

Radial and longitudinal variation of wood density and mixed equations for estimating biomass of pioneer species in secondary forests

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ABSTRACT: The search for accuracy on biomass estimation is growing significantly, however density measurements are still essential to reduce bias in biomass estimations. The objective of this research was to: (1) test longitudinal and radial variations in wood density of *Distemonanthus benthamianus*, *Musanga cecropioides* and *Trema orientalis*. (2) Fitting mixed models of secondary forests pioneer species. Data for density determinations and fitting allometric equations were obtained by destructive method, on a sample of 115 trees. Archimedes' principle applied to the biomass data yielded the average densities of the three respective species (0.726; 0.214 and 0.35 in g.cm⁻³). This variable associated with tree height, crown diameter and diameter at breast height were used to explain tree biomass through ten fitted mixed models. The model, Aboveground biomass = $\text{Exp}(-0.85 + 2.19 \times \ln(\text{DBH}) + 1.1 \times \ln(\phi))$, with a low Akaike Information Criterion (AIC = 78.76), the high correlation coefficient (Adjusted.R² = 96.4%), the low rate of residual standard error (RSE = 0.33) and the Relative Root Mean Square Error (RRMSE = 0.39), was selected as the best mixed model. The full model (Aboveground biomass = $\text{Exp}(-0.84 + 0.63 \times \ln(\text{DBH}^2 \times H) + 0.85 \times \ln(\phi) + 0.54 \times \ln(C))$) under the validation criteria was found to be efficient (adjusted R² = 0.96; RRMSE = 0.41; average error = 15,95). However, density variations must be considered to reduce bias in the estimation. In addition, increased collection of large amounts of secondary forest data remains essential for fitting more robust mixed models.

KEYWORDS: allometric equations; pioneer species, secondary forests, biomass, wood density.

1 INTRODUCTION

Wood is the essential material of the trunk, it plays multiple functions such as the transport of raw sap from the roots to the aerial parts of the tree, the mechanical support of the tree and the storage of reserves. In addition to these functions, the wood with this mechanical property, physiologically influences the storage of carbon and makes forest ecosystems an excellent carbon sink. It's important to appreciate the effect of density variations in the estimation of tree biomass. Within each tree, wood density varies among compartments (branches, trunk, stump, and roots) and can also vary radially within the trunk during growth (Henry *et al.*, 2010). In a rainforest plantation in Venezuela in 2004, some authors reported a decrease in wood density from the bark to the heartwood, a decrease from the stump to the middle of the bole, and then an increase toward the top of the stem for *Gmelina arborea*. Furthermore Nogueira (2005) showed that along the same tree, wood density varies from the base to near the top, radially from the cambium to the heartwood. In the same facet, Djomo (2017) showed that this density decreased from the base towards the top. Different biological and eco-physiological aspects such as structural requirements, tree architecture, age, compartment where the sample was measured within the tree, phytogeography, light and rapid growth are reported to be responsible for variation in trunk density (Favrichon, 1994; Ter Steege *et al.*, 2001; Williamson, 1984) and would be related to density variations, a variable reported to be reliable in explaining biomass.

In Cameroon, studies on biomass estimates with the development of allometric equations are in full growth, however the available results are very weak, compared to the current need for biomass estimation which can be done not only at the tree scale but also at the stand or ecosystem scale by allometric equations or by remote sensing method (Goodman *et al.*, 2014; P. Ploton *et al.*, 2016). The models fitted up to

now are for the majority, those of a genus, species, ecosystem or a region. Beyond the work of Feukeng (2020) on single-species equations for estimating biomass of some pioneer species, very few studies have been done on allometric equations of secondary forests species. The development of allometric equations for biomass estimation is done by the destructive method, inventory data or dendrometric variables are converted to biomass through these equations once tested and validated (Chave *et al.*, 2014).

The objective of this study was to analyze radial and longitudinal variations in wood density of *Distemonanthus benthamianus*, *Musanga cecropioides* and *Trema orientalis*, to associate *Polyscias fulva* and *Pycnanthus angolensis* with the above species to fit mixed models for estimating tree biomass in semi-deciduous forests.

2 MATERIAL AND METHODS

2.1 STUDY SITE

The study area is located in the Center region of Cameroon, specifically in the Mbankomo subdivision in the Mefou and Akono Division, about 22 Km from Yaounde. This subdivision covers an area of 1300 km² between 11°13' and 11°39' East longitude and between 3°37'30 and 3°52' North latitude. Phytogeographically, this area belongs to the domain of semi-deciduous forests with savannas included (Letouzey *et al.*, 1985). The intensity of human activity in this area is responsible for its overall appearance of secondary semi-deciduous forest, with altitude ranging from 650 to 900 m above sea level. Mbankomo is topographically located on the upper basins of the Nyong and Sanaga rivers (PNDP, 2011).

2.2 DATA COLLECTION

The collection of biomass data for the establishment of allometric equations and the study of density variations was obtained by the destructive sampling of 115 trees across a huge range of diameter (5 – 97.5 cm). Five pioneer species have been identified at the taxa level (*Distemonanthus benthamianus* (35 trees), *Musanga cecropioides* (38 trees), *Trema orientalis* (30 trees), *Polyscias fulva* (09 trees) and *Pycnanthus angolensis* (03 trees). Thus, each selected tree was felled at ground level, cut and then weighed separately according to the compartments. This collection had for objective to obtain the fresh weight of each compartment of the felled tree (stump, trunk, branches without leaves and isolated leaves). The weighing of the compartments required an electronic balance. Disc samples were collected from different levels of the stump, trunk and branches. These samples were immediately weighed using a high precision electronic balance and then taken to the Botany and Systematics Laboratory of the University of Yaoundé I where they were oven dried at 105° C for the woody samples and 70° C for the leaves samples until constant weight was obtained. The dry mass obtained for each fraction was used to estimate the total dry mass of each compartment and then that of the entire tree. In addition to the biomass data that were collected on each sampled tree, dendrometric parameters were also measured (diameter at breast height and total tree height). As for the crown diameter, the average of the crown diameters according to the orientations (North-South, East-West, North-East/South-West and North-West/South-East) was used to calculate the average crown diameter of the sampled tree.

2.3 DATA ANALYSIS

2.3.1 WOOD DENSITY

The fresh weight was measured directly in the field and the volume was calculated using Archimedes principle. According to this principle, a solid immersed in water experiences an upward force equal to the weight of the water it displaces because the wood density of water is 1 g/cm³ (Djomo *et al.*, 2017). For volume determination, each fresh sample was fully immersed in water on a graduated cylinder and the weight of displaced water was read on the electronic balance calibrated to 0. The dry weight was obtained by drying the samples in an oven at a constant weight for 48 to 72 hours depending on the type of species. The constant weight was obtained after several weighing of the samples at regular intervals every seven hours until weight stabilization. The volume and dry weight measurements were used to calculate the density of the wood using the formula:

$$\phi_i = \frac{M_i}{V_i} \text{ (Fearnside et al., 1997)}$$

Where M_i is the dry mass (g), V_i is the fresh sample volume in cm³, and WD_i is the wood density (g/cm³) of wood sample i . For each tree, densities at the base, mid-trunk, and crown portions were calculated. The average density of the tree is the average of the wood densities of the three levels.

$$\phi_{\text{mean}} = \frac{\phi_{\text{basis}} \times V_{\text{basis}} + \phi_{\text{middle}} \times V_{\text{middle}} + \phi_{\text{top}} \times V_{\text{top}}}{V_{\text{basis}} + V_{\text{middle}} + V_{\text{top}}} \text{ (Pearson et al., 2005)}$$

With ϕ_{basis} , ϕ_{middle} , ϕ_{top} the densities respectively at the base of the bole, the middle of the bole and near the top; V_{base} , V_{middle} and V_{top} the wood volumes respectively at the base of the bole, at the middle and the top (Nogueira *et al.*, 2007).

2.3.2 ALLOMETRIC EQUATIONS

For the establishment of the mixed allometric equations, we selected the variables diameter at breast height, total height, crown diameter and average wood density. The response variable was the total dry mass. To avoid problems of heteroscedasticity, we used the logarithm function to linearize the variables (Mascaro *et al.*, 2014; Xiao *et al.*, 2011), this is the most recommended function in the establishment of allometric equations for tree biomass estimation (Djomo *et al.* 2016; Picard *et al.*, 2012;).

We also did combinations of variables such as $(DHP)^2 \times H$, $(DHP)^2 \times C$, $(DHP)^2 \times H \times C$, and $(DHP)^2 \times H \times C \times \phi$ in the case of multiple linear regression. Since logarithmic transformations introduce biases in the models, these biases were corrected using the correcting factor (CF) which is expressed by the relationship $CF = (RSE)^2/2$ (Djomo *et al.*, 2016), RSE being the Residual Standar Error. Several additional tests that indicate the goodness of fit of the tested equations were also performed from this study. The following parameters were calculated: Akaike Information Criterion (AIC), RSE, adjusted R^2 (Akaike *et al.*, 1974; Djomo *et al.*, 2017). Parameters such as the mean error and RRMSE (Relative Root Means Square Error) were also calculated for each model. These errors are calculated by the following formulas respectively:

$$\text{Average error or Deviation (\%)} = 100 \times \frac{1}{n} \sum_{i=1}^n \left(\frac{M_{pi} - M_i}{M_i} \right)$$

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

M_{pi} represents the dry weight of the tree predicted by the regression equation, M_i the observed weight and n the total number of trees.

$$\text{AIC} = 2k - 2 \ln L$$

k - number of parameters in the regression model,

L - probability of the fitted regression model (Nelson *et al.*, 1999; Basuki *et al.*, 2009)

3 RESULTS

The Archimedes principle described in the methodological section and applied to fresh samples of *D. benthamianus*, *M. cecropioides* and *T. orientalis* gave the average wood densities recapitulated in Table 1:

Table 1. Longitudinal Variation of the wood density of *Distemonanthus benthamianus*, *Musanga cecropioides* and *Trema orientalis* species

| Family | Scientific name | N | (ϕ_1) | (ϕ_2) | (ϕ_3) | ϕ mean GWD |
|--------------|------------------------|----|--------------|--------------|--------------|-----------------|
| Fabaceae | <i>D. benthamianus</i> | 07 | 0,736 | 0,733 | 0,710 | 0,726 0,73 |
| Cecropiaceae | <i>M. cecropioides</i> | 08 | 0,232 | 0,210 | 0,200 | 0,214 0,22 |
| Canabaceae | <i>T. orientalis</i> | 09 | 0,371 | 0,348 | 0,331 | 0,350 0,37 |

ϕ_1 = Wood density taken at the base, ϕ_2 = wood density taken from the middle of the bole, ϕ_3 = wood density collected at the crown, ϕ mean = average wood density and GWD = represents the Global Wood Density (Zane *et al.*, 2009).

3.1 LONGITUDINAL VARIATION IN WOOD DENSITY

Figure 1a in *Distemonanthus benthamianus* shows drop in density from the base to the middle of the trunk and then from the middle to near the top (0.736 - 0.733 - 0.710) (Figure 1a). In *Musanga cecropioides*, the density decreased from the base to the middle of the trunk and up to near the top (0.232 - 0.209 - 0.200) (Figure 1b). The same observation was made in *Trema orientalis* (c) (0.365 - 0.347 - 0.331) (Figure 1c).

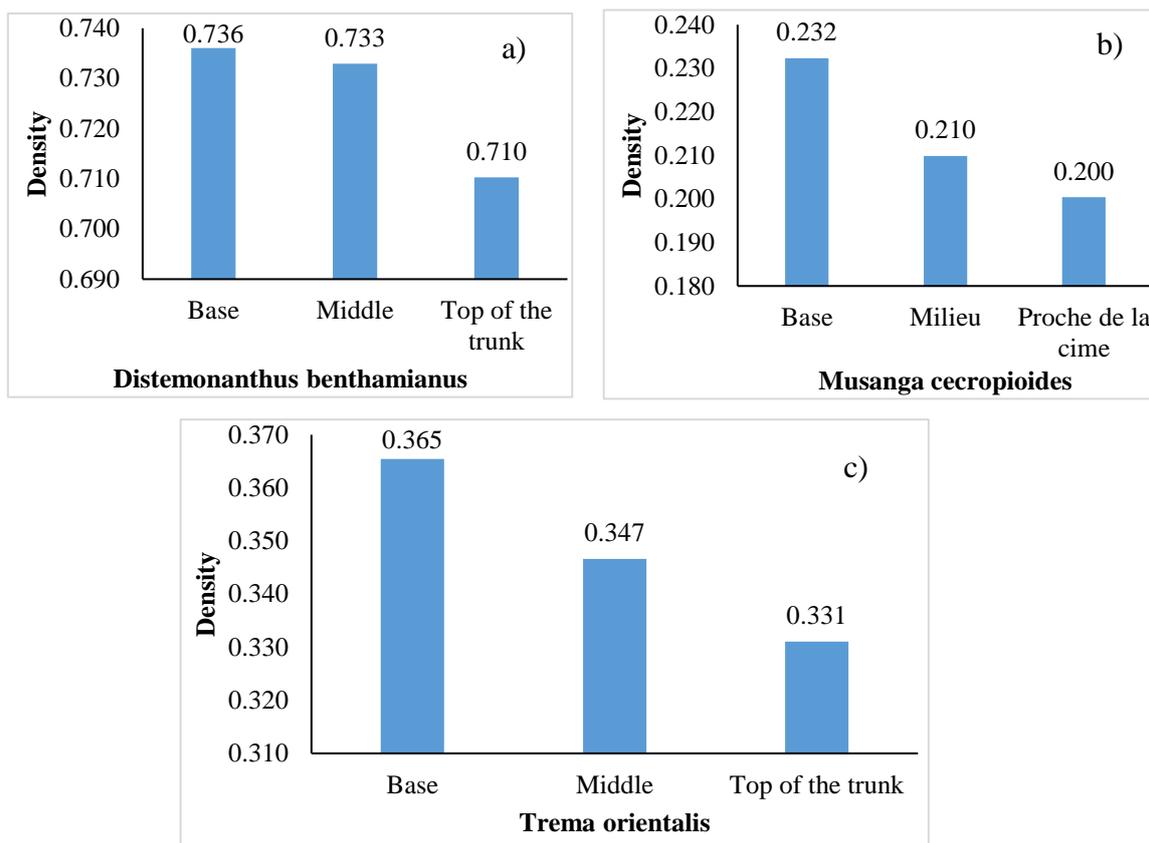


Fig. 1. Longitudinal density variation of *Distemonanthus benthamianus* (a), *Musanga cecropioides* (b) and *Trema orientalis* (c)

The Student's t test applied to the density data of the pairs (Base/Mid-bole), (Base/Near-top), and (Mid-bole/Near-top) yielded Table 2.

Table 2. Student's test for comparison of base, middle and top of the trunk wood densities for the three species (*Distemonanthus benthamianus*, *Musanga cecropioides* and *Trema orientalis*).

Distemonanthus benthamianus

| Pair of densities to be compared | t | df | p-value | Confidence interval | Average base | Average average Middle Top of the trunk | Test result |
|--|--------|--------|---------|---------------------|--------------|---|-----------------------------|
| Base – Middle of the trunk | 1.3546 | 11.228 | 0,2022 | [-0.0018; 0.0078] | 0.7360 | 0.7330 - | No difference |
| Base – Top of the trunk | 4.7881 | 6.7904 | 0.0022* | [0.0130; 0.0387] | 0,7360 | - 0.7101 | The densities are different |
| Middle of the trunk - Top of the trunk | 4.1422 | 7.3407 | 0.0039* | [0.0099; 0.0357] | - | 0.7330 0.7101 | The densities are different |

Musanga cecropioides

| | | | | | | | |
|--|---------|--------|--------|-------------------|----------|-----------------|---------------|
| Base – Middle of the trunk | 1.2599 | 7.6306 | 0.2449 | [-0.0191; 0.0643] | 0.232250 | 0.2096 - | No difference |
| Base – Top of the trunk | 1.5718 | 11.194 | 0.1438 | [-0.0126; 0.0764] | 0.232250 | - 0.2003 | No difference |
| Middle of the trunk – Top of the trunk | 0.85662 | 8.8646 | 0.4142 | [-0.0152; 0.0337] | - | 0.209625 0.2003 | No difference |

Trema orientalis

| | | | | | | | |
|--|--------|--------|--------|----------------------|---------|----------------|---------------|
| Base – Middle of the trunk | 0.9993 | 9 | 0.3438 | [-55.6514; 143.7277] | 44.3847 | 0.3465 - | No difference |
| Base – Top of the trunk | 0.9996 | 9 | 0.3436 | [-55.6359; 143.7433] | 44.3847 | - 0.3310 | No difference |
| Middle of the trunk - Top of the trunk | 0.6807 | 15.848 | 0.5059 | [-0.0329; 0.0640] | - | 0.34655 0.3310 | No difference |

t is the student's statistic, df the degree of freedom, p-value is the degree of significance of the test, confidence interval of the difference of the means to 95%; average at the base of the trunk, in the middle of the trunk, and near the top of the trunk, test result.

3.2 DENSITY VARIATION OF WOOD IN THE RADIAL DIRECTION

Analyses are done to evaluate radial variations in wood density of the three species. The radial decrease in density is conspicuous in *D. benthamianus* from the 5% (D/2) position towards the center of the wood through the 50% (D/2) position (Figure 2a). In *M. cecropioides*, this variation is conspicuous; the drop goes from the 5% (D/2) position towards the center of the wood (Figure 2b). However, in *Trema orientalis*, after the fall from the position 5% (D/2) to 50% (D/2), there is a slight variation of this position from 50% (D/2) towards the center (Figure 2c).

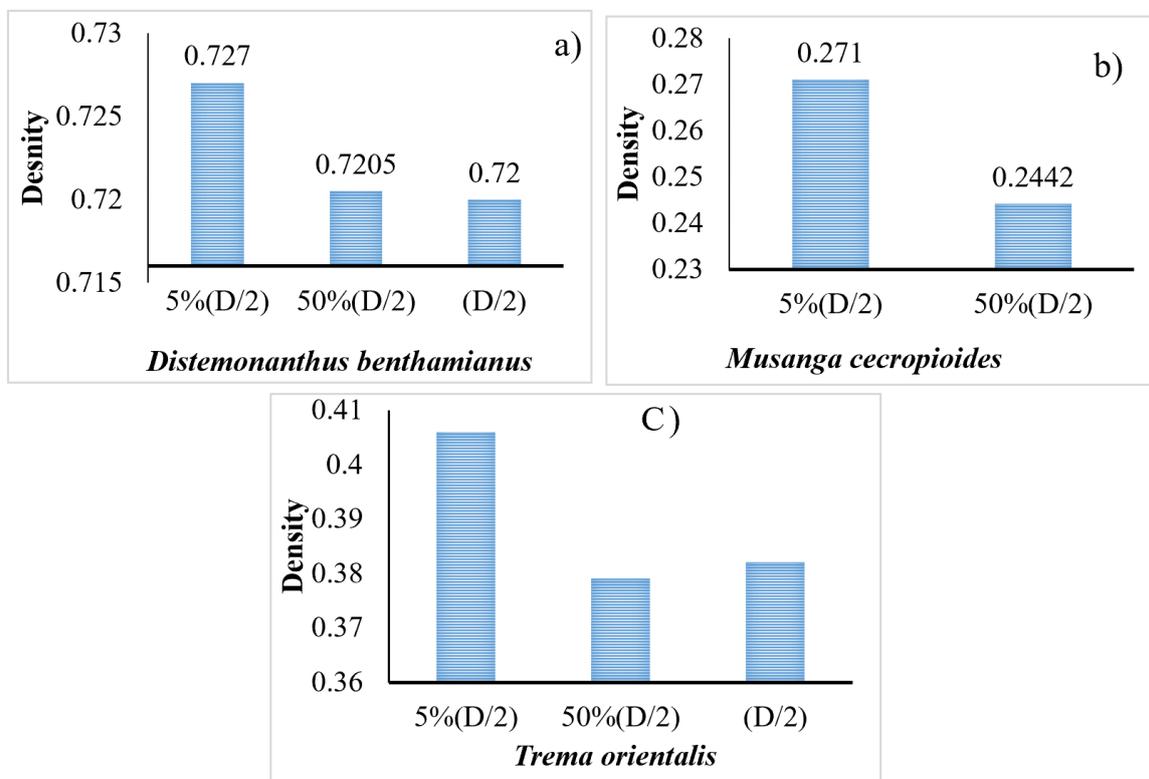


Fig. 2. Radial density variation in *Distemonanthus benthamianus* (a), *Musanga cecropioides* (b) and *Trema orientalis* (c)

The Student's test was also used to compare densities in the radial direction. The results of this test for the three species are reported in Table 3.

Table 3. Student's test for comparison of wood densities of the (5%D/2), (50%D/2) and D/2 levels, from the periphery to the center for the three species *Distemonanthus benthamianus*, *Musanga cecropioides* and *Trema orientalis*

Distemonanthus benthamianus

| Pairs to compared | t | Df | p-value | Confidence interval | Average 5% (D/2) | Average Average 50% (D/2) (D/2) | Test result |
|----------------------|--------|--------|---------|---------------------|------------------|---------------------------------|---------------|
| 5% (D/2) - 50% (D/2) | 0.6766 | 7.0889 | 0.5201 | [-0.0103; 0.0186] | 0.727 | 0.722 - | No difference |
| 5% (D/2) - (D/2) | 0.9408 | 7.9989 | 0.3743 | [-0.0097; 0.0230] | 0.726 | - 0.720 | No difference |
| 50% (D/2) - (D/2) | 0.4167 | 7.1352 | 0.6891 | [-0.012; 0.0168] | - | 0.722 0.720 | No difference |

Musanga cecropioides

| | | | | | | | |
|----------------------|---------|--------|--------|-------------------|-------|-------|---------------|
| 5% (D/2) - 50% (D/2) | 0.68803 | 5.9959 | 0.5172 | [-0.0704, 0.1254] | 0.272 | 0.244 | No difference |
|----------------------|---------|--------|--------|-------------------|-------|-------|---------------|

Trema orientalis

| | | | | | | | |
|----------------------|---------|--------|--------|-------------------|-------|-------------|---------------|
| 5% (D/2) - 50% (D/2) | 1.1217 | 7.1631 | 0.2982 | [-0.0296, 0.0835] | 0.406 | 0.379 - | No difference |
| 5% (D/2) - (D/2) | 0.9264 | 6.6985 | 0.3864 | [-0.0380, 0.0863] | 0.406 | - 0.382 | No difference |
| 50% (D/2) - (D/2) | -0.0946 | 7.8928 | 0.9270 | [-0.0712, 0.0656] | - | 0.379 0.382 | No difference |

Note: t is student's statistic, df is the degree of freedom, p-value is the degree of significance of the test, confidence interval of the difference of means at 95%.

3.3 MIXED ALLOMETRIC EQUATIONS

The second objective of this research was to associate *Polyscias fulva*, *Pycnanthus angolensis* with *Distemonanthus benthamianus*, *Musanga cecropioides* and *Trema orientalis* to fit mixed models. Thus, a total of 115 trees were sampled to establish the allometric equations. In the fits, several models were tested. Figure 3 shows the scatter plot of the relationship between total dry above ground biomass and the main explanatory variable (DBH)

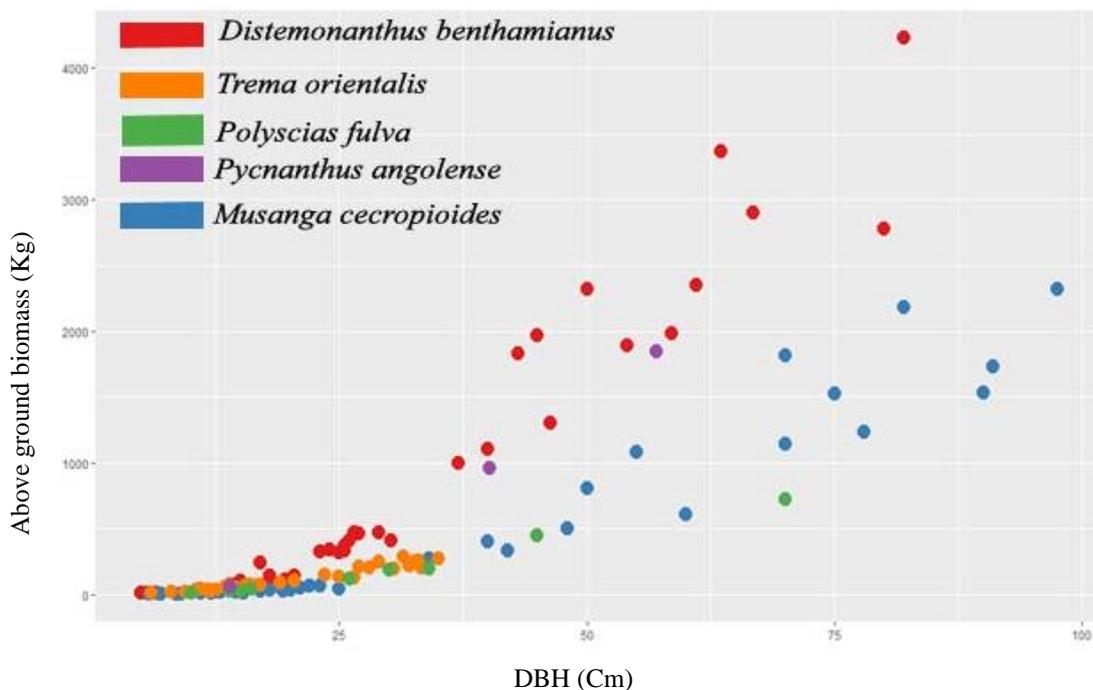


Fig. 3. Correlation between the diameter and aboveground biomass for the 115 trees sampled for mixed model fitting

In order to reduce the gaps and stabilize the variance, the transformation of the variables by the logarithm function allowed to refine the relationship. This linearization allowed us to obtain the figure 5.

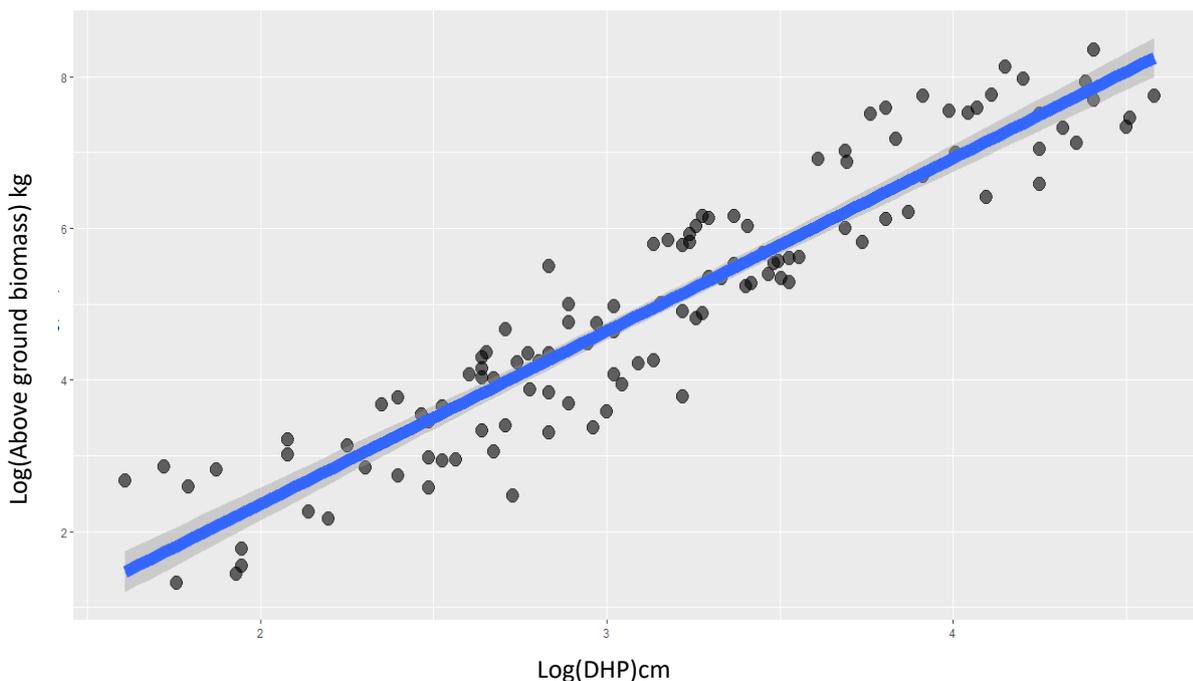


Fig. 4. Correlation between Log (DBH) and Log (Aboveground biomass) for the 115 trees sampled for mixed model fitting

Correcting factor was calculated from the Residual Standard Error and used to correct biases generated by the log transformation. The AIC was also calculated for model comparison. The Relative root mean square error (RRMSE) was also calculated as well as the adjusted R². The results of the mixed model fits are summarized in Table IV.

Table 4. Allometric equations for estimations of total aboveground biomass (M); DBH: Diameter of the trees analyzed (DBH); H: tree height; ϕ: wood density; C: crown diameter; N: the sample size; a, b, c and d are the model's fitted parameters; RRMSE: Relative Root Mean Square Error; RSE: Residual Standard Error of the estimate; Adj R²: coefficient of determination; AIC: Akaike Information Criterion and CF: correction factor

| Models | N | DBH range | a | b | C | d | RRMSE | RSE | Adj.R ² | AIC | CF |
|---|-----|-----------|-----------|---------|---------|------|-------|------|--------------------|--------|-------|
| DBH | | | | | | | | | | | |
| M1 lnBtot = a + b x ln (DBH) | 115 | 5-97.5 | -2.204*** | 2.28*** | | | 1.02 | 0.62 | 0.874 | 220.94 | 0.19 |
| M2 lnB = a + b x ln (DBH ² x H) | 115 | 5-97.5 | -2.77*** | 0.86*** | | | 0.80 | 0.58 | 0.88 | 206.91 | 0.17 |
| M3 lnBtot = a + b x ln (DBH) + c x ln (ϕ) | 115 | 5-97.5 | -0.85*** | 2.19*** | 1.10*** | | 0.39 | 0.33 | 0.964 | 78.76 | 0.05 |
| M4 lnBtot = a + b x ln (DBH) + c x ln (C) | 115 | 5-97.5 | -1.36*** | 1.54*** | 0.74*** | | 0.75 | 0.55 | 0.89 | 196.83 | 0.15 |
| M5 lnB = a + b x ln (DBH ² xH) + c x ln (ϕ) | 115 | 5-97.5 | -1.84*** | 0.60*** | 0.70*** | | 0.50 | 0.51 | 0.912 | 180.15 | 0.10 |
| M6 lnB = a + b x ln (DBH ² xH) + c x ln (ϕ) + d x ln (C) | 115 | 5-97.5 | -0.90*** | 0.63*** | 0.85*** | 0,54 | 0.41 | 0.34 | 0.96 | 81.54 | 0.058 |
| Crown diameter (C) | | | | | | | | | | | |
| M7 lnBtot = a + b x ln (C) | 115 | 5-97.5 | 1.076*** | 1.95*** | | | 1.41 | 0.76 | 0.81 | 266.75 | 0.28 |
| M8 lnBtot = a + b x ln (C) + c x ln (H) | 115 | 5-97.5 | -1.702*** | 1.13*** | 1.64*** | | 0.87 | 0.55 | 0.90 | 194.06 | 0.15 |
| M9: lnBtot = a + b x ln (C) + c x ln (ϕ) | 115 | 5-97.5 | 2.04*** | 1.85*** | 0.77*** | | 1.38 | 0.67 | 0.85 | 239.32 | 0.22 |
| M0: lnBtot = a + b x ln (C) + c x ln (H) + d x ln (ϕ) | 115 | 5-97.5 | -0.71*** | 1.14*** | 1.46*** | 0,54 | 0.68 | 0.49 | 0.92 | 169.69 | 0.12 |

Note: The statistical analyses are significant at 95% confidence interval. **p < 0.01; *p < 0.05; and ns (non-significant) p > 0.05. P-value of all models: 2.2e_16. ***p < 0.001.

The Q-Q plot, showed a group of points that form a straight line, this is evidence of the normality of the residuals (Figure 5).

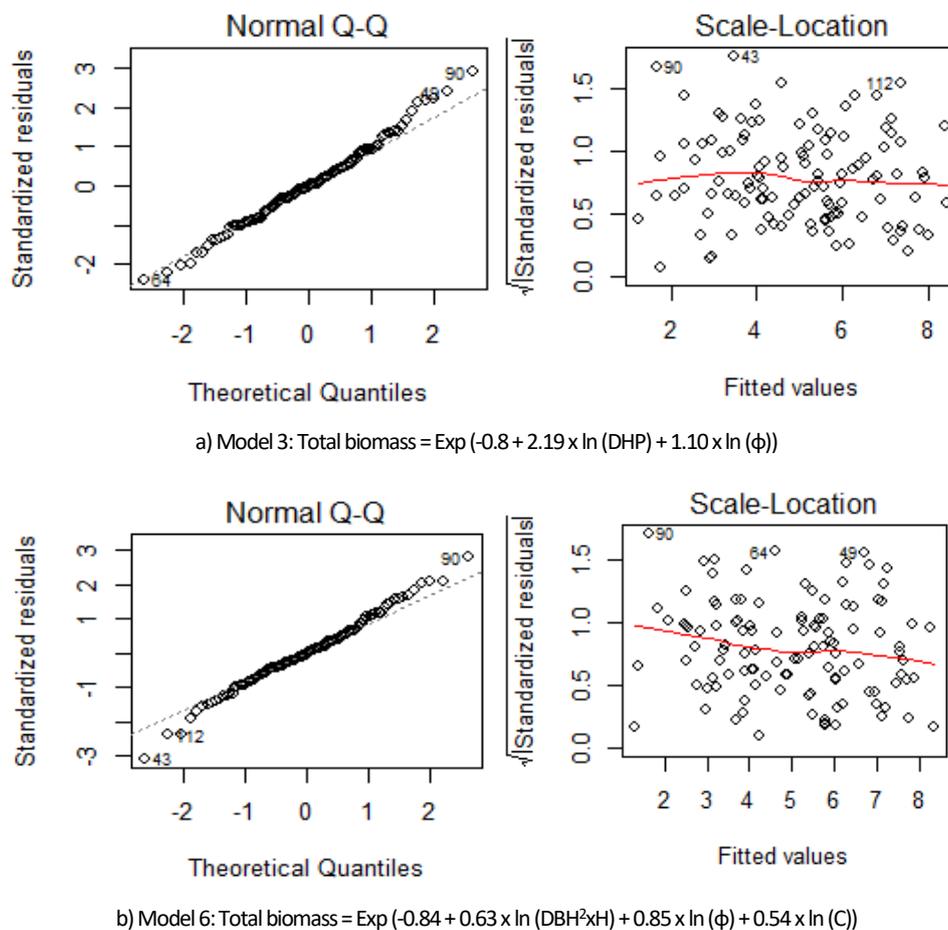


Fig. 5. Distribution of residues as a function of the predicted values (right) and of Q-Q graph (left) issued from the M3 and M6 mixed models.

Statistical tests were applied for validation the scattered residuals. The residuals follow a normal distribution with the mixed models, especially with the Q-Q plots. Visually the group of points forms a straight line. Moreover, in all models (M1 to M10) the p-value of the Shapiro-Wilk test is higher than 0.005, which is proof of the normality of the residuals (Table V).

Table 5. Statistical tests for model validation

| Models | Shapiro-Wilk | p-value | Breusch-Pagan | p-value | Durbin-Watson | p-value |
|--------------|--------------|----------|---------------|---------|---------------|-----------|
| Mixed models | | | | | | |
| M1 | 0.97786 | 0.05362 | 1.0448 | 0.3067 | 0.4404 | < 2.2e-16 |
| M2 | 0.97394 | 0.02417 | 3.9399 | 0.0471 | 0.7276 | 2.167e-12 |
| M3 | 0.9924 | 0.786 | 4.348 | 0.430 | 1.3624 | 0.000175 |
| M4 | 0.96537 | 0.004525 | 4.5846 | 0.1010 | 0.5967 | 6.878e-15 |
| M5 | 0.99004 | 0.5698 | 9.8226 | 0.0074 | 1.4630 | 0.0012000 |
| M6 | 0.99217 | 0.762 | 4.0748 | 0.2535 | 1.6749 | 0.0269000 |
| M7 | 0.98694 | 0.3336 | 0.5524 | 0.4573 | 1.0741 | 0.0000002 |
| M8 | 0.98889 | 0.4725 | 0.5523 | 0.4573 | 1.4305 | 0.0007960 |
| M9 | 0.98777 | 0.388 | 5.8800 | 0.0528 | 1.3617 | 0.0001680 |
| M0 | 0.99454 | 0.9357 | 1.3210 | 0.7241 | 1.6949 | 0.0352200 |

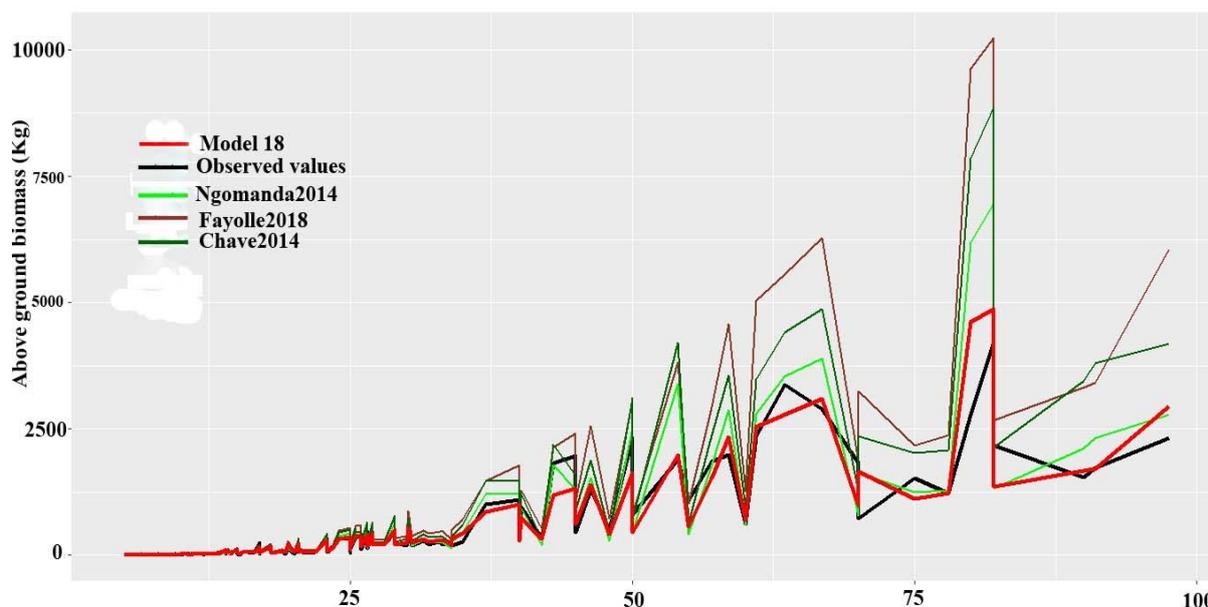


Fig. 6. Comparison of the mixed model M3 with the previous equations

4 DISCUSSION

4.1 RADIAL AND LONGITUDINAL VARIATION OF WOOD DENSITY

Concerning the densities of the species and their evolution in the radial and longitudinal directions, the results showed the mean values of densities at different levels were 0.736 g/cm³, 0.7323 g/cm³ and 0.710 g/cm³, respectively at the base, middle and near the crown of *D. benthamianus*. The Student's test shows that in *D. benthamianus*, the density of wood at the base and that of the middle does not differ significantly (P-value > 0.05). It was observed that, the density of wood at the base and near the top (Base - top of the trunk) on the one hand, and the density of wood in the middle and near the top (Middle - near the top) on the other hand, showed a significant difference respectively, with P-value 0.002168 and 0.003911, both values lower than 0.05. These results reflected those of Djomo *et al.* (2017) who worked in the tropical rainforest. They showed that, of about 30 species studied, wood densities decreased significantly from the base to the middle and then to near the top. For the species *Guarea sp.*, these observations were slightly different (0.691 g/cm³ at the base, 0.605 g/cm³ in the middle and 0.648 g/cm³ at the top); falling from the base to the middle and rebounding from the middle to the top (Nogueira *et al.*, 2005). In the same logic, Henry *et al.* (2010) showed that the density of the tree decreases with size as confirmed in this study.

In the other two species *Musanga cecropioides* and *Trema orientalis*, from the base to the middle and from the middle to near the top, the density also decreased. However, statistically, these differences in density were not significant. All tests had a P-value greater than 0.05. Radially, there was no significant difference from the periphery of the wood to the center. Overall, variation in wood density between trees of different species is more significant than variation within individuals of the same species (Quentin *et al.*, 2013) in accordance with this study. Major environmental variations (abiotic and biotic factors) such as physiological, mechanical, anatomical, genetic and morphological stresses observed in a forest stand would explain the causes of wood density variation among species (Fearnside, 1997). Tree architecture, age, phytogeography and the compartment in which the sample was measured within the tree (Williamson, 1984) are thought to be related to density variations. In conclusion, different biological and eco-physiological aspects such as structural requirements, climatic zone, light and rapid growth are reported to be responsible for the variation in trunk density (Favrichon, 1994; Ter Steege *et al.*, 2001). Wood density is known to be a strong indicator of the successional state of tropical trees, with pioneer secondary forest species being lighter than trees belonging to other ecosystems. Their fast initial growth is responsible for the production of low-density wood (Wiemann and Williamson, 1998), as is the case in *Musanga cecropioides* and *Trema orientalis* in this study.

4.2 MIXED MODELS FOR BIOMASS ESTIMATION

4.2.1 ANALYSIS OF RESIDUALS DERIVED FROM THE MIXED MODELS M3 AND M6 FOR ESTIMATING PIONEER SPECIES BIOMASS

The best fit models, fitted to the pioneer species were confirmed by testing the regression hypotheses to provide all the conditions for its validation. Among these models tested, we have selected ten that are predictive, and the validation criteria of the models through the analysis of the residuals have been carried out. However, model 3 (Dry biomass = $\text{Exp}(-0.85 + 2.19 \times \ln(D) + 1.1 \times \ln(\phi))$), based on the AIC comparison criterion, is considered more efficient. Djomo *et al.* (2016) had similar results, mentioning that the combination of DBH with wood density optimized the prediction of biomass. Studies on allometric equations for biomass estimation have shown that mono-specific models are more reliable than mixed models (Nelson *et al.*, 1999; Basuki *et al.*, 2009; Chave *et al.*, 2014; Djomo *et al.*, 2016). However, in the absence of mono-specific models, mixed models can be used, especially if they are efficient and eventually validated. The Shapiro-Wilk, Studentized Breusch-Pagan and Durbin-Watson tests were applied to the ten models to check the normality, heterogeneity and independence of the residuals. They are all predictive, this model overestimates the biomass by 0.098% with RRMSE = 0.39; RSE = 0.33 and adjusted $R^2 = 0.964$. At the same time, model 6, qualified as a full model integrating all the explanatory variables of this research (Biomass = $\text{Exp}(-0.84 + 0.63 \times \ln(\text{DBH}^2 \times H) + 0.85 \times \ln(\phi) + 0.54 \times \ln(C))$) is also efficient (RSE = 0.34; AIC = 81.54; Adj $R^2 = 0.96$; RRMSE = 0.41). Furthermore, the plot of residuals versus fitted values showed no particular trend (Picard *et al.*, 2012), this confirms the assumption of homoscedasticity of model 3, 6 and also those of the other eight predictive models. The hypothesis of independence was tested by the Durbin-Watson statistics, whose values vary between 0 and 4. However, the residuals are considered uncorrelated (independent) if the Durbin-Watson statistic is between 1.5 and 2.5 (Field, 2009). The Durbin-Watson statistic for the mixed models is less than 2.5; this indicates that the residuals for all models are uncorrelated. Therefore, the independence assumption is met in this modeling.

4.2.2 COMPARISON OF THE MIXED PIONEER SPECIES MODEL TO PREVIOUSLY PUBLISHED EQUATIONS

The models of Ngomanda *et al.* (2014), Chave *et al.* (2014) and Fayolle *et al.* (2018) estimate with biases of the order of -4.8%, 29.77% and 60.22% respectively. Given the low rate of bias in Ngomanda (-4.8%), this model is efficient. On the other hand, the models of Chave (2014) and Fayolle (2018) tested in this comparison are not reliable, their biases are 29.77% and 60.22% hence the gap between their curve and that of the biomass really observed. Model 3 (Btot = $\text{Exp}(-0.8 + 2.19 \times \ln(\text{DHP}) + 1.10 \times \ln(\phi))$) and model 6 (Biomass = $\text{Exp}(-0.84 + 0.63 \times \ln(\text{DBH}^2 \times H) + 0.85 \times \ln(\phi) + 0.54 \times \ln(C))$) tested and validated are recommended for the prediction of biomass of *D. benthamianus*, *M. cecropioides* and *T. orientalis*, *P. fulva* and *P. angolensis* species.

5 CONCLUSION

The objective of this work was to establish mixed allometric equations for the species *Distemonanthus benthamianus*, *Musanga cecropioides*, *Trema orientalis*, *Polyscias fulva* and *Pycnanthus angolensis*, to estimate the biomass of the pioneer species in the zone of semi-deciduous degraded forest. Among the models selected by their efficiency, we had under the adjusted R^2 , AIC, RSE, RRMSE, residual error comparison criteria, retained two mixed models for the estimation of the biomass of these pioneer species of secondary forests (M3: Dry biomass = $\text{Exp}(0.85 + 2.19 \times \ln(D) + 1.1 \times \ln(\phi))$) and (M6: Dry biomass = $\text{Exp}(-0.84 + 0.63 \times \ln(\text{DBH}^2 \times H) + 0.85 \times \ln(\phi) + 0.54 \times \ln(C))$). In order to avoid an underestimate prediction, the application of the correcting factor allowed for a considerable reduction of the biases coming from the logarithmic transformation, so that about ten models were retained, predictive with high correlation coefficients and with relatively low residual errors. Density measurements are essential to reduce uncertainties in carbon stock estimates, the density of the studied species was also calculated and the existence of a radial and longitudinal variation gradient within the wood was shown for the species *D. benthamianus*, *M. cecropioides* and *T. orientalis*.

PERSPECTIVES

In a large scale, important data on pioneers of semi-deciduous forests as well as several other ecosystems, remain essential for the fitting of mixed models with a large sample. This being the case, in order to optimize the effort to improve the estimates, it would also be necessary to set up a data archiving system, which would be the starting point for the improvement of future predictions as initiated in the PREREDD+ platform. This work through the MRV protocol is a main objective of the REDD+ mechanism and would effectively contribute to climate change mitigation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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