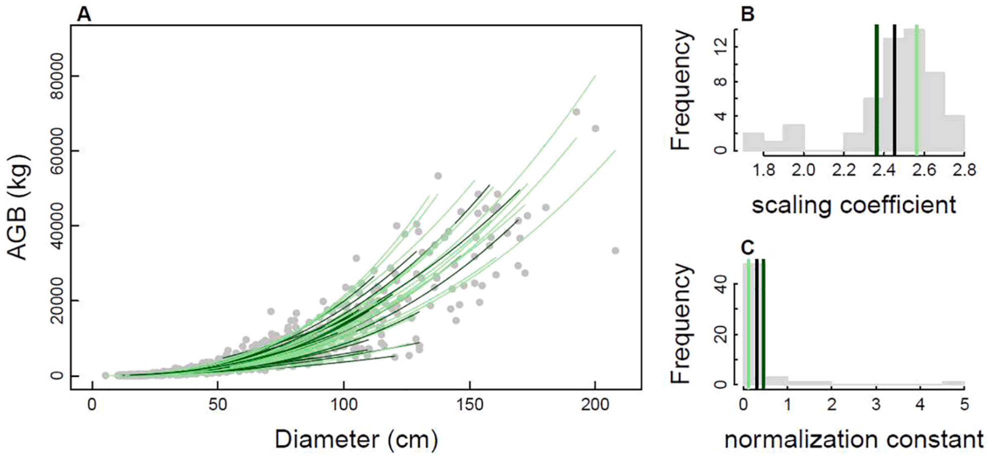

Fig. 2. Interspecific variation in biomass allometry across the 54 tropical tree species destructively sampled in eight sites across central Africa. Species-specific power models relating tree AGB (in kg) and D (cm) are shown for all species (A). One point represents one tree, and fitted lines represent species-specific relationships. The colors indicate the species leaf phenology, deciduous (light green) *vs* evergreen (dark green) species. The frequency distribution of the two model coefficients, scaling coefficient (B) and normalization constant (C), is also given. The vertical lines indicate the mean value of the coefficients across all species (black), and for deciduous species (light green) and evergreen species (dark green), separately. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

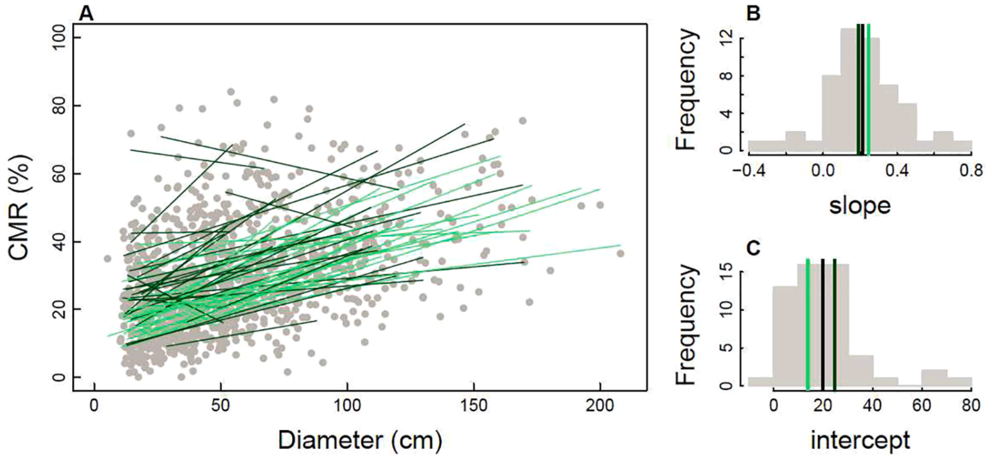

Fig. 3. Interspecific variation in biomass allocation to crown across the 54 tropical tree species destructively sampled in eight sites across central Africa. Species-specific linear relationships relating the tree Crown Mass Ratio (CMR, %) and D (cm) are shown for all species (A). One point represents one tree, and fitted lines represent species-specific relationships. The colors indicate the species leaf phenology, deciduous (light green) *vs* evergreen (dark green) species. The frequency distribution of the two model coefficients, slope (B) and intercept (C), is also given. The vertical lines indicate the mean value of the coefficients across all species (black), and for deciduous species (light green) and evergreen species (dark green), separately. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tropical tree species, the relationships were mostly positive, though for some species, no and also, negative relationships, were also found, with a mean of 0.21 (± 0.2) found for the slope and of 20% (± 15.7) for the intercept (Fig. 3B-C). The intercept tended to be higher in average for evergreen species with a mean of 25% *vs* 14% for deciduous species, and this difference was significant according to the result of a *t*-test (*P-value* = 0.007). Again the two coefficients were related, though the relationship was slight ($r_{\text{Pearson}} = -0.64$). We also examined the relationships between the tree CMR and AGB for each individual species, and the pattern reported by Ploton et al. (2016) of a relatively constant CMR below 10 Mg, and of an increase in CMR with AGB above the 10 Mg threshold, was also retrieved (results not shown).

3.3. Relating traits to allometry and allocation

The PCA performed on quantitative traits highlighted on the first axis (describing 35.8% of variation) a continuum of species between species reaching large stature (both in terms of diameter and height) that were mostly also tall at 10 cm diameter, light-demanding (P or NPLD), deciduous and wind-dispersed, and species with opposite attributes (Fig. 4). The latter species, i.e., with negative scores on PC1, tended to be shade-bearer, evergreen, and to have animal or unassisted dispersal. The second axis (describing 18.7% of variation) was less clearly defined, highlighting a positive correlation between crown exposure (CEI) and bark thickness (BT). Including the coefficients of species-specific allometry and allocation models as supplementary variables on the correlation circle showed that biomass allometry was somehow related to the second axis, while the intercept of species-specific CMR models was related to the first axis describing species stature, and which appeared also related to the dispersal mode (Fig. 4B), the leaf phenology (Fig. 4C) and the regeneration guild (Fig. 4D).

3.4. Modelling AGB and CMR in response to species traits

We then included species traits directly in multi-specific allometry and allocation models. Among the set of tested models potentially including all AGB predictors at the tree level and all traits at the species level, log-transformed AGB was best modelled (lowest AIC and BIC) with equation 1 (Table 2), and the selected response variables were tree diameter (D), wood density computed at species level (WD), height at 10 cm in diameter (*H*10) and regeneration guild (RG). α_j and ε_{ij} were respectively the species-specific and residual random effects. Both effects are fitted as centered normal distributions of fitted variances. α_j depicted the interspecific variation in AGB whereas ε_{ij} depicted the intraspecific variation. Among the fixed effects, besides tree D, WD was the most sensitive effect then followed by two traits related to the species light demand, *H*10 and RG (Appendix C). This suggest that the contrasted allometry between deciduous and evergreen (Fig. 1) is driven

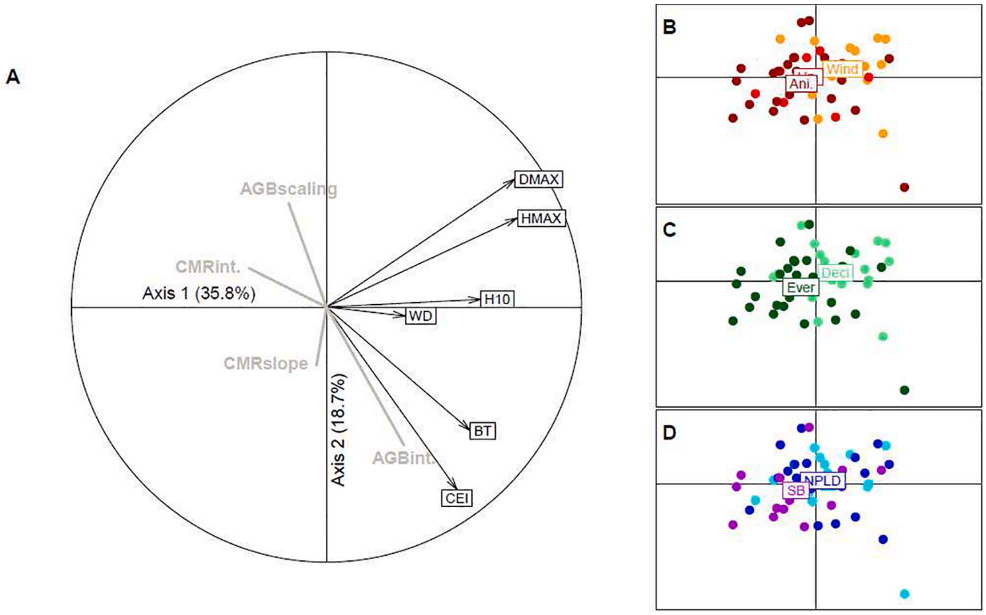

Fig. 4. Trait covariations among the 50 tropical tree species for which trait data were available. The correlation circle resulting from the PCA on quantitative traits is shown in (A) with coefficients of species-specific allocation and allometry models added as supplementary variables (in grey). Species scores were colored according to the dispersal mode (B), the leaf phenology (C) and the regeneration guild (D).

Table 2
Equations and parameters of the multi-specific allometry and allocation models retained. The estimate, standard deviation, degree of freedom and *P-value* are given for the fixed parameters whereas only the standard deviation is given for the random effect terms.

Parameter	Estimate	Std Dev.	df	*P-value*
Allometry model (equation 1)				
$log(AGB_{ij}) = a + b\ log(D_{ij}) + c\ log(WD_j) + d\ log(H10_j) + e_{RG,j} + \alpha_j + \varepsilon_{ij}$				
a	−2.330	0.347	49.0	<0.001
b	2.516	0.013	950.0	<0.001
c	1.064	0.094	41.3	<0.001
d	0.287	0.113	46.9	0.015
$e_{RG=NPLD}$	−0.128	0.057	39.2	0.032
$e_{RG=SB}$	0.031	0.064	41.3	0.636
α_j		0.147		
ε_{ij}		0.246		
Allocation model (equation 2)				
$CMR_{ij} = a + b\ D_{ij} + c\ HMAX_j + d_{DISP,j} + \alpha_j + \varepsilon_{ij}$				
a	38.34	7.96	45.3	<0.001
b	0.20	0.01	947.8	<0.001
c	−0.47	0.16	45.1	0.004
$d_{DISP=unassisted}$	10.90	3.75	42.4	0.006
$d_{DISP=animal}$	1.68	3.01	42.7	0.579
α_j	8.12			
ε_{ij}	11.10			

by other traits (WD, *H*10 and RG). Looking into the effect of the RG, we noted that model intercept was significantly lower for NPLD species than for both the SB and P species, probably because our set of P included extremely dense-wooded species (Appendix A). The standard deviations of α_j and ε_{ij} were respectively 0.147 and 0.246 when fitting a model without any species-trait covariable. Adding the species-specific trait as covariable significantly reduced (73%) the standard deviation of α_j meaning that a great part of the interspecific variation on model intercept was explained adding the fixed parameters.

The crown mass ratio (CMR) was best modelled (lowest AIC and BIC) with equation 2 (Table 2) and the selected response variables were tree diameter, species-specific maximum height (HMAX) and species dispersal mode (DISP). Again, this suggest that the contrasted allocation between deciduous and evergreen (Fig. 2) is driven by other traits (HMAX and DISP). Though the *P-value* associated with the effect of DISP was greater than that of HMAX, the effect of the DISP affected more model predictions (Table 2, Appendix C). The crown mass ratio of the species with unassisted seed dispersal was found to be significantly greater than that of wind-dispersed species and of animal-dispersed species. Species with unassisted dispersal predominantly belong to the Fabaceae (n = 10 species whose diaspore are classified as ballochore, i.e., ejected) with only one other species (*Macaranga barteri*, Euphorbiaceae, whose diaspores are classified as sclerochore, i.e. small diaspores without any specific morphological adaptations). The standard deviations of α_j and ε_{ij} were respectively 10.25% and 11.10% when fitting a model without any species-trait covariable. Adding the species-specific trait as covariable reduced the standard deviation of α_j to 8.12% meaning that about 20% of the interspecific variation on model intercept was explained by HMAX and DISP covariables.

4. Discussion

In accordance with the predictions of the metabolic theory, under certain hypotheses of biomechanical constraints of tree stability and hydraulic resistance in conductive cell networks, tree AGB scales with tree diameter with an exponent of 8/3 (West et al., 1997). The metabolic theory has been hotly debated, specifically its general nature and its underlying assumption of invariant scaling coefficient (Zianis and Mencuccini, 2004; Muller-Landau et al., 2006). Here, the scaling coefficient of species-specific AGB models varied across species, with a mean of 2.45 (± 0.24), only slightly different from the theoretical average of ~ 2.67 (West et al., 1997). While the values of the scaling coefficient was found to vary between 2 and 3 among European trees (Zianis and Mencuccini, 2004), here, for a few species with limited sampling (n ≤ 11 trees) the value of the scaling coefficient was slightly below 2. We observed strong interspecific variation in scaling coefficient, however, other AGB predictors commonly used in multi-specific models were not included, notably wood density and height (Chave et al., 2005, 2014), and also crown dimensions (Goodman et al., 2014; Fayolle et al., 2018) and mass (Ploton et al., 2016) which were more recently proposed.

Including species traits directly in multi-specific AGB models, we found that interspecific variation is strongly related to wood density as already demonstrated (Chave et al., 2005; Fayolle et al., 2013; Ketterings et al., 2001). Our results using regional species average for central Africa complemented with the global database (Chave et al., 2009; Zanne et al., 2009) confirmed the importance of wood density though acquiring tree level information from wood samples or cores is practically unrealistic. It has been earlier demonstrated that species averages (Molto et al., 2013) and even genus averages (Slik, 2005) are sufficient for biomass estimates. Though we observed a slight difference in scaling coefficient between evergreen and deciduous species, leaf phenology was not selected in the multi-specific model in contrasts to the regeneration guild and the height at 10 cm, both being related to the light demand of tropical tree species (Loubota Panzou et al., 2018; Poorter et al., 2006; Sheil et al., 2006). Unfortunately tree height was not measured in the Mindourou site (Fayolle et al., 2013), but if available, it would have probably raised as a significant covariable (Chave et al., 2014; 2005; Molto et al., 2013). The contribution of tree height to the AGB predictors was tested on a restricted dataset (Appendix D) and its inclusion in the AGB predictors decreased the effect of the species light demand, removing the height at 10 cm and weakening the effect of the regeneration guild. This is probably because the height-diameter allometry is associated with species life-history strategy, notably light demand. Indeed, height at 10 cm and maximum height were both found related to the regeneration guild in the trait ordination.

The biomass allocation to crown (CMR) was found highly variable among trees and linearly related to tree size, as previously highlighted by Ploton et al. (2016) though in the latter study the tree biomass was used instead of tree diameter. Interspecific variation in CMR, which was found to be important, was to our knowledge considered for the first time here. We found a contrasted allocation between deciduous and evergreen species but leaf phenology was not selected in the multi-specific model in contrasts to species dispersal mode. Species that are wind-dispersed, light-demanding and taller for a certain diameter tended to have lower crown mass ratios. This result is in line with a biomass allocation toward efficient height growth (King, 1990). In contrast, shade-bearing species showed a greater biomass allocation to the crown for a given diameter, in line with the maximization of light interception and the persistence in the shaded understory. This compensation between height growth and crown development has consequences on tree allometry (Goodman et al., 2014) and forest biomass estimates (Ploton et al., 2016). Here, a phylogenetic signal is suspected, since the trend in biomass allocation to crown was driven by a few species with unassisted dispersal, mostly Fabaceae, a plant family that is specifically concentrated in the Neotropics and tropical Africa. In the same line of evidence, Kearsley et al. (2013) showed that the trees inventoried in the Yangambi Man and Biosphere Reserve, in the Democratic Republic of Congo (DRC), were significantly shorter in height than predicted by regional models (Feldpausch et al., 2011), although the trees sampled in the same region (site #8, Fig. 1), mostly Fabaceae, were found to develop extremely large crowns (Fayolle et al., 2018), and to reach huge AGB though shorter in height.

Our species-specific allometries were used to derive allometric traits, notably height, crown exposure and bark thickness at 10 cm diameter, and height at maximum diameter (Appendix A), although the complete adult stature of species was probably not fully captured here. The crown exposure index at 10 cm (elsewhere noted $\mathrm{CEI}_{\mathrm{juv}}$) is known to be a key indicator of species light requirement (Poorter et al., 2006; Sheil et al., 2006), while the bark thickness at 10 cm diameter is a key indicator of fire tolerance, with value assigned for only three forest species in tropical Africa (Pellegrini et al., 2017) prior to this study. Providing such information for 50 new species might be extremely useful in a vastly different context, comparing species characteristics of the forest and savanna biome (Pellegrini et al., 2017). Architectural traits, and specifically, at adult stature, are also extremely important. Maximum height is a key functional trait for tropical and temperate trees (King et al., 2006), representing a fundamental functional axis (Westoby et al., 2002). Here, the power model provided a good fit to the relationships between tree diameter and height (Brown et al., 1989; Feldpausch et al., 2011) and between tree diameter and bark thickness (Pellegrini et al., 2017). While the use of the power model to depict the height-diameter allometry has been questioned earlier (notably in central Africa, Fayolle et al., 2016) and is known for overestimating the height of the large trees (Feldpausch et al., 2011), the power model was found suitable here on this relatively restricted dataset. For the relationship between tree diameter and crown exposure index, we used ordinal regressions as recently suggested (Jucker et al., 2014) instead of the multinomial regressions earlier proposed (Poorter et al., 2006; Sheil et al., 2006). Examining the relationships between allometry, allocation, and traits, in the light of contrasted strategies for occupying space, capturing resources, and resisting mechanical stress, our results confirmed the continuum of species between large-statured and understory species (Swaine and Whitmore, 1988) though the latter might have been undersampled since sampled trees showed diameter $\geq$ 10 cm. Large-statured species tended to be wind-dispersed and deciduous, and for a given diameter, they have lower biomass allocation to the crown, but still store most of the biomass (Loubota Panzou et al., 2018).

Common allometric patterns have been reported across the tropics and there is no general agreement on the necessity to develop new allometric models for specific taxa to improve the estimation and monitoring of forest biomass and carbon stocks (Chave et al., 2014; Fayolle et al., 2018). Developing species-, genus-, or forest-specific biomass allometries would be extremely costly and practically unrealistic, and the biomass estimates provided by general models through sometimes biased locally are valid across large landscapes due to error compensation. Specific allometric models, as the one developed here, for specific species, including most timber species of central Africa, are, however, of key importance for integrating remote sensing imagery into large-scale forest monitoring programs, and for parameterizing the next generation of dynamic models. The latter models also need information on biomass allocation which has yet been little explored for tropical tree species. Crown measurements are extremely difficult in the field, but high resolution remote sensing offers new possibilities to derive crown measurements for emergent and canopy trees. In the future, forest monitoring programs will certainly integrate high resolution remote sensing routinely and a new generation of allometric models will be needed (Jucker et al., 2017).

5. Conclusions

Using published destructive biomass data of tropical trees in eight sites representative of terra firme forests across central Africa we were able to provide new information on biomass allometry and allocation, for a set of 54 tropical tree species widespread and/or locally abundant, and phylogenetically dispersed. New allometric traits were derived for 50 species and were both related to the coefficients of the allometry and allocation models, and were also included in multi-specific models in addition to the tree level information. Our results showed strong interspecific variation in the allometric relationship between tree diameter and aboveground biomass, which was mostly driven by wood density, confirming its importance in the aboveground biomass predictors of multi-specific models. Our results showed that biomass allocation to crown increases linearly with tree diameter, and that interspecific variation is important and associated with the species dispersal mode and maximum height.

CRediT authorship contribution statement

Géraud Sidoine Mankou: Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Gauthier Ligot:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Grace Jopaul Loubota Panzou:**

Conceptualization, Investigation, Writing - review & editing. **Faustin Boyemba:** Data curation, Funding acquisition, Project administration, Writing - review & editing. **Jean-Joël Loumeto:** Data curation, Funding acquisition, Project administration, Writing - review & editing. **Alfred Ngomanda:** Data curation, Funding acquisition, Project administration, Writing - review & editing. **Diosdado Obiang:** Data curation, Funding acquisition, Project administration, Writing - review & editing. **Vivien Rossi:** Project administration, Supervision, Writing - review & editing. **Bonaventure Sonke:** Data curation, Funding acquisition, Project administration, Writing - review & editing. **Olga Diane Yongo:** Data curation, Funding acquisition, Project administration, Writing - review & editing. **Adeline Fayolle:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Species traits

Characteristics of the study species in terms of life-history traits, including dispersal mode, leaf phenology and regeneration guild, and newly developed traits, including maximum diameter (DMAX, in cm), height at 10 cm diameter (*H*10, in m) and at DMAX (HMAX, in m), mean wood density (WD, in g.cm^{-3}), and crown exposure (CEI) and bark thickness (BT, in cm), both at 10 cm diameter. The abbreviations corresponds to Ani.: Animal, Unas.: Unassisted and Wind: Wind dispersal for the dispersal mode; to Dec.: Deciduous and Ev.: Evergreen species for the leaf phenology; and to P: Pioneer, NPLD: Non-Pioneer Light Demander, and SB: Shade Bearer for the regeneration guild. Species are sorted by botanical family according to APGIII available on the African Plant Database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php). Species-specific coefficients (normalization constant and scaling coefficient) are given for the power model relating AGB (in kg) to tree diameter (in cm).

Family	Species	disp. mode	leaf. pheno	rege. guild	n	DMAX	*H*10	HMAX	WD	CEI	BT	AGB model coef.	
												norm. cst	scaling
Anisophylleaceae	*Poga oleosa*	Ani.	Ev.	NPLD	7	124.2	23.4	41.6	0.421	3.14	0.69	0.525	2.000
Annoceae	*Annickia affinis*	Ani.	Ev.	SB	5	50.1	15.1	40.8	0.449	2.28	0.40	0.194	2.317
	Anonidium mannii	Ani.	Ev.	SB	13	71.4	9.9	31.2	0.329	1.22	0.46	0.026	2.699
	Polyalthia suaveolens	Ani.	Ev.	SB	21	50.8	12.3	39.2	0.597	2.71	0.31	0.176	2.457
	Xylopia aethiopica	Ani.	Ev.	P	26	76.3	20.5	44.2	0.529	1.44	0.24	0.227	2.374
Apocyceae	*Alstonia boonei*	Wind	Dec.	P	11	122.9	12.4	44.6	0.380	3.05	0.45	0.071	2.536
Aptandraceae	*Ongokea gore*	Ani.	Ev.	SB	8	71.7	17.8	36.3	0.699	3.34	0.27	0.071	2.703
Burseraceae	*Aucoumea klainena*	Wind	Ev.	P	36	160.2	18.4	55.8	0.384	2.62	0.28	0.062	2.613
	Carium schweinfurthii	Ani.	Dec.	P	8	154.1	24.0	34.8	0.411	2.05	0.31	0.113	2.470
	Santiria trimera	Ani.	Ev.	SB	9	52.4	9.2	40.4	0.548	1.40	0.18	0.191	2.418
Cannabaceae	*Celtis adolfi-friderici*	Ani.	Dec.	NPLD	14	69.2	17.8	37.6	0.621	1.39	0.31	0.070	2.698
Combretaceae	*Termilia superba*	Wind	Dec.	P	34	110.7	15.4	55.7	0.492	2.44	0.37	0.058	2.699
Euphorbiaceae	*Macaranga barteri*	Unas.	Ev.	P	12	53.4	17.1	33.2	0.346	2.28	0.15	0.069	2.563
	Plagiostyles africana	Ani.	Ev.	NPLD	12	50.1	13.8	28.3	0.575	1.96	0.33	0.132	2.434
	Ricinodendron heudelotii	Ani.	Dec.	P	23	119.0	12.6	36.2	0.269	2.23	0.28	0.033	2.582
Fabaceae	*Baphia leptobotrys*	Unas.	Ev.	SB	6	65.4	17.7	29.8	0.801	2.00	0.41	0.937	1.997
	Brachystegia laurentii	Unas.	Ev.	NPLD	9	142.3	16.1	35.7	0.438	2.00	0.24	0.075	2.600
	Calpocalyx heitzii	Unas.	Ev.	NPLD	7	84.8	20.6	44.9	0.684	4.00	0.17	0.162	2.498
	Cylicodiscus gabunensis	Wind	Dec.	NPLD	19	157.0	20.8	60.5	0.749	2.01	0.43	0.183	2.470
	Cynometra hankei	Unas.	Ev.	SB	12	110.8	16.8	33.1	0.693	2.26	0.29	0.170	2.534
	Dialium pachyphyllum	Ani.	Ev.	SB	23	114.9	16.8	52.6	0.740	1.05	0.13	0.283	2.402
	Erythrophleum ivorense	Unas.	Dec.	P	10	159.6	17.3	52.0	0.705	3.08	0.48	0.307	2.313
	Erythrophleum suaveolens	Unas.	Dec.	P	36	128.2	16.4	44.7	0.839	1.76	0.27	0.096	2.667
	Gilbertiodendron dewevrei	Unas.	Ev.	SB	39	154.6	18.9	44.1	0.668	2.50	0.33	0.191	2.468
	Millettia laurentii	Unas.	Dec.	P	10	78.0	17.6	38.9	*0.761			0.133	2.587
	Pentaclethra macrophylla	Unas.	Ev.	NPLD	23	109.8	15.1	44.1	0.744	1.38	0.43	0.183	2.443
	Pericopsis elata	Wind	Dec.	P	25	149.6	19.5	36.7	0.624	1.00	0.46	0.225	2.393
	Piptadeniastrum africanum	Wind	Dec.	NPLD	11	99.9	13.2	45.4	*0.605			0.084	2.546
	Prioria oxyphylla	Wind	Ev.	NPLD	10	105.8	16.3	41.6	0.534	1.12	0.17	0.067	2.652
	Pterocarpus soyauxii	Wind	Dec.	NPLD	60	111.1	18.4	49.5	0.594	2.69	0.31	0.102	2.594
	Scorodophloeus zenkeri	Unas.	Ev.	SB	18	95.8	14.6	36.7	0.660	2.00	0.16	0.302	2.302
Irvingiaceae	*Desbordesia glaucescens*	Wind	Ev.	SB	12	157.9	20.3	56.4	0.807	3.09	0.32	0.462	2.255

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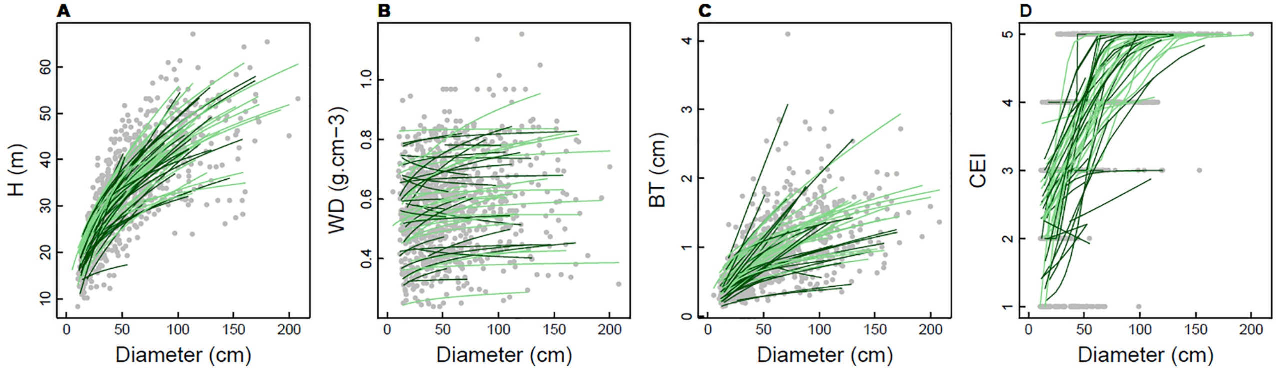
Family	Species	disp. mode	leaf. pheno	rege. guild	n	DMAX	*H*10	HMAX	WD	CEI	BT	AGB model coef.	
												norm. cst	scaling
	Irvingia grandifolia	Ani.	Dec.	NPLD	8	125.5	12.9	50.8	0.756	1.00	0.20	0.061	2.772
	Klainedoxa gabonensis	Ani.	Ev.	P	5	101.5	11.6	54.3	0.781	4.00	1.69	4.726	1.750
Lecythidaceae	*Petersianthus macrocarpus*	Wind	Dec.	NPLD	50	108.1	17.9	46.6	0.588	2.20	0.39	0.118	2.485
Malvaceae	*Duboscia macrocarpa*	Ani.	Ev.	NPLD	8	117.2	11.4	42.9	0.550	2.32	0.16	0.516	1.927
	Eribroma oblongum	Ani.	Dec.	SB	13	98.1	17.9	55.0	0.521	2.00	0.73	0.047	2.777
	Mansonia altissima	Wind	Dec.	NPLD	14	73.4	19.4	46.9	0.535	2.00	0.46	0.053	2.753
	Triplochiton scleroxylon	Wind	Dec.	P	22	196.4	20.1	59.4	0.377	2.21	0.64	0.060	2.590
Meliaceae	*Entandrophragma candollei*	Wind	Dec.	NPLD	9	161.6	19.7	50.7	0.547	2.08	0.49	0.090	2.571
	Entandrophragma cylindricum	Wind	Dec.	NPLD	57	168.4	19.9	48.6	0.568	2.59	0.53	0.101	2.538
	Guarea cedrata	Ani.	Ev.	SB	8	69.3	13.8	42.5	0.562	2.08	0.50	0.108	2.612
	Khaya anthotheca	Wind	Dec.	NPLD	8	108.0	20.7	32.4	0.520	3.68	0.28	0.101	2.578
	Lovoa trichilioides	Wind	Dec.	NPLD	6	104.8	30.3	41.6	0.599	4.00	0.57	0.163	2.466
Moraceae	*Milicia excelsa*	Ani.	Dec.	P	21	112.6	16.3	39.5	0.515	2.31	0.48	0.079	2.569
Myristicaceae	*Coelocaryon preussii*	Ani.	Ev.	SB	10	87.6	17.0	43.5	*0.495			1.817	1.760
	Pycnanthus angolensis	Ani.	Ev.	NPLD	69	109.7	13.7	45.1	0.411	2.34	0.30	0.041	2.660
	Scyphocephalium mannii	Ani.	Ev.	NPLD	12	107.4	19.9	42.0	0.446	2.05	0.42	0.100	2.442
	Staudtia kamerunensis	Ani.	Ev.	SB	54	101.3	16.9	49.4	0.675	2.54	0.24	0.116	2.539
Ochnaceae	*Lophira alata*	Wind	Dec.	P	35	141.3	19.2	50.1	0.833	2.81	0.50	0.375	2.357
Pandanaceae	*Panda oleosa*	Ani.	Ev.	SB	11	106.3	18.3	31.9	*0.565			1.240	1.837
Sapotaceae	*Autranella congolensis*	Ani.	Dec.	NPLD	12	191.4	20.6	51.2	0.732	2.48	0.62	0.140	2.502
	Manilkara mabokeënsis	Ani.	Ev.	SB	14	98.3	18.4	44.0	0.738	2.89	0.41	0.221	2.421
Strombosiaceae	*Strombosia grandifolia*	Ani.	Ev.	SB	8	53.0	13.3	17.2	0.646	2.29	0.22	0.336	2.216

* indicates species average wood density extracted from the global database (Chave et al., 2009; Zanne et al., 2009).

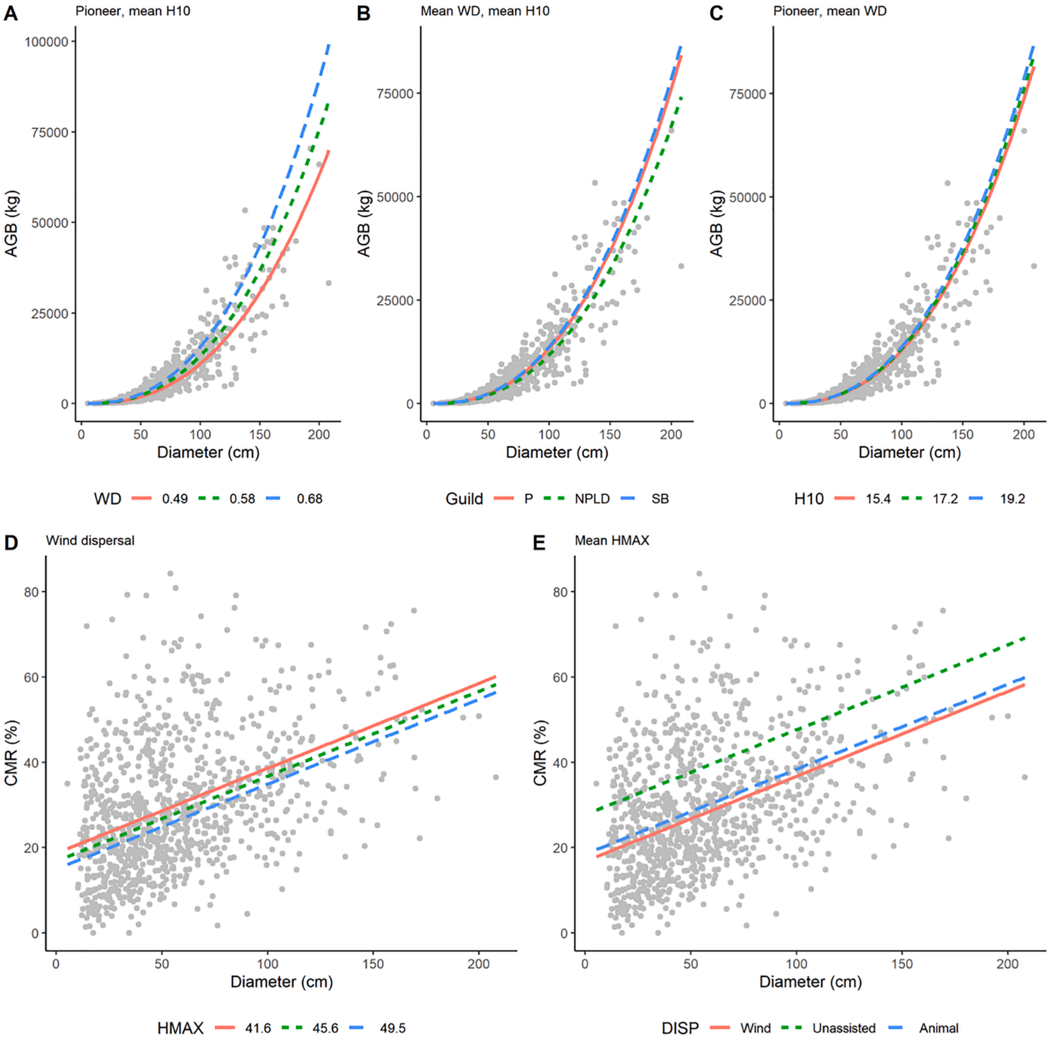
Appendix B. Allometric traits

Species-specific allometric relationships between tree diameter and other tree measurements including total tree height (A), wood density (B) and bark thickness (C) using Ordinary Least Squares regressions after log-transformation are given, and using ordinal regressions for the relationships between tree diameter and the crown exposure index (D). One point represents one tree, and fitted lines represent species-specific relationships. The colors indicate the species leaf phenology, deciduous (light green) *vs* evergreen (dark green) species.



Appendix C. Predictions of multi-specific AGB and CMR models including species traits in the predictors

Points correspond to observations used to fit the model and lines show model predictions for some particular value of model covariables. The allometry model which was finally retained predicts the aboveground biomass (AGB, in kg) in response to tree diameter, species-specific wood density (WD, in g.cm^{-3}), species guild and species-specific height at 10 cm in diameter (*H*10, in m). Panel A shows the variation in AGB predictions across a range of wood density (1st quantile, mean, 3rd quantile) for pioneer tree species and mean *H*10. Panel B shows the variation in AGB predictions for the different species regeneration guild and mean values of WD and *H*10. Panel C shows the variation in AGB prediction across a range of *H*10 for pioneer species and mean WD. The allocation model which was finally retained predicts the crown mass ratio (CMR, in %) in response to tree diameter, species-specific maximum height (HMAX, in cm) and species dispersal mode (DISP). Panel D shows the variation in CMR predictions across a range of maximum height (1st quantile, mean, 3rd quantile) for trees of wind-dispersed species. Panel E shows the variation in CMR predictions for the different species dispersal mode and mean value of HMAX.



Appendix D. Multi-specific AGB and CMR models including tree height in the predictors

Equations and parameters of the multi-specific allometry and allocation models retained for the subset of species for which all traits were available (n = 50 species) and for the subset of trees for which all classical AGB predictors (including H) were available (n = 981 trees). As in Table 2, the estimate, standard deviation, degree of freedom and *P-value* are given for the fixed parameters whereas only the standard deviation is given for the random effect terms.

Parameter	Estimate	Std Dev.	df	*P-value*
Allometry model (equation 1)				
$log(AGB_{ij}) = a + b\ log(D_{ij}) + c\ log(WD_j) + d\ log(H_{ij}) + e_{RG,j} + \alpha_j + \varepsilon_{ij}$				
a	−2.518	0.119	208.7	<0.001
b	2.244	0.023	894.4	<0.001
c	1.027	0.091	11.3	<0.001
d	0.588	0.043	13.6	0.062
$e_{RG=NPLD}$	−0.110	0.057	41.9	0.062
$e_{RG=SB}$	0.033	0.062	0.5	0.602
α_j		0.149		
ε_{ij}		0.224		
Allocation model (equation 2)				
$CMR_{ij} = a + b\ D_{ij} + c\ HMAX_j + d\ H_{ij} + \alpha_j + \varepsilon_{ij}$				
a	37.71	7.68	45.6	<0.001
b	0.23	0.02	878.0	<0.001
c	−0.61	0.15	48.0	<0.001

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Parameter	Estimate	Std Dev.	df	*P-value*
d	−0.13	0.06	872.3	0.031
α_j	8.40			
ε_{ij}	11.13			

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