Taller trees, denser stands and greater biomass in semi-deciduous than in evergreen lowland central African forests

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Abstract

Accurate height-diameter allometry is crucial for the estimation of forest biomass and carbon stocks. Tree height measurements over a large range of diameters and species are urgently needed in the tropics, specifically in central Africa, for the development of locally derived height-diameter allometric equations and the conversion of forest inventory data into biomass estimates, and for the validation of remotely sensed canopy height that mostly rely on a few specific field sites. In this study, we aimed to identify the variation in height-diameter allometry of tropical trees between forest types and among species in central Africa, and we examined the consequences for biomass estimation. Height and diameter were measured for a total of 521 trees over a large range of diameters in two forest types in southern Cameroon, 10–240 cm in the evergreen forest and 11–182 cm in the semi-deciduous forest. A total of ten allometric models including asymptotic and non-asymptotic models were fitted to the height-diameter data. Measured tree diameters, grouped into 10 cm wide diameter classes up to 150, from commercial forest inventory data at genus level, and both allometry and forest structure (taller trees and denser stands) contributed to the greater biomass per hectare of the semi-deciduous forest.

Keywords:
Allometry
Biomass estimation
Forest deciduousness
Maximum tree height
Tropical forest

1. Introduction

The Congo basin forms the second largest continuous block of tropical forests in the world with up to 200 Mg of carbon per hectare in standing trees (diameters greater than 10 cm, Lewis et al., 2009, 2013). Due to the lack of agreement in central Africa between the biomass maps produced (Baccini et al., 2008, 2011; Mitchard et al., 2011), a lot of uncertainty remains about the amount and spatial variation in biomass and carbon stocks. This is mainly due to the lack of appropriate allometric models to convert forest inventory data over large spatial scales. Forest inventory data in central Africa covers more than 12 million hectares (De Wasseige et al., 2012, p. 46) and national forest inventories have been
conducted in several countries (http://www.fao.org/forestry/fma/73410/en/). If all these data could be gathered and jointly analyzed, a good picture of the biomass distribution may be obtained.

The choice of the allometric model is a critical step in the estimation of forest biomass (Chave et al., 2004; Molto et al., 2013). Until recently, there were only few available data on the biomass allometry of tropical African trees, and data were restricted to particular species and sites (Henry et al., 2011). The pantropical allometric models developed by Chave et al. (2005) were thus used to convert inventory data into estimates of biomass and carbon stocks, either including only diameter and wood specific gravity in the set of predictors (e.g. Gourlet-Fleury et al., 2011; Maniatis et al., 2011) or including diameter, wood specific gravity, as well as tree height (Kearsley et al., 2013; Lewis et al., 2013, 2009). Multi-species allometric equations have been recently established in south-eastern Cameroon (Fayolle et al., 2013) and in northern Gabon (Ngomanda et al., 2014) but with conflicting results. The local allometric equation we developed for south-eastern Cameroon (Fayolle et al., 2013) was found not to be different from the pantropical equation developed by Chave et al. (2005) for moist forests, while the local allometric equation of northern Gabon strongly differed from the pantropical equation developed for moist forests (40% overestimation of biomass) but was not different from the pantropical equation for wet forests (Ngomanda et al., 2014). While both sites have been assigned to a transition type between evergreen and semi-deciduous forests (White, 1983), the sampled trees, however, tended to be more deciduous in south-eastern Cameroon (79 trees and 15 species, out of 138 and 42, respectively) and to be more evergreen in northern Gabon (72 trees and 7 species, out of 101 and 10, respectively). According to Holdridge’s classification system (1967), most of the central African forests are climatically attributed to moist forests. Strong variation in tree species composition from wet evergreen forests rich in Caesalpinioideae to semi-deciduous forests rich in Ulmaceae and Sterculiaceae (now included in Malvaceae) has, however, long been reported (Fayolle et al., 2014; White, 1983, and references therein). We suspect that this variation in species composition and overall deciduousness is correlated with variations in forest structure and tree allometry, and that the bioclimatic thresholds of the Holdridge’s classification system (1967) are not suitable for distinguishing wet, moist and dry forests of Africa. In their recent synthesis work on the allometry of tropical trees, Chave et al. (2014) indeed abandoned these forest types and directly linked variation in tree allometry to a bioclimatic stress variable which compounds indices of temperature variability, rainfall variability and drought intensity.

According to Ketterings et al. (2001), between site differences in biomass allometry are due to two characteristics of the forest, the height-diameter allometry and the wood specific gravity of the trees. Since the wood specific gravity is generally included in the set of predictors of tree biomass, architectural differences between sites including height-diameter allometry, but also crown-diameter allometry (Goodman et al., 2013; Ploton et al., 2015), determine the variation in biomass allometry. It has been recently demonstrated that crown-diameter allometry is relatively stable while height-diameter allometry is highly variable, supporting the idea that tropical trees preferentially adjusted their height to growth conditions (Antin et al., 2013). The variation in height-diameter allometry has indeed been shown to be of extreme importance for the estimation of biomass and carbon stock (Chave et al., 2014; Feldpausch et al., 2012; Kearsley et al., 2013; Molto et al., 2014). In sites with specific height-diameter allometry, the use of conventional height-diameter allometric equations, i.e. those that have not been locally fitted, can induce a significant bias in the estimation of biomass and carbon stocks (as demonstrated in Indonesia by Rutishauser et al. (2013); and in Yangambi, DR Congo by Kearsley et al. (2013)). Total tree height is, however, extremely difficult to measure accurately in structurally complex and species-rich tropical forests (Larjavaara and Muller-Landau, 2013). As a result tree height measurements are rarely available in forest inventory data in central Africa and tree height is estimated from a height–diameter allometric equation established at a global (Lewis et al., 2009), regional (Feldpausch et al., 2012; Lewis et al., 2013) or local (Kearsley et al., 2013) scale. There is, however, no consensus on which height–diameter allometric equation should be used in central Africa. When tree height data are not available for the estimation of biomass, Chave et al. (2014) developed a pantropical biomass model incorporating wood specific gravity, tree diameter, and a bioclimatic stress variable. The validity of this recently developed pantropical model has not yet been tested on a validation dataset.

There is general agreement on the need for tree height data over a large range of diameters and species in the tropics for the development of locally derived height-diameter allometric equations (Chave et al., 2014; Kearsley et al., 2013; Molto et al., 2014; Rutishauser et al., 2013) and the conversion of forest inventory data into biomass estimates (Chave et al., 2004; Clark and Kellner, 2012; Molto et al., 2013). Tree height data are also needed for the validation of global and regional remotely sensed canopy height (e.g. Wang et al., 2016) that mostly rely on a few specific field sites, specifically for central African forests. In addition to these practical questions, both related to the estimation of forest biomass and carbon stocks, tree height data are also needed for addressing theoretical questions. There has been a historical debate on the shape of the height-diameter allometry for tropical trees. The origin of this debate can be found in the fact that Malaysian tree species supported an asymptotic shape and thus a determinate height growth (Thomas, 1996) while Ecuadorian tree species tended to support a power law model and thus an indeterminate growth (King, 1996). It was later demonstrated that similarly to Ecuadorian trees, Brazilian tree species also supported an indeterminate growth at species level, but based on a log-linear rather than a power law model (Nogueira et al., 2008). The recent need for height-diameter equations for the estimation of biomass and carbon stocks in tropical forests motivated scientists to establish plot-level height-diameter allometric equations, and thus renewed the debate. Some authors argued in favour of a truly asymptotic model (Kearsley et al., 2013; Lewis et al., 2009; Molto et al., 2014; Rutishauser et al., 2013), or a second order polynomial of the log–log data (Chave et al., 2014; Niklas, 1995) mimicking the saturation of tree height with tree diameter, while others argued in favour of the power law model (Djomo et al., 2010; Feldpausch et al., 2011; Hunter et al., 2013) such as predicted by the metabolic theory of ecology (West et al., 1997, 1999). The metabolic theory moreover predicts invariant morphological scaling between several tree dimensions, and specifically a 2/3 exponent between tree height and diameter (Muller-Landau et al., 2006).

In this study, we investigated the variation in height-diameter allometry between two forest types and among species in southern Cameroon, and we examined the consequences for biomass estimation using commercial inventory data. Given the quantitative information they contain (diameters are measured and trees are identified to species when possible) and the spatial extent they cover (De Wasseige et al., 2012), commercial inventory data as they are performed in central Africa (consecutive 0.5 ha plots, with a sampling rate of 1%) are reliable for biomass estimates (Gourlet-Fleury et al., 2011; Maniatis et al., 2011). In this study, we addressed the following research questions. (1) Are differences in height-diameter allometry due to the local conditions of the site or to the identity of species? We specifically tested the hypothesis that the evergreen and the semi-deciduous forests show contrasted height-diameter allometry. (2) Are published (regional
and/or local) height-diameter allometric relationships in central Africa appropriate for both the evergreen and the semi-deciduous forests? (3) What are the consequences of the height-diameter allometry on the estimation of biomass? We additionally examined an ancillary question on the shape of the allometric relationship between tree height and diameter. (4) Is there continuous height growth (versus saturation)?

2. Material and methods

2.1. Study sites

Height and diameter measurements were conducted in two sites characteristic of two major forest types in central Africa. The Ma’an site is located in south-western Cameroon, east of the Campo-Ma’an National Park. Measurements were performed in two forest management units managed by the Wij’ma logging company. The annual rainfall is up to 2080 mm with a distinct dry season (December to February) and the mean annual temperature is 23.3 °C (Hijmans et al., 2005). Forests in the Ma’an site are assigned to Wet Central Africa in our terminology for the African floristics (Fayolle et al., 2014) and correspond to lowland evergreen forests with a canopy dominated by Lophira alata and Saccoglottis gabonensis (Letouzey, 1985). The Mindourou site is located in south-eastern Cameroon, east of the Dja reserve. Measurements were performed in five forest management units managed by the Pallisco logging company. The annual rainfall is up to 1640 mm with a distinct dry season (December to February) and the mean annual temperature is 23.1 °C. Forests in the Mindourou site are assigned to Moist Central Africa (Fayolle et al., 2014) and have been previously described as a transition type between the evergreen and the semi-deciduous forests with a canopy dominated by species of the Meliaceae, Sterculiaceae (now included in Malvaceae) and Ulmaceae families indicating a strong floristic affinity with the semi-deciduous forests (Letouzey, 1985). In both sites, the topography is undulating, with elevation varying between 600 and 800 m, and between 500 and 650 m, in the Ma’an and Mindourou sites, respectively; the geological substrate consists of volcanic intrusions and metamorphic rocks, and soils are generally attributed to Ferralsols (Jones et al., 2013).

2.2. Height and diameter measurements

A total of 12 focal species, 7 and 8 in the Ma’an and Mindourou sites, respectively, with three species shared by the two sites, were selected to establish site- and species-specific height-diameter allometric equations (Table 1). Focal species corresponds to timber species characteristic of the evergreen and semi-deciduous forest in Cameroon (Doucet, pers.com), some of them already identified as hyperdominant in terms of biomass (Bastin et al., 2015). Non-destructive height and diameter measurements were performed in 2014 by the same operator (Loubota Panzou) for a total of 251 destructive height and diameter measurements were performed in unlogged terra firme forests, except for L. alata in the Mindourou site which was measured along the Boumba River. Height measurements were performed with a VERTEX IV dendrometer. For each standing tree, height was measured from two different points at a distance of at least one tree height and the average between the two measurements was used for the analyses. Diameter was measured at breast height, or 30 cm above the deformation following Picard et al. (2012). Since tree height measurements are difficult in the tropics (Larjavaara and Muller-Landau, 2013), we first evaluated how accurate are non-destructive tree height measurements in comparison with destructive measurements on a total of 60 felled trees, 30 in each site (Appendix A). The trees of the validation data set mostly belonged to the 12 focal species, but also to six additional species frequently logged on the sites and that were only used for the validation of height measurements (n = 10 trees, Table 1). Given the strong correlation (r² = 0.89, P < 0.001) and the very small bias between the non-destructive and destructive height measurements, we had confidence in using our non-destructive height measurement to establish site- and species-specific height-diameter allometric equations. Our measurements were, however, performed in good visibility conditions on selected trees and systematic height measurements remain difficult in tropical forests (Larjavaara and Muller-Landau, 2013).

2.3. Forest inventory data

We gathered forest inventory data performed by the two logging companies prior to the implementation (or revision) of their management plan. The sampling design was systematic and consisted of parallel transects 2 or 3 km apart, and divided into consecutive rectangular plots (20 × 250 m, i.e. 0.5 ha). Within each plot, all trees with a dbh ≥ 20 cm were identified and measured with a tape. In the management process, trees were assigned to 10 cm wide diameter classes and large trees were grouped in the dbh ≥ 150 cm class. Vernacular names were converted to species-level scientific names. Taxonomy was homogenized according to the African plant database (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php) on 19 June 2014. Because vernacular names are more reliable at the genus level than at the species level (Réjou-Mechain et al., 2011), inventory data were used at the genus level for biomass estimation. A total of 311 genera (76 families according to APGIII, The Angiosperm Phylogeny Group, 2009) were identified in the 7253 inventoried plots. The unidentified trees represented a total of 4077 trees (3.92%) with an average of 1.75 per 0.5 ha plot for the evergreen forest of the Ma’an site, and a total of 14201 trees (3.11%) with an average of 1.45 per 0.5 ha plot for the semi-deciduous forest of the Mindourou site. The three most abundant genera were Xylopia, Strombosioptis, and Annickia for the Ma’an site, and Polyalthia, Strombosia, and Strombosioptis for the Mindourou site.

2.4. Height-diameter models

A total of ten different allometric models were fitted at site or species level (Table 2). Fitted models include the linear model (m1), the log-linear model (m2, Nogueira et al., 2008), the power law model (m3, Feldpausch et al., 2011; King, 1996; Niklas, 1994); a second order polynomial of the previous models (m1–3), of the linear model (m4), of the log-linear model (m5) and of the power law model (m6, see Chave et al., 2014; Niklas, 1995 for a log–log transformation); as well as four asymptotic models, the monomolecular (or three-parameters exponential) model (m7, Banin et al., 2012; Feldpausch et al., 2012; Ngomanda et al., 2014), the Gompertz model (m8), the Weibull model (m9, Bailey, 1980; Feldpausch et al., 2012; Rutishauser et al., 2013) and the Michaelis–Menten model (m10, Molto et al., 2014, 2013). The best models at site and species level were selected according to the Akaike Information Criterion (AIC) and the Residual Standard Error (RSE). To better interpret the AIC values we also computed the Akaik weights (Aw), an indicative probability for a model to be the best model given the data and the set of models tested. To test for a significant difference between forest types in height-diameter allometry, we used the Michaelis–Menten model (m10), that was identified as the most likely model, and fitted on the whole data a set of four derivative models: with invariant coefficients (m10.1) and with coefficients that vary between forest types (m10.2 site-specific a and b, m10.3 site-specific a and fixed b,
Our height observations were compared to height predictions in m) to tree diameter (D in cm). A total of ten different allometric models were fitted to the height-diameter data. The Akaike Information Criterion (AIC), the Akaike weights (Aw), the Residual Standard Error (RSE) and parameter estimates are given for each model. The best model (lowest AIC and RSE, highest Aw) relating height to diameter is shown in bold for each forest type.

### Table 1

<table>
<thead>
<tr>
<th>Commercial name</th>
<th>Species</th>
<th>Family</th>
<th>WSG (g cm⁻³)</th>
<th>Sampling effort (number of sampled trees)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ma'an site (evergreen forest)</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mindourou site (semi-deciduous forest)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>[diameter range]</td>
</tr>
<tr>
<td>Focal species</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Assamela (Afromosia)</td>
<td><em>Pericopsis elata</em></td>
<td>Fabaceae</td>
<td>0.639 ± 0.0410</td>
<td>32 [12.2–110.5]</td>
</tr>
<tr>
<td>Azbé</td>
<td><em>Lophira alata</em></td>
<td>Ochnaceae</td>
<td>0.897 ± 0.0563</td>
<td>41 [10.5–123.3]</td>
</tr>
<tr>
<td>Bibolo (Dibotou)</td>
<td><em>Lova trichiloides</em></td>
<td>Meliaceae</td>
<td>0.455 ± 0.0401</td>
<td>42 [10.4–138.8]</td>
</tr>
<tr>
<td>Daréma</td>
<td><em>Piptadeniastrom africanum</em></td>
<td>Fabaceae</td>
<td>0.605 ± 0.0532</td>
<td>35 [16.6–142.1]</td>
</tr>
<tr>
<td>Fraké</td>
<td><em>Terminalia superba</em></td>
<td>Combretaceae</td>
<td>0.459 ± 0.0641</td>
<td>–</td>
</tr>
<tr>
<td>Iroko</td>
<td><em>Milicia excelsa</em></td>
<td>Moraceae</td>
<td>0.575 ± 0.0699</td>
<td>14 [12.2–115.6]</td>
</tr>
<tr>
<td>Mavingui</td>
<td><em>Distemonanthus benthamianus</em></td>
<td>Fabaceae</td>
<td>0.695 ± 0.0634</td>
<td>34 [14.1–135.7]</td>
</tr>
<tr>
<td>Okan</td>
<td><em>Cylindicus gabunensis</em></td>
<td>Fabaceae</td>
<td>0.790 ± 0.0792</td>
<td>23 [11.7–240.0]</td>
</tr>
<tr>
<td>Padouk</td>
<td><em>Pterocarpus soyauxii</em></td>
<td>Fabaceae</td>
<td>0.658 ± 0.0716</td>
<td>31 [11.7–119.3]</td>
</tr>
<tr>
<td>Sapelli</td>
<td><em>Entandrophragma cylindricum</em></td>
<td>Meliaceae</td>
<td>0.572 ± 0.0368</td>
<td>–</td>
</tr>
<tr>
<td>Tali</td>
<td><em>Erythrophleum suaveolens</em></td>
<td>Fabaceae</td>
<td>0.872 ± 0.0919</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td><em>Erythrophleum ivorense</em></td>
<td>Fabaceae</td>
<td>0.774 ± 0.0597</td>
<td>38 [14.7–127.2]</td>
</tr>
</tbody>
</table>

Additional species/trees used for validation of the non-destructive measurements:

Abel (Aïdlé) - *Canarium schweinfurthii* Bursereaceae | 0.409 ± 0.0623 | – | 1 [123.0]
Besse – *Guarea cedrata* Meliaceae | 0.510 ± 0.0329 | – | 1 [87.6]
Iatandza – *Albicic ferruginea* Fabaceae | 0.494 ± 0.0525 | – | 1 [88.5]
Kossipo – *Entandrophragma candolleti* Meliaceae | 0.574 ± 0.0712 | 1 [112.0]
Ngolon (Acajou de Bassam) – *Khowa ivorensis* Meliaceae | 0.444 ± 0.0277 | 2 [87.6–95.5] |
Tiana – *Entandrophragma angolense* Meliaceae | 0.483 ± 0.0395 | 1 [97.9] |
Wengué – *Milletia laurentii* Fabaceae | 0.761 ± 0.0403 | 3 [73.1–83.5] |

### Table 2

Local site-specific allometric equations relating total tree height (H in m) to diameter (D in cm). A total of ten different allometric models were fitted to the height-diameter data. The AIC, the Akaike weights (Aw), the RSE and parameter estimates are given for each model. The best model (lowest AIC and RSE, highest Aw) relating height to diameter is shown in bold for each forest type.

### Table 3

Values of E for the two sites were extracted from the global gridded layer at 2.5 arc sec resolution available online (http://chave-ups-tlse.fr/panropical_allometry.htm). We obtained E = –0.126 for the Ma’an site (Lon = 10.63, Lat = 2.37) and E = –0.063 for the Mindourou site (Lon = 13.41, Lat = 3.58). To quantify the error in tree height estimates from published height-diameter equations, we additionally used paired t-tests (error, in m and significance) and linear regressions (intercept and slope) between estimated and observed values for each forest type separately. We examined the significance of the intercept and for the slope the confidence interval at 95% to test for significant difference from unity. We used the R environment for model fitting and statistical analyses (R Development Core Team, 2014).

2.5. Biomass estimation

We examined how the inclusion of tree height in biomass allometric equations affected the estimation of biomass. Above-ground biomass (AGB in Mg) of each 0.5 ha plot was estimated as the sum of the above-ground biomass of the inventoried trees. Tree diameters were converted into biomass estimates with the two pantropical allometric equations (without and with height in the set of predictors) developed by Chave et al. (2005) for moist forests,
Table 3

<table>
<thead>
<tr>
<th>Source</th>
<th>Location</th>
<th>Equation</th>
<th>Site (forest type)</th>
<th>RMSE</th>
<th>Intercept</th>
<th>Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chave et al. (2014)</td>
<td>Pantropical</td>
<td>log((H)) = 0.893 - E + 0.760 \times \log(D) - 0.0340 - (\log(D))^2</td>
<td>Ma’an (evergreen)</td>
<td>7.6</td>
<td>6.1 (P &lt; 0.001)</td>
<td>0.66 [0.63–0.70]</td>
</tr>
<tr>
<td>Lewis et al. (2009)</td>
<td>Tropical Africa</td>
<td>H = 54.01 \times (1 - \exp(-0.053 \times D^{0.76}))</td>
<td>Ma’an (evergreen)</td>
<td>7.8</td>
<td>7.1 (P &lt; 0.001)</td>
<td>0.77 [0.73–0.81]</td>
</tr>
<tr>
<td>Feldpausch et al. (2011)</td>
<td>Central Africa</td>
<td>log((H)) = 1.1525 + 0.5547 \times \log(D)</td>
<td>Ma’an (evergreen)</td>
<td>6.0</td>
<td>4.0 (P &lt; 0.001)</td>
<td>0.92 [0.86–0.98]</td>
</tr>
<tr>
<td>Feldpausch et al. (2012)</td>
<td>Central Africa</td>
<td>H = 50.453 \times (1 - \exp(-0.0471 \times D^{0.12}))</td>
<td>Ma’an (evergreen)</td>
<td>6.9</td>
<td>6.2 (P &lt; 0.001)</td>
<td>0.79 [0.75–0.82]</td>
</tr>
<tr>
<td>Banin et al. (2012)</td>
<td>Africa</td>
<td>H = 45.1 - 42.8 \times \exp(-0.025 \times D)</td>
<td>Ma’an (evergreen)</td>
<td>5.4</td>
<td>4.5 (P &lt; 0.001)</td>
<td>0.80 [0.76–0.84]</td>
</tr>
<tr>
<td>Kearsley et al. (2013)</td>
<td>Yangambi, DR</td>
<td>H = (36.3576–31.6591) \times \exp(-0.0221 \times D)</td>
<td>Ma’an (evergreen)</td>
<td>3.8</td>
<td>2.7 (P &lt; 0.001)</td>
<td>1.06 [1.01–1.11]</td>
</tr>
<tr>
<td></td>
<td>Congo</td>
<td>H = (36.3576–31.6591) \times \exp(-0.0221 \times D)</td>
<td>Mindourou (semi-dec.)</td>
<td>7.7</td>
<td>6.0 (P &lt; 0.001)</td>
<td>1.28 [1.19–1.36]</td>
</tr>
</tbody>
</table>

\* A positive error corresponds to overestimation (prediction > observation).

Eqs (1) and (2); for wet forests, Eqs (3) and (4); and developed by Chave et al. (2014) for all forests, Eqs (5) and (6).

\[ AGB = \rho \times \exp(-1.499 + 2.148 \times \ln D + 0.207 \times (\ln D)^2 - 0.0281 \times (\ln D)^3) \]  
\[ AGB = 0.0509 \times \rho D^2 H \]  
\[ AGB = \rho \times \exp(-1.239 + 1.980 \times \ln D + 0.207 \times (\ln D)^2 - 0.0281 \times (\ln D)^3) \]  
\[ AGB = 0.0776 \times (\rho D^2 H)^{0.940} \]  
\[ AGB = \exp(-1.803 - 0.976 E + 0.976 \times \ln \rho + 2.673 \times \ln D - 0.299 \times (\ln D)^2) \]  
\[ AGB = 0.0673 \times (\rho D^2 H)^{0.976} \]  

where \( \rho, D, H \) and \( E \) are wood specific gravity (in g cm\(^{-3}\)), tree diameter (in cm), tree total height (in m) and a measure of environmental stress, respectively. Wood specific gravity values at species level were extracted from the global wood specific gravity data base (Chave et al., 2009; Zanne et al., 2009). We obtained reliable wood specific gravity values at the genus level for 192 tropical African genera. When no information was available for the genus, we assigned the average value at family level (n = 89 genera), and when no information was available for the family, we assigned the overall average value for the site (n = 30 genera). The calculation of AGB required information on exact \( D \) values that were not available in the inventory data. We replaced this information by the mid-point of diameter class (Maniatis et al., 2011). \( H \) was estimated from the diameter data with the best site-specific allometric equations. For an easier comparison of our results with results obtained with an inventory threshold of 10 cm, we estimated the number of trees within the [10–20] cm diameter class in each site by fitting a relationship between tree diameter and frequency (Appendix B). We assigned the mean wood specific gravity across genera to these trees.

3. Results

3.1. Site-specific height-diameter allometric equations

Our results tended to support an asymptotic shape of the height-diameter allometry at site level for both forest types (Table 2). Given the RSE values, all models with the exception of the linear model (m1) fitted satisfactorily to the height-diameter data. According to the Akaike weights, two truly asymptotic models, the Michaelis–Menten model (m10) and the Weibull model (m9), and the m5 and m6 polynomial models that can both mimic height saturation, tended to perform a little better than the other models.

We identified a significant variation in height-diameter allometry between sites. Based on AIC values (results not shown), we found that the two parameters of the Michaelis–Menten model varied with the forest type, with coefficient estimates and confidence interval at 95% for the evergreen forest of the Ma’an site \( a = 46.7 [44.69–48.82] \) and \( b = 31.1 [27.02–35.72] \), and for the semi-deciduous forest of the Mindourou site \( a = 55.2 [53.11–57.57] \) and \( b = 38.2 [33.96–42.98] \). For a given diameter, trees tended to be taller in the semi-deciduous Mindourou site than in the evergreen Ma’an site, and these differences, maintained across the diameter range, lead to a difference in maximum height \( H_{\text{max}} \) hereafter, a parameter of the asymptotic models. \( H_{\text{max}} \) was indeed lower for the evergreen Ma’an site (with an average of 37.4 m for the four asymptotic models) than for the semi-deciduous Mindourou site (with an average of 45.5 m). It is, however, important to note that \( H_{\text{max}} \) estimates varied with the asymptotic model considered, with taller estimates reported from the Michaelis–Menten model (m10, Table 2).

For the two forest types, height observations significantly differed from the predictions of published regional or local equations (Table 3). The pantropical model of Chave et al. (2014) including a measure of environmental stress in the set of predictors and the regional models of Lewis et al. (2009), Feldpausch et al. (2011, 2012), and Banin et al. (2012) tended to significantly overestimate tree height in the two study sites with the exception of Feldpausch et al. (2011) that slightly (but significantly) underestimated tree height in the semi-evergreen forest. The height overestimation of these general models was stronger for the evergreen than for the semi-deciduous forest. The local model developed by Kearsley et al. (2013) for mixed moist forests in Yangambi significantly underestimated tree height in both sites.

3.2. Between and within-species variations in height-diameter allometry

Our results tended to support asymptotic models at species level. We fitted the ten allometric models to the 12 focal species and separately for the two sites for the three species (Cylicodiscus gabunensis, L. alata, and Pterocarpus soyauxii) shared by the forest
types (Appendix C). Given the RSE values, all models, with the exception of the linear model (m1, Aw < 0.001), fitted satisfactorily to the height-diameter data at species-site level. The Michaelis–Menten model (m10, Aw = 0.170) tended to be the most likely model of height-diameter allometry at the species level, followed by the other asymptotic models, i.e. Weibull (m9, Aw = 0.152), monomolecular (m7, Aw = 0.139), and Gompertz (m8, Aw = 0.126) and the m6 model (Aw = 0.143). The power law model (m3) was the second worst model (Aw = 0.20). The value of the parameter b (scaling coefficient) for the 15 species- and site-specific power law models was lower than the theoretical 2/3 exponent predicted by the metabolic theory. Species of the evergreen Ma'an site tended to show lower exponents and higher intercepts than species of the semi-deciduous Mindourou site (Fig. 1).

We identified a slight variation in height-diameter allometry between species for the same site (Fig. 2). *C. gabunensis* was the tallest species in the two forest types, while *Erythrophleum ivorense* and *Erythrophleum suaveolens* were the smallest species in the evergreen and in the semi-deciduous forest, respectively. For the three species common to the two forest types, we identified a significant variation in height-diameter allometry between sites. We found that the two parameters of the Michaelis–Menten model varied with the forest type for *L. alata* (n = 73 trees), with coefficient estimates and confidence interval at 95% for the evergreen forest of the Ma’an site a = 44.7 [41.63–48.43] and b = 24.6 [18.77–31.95], and for the semi-deciduous forest of the Mindourou site a = 53.44 [48.53–59.42] and b = 37.4 [28.42–49.23]. In contrast, we found that only the a coefficient (Hmax) varied with the forest type for *C. gabunensis* (n = 57 trees) and *P. soyauxii* (n = 56), with respectively a = 49.3 [45.23–53.92] for the evergreen forest and a = 58.3 [54.48–62.70] for the semi-deciduous forest, and b = 37.8 [29.58–48.00] for *C. gabunensis*, and a = 48.7 [45.49–52.50] for the evergreen forest and a = 57.6 [53.64–62.27] for the semi-deciduous forest, and b = 32.5 [26.54–52.50] for *P. soyauxii*.

### 3.3. Between-site variation in forest structure

We found that the two forest types showed strong differences in stand structure and biomass (Table 4). Considering the most recent pantropical model (Chave et al., 2014) combined with a site-specific height-diameter allometry (m5 for the evergreen forest of the Ma’an site and m10 for the semi-deciduous forest of the Mindourou site, Table 2), we found that the aboveground biomass per hectare was lower for the evergreen Ma’an site with 213.1 ± 1.8 Mg dry mass ha$^{-1}$ for trees with a diameter ≥20 cm and 259.8 Mg for trees ≥10 cm than for the semi-deciduous Mindourou site with 281.8 ± 1.4 and 347.6 Mg dry mass ha$^{-1}$ respectively for trees ≥20 cm and ≥10 cm. The lower biomass per hectare in the evergreen Ma’an forest than in the semi-deciduous Mindourou forest was, however, attributable to height-diameter allometry (shorter trees), stand structure (lower stem density and basal area), and to a lesser extent to wood specific gravity (lighter wood). The estimated biomass strongly varied with the choice of the allometric model. In the Ma’an site, the models developed by Chave et al. (2005) for moist forests tended to predict higher biomass values while the models developed for wet forests tended to predict much lower biomass values than the most recent pantropical model (Chave et al., 2014) including site-specific
height-diameter allometry. In the Mindourou site, the models developed by Chave et al. (2005) for moist forests provided good biomass estimates while the models developed for wet forests predicted much lower biomass values, and this was even much lower for the Ma'an site. The biomass predictions of the most recent pantropical model (Chave et al., 2014), including a measure of environmental stress in the set of predictors, tended to be higher in the Ma'an site (+16%) but were much closer for the Mindourou site (-1%) to the values predicted by this most recent pantropical model but including site-specific height-diameter allometry.

4. Discussion

4.1. Toward a unique height-diameter allometric model?

There has been a historical debate on the shape of the height-diameter allometric equation for tropical trees. Our results based on height measurements over a wide range of diameters (up to 240 cm) clearly support an asymptotic height-diameter allometry at both site and species level. All models except the linear model should be carefully addressed for establishing adequate site-specific height-diameter allometric equations.

4.2. The determinant of the height-diameter allometry

We found strong support for the hypothesis that height-diameter allometry varies between forest types. Similarly to Molto et al. (2014) at plot level in French Guiana, we found that the two parameters of the Michaelis–Menten model varied with the forest type. We specifically showed that trees tended to be significantly smaller for a given diameter in evergreen than in semi-deciduous forest in agreements with pantropical studies have already demonstrated that for a given diameter, trees in the semi-deciduous forest tended to be shorter than trees in moist (semi-deciduous) forests (Brown, 1997; Chave et al., 2005). This contrasted allometry was attributed to the more acid and shallower soils in the wet ecological zone (Henry et al., 2011) and we used additional soil data to test this hypothesis (Appendix D). A negative correlation between rainfall and soil fertility has already been demonstrated in Ghana (Swaine, 1996) and a similar allometric pattern has been reported across Ghanaian forests (Hall and Swaine, 1976; Longman and Jenik, 1974). $H_{\text{max}}$ has been shown to increase with increasing rainfall until a maximum is reached in the 1250–1750 mm class, and thereafter, $H_{\text{max}}$ decreases with increasing rainfall (Longman and Jenik, 1974). This variation is not simply the result of the floristic composition, and specifically due the absence from the driest and wettest forests of the tallest species, since the same trends were shown by the ubiquitous large tree Ceiba pentandra (Hall and Swaine, 1976). In this study, we also found for the three species shared by the two forest types, that for a given diameter, trees tended to be shorter in the (wet) evergreen forest than in the (moist) semi-deciduous forest. This suggests an environmental control on tree allometry, though in southern Cameroon, we did not find evidence of strong soil variations between the two sites, with the exception of the plant-available P content (Appendix D). The height-diameter allometry has also been shown to be influenced by light availability (Muller-Landau et al., 2006) and the effect of forest structure (basal area and stem density) was indeed found to be stronger than those of environmental factors and trees tended to be higher for a given diameter in denser stands (Banin et al., 2012; Molto et al., 2014). This is also the pattern reported in this study, with denser stands and taller trees in the semi-deciduous forest than in the evergreen forest. Other factors could also be invoked to explain the between-site variation in tree allometry, and among them wind exposure model. The power function is widely found in biology and has been used to describe height-diameter allometry for a wide range of plants (Niklas, 1994), including plot-level allometry for tropical trees (Feldpausch et al., 2011; Hunter et al., 2013) and specifically in southern Cameroon close to the Ma'an site (Djomo et al., 2010, but for only a small range of diameters). In this study, we showed that the power law model does not necessarily hold true when large trees are included in the analyses (it overestimates the height of large trees, Feldpausch et al., 2011) and asymptotic models should be preferred. The power law model is indeed useful for restricted datasets but unrealistic biologically because of the basic assumption of factors limiting tree growth in height but not in diameters (Molto et al., 2014). In addition, we found that the value of the scaling coefficient for the 15 species- and site-specific power law models fitted in this study was lower than the theoretical 2/3 exponent predicted by the metabolic theory (West et al., 1997) in agreement with the results of Muller-Landau et al. (2006) for ten old-growth tropical forests. Given the importance of large trees for forest structure and specifically the estimation of above-ground biomass (Bastin et al., 2013; Slik et al., 2013), the questions of both the sampling of species and trees, and the model choice should be carefully addressed for establishing adequate site-specific height-diameter allometric equations.

### Table 4

Above-ground-biomass stock in relation to forest structure in the evergreen forest of the Ma’an site and in the semi-deciduous forest of the Mindourou site in Cameroon. Stem density and basal area per hectare were computed for trees with a diameter > 20 cm. Wood specific gravity values at species level were extracted from the global data base (Chave et al., 2009; Zanne et al., 2009) and averaged at the genus level. Mean value for the trees (and genera) are given for each site. The above-ground biomass (AGB, in kg ha$^{-1}$) for trees with a diameter > 20 cm from inventory data, and for trees with a diameter >10 cm biomass was estimated from stem number estimates in the [10–20] cm diameter class and mean wood specific gravity. A set of six allometric equations without and with height included in the set of predictors were used for AGB estimation: the two models developed by Chave et al. (2005) for moist forests, Eqs. (1) and (2); the two models developed by Chave et al. (2005) for wet forests, Eqs. (3) and (4); and the two models developed by Chave et al. (2014) for all tropical forests, Eqs. (5) and (6). $H$ was estimated from the diameter data with the best site-specific equations (m5 and m10 for the Ma’an and Mindourou sites, respectively, Table 2).

<table>
<thead>
<tr>
<th>Forest structure</th>
<th>Ma'an site (evergreen forest)</th>
<th>Mindourou site (semi-deciduous forest)</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>2101 plots</td>
<td>5152 plots</td>
</tr>
<tr>
<td>Stem density (ha$^{-1}$)</td>
<td>124.8 ± 1.07</td>
<td>142.8 ± 0.49</td>
</tr>
<tr>
<td>Basal area (m$^2$ ha$^{-1}$)</td>
<td>15.2 ± 0.12</td>
<td>17.5 ± 0.08</td>
</tr>
<tr>
<td>Wood density (g cm$^{-3}$)</td>
<td>0.608 (0.611)</td>
<td>0.621 (0.606)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Above-Ground Biomass (kg ha$^{-1}$)</th>
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<tbody>
<tr>
<td>For trees with a diameter &gt; 20 cm</td>
</tr>
<tr>
<td>AGB = $f(D)$, D) moist (1)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, H) moist (2)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, wet (3)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, H, wet (4)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, E,5 (5)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, H, (6)</td>
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</table>

<table>
<thead>
<tr>
<th>For trees with a diameter &gt; 10 cm</th>
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<tbody>
<tr>
<td>AGB = $f(D)$, D) moist (1)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, H) moist (2)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, wet (3)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, H, wet (4)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, E,5 (5)</td>
</tr>
<tr>
<td>AGB = $f(D)$, D, H, (6)</td>
</tr>
</tbody>
</table>
4.3. The low biomass per hectare in central African forests

Our biomass estimates, 259.7 and 347.6 Mg dry mass ha⁻¹ for trees with a diameter >10 cm for the evergreen and the semi-deciduous forests, respectively, are in the range of reported values across the Congo basin (Djuikouo et al., 2010; Gourlet-Fleury et al., 2011; Kearsley et al., 2013; Lewis et al., 2013; Maniatis et al., 2011; Mermoz et al., 2015). In agreement with the results of Kearsley et al. (2013) in Yangambi, our biomass estimates are lower than the average values of 395.7 Mg dry mass ha⁻¹ across 260 plots in central Africa reported by Lewis et al. (2013) and of 418.3 Mg dry mass ha⁻¹ across 45 plots reported by Slik et al. (2013) for tropical Africa, though these low biomass values are not necessarily attributed to low tree height values. The choice of an appropriate allometric model is the most critical step in the estimation of forest biomass and carbon stocks (Chave et al., 2004; Molto et al., 2013) and we found strong differences in biomass estimates depending on the choice of the allometric model. The predictions of the allometric models developed by Chave et al. (2005) for moist forests were not strongly different from that of the reference model, i.e. the most recent pantropical model (Chave et al., 2014) including site-specific height-diameter allometry, in the Mindourou site, thus confirming our previous results of a moist allometry based on destructive measurements (Fayolle et al., 2013). In contrast, the intermediate height-diameter allometry between wet and moist forests reported for the M’a’an site in this study needs further investigation. This specific result and the significant biases associated with regional height-diameter models (Kearsley et al., 2013; Rutishauser et al., 2013; Thomas et al., 2015) confirmed the need for local site-specific models (Chave et al., 2014).

5. Conclusions

The aim of this study was to identify the variation in tree height-diameter allometry of tropical trees between forest types and/or among species in southern Cameroon. We identified that the shape of the height-diameter allometry was clearly asymptotic at species level. We demonstrated that height-diameter allometry strongly varies between forest types, and that published regional and local models produced biased height predictions for the studied forest types. We also showed strong between-site differences in height-diameter allometry, and similar trends were observed within species for the three species shared by both forest types, suggesting an environmental control on tree height-diameter allometry. In addition to tree allometry variation, structural differences (basal area and density) were also identified between the two forest types, and both allometry and forest structure (taller trees and denser stands) contributed to the greater biomass of the semi-deciduous forest.

Acknowledgments

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Appendix A-D: Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.04.033.

References


