*Acta Botanica Brasilica*, 2022, 36: e2020abb0475
doi: 10.1590/0102-33062020abb0475

Original article

# Complementary allometric model of understory tree biomass in the semi-deciduous rainforest of Cameroon

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Received: November 03, 2020
Accepted: April 20, 2022

## ABSTRACT

Forest understorey contains remarkable plant diversity, contributing to the heterogeneous environments for other biotic gatherings and soil supplement aggregations. Nonetheless, the biomass of the understorey vegetation is neglected because of the lack of appropriate allometric equations without which there are uncertainties in biomass estimation. This study was aimed at developing multispecies allometric equations that will be used to estimate the aboveground biomass of different compartments (trunk, crown, and leaves) of understorey trees in the semi-deciduous rainforest of Cameroon. Understorey tree diameter (1.0-10.0 cm), height, and crown diameter were measured on 1023 trees as biomass predictors. The results showed that the fit of the model improves with more predictive variables, four of which were considered in all studied compartments (trunk, crown, and leaves). Existing specific and pantropic allometries based on diameter tend to overestimate the aboveground biomass of understorey trees when compared to the allometry developed in this study. This study highlighted the importance of a specific aboveground biomass allometric equation for understorey trees. Furthermore, the multispecies allometric equation developed for understorey trees complements those recently developed for overstorey trees, thereby contributing to the total aboveground woody biomass estimation in semi-deciduous forest in the Congo Basin.

**Keywords:** understorey trees, multispecies allometric equations, aboveground biomass, predictive variables, semi-deciduous rainforest, Cameroon

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## Introduction

There is a remarkable plant diversity in the forest understorey stratum (Nilsson & Wardle 2005), contributing to auxiliary multifaceted nature, heterogeneous environments for other biotic gatherings, disintegration, supplement stream, and soil supplement aggregation (Whigham 2004; Su *et al*. 2019). Despite that understory, vegetation represents a moderately small amount of biomass within a forest ecosystem (Kabelong *et al*. 2018; Zekeng *et al*. 2020), it plays an essential role in energy cycling because of its high turnover rate (Kumar *et al*. 2018; Hubau *et al*. 2019). Although large trees are being projected as the major carbon sinks in mature forests (Bastin *et al*. 2015; Hubau *et al*. 2019), it is essential to consider the undergrowth biomass. This is vital for climate change mitigation in the context of different strata of the forest carbon pool. For instance, undergrowth in a semi-deciduous rainforest in Cameroon contribute a non-negligible amount of 3 % total aboveground biomass (AGB) (Chimi *et al*. 2018), revealing the necessity of taking into account all carbon pools within a forest ecosystem (Zekeng *et al*. 2020). Nevertheless, harvesting woody plants to calibrate an allometric equation is labour intensive especially for trees less than 10 cm in diameter at breast height. As a result, small diameter understorey trees have been disregarded when assessing forest biomass and consequently underestimating total aboveground biomass (Tabue *et al*. 2016).

Several studies on forest biomass assessment using allometric equations have focused solely on estimating tree biomass for large trees with a diameter at breast height (DBH) ≥ 5 cm. The existence of a multitude of allometric equations developed for those large trees (Chave *et al*. 2005; 2014; Fayolle *et al*. 2018) is not necessarily applicable for stems less than 5 cm in diameter even though understorey species are also important. These trees' allometric equations are not suitable for estimating the aboveground biomass (AGB) of understory vegetation because of their restriction in the DBH range and different growth forms and physiognomies compared to trees (Ali *et al*. 2015). The choice of the allometric equation is among the factors responsible for inflating uncertainties in AGB prediction and this can contribute up to 76 % of error in AGB estimates (Quentin *et al*. 2014; Picard *et al*. 2015). The specific equations linked to a site, to an ecosystem, to a species (Basuki *et al*. 2009), or across a large pantropical zone (Chave *et al*. 2014) will reduce uncertainties and increase precision in estimating biomass. For example, despite the fact that the use of the pantropical equation of Chave *et al*. (2005) had been validated using data from South Cameroon (Fayolle *et al*. 2013), this is often criticised for not taking into account data from tropical Africa (Djomo *et al*. 2010). This deficiency is corrected by introducing the Congo Basin data and developing general equations for moist tropical forests (Chave *et al*. 2014).

Site-specific allometric equations for seven forest types/strata in the Congo Basin have been developed (Fayolle *et al*. 2018). However, they do not take into account stems less than 10 cm in diameter. Studies report that in the error structure, a systematic AGB overestimation is more critical for small trees (*e.g.* Chave *et al*. 2014). Considering that very few allometric equations for understorey trees have been developed in the past (Djomo *et al*. 2010; Conti *et al*. 2013; Ali *et al*. 2015; Djomo & Chimi 2017; Puc-Kauil *et al*. 2020), it is crucial and necessary to improve knowledge in this discipline as understorey vegetation is an essential component of forest productivity (Kabelong *et al*. 2018; Zekeng *et al*. 2020) and structure (Wu *et al*. 2016). Forest biomass and/or carbon stocks are essential in international policy implementation, such as the REDD+ mechanism and payment for ecosystem services (Ebeling & Yasue 2008). Therefore, this research is useful because allometric equations can contribute to researchers' needs in assessing total and component biomass for carbon accounting.

Few studies (Djomo *et al*. 2010; Djomo & Chimi 2017) have so far developed the allometric equations for understorey trees in Cameroon. However, these studies show some limitations. For example, increasing the sample size in the field to decrease sampling error and hence reduce uncertainty in biomass estimation requires additional costs and time, energy, and funds. Djomo & Chimi (2017) attempted to improve the quality of such equations developed in the past (Djomo *et al*. 2010). They noted that: (i) multispecies equations used for biomass estimation are more performant than general equations; (ii) consistent with the results of Xu *et al*. (2015), consideration of several variables in the development of an equation for biomass estimation reduces uncertainty. Despite all improvement, the specific equations for understory trees developed by Djomo & Chimi (2017) are still criticised due to the low sample size and inclusion of a large range of diameter classes. Another study in a semi-evergreen forest of Mexico, considered only 311 trees belonging to 22 species to develop general allometric equations for understorey trees (Puc-Kauil *et al*. 2020). However, it did not consider the tree crown diameter, which appears to be an essential additional predictive variable that could improve the model's adjustment (Djomo & Chimi 2017).

Our objective was to develop a local multispecies allometric equation needed to estimate the biomass of understorey trees, and their compartments (trunk, crown, and leaves). Specifically, the relative performance of different measurement variables in predicting AGB were tested and compared with the existing models.

## Material and methods

### Study area

This study was carried out in a semi-deciduous rainforest in the East region of Cameroon. The site for data collection was geographical located between 3° 20' and 3° 63' N and 13°

25' and 13° 85' E. The elevation of this site varies between 561 to 620 m (average~600 m). The annual precipitation varies from 1500 to 2000 mm with an average of 1800 mm.year$^{-1}$. The mean annual temperature is between 23 and 25 °C during the year. The climate is of the equatorial type with four seasons including two dry seasons: long (December to February) and short (July to August); and two rainy seasons: long (March to June) and short (September to November) (Anonymous 2012). The soil is lateritic and the bedrock is made up of granite and metamorphic rocks (Moby *et al*. 1979). This area belongs to the semi-deciduous rainforest (Letouzey 1985). The most common tall canopy species prominent in this forest type are *Staudtia kamerunensis* Warb., *Pausinystalia macroceras* (K.Schum.) Pierre ex Beille, *Celtis* spp., *Chrysophyllum* spp., *Terminalia superba* Engl. & Diels and *Antiaris toxicaria* (Engl.) C. C. Berg. etc., while species with large trunks and undulating canopies (*e.g.*, *Entandrophragma* spp., *Triplochiton scleroxylon* K.Schum. *Milicia excelsa* (Welw.) C.C.Berg) characterize this forest type (Letouzey 1985). The floristic composition of the study forest with the common species found in the understorey strata as follows: *Tabernaemantana crassa* (8.53 %), *Rinorea batesii* (8.19 %), *Drypetes* sp. (5.69 %), *Polyalthia suaveolens* (3.87 %), *Voacanga africana* (3.41 %), *Diospyros gabunensis* (3.07 %), *Trichilia heudellotii* (2.16 %) and *Calpocalyx dinklagei* (2.05 %) (Ntonmen *et al*. 2020).

## Data collection

AGB and several measurement variables (diameter, height, crown diameter, and wood density) were measured on 1023 understorey stems belonging to 184 species before the extraction of physical samples through the destructive method (Tab. 1). For the 230 stems with a diameter class 5-10 cm, hereafter call saplings, measurement of variables was conducted in 15 random plots of 20 m x 20 m, while 793 stems of diameter class 1-5 cm hereafter called seedlings were collected in each sub-plots 10 m x 10 m of the 20 m x 20 m plots.

The diameter was measured at 30 cm aboveground level, representeding the reference level for diameter measurement of trees with diameter <10 cm (Djomo & Chimi 2017). The total height was obtained directly on felled trees. The crown diameter of the upright stem was obtained by averaging the North/South and East/West orientations of crown diameters (Djomo & Chimi 2017).

Wood density was determined using three samples collected at the base, trunk, and branches of the stems. It was calculated using the following formula (Nogueira *et al*. 2005): $wood\ density\ (\rho) = \dfrac{dry\ weight}{fresh\ volume}$ (1).

This formula is recommended for wood density determination. It applies for biomass estimation using allometric equations (Henry *et al*. 2010). The wood density of each understorey stem used to develop allometric equations corresponds to the mean wood density of the three compartments (base, trunk, and branches of the tree).

The total fresh weight of the trunk, the branches, and the leaves of each stem was weighed with an electronic suspension balance (max = 40 kg; precision = 1g). The total fresh aboveground biomass of each stem corresponds to the sum of the fresh mass of trunk + branches without leaves + leaves. Samples of these compartments were collected (samples having an average weight of 50 g) on each stem and their fresh mass, and fresh volume measured directly on the field with the help of the laboratory balance (max=2000g; precision=0.01g) (Djomo *et al*. 2017). The water displacement method (Archimede's principle) was applied to fresh volume determination (Henry *et al*. 2010). Leaf biomass was measured on collected samples using the laboratory balance. For each stem, samples (the base, trunk, and branches) were collected for further laboratory analysis.

Dry weight and wood density for each samples collected in the field were oven-dried at 105 °C (for tree samples) and 70 °C (for leaf samples) in the Plant Systematics and Ecology laboratory of the University of Yaoundé 1 (Brown & Pearson 2005).

## Data analysis

### Covariables and model form

The relationships between the response variables representing the understorey biomass (i.e., total AGB, AGB of the trunk, the biomass of the crown, and the leaves) and measurement variables (i.e., diameter, height, crown diameter, and wood density) were tested. Several existing allometric forms frequently used in the literature (*e.g.* Djomo *et al*. 2010; Alvarez *et al*. 2012; Picard *et al*. 2012; Fayolle *et al*. 2018) to establish relationships between biomass and predictors were also tested. The model form that satisfied the heteroscedasticity of variance and whose residues satisfied the conditions for normality after logarithmic

**Table 1.** Descriptive analysis of data used in the establishment of understorey allometric equations.

| Statistics | Diameter (cm) | Height (m) | Wood density (g.cm$^{-3}$) | Crown diameter (cm) | Leaves biomass (kg) | Branches biomass (kg) | Trunk biomass (kg) | Aboveground biomass (kg) |
|---|---|---|---|---|---|---|---|---|
| Mean | 3.15 | 4.00 | 0.561 | 1.49 | 0.141 | 0.755 | 1.43 | 2.228 |
| SD | 2.19 | 2.50 | 0.100 | 0.92 | 0.193 | 1.586 | 2.625 | 3.981 |
| Min | 1.00 | 0.86 | 0.156 | 0.19 | 0.002 | 0.003 | 0.002 | 0.008 |
| Max | 9.99 | 15.55 | 0.914 | 7.55 | 1.274 | 16.788 | 20.877 | 35.549 |
| Number | 1023 | 1023 | 1023 | 1010 | 311 | 1023 | 1023 | 1023 |

transformation were selected (Xiao *et al*. 2011; Djomo & Chimi 2017).

Figure 1 shows the log-linear relationship between the biomass of leaves, crown diameter, trunk, and total AGB with tree diameter considered by several authors (*e.g.* Djomo *et al*. 2010, Xiao *et al*. 2011; Djomo & Chimi 2017; Fayolle *et al*. 2018) as principal predictive variable. Over 30 models were tested. The first tested models were those that employ the diameter of the understorey as the main principal variable. Secondly, different multiplicative combinations of variables of diameter, total height, wood density, and crown diameter were tested. The general model established was in the form: $ln(M) = a + b \times ln(X1) + c \times ln(X2) + \ldots + n \times ln(Xn)$ (3) and exponential transformation $M = e^{(a + b \times lnln(X1) + c \times lnln(X2) + \ldots + n \times lnln(Xn))}$ (4); where M is the biomass, a, b, c, ..., n the coefficients and X1, X2,...Xn the predictive variables. The correction factor (CF) calculated by the formula CF= $RSE^2/2$ (5); was used to correct the systematic bias due to the log transformation applied to the models (Djomo *et al*. 2016).

### *Performance criteria of the models' estimation*

Three performance parameters were calculated and used to compare the performances of the different models. The performance parameters were used to select the best models for the prediction of total AGB and AGB compartments. These performance parameters include (i) Akaike Information Criterion (AIC) (Akaike 1974), which measures the goodness of fit in a regression model. The allometric equation with the least AIC value is considered the best estimator (Chave *et al*. 2005); (ii) Residual Standard Error of the model (RSE): square root of the residual variance around the regression function. The allometric equation with the least AIC and RSE value are considered the best estimator (Chave *et al*. 2005). (iii) The Adjusted coefficient of determination (Adj. $R^2$) corrects the coefficient of determination by accounting for an increasing number of independent variables.

### *Validation of the models*

The model validation was done by comparing the predicted biomass using the model(s) with those of biomass observed in the field. These models were evaluated based on parameters like the Relative Root Mean Square Error (RRMSE) and the average error (%). The following formulae used for the determination of RRMSE and average error (in %) were respectively:

$$RRMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(\frac{M_{pi} - M_i}{M_i}\right)^2} \quad (6);$$

and the $average\ error\,(\%) = 100 \times \frac{1}{n}\sum_{i=1}^{n}\left(\frac{M_{pi} - M_i}{M_i}\right)$ (7)

$M_{pi}$ represents the predicted dry weight of understorey tree i, $M_i$ the observed dry weight, and n number of understorey trees used.

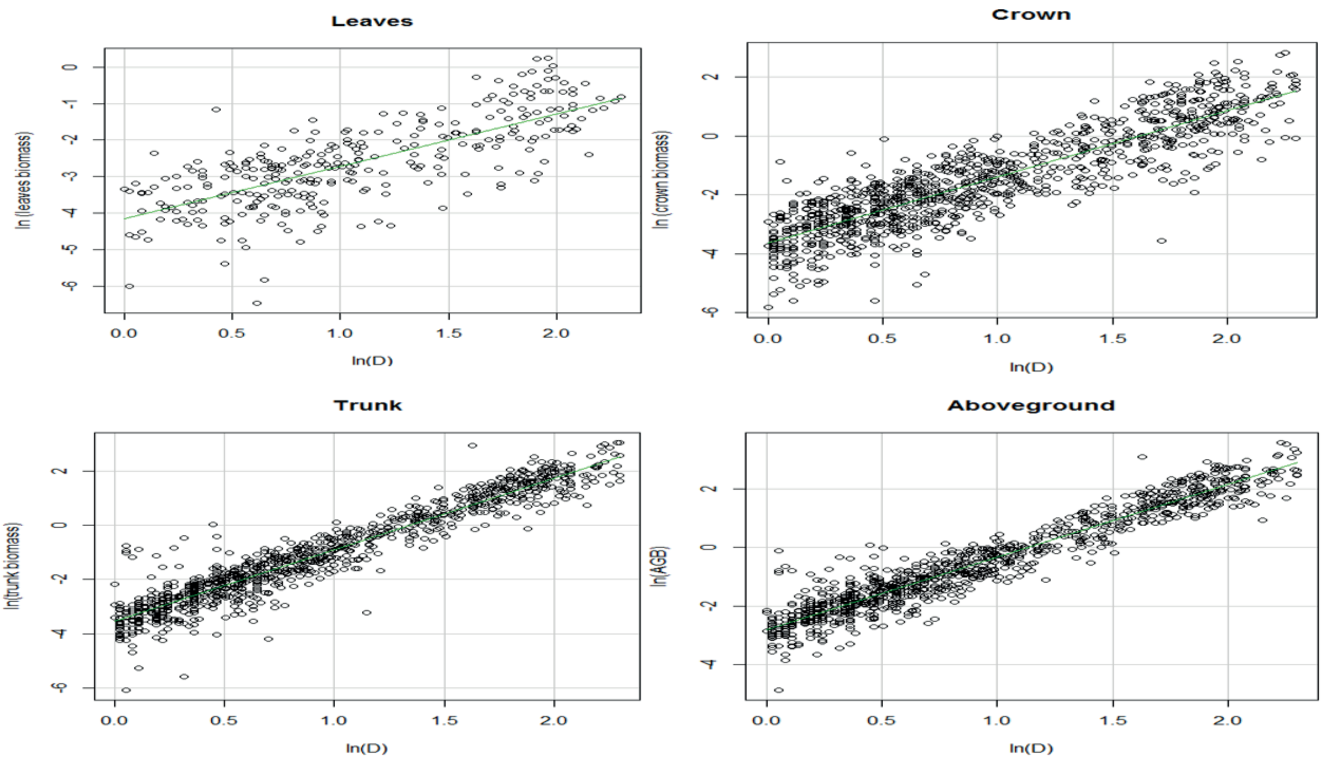

**Figure 1.** Log-log relationship between leaves, crown, trunk versus aboveground biomasses and principal predictive variable (diameter) of understorey.

### *Fitting strategy comparison with existing equation*

Some authors have established equations for aboveground biomass estimation which include data of sapling (diameter 5-10 cm) (Chave *et al*. 2005; 2014; Fayolle *et al*. 2013). Others consider in their data set those of seedlings (diameter 1-5 cm) in the Congo Basin forest (Djomo & Chimi 2017). Average error (in %), RMSE, RRMSE, total AGB (kg), mean biomass, and % ratio (estimated total or mean biomass-observed biomass/ observed biomass) have been used to compare these equations based on biomass data measured on the field during this study. The equations that considered AGB were those of Djomo *et al*. (2010; 2016), Chave *et al*. (2005; 2014), and Djomo & Chimi (2017). Furthermore, the best local multispecies or pantropical equations used so far are reported by these authors. The same rules were also applied for leaves, trunk, and crown biomass equations in this study area. For leaf biomass equations, comparisons was made with equations of Djomo *et al*. (2010) and Henry *et al*. (2010), while for the trunk biomass equations, equations of Henry *et al*. (2010); Djomo & Chimi (2017) established respectively in a dry and moist tropical forest were considered. For the crown biomass equation, only the equation of Djomo & Chimi (2017) was considered.

## Results

### *Allometric equations for aboveground biomass of understorey stems*

Multispecies allometric equations were developed for the estimation of AGB for seedlings, saplings, and understorey trees. The best model for estimating biomass of understorey trees was obtained using the four predictive variables (diameter, height, crown diameter, and wood density). These models accounted for 76 % to 96 % of the AGB variations (Tab. 2).

Moreover, it was found that the quality of the fit improved with the increasing number and nature of predictors considered in the model. Hence, equations taking into account the diameter alone only accounted for 39-92 % of the variation in AGB. Considering two variables, the model improved with respect to the predictive variables. The equation involving diameter and wood density was the best, accounting for 59-94 % of the variation in AGB,

**Table 2.** Allometric equations for the estimation of total aboveground biomass of the understorey.

| Models | Model parameters | | | | | Performance criteria | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | a | b | c | d | RRMSE | RSE | Adj.R$^2$ | AIC | CF | Average error (%) |
| **1≤ diameter ≤5 cm (seedlings)** | | | | | | | | | | | |
| $\ln M= a + b \times \ln(D)$ | 793 | $-2.785^{***}$ | $2.416^{***}$ | | | 0.243 | 0.483 | 0.816 | 1101 | 0.12 | 1.68 |
| $\ln M= a + b \times \ln(D) + c \times \ln(H)$ | 793 | $-3.180^{***}$ | $1.599^{***}$ | $0.954^{***}$ | | 0.219 | 0.432 | 0.853 | 926 | 0.09 | 1.86 |
| $\ln M= a + b \times \ln(D) + c \times \ln(\rho)$ | 793 | $-2.145^{***}$ | $2.451^{***}$ | $1.120^{***}$ | | 0.200 | 0.433 | 0.852 | 928 | 0.09 | 0.22 |
| $\ln M= a + b \times \ln(D) + c \times \ln(C)$ | 793 | $-2.527^{***}$ | $0.593^{***}$ | $1.989^{***}$ | | 0.308 | 0.447 | 0.844 | 967 | 0.10 | -15.12 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln(\rho)$ | 793 | $-2.529^{***}$ | $0.860^{***}$ | $1.077^{***}$ | | 0.185 | 0.381 | 0.886 | 723 | 0.07 | 0.65 |
| $\ln M= a + b \times \ln(D) + c \times \ln(H) + d \times \ln(C)$ | 793 | $-2.924^{***}$ | $1.400^{***}$ | $0.807^{***}$ | $0.452^{***}$ | 0.197 | 0.410 | 0.868 | 835 | 0.08 | 1.44 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln(\rho) + d \times \ln(C)$ | 793 | $-2.377^{***}$ | $0.767^{***}$ | $0.997^{***}$ | $0.365^{***}$ | 0.170 | 0.364 | 0.896 | 648 | 0.07 | 0.61 |
| **5< diameter ≤10 cm (saplings)** | | | | | | | | | | | |
| $\ln M= a + b \times \ln(D)$ | 230 | $-1.768^{***}$ | $1.944^{***}$ | | | 0.577 | 0.432 | 0.394 | 271 | 0.09 | 19.74 |
| $\ln M= a + b \times \ln(D) + c \times \ln(H)$ | 230 | $-2.576^{***}$ | $1.371^{***}$ | $0.937^{***}$ | | 0.434 | 0.382 | 0.527 | 215 | 0.07 | 14.54 |
| $\ln M= a + b \times \ln(D) + c \times \ln(\rho)$ | 230 | $-1.494^{***}$ | $2.206^{***}$ | $1.247^{***}$ | | 0.479 | 0.357 | 0.587 | 184 | 0.06 | 13.45 |
| $\ln M= a + b \times \ln(D) + c \times \ln(C)$ | 230 | $-1.643^{***}$ | $1.602^{***}$ | $0.555^{***}$ | | 0.496 | 0.389 | 0.485 | 218 | 0.08 | 16.45 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln(\rho)$ | 230 | $-2.230^{***}$ | $0.836^{***}$ | $1.151^{***}$ | | 0.356 | 0.308 | 0.692 | 116 | 0.05 | 10.23 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln(C)$ | 230 | $-2.464^{***}$ | $0.671^{***}$ | $0.509^{***}$ | | 0.394 | 0.341 | 0.605 | 159 | 0.06 | 11.73 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln(\rho) + d \times \ln(C)$ | 230 | $-2.151^{***}$ | $0.738^{***}$ | $1.088^{***}$ | $0.473^{***}$ | 0.889 | 0.266 | 0.760 | 49 | 0.04 | 70.06 |
| **All (1≤ diameter <10 cm)** | | | | | | | | | | | |
| $\ln M= a + b \times \ln(D)$ | 1023 | $-2.811^{***}$ | $2.474^{***}$ | | | 0.199 | 0.475 | 0.918 | 1384 | 0.11 | 0.11 |
| $\ln M= a + b \times \ln(D) + c \times \ln(H)$ | 1023 | $-3.215^{***}$ | $1.665^{***}$ | $0.958^{***}$ | | 0.192 | 0.423 | 0.935 | 1149 | 0.09 | 2.45 |
| $\ln M= a + b \times \ln(D) + c \times \ln(\rho)$ | 1023 | $-2.144^{***}$ | $2.505^{***}$ | $1.164^{***}$ | | 0.184 | 0.419 | 0.936 | 1126 | 0.09 | 1.16 |
| $\ln M= a + b \text{ v } \ln(D) + c \times \ln(C)$ | 1023 | $-2.550^{***}$ | $2.041^{***}$ | $0.595^{***}$ | | 0.187 | 0.437 | 0.930 | 1196 | 0.10 | 2.16 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln(\rho)$ | 1023 | $-2.554^{***}$ | $0.880^{***}$ | $1.100^{***}$ | | 0.158 | 0.367 | 0.951 | 854 | 0.07 | 1.10 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln(C)$ | 1023 | $-2.924^{***}$ | $0.750^{***}$ | $0.473^{***}$ | | 0.167 | 0.397 | 0.942 | 1005 | 0.08 | 1.99 |
| $\ln M= a + b \times \ln(D^2 \times H) + c \times \ln (\rho) + d \times \ln(C)$ | 1023 | $-2.385^{***}$ | $0.779^{***}$ | $0.779^{***}$ | $0.392^{***}$ | 0.373 | 0.346 | 0.956 | 728 | 0.06 | 13.36 |

Note: The statistical analyses are significant at 95% confidence interval. $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$. P-value of all models: <0.0001; D: diameter of trees analysed (in DBH); H: height of trees; ρ: wood density; C: crown diameter; N: sample size; a, b, c and d are the model's fitted parameters; RRMSE: Relative Root mean error; RSE: residual standard error of the estimation; AdjR2: adjusted coefficient of determination; AIC: Akaike Information Criterion and CF: correction factor.

followed by the one involving diameter and height (Adj.$R^2$ = 53-94 %) and finally by the one considering the diameter and crown diameter (Adj.$R^2$= 39-45 %). The results also showed that model adjustment increase more when using three variables and that the model which took into account the diameter, height, and the wood density account for 69-95 % of AGB variation and was better than the one taking into accounted the diameter, height, and diameter of the crown (Adj.$R^2$=61-94 %; Tab. 2).

## *Allometric equations for estimating aboveground biomass of understorey compartments*

Such as the local multispecies model, the equations using a combination of the four predictive variables were the best models accounting for 65 to 94 % of the biomass of tree compartments (Tab. 3). Furthermore, the trunk of the trees showed the best model adjustment (Adj.$R^2$>90 %) compared to the tree crown (Adj.$R^2$>75 %) and leaves (Adj.$R^2$>55 %). The crown diameter and tree diameter, compared to the height and wood density variables taken individually improved the model fit of different compartments; except for the tree trunk. Indeed, for the trunk biomass estimation models, the tree diameter appears to be a good predictor of its biomass (AIC=1633; RSE=0.537; Adj.$R^2$=0.908). When combined with the diameter and the height (AIC=1367; RSE=0.471; Adj.$R^2$=0.929), the second parameter that improved the model's adjustment was noted, followed by the crown diameter (AIC=1606; RSE=0.534; Adj.$R^2$=0.909). When four variables were considered in the same model, the quality of the adjustment was the best (AIC=1206; RSE=0.438; Adj.$R^2$=0.939).

The crown diameter was another principal predictive variable for the leaves and crown biomass model, such as the tree diameter. It was shown that when only one principal predictive variable in the leaves and crown models was considered, the leave biomass model adjustment was better improve with the tree diameter (AIC=730; RSE=0.781; Adj.$R^2$=0.553) than the crown diameter (AIC=729; RSE=0.785; Adj.$R^2$=0.550). A similar result was obtained for the crown model. Meanwhile, models for the trunk and the crown biomass

**Table 3.** Allometric equations for estimations of the total aboveground biomass of leaves, crown and trunk of understorey (M).

| Models | Model parameters | | | | | | Performance criteria | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | a | b | c | d | e | RRMSE | RSE | Adj.$R^2$ | AIC | CF | Average error (%) |
| **Leaves** | | | | | | | | | | | | |
| $\ln M = a + b \times \ln(D)$ | 311 | -4.158$^{***}$ | 1.436$^{***}$ | | | | 0.168 | 0.781 | 0.553 | 730 | 030 | 0.21 |
| $\ln M = a + b \times \ln(C)$ | 311 | -3.229$^{***}$ | 1.679$^{***}$ | | | | 0.170 | 0.785 | 0.550 | 729 | 0.31 | -0.44 |
| $\ln M = a + b \times \ln(D^2 \times H)$ | 311 | -4.371$^{***}$ | 0.505$^{***}$ | | | | 0.165 | 0.772 | 0.563 | 723 | 0.30 | 0.36 |
| $\ln M = a + b \times \ln(D) + c \times \ln(\rho)$ | 311 | -3.507$^{***}$ | 1.474$^{***}$ | 1.111$^{***}$ | | | 0.166 | 0.743 | 0.593 | 701 | 0.28 | 0.19 |
| $\ln M = a + b \times \ln(D) + c \times \ln(C)$ | 311 | -3.833$^{***}$ | 0.826$^{***}$ | 0.917$^{***}$ | | | 0.165 | 0.724 | 0.618 | 680 | 0.26 | 0.02 |
| $\ln M = a + b \times \ln(D^2 \times H) + c \times \ln(\rho)$ | 311 | -3.755$^{***}$ | 0.515$^{***}$ | 1.047$^{***}$ | | | 0.164 | 0.739 | 0.600 | 696 | 0.27 | 0.28 |
| $\ln M = a + b \times \ln(D^2 \times H) + + c \times \ln(C)$ | 311 | -3.700$^{***}$ | 0.299$^{***}$ | 0.878$^{***}$ | | | 0.149 | 0.722 | 0.620 | 679 | 0.26 | 1.65 |
| $\ln M = a + b \times \ln(D) + c \times \ln(H) + d \times \ln(\rho) + e \times \ln(C)$ | 311 | -3.505$^{***}$ | 0.817$^{***}$ | 0.160$^{ns}$ | 0.895$^{***}$ | 0.779$^{***}$ | 0.105 | 0.698 | 0.645 | 659 | 0.24 | 12.99 |
| **Crown (branches+leaves)** | | | | | | | | | | | | |
| $\ln M = a + b \times \ln(D)$ | 1021 | -3.630$^{***}$ | 2.239$^{***}$ | | | | 0.574 | 0.772 | 0.775 | 2374 | 0.30 | 12.87 |
| $\ln M = a + b \times \ln(C)$ | 1021 | -2.147$^{***}$ | 2.515$^{***}$ | | | | 0.502 | 0.801 | 0.758 | 2415 | 0.32 | 13.97 |
| $\ln M = a + b \times \ln(D^2 \times H)$ | 1021 | -3.958$^{***}$ | 0.786$^{***}$ | | | | 0.589 | 0.756 | 0.785 | 2330 | 0.29 | 13.46 |
| $\ln M = a + b \times \ln(D) + c \times \ln(\rho)$ | 1021 | -2.807$^{***}$ | 2.278$^{***}$ | 1.439$^{***}$ | | | 0.552 | 0.721 | 0.804 | 2234 | 0.26 | 10.01 |
| $\ln M = a + b \times \ln(D) + c \times \ln(C)$ | 1021 | -3.060$^{***}$ | 1.296$^{***}$ | 1.300$^{***}$ | | | 0.548 | 0.651 | 0.841 | 1997 | 0.21 | 8.23 |
| $\ln M = a + b \times \ln(D) + c \times \ln(H) + d \times \ln(\rho)$ | 1021 | -3.099$^{***}$ | 1.745$^{***}$ | 0.629$^{***}$ | 1.392$^{***}$ | | 0.574 | 0.707 | 0.812 | 2196 | 0.25 | 10.42 |
| $\ln M = a + b \times \ln(D) + c \times \ln(H) + d \times \ln(C)$ | 1021 | -3.235$^{***}$ | 1.035$^{***}$ | 0.356$^{***}$ | 1.247$^{***}$ | | 0.554 | 0.646 | 0.843 | 1984 | 0.21 | 8.60 |
| $\ln M = a + b \times \ln(D) + c \times \ln(H) + d \times \ln(\rho) + e \times \ln(C)$ | 1021 | -2.603$^{***}$ | 1.162$^{***}$ | 0.318$^{***}$ | 1.145$^{***}$ | 1.155$^{***}$ | 0.507 | 0.606 | 0.861 | 1864 | 0.18 | 6.69 |
| **Trunk** | | | | | | | | | | | | |
| $\ln M = a + b \times \ln(D)$ | 1023 | -3.532$^{***}$ | 2.633$^{***}$ | | | | 1.279 | 0.537 | 0.908 | 1633 | 0.14 | 3.44 |
| $\ln M = a + b \times \ln(D) + c \times \ln(H)$ | 1023 | -4.014$^{***}$ | 1.667$^{***}$ | 1.143$^{***}$ | | | 1.335 | 0.471 | 0.929 | 1367 | 0.11 | 3.33 |
| $\ln M = a + b \times \ln(D) + c \times \ln(\rho)$ | 1023 | -2.972$^{***}$ | 2.659$^{***}$ | 0.978$^{***}$ | | | 1.230 | 0.502 | 0.919 | 1500 | 0.13 | 2.53 |
| $\ln M = a + b \times \ln(D) + c \times \ln(C)$ | 1023 | -3.454$^{***}$ | 2.504$^{***}$ | 0.175$^{***}$ | | | 1.209 | 0.534 | 0.909 | 1602 | 0.14 | 3.60 |
| $\ln M = a + b \times \ln(D) + c \times \ln(H) + d \times \ln(\rho)$ | 1023 | -3.480$^{***}$ | 1.731$^{***}$ | 1.096$^{***}$ | 0.897$^{***}$ | | 1.318 | 0.438 | 0.939 | 1220 | 0.10 | 2.44 |
| $\ln M = a + b \times \ln(D) + c \times \ln(H) + d \times \ln(\rho) + e \times \ln(C)$ | 1023 | -3.509$^{***}$ | 1.766$^{***}$ | 1.113$^{***}$ | 0.912$^{***}$ | -0.067$^{ns}$ | 1.209 | 0.438 | 0.939 | 1206 | 0.10 | 2.31 |

Note: The statistical analyses are significant at 95% confidence interval. $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; and ns (non-significant) $p > 0.05$. P-value of all models: <0.0001 ; D: Diameter of the trees analysed (dbh) ; H : tree height; ρ: wood density ; C : crown diameter; N : the sample size; a, b, c, d and e are the model's fitted parameters; RRMSE : Relative Root Mean Square Error; RSE : residual standard error of the estimate ; Adj.R2 : adjusted coefficient of determination ; AIC : Akaike Information Criterion and CF : correction fator.

estimations were best when the wood density or height was substituted by the crown diameter. As seen with the tree trunk, when four variables were considered in the same model, the adjustment quality was the best, and the trunk adjustment quality was better than for the crown (Tab. 3).

### *Comparing models used in the study area*

This study showed that pantropical equations overestimate the understorey biomass compared to those developed locally by this study (Fig. 2). Figure 2 presents only the overestimation of biomass with the existing equations, which have considered trees with diameter ≥ 1cm in their data set. For trees with a diameter ≥ 1cm, the specific equation of Djomo *et al*. (2010) gave values close to those measured on the field with a difference of +20 %. It was followed by the model of Djomo & Chimi (2017) with the ratio (estimated-measured)/measured) of 46 %. Moreover, the model of Djomo & Chimi (2017) gave a very weak mean error of 55 % (Tab. 4). For trees of diameter ≥5 cm, the equation of Chave *et al*. (2014) provided estimated values nearest to those measured on the field with the ratio (calculated/measured of 54 %) and a mean error of 65 % (Tab 4).

## Discussion

### *Aboveground biomass equations for understorey trees*

Several studies in the moist tropical forest of African ecosystems investigating the composition, structure, diversity, and the potentials of forest carbon stocks are limited to trees of diameter ≥10 cm (Day *et al*. 2013; Lewis *et al*. 2013; Tabue *et al*. 2016). However, considering its temporal dynamics, trees of diameter < 10 cm which represents the future forest cover are currently overlooked (Hakizimana *et al*. 2011). Due to its high turnover rate, understory vegetation plays an essential role in nutrient cycling and energy flow (Kumar *et al*. 2018; Hubau *et al*. 2019). Understorey vegetation also plays a vital role in climate change mitigation (Chimi *et al*. 2018), hence the need for it to be part of carbon quantification in the REDD+ mechanism.

Evaluating forest carbon/biomass potentials requires specific imperative equations (Picard *et al*. 2015). The results of this study appear to be a significant contribution towards assessing the understorey vegetation of the semi-deciduous forests of the Congo Basin. The multispecies equations of this study complete those existing for overstorey trees in the same forest stratum (Fayolle *et al*. 2018), allowing the total quantification of woody biomass in the semi-deciduous forests of the Congo Basin.

Allometric equations represent the proportionality relationship between individual dimensions (*e.g.*, biomass) and tree measurements (Brown *et al*. 1989). The results of this study and those of many other studies (Basuki *et al*. 2009; Chave *et al*. 2005; Fayolle *et al*. 2018) confirm the existence of a direct link between the understorey dendrometric variables and their biomass. These results show that tree diameter is a significant variable in the prediction of forest biomass. Indeed, the percentage of

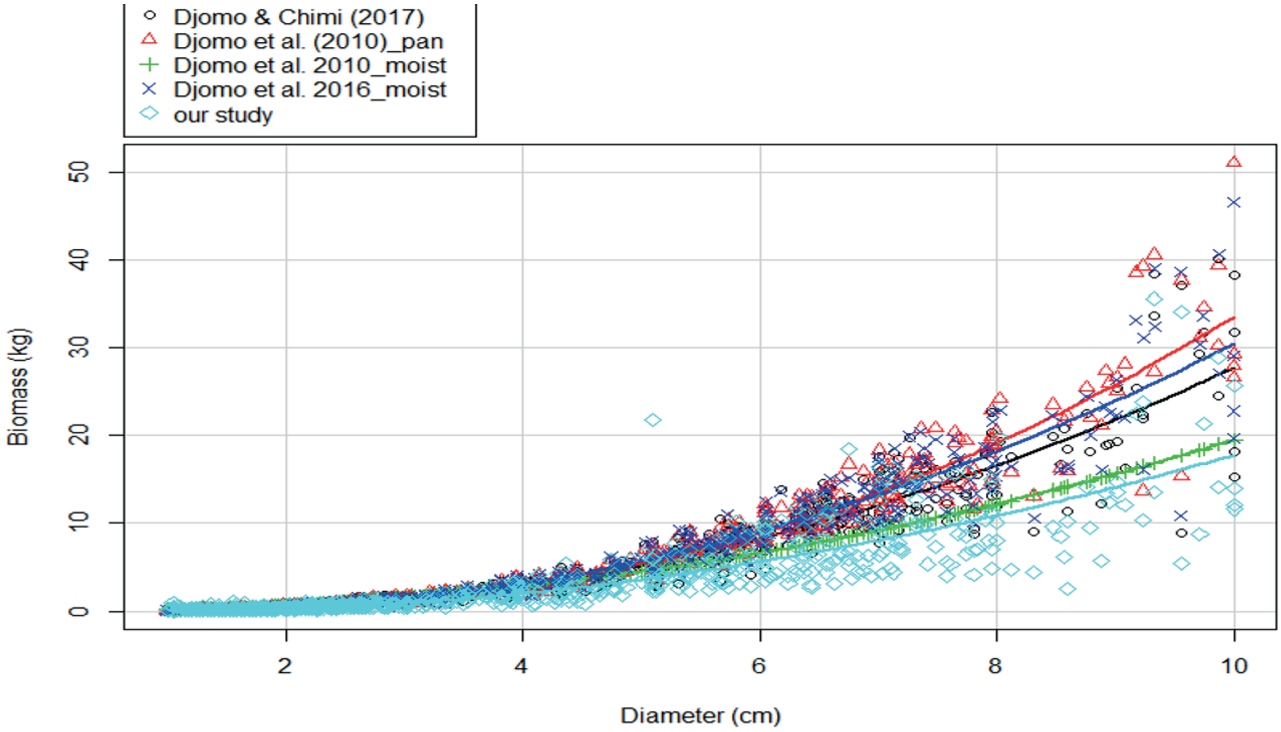

**Figure 2.** Scatter plot of the aboveground biomass of LFST with respect to diameter (cm).

**Table 4.** Comparison of existing and applicable models in our study area. N: the sample size; D: diameter range of trees analysed; RMSE: Root mean square error; RRMSE: Relative Root mean square error; RSE: residual standard error of the estimate.

| Models | Forest type | N | D(cm) | RMSE | RRMSE | Average error (%) | Total (kg) | Mean (kg) | Ratio (% of difference to total or mean) |
|---|---|---|---|---|---|---|---|---|---|
| Aboveground biomass | | | | | | | | | |
| **Comparison of existing and applicable models for tropical moist forest which considered trees diameter>1 cm** | | | | | | | | | |
| Our study (measured AGB; trees≥1 cm) | moist | 1023 | 1-9.9 | - | - | - | 2279.415 | 2.228 | - |
| Djomo *et al.* (2010) | moist | 71 | 1-10 | 2.027 | 1.676 | 105.42 | 2744.763 | 2.683 | 20 |
| Djomo *et al.* (2010) | Pan tropical | 274 | 1-138 | 3.295 | 0.991 | 66.97 | 3647.510 | 3.566 | 60 |
| Djomo *et al.* (2016) | Pan tropical | 570 | 1-212 | 2.951 | 0.875 | 59.71 | 3576.602 | 3.496 | 57 |
| Djomo and Chimi (2017) | moist | 237 | 1-121 | 2.628 | 0.879 | 55.13 | 3317.026 | 3.242 | 46 |
| **Comparison of existing and applicable models for tropical moist forest which considered trees diameter >5 cm** | | | | | | | | | |
| Our study (measured AGB; trees>5 cm) | moist | 230 | 5-9.9 | | | | 1821.356 | 7.908 | |
| Chave *et al.* (2005) | pan tropical | 2410 | 5-315 | 7.386 | 1.251 | 93.51 | 3137.456 | 13.616 | 72 |
| Fayolle *et al.* (2013) | moist | 133 | 5-193 | 7.667 | 1.312 | 100.21 | 3227.529 | 14.001 | 77 |
| Chave *et al.* (2014) | pan tropical | 4004 | 5-315 | 5.987 | 0.830 | 64.99 | 2809.971 | 12.179 | 54 |
| Compartments biomass | | | | | | | | | |
| Our study (leaves biomass measured) | moist | 309 | 1-9.9 | - | - | - | 35.017 | 0.304 | - |
| Djomo *et al.* (2010) | moist | 71 | 1-79 | 0.129 | 1.178 | 30.45 | 31.264 | 0.136 | -11 |
| Henry *et al.* (2010) | Dry forest | 109 | 3-180 | 0.140 | 1.190 | 23.27 | 41.562 | 0.181 | 19 |
| Our study (trunk biomass measured) | moist | 286 | 4-9.9 | - | - | - | 1068.183 | 4.646 | - |
| Henry *et al.* (2010) | Dry forest | 109 | 3-180 | 2.141 | 0.603 | 25.24 | 1150.987 | 5.010 | 8 |
| Djomo and Chimi (2017) | moist | 96 | 4-121 | 5.438 | 1.414 | 105.93 | 2182.506 | 9.500 | 104 |
| Our study (crown biomass measured) | moist | 286 | 4-9.9 | - | - | - | 569.580 | 2.487 | - |
| Djomo and Chimi (2017) | moist | 96 | 4-121 | 1.926 | 3.431 | 60.14 | 451.251 | 1.965 | -21 |

$$1: M = e^{\left(-1.897+2.114\times lnln\,(D)\right)};\quad 2: M = e^{\left(-2.378+0.289\times(ln(D))^2-0.037\times\left(ln(D)\right)^3+0.742\times lnln\,\left(D^2\times H\right)+0.284\times lnln\,(\rho)\right)};\quad 3: M = e^{\left(-2.359+1.325\times lnln\,(D)+0.469\times lnln\,\left(D^2\times H\right)+0.802\times lnln\,(\rho)\right)};$$

$$4: M = e^{\left(-1.836+2.619\times lnln\,(D)+1.268\times lnln\,(\rho)\right)};\quad 5: M = \rho\times e^{\left(-1.499+2.148\times lnln\,(D)+0.207\times(ln(D))^2-0.028\times\left(ln(D)\right)^3\right)};\quad 6: M = \rho\times e^{\left(-1.183+1.940\times ln(D)-0.239\times(l(D))^2-0.029\times\left(lnln\,(D)\right)^3\right)};$$

$$7: M = 0.0673\times(D^2\times H\times\rho)^{0,976}; 8: M = e^{\left(-4.203+1.614\times lnln\,(D)\right)}; 9: M = 0.01\times D^{1.62}\times C^{0.79}; 10: M = 0.09\times D^{2.2}\times\rho^{0.17}; 11: M = e^{\left(-2.931+0.896\times ln(D\hat{}2\times H)\right)};$$

$$12: M = e^{\left(-2.988+2.474\times lnln\,(D)+1.652\times lnln\,(\rho)\right)}.$$

prediction using only the diameter meets the determination coefficient ($R^2$) of more than 90 % obtained in other studies (Brown *et al*. 1989; Basuki *et al*. 2009; Djomo *et al*. 2016).

Some studies have shown that the prediction of biomass can be overestimated if the height or the wood density variables are ignored in the model (Nogueira *et al*. 2005; Ngomanda *et al*. 2014). Faced with this many decades ago, researchers acknowledged that the integration of variables of diameter, height, and wood density permit to take into account all the variability of the trees on a site to provide the best estimation of their biomasses (Nelson *et al*. 1999; Vieilledent *et al*. 2012; Ngomanda *et al*. 2014; Djomo *et al*. 2016; Djomo & Chimi 2017; Fayolle *et al*. 2018). This study confirms the latter. More so, Xu *et al*. (2015) reported that with more than three variables, the consideration of crown diameter as the 4th additional variable in the model provides the best adjustment of the model. Similar results exist in the Chinese forest (Xu *et al*. 2015) and the semi-deciduous forest of East Cameroon (Djomo & Chimi 2017). These four variables permit the understanding of tree architecture's impacts on the dynamics of forest biomass (Goodman *et al*. 2014).

### *Equations for the estimation of biomass in tree compartments*

The models obtained for the leaves and the crown show the importance of considering the crown diameter to estimate their biomass. It is clear that in most cases, during tree growth, architectural morphology also increases (Goodman *et al*. 2014). Theoretically, as a tree grows, its crown becomes more predominant, and the leaves are more abundant. However, such a parameter may be challenging to measure in the field, especially with taller trees (diameter between 5 and 10 cm). In the Congo Basin, this study and the one of Djomo & Chimi (2017) are the only ones to have established the allometric equation for crow diameter estimation.

Moreover, considering the leaves as a tree variable, few studies (Djomo *et al*. 2010; Henry *et al*. 2010) developed equations to estimate the leaf biomass. Contrary to the trunk and crown variables, this study confirms the assertion of previous studies, which indicate that leaf biomass estimation models are less accurate. Indeed, in the tropical forest characterized by an immense floral diversity, leaf size varies mainly according to the species. For example, mega leaves or small leaves describe some species while others, on the contrary, have a tiny number of leaves, and some have many leaves. The low correlation (Fig. 1) could be explained by the high specific diversity (i.e., 184 understorey species) as well as their architectural variability, particularly in their leaves. Therefore, it is recommended that leaf species-specific allometries be developed for more precision in estimating their biomass.

The trunk of the tree is generally assimilated to a more or less cylindrical disc; the quality of adjustment of its model is more precise than those of leaves and crowns. The tree crown like the leaves gives information about the architecture, and this is usually different from one tree to the other in the tropical forest. Contrary to the trunk, given its shape, which is often very cylindrical, whatever the model considers, the allometric equations developed give a more accurate fit (Adj.$R^2 > 0.9$). Similar results exist in the tropical semi-deciduous forest of Cameroon for trees in the group of larger diameter (Ploton *et al*. 2016; Djomo & Chimi 2017).

### Comparison of existing equations

Results of this study were compared with those of specific and pantropical allometric equations available in the literature. These equations, which take into account a wide range of diameters, include those greater than 5 cm in diameter (Chave *et al*. 2014) and greater than 1 cm in diameter (Djomo & Chimi 2017) for the aboveground biomass and estimation for tree components biomass. The comparison shows that the equation of Djomo *et al*. (2010) equations give the estimated aboveground biomass value closest to that measured in the study area. This study shows that the sample size plays a primordial role in the accuracy of the model fit. The sample size seems to be the major cause of the observed differences between our equation and the other equations since their sample size consisted of 96 % of the trees with a diameter <10 cm.

A specific allometric equation is needed for an accurate and reliable estimation of the undergrowth biomass of the semi-deciduous forests of the Congo Basin. Reports show that a specific allometric equation is more efficient and limits the propagation of estimation errors than the pantropical equation (Basuki *et al*. 2009). This explains the deviation observed between measured biomass data on the field in this study's framework with those of the pantropical equation (Djomo *et al*. 2010; 2016). The comparison of equations for the biomass estimation of understorey compartments equally show that: for the leaves, the equation of Djomo *et al*. (2010) underestimate the biomass of leaves in the study area (ratio = -11 %) compared to that of Henry *et al*. (2010) which had a higher value compared to that measured on the field with the ratio = + 19 %. For the trunk biomass, the equation of Henry *et al*. (2010) has the value of biomass nearest to that measured on the field (ratio = +8 %). For the crown's biomass, only the equation of Djomo & Chimi (2017) was considered. The results show that this equation underestimated biomass since it has the most practical value compared to those measured on the field (Tab. 4).

### Conclusion

The choice of the allometric equation in estimating forest biomass is determinant for the efficiency of the expected results. Given the limited number of equations available to estimate understorey biomass, equations developed in the present study appear to constitute a significant contribution and tool for biomass estimation in the semi-deciduous forest of the Congo Basin. This study shows that the quality of the model fit is best (Adj.$R^2 \geq 0.956$) when four predictive variables (diameter, height, wood density, and crown diameter) are considered. The use of available allometric equations (specific and pantropical), with this range of diameter, underestimated 20-77 % of aboveground biomass of understorey trees. Therefore, this study could contribute to the successful implementation of the REDD+ policy as it develops equations/tools necessary for an accurate estimation of understorey biomass using a non-destructive method. Furthermore, the results of this study complement those of Fayolle *et al*. (2018) for the total evaluation of woody aboveground biomass of semi-deciduous forests in the Congo Basin.

## Acknowledgments

We express our gratitude to Dr. Kringel Robert, who provided us with the financial support for field data collection. We also thank the Plant Systematic and Ecology's laboratory at the Department of Plant Biology, University of Yaounde I for the assistance and materials put at our disposal during the laboratory activities. We also express our gratitude to Dr. Moses LIBALAH and Dr. Godswill NTSOMBOH NTSEFONG, Seniors Lecturers (Department of Plant Biology, University of Yaounde 1), for English language proofreading of this article.

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