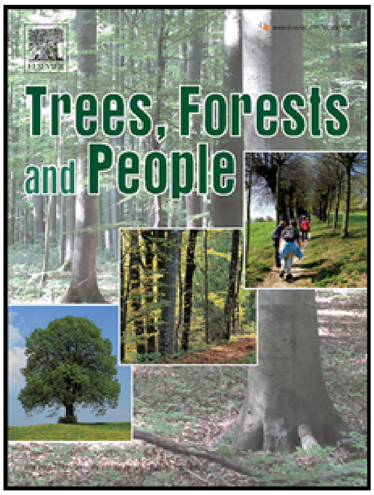
Journal Pre-proof



Tree allometry and stand structure in dryland forests relics of northern Côte d'Ivoire

Nina Gueulou , Brahima Coulibaly , Adeline Fayolle , Noufou Doudjo Ouattara , Assandé Ahoba , Anatole Kanga N'Guessan , Adama Bakayoko

PII: S2666-7193(23)00110-3
DOI: https://doi.org/10.1016/j.tfp.2023.100478
Reference: TFP 100478

To appear in: *Trees, Forests and People*

Received date: 18 October 2023
Revised date: 10 December 2023
Accepted date: 11 December 2023

Please cite this article as: Nina Gueulou , Brahima Coulibaly , Adeline Fayolle , Noufou Doudjo Ouattara , Assandé Ahoba , Anatole Kanga N'Guessan , Adama Bakayoko , Tree allometry and stand structure in dryland forests relics of northern Côte d'Ivoire, *Trees, Forests and People* (2023), doi: https://doi.org/10.1016/j.tfp.2023.100478

Tree allometry and stand structure in dryland forests relics of northern Côte d'Ivoire

Nina Gueulou [a,b*], Brahima Coulibaly [b], Adeline Fayolle [c], Noufou Doudjo Ouattara [a,d], Assandé Ahoba[b], Anatole Kanga N'Guessan [b], Adama Bakayoko [a,d]

[a] UFR des Sciences de la Nature (SN), Université Nangui Abrogoua, 02 BP 801 Abidjan 02, Côte d'Ivoire

[b] Station de Recherche Technologique, Centre National de Recherche Agronomique (CNRA), 08 BP 33 Abidjan 08, Côte d'Ivoire

[c] Université de Liège - Gembloux Agro-Bio Tech, Passage des Deportés 2, B-5030, Gembloux, Belgium

[d] Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, 01 B.P. 1303 Abidjan 01, Côte d'Ivoire

***E-mail address of corresponding author : ninagueulou@gmail.com**

Abstract

The contribution of dryland forests in West Africa to carbon stocks remains poorly documented due to the lack of appropriate allometric models and inventory data. In this study, we gathered such data for dryland forest relics of northern Côte d'Ivoire that were used to determine and sample the dominant species, to develop local mixed-species allometric models for estimating tree aboveground biomass (AGB), to test the validity of existing allometric models, and to characterize the stand structure (including carbon stock). A total of 118 tree species belonging to 102 genera and 36 families were inventoried in 41 plots of 25 × 25 m (625 m² each, totalling 2.56 ha) sampled in three sites in the Korhogo department. Among them, seven predominant species, including one exotic, were selected for destructive sampling in one site, the Lataha Forest Research Station. Destructive biomass data for 34 trees belonging to these dominant species and with diameter at breast height between 6 and 41 cm were used to fit allometric equations specific to this vegetation type and to test the predictions of existing equations earlier developed for the global tropics and for African dry forests. Six equations integrating three predictors, trunk diameter (D), total tree height (H) and wood specific gravity (ρ) were developed and the models with the three predictors showed the best performance. Pantropical models significantly over-estimated tree AGB by 20% while models developed for African dry forests provided reliable estimates, suggesting a specific allometry of trees in dryland forest relics. With our best local equation, a quantity of 141.26 ± 92.72

tDM.ha^{-1} was estimated confirming that these dryland forest relics are important carbon stocks for this region where open vegetation dominates. This study constitute an important contribution for the carbon accounting programs related to the implementation of REDD+ initiatives in Côte d'Ivoire.

Key words: mixed-species allometric models, dryland forests, aboveground biomass, Africa

1. Introduction

Rapidly increasing atmospheric CO_2 concentrations have prompted attention to the preservation of carbon stocks (Ryan et al., 2011) and the sequestration of carbon (Lewis et al., 2013) in tropical ecosystems for mitigating climate changes. It is especially important for the implementation of the mechanism for Reducing Emissions from Deforestation and forest Degradation (REDD+), an emerging carbon credit market mechanism under discussion in international climate negociations (Gibbs et al., 2007; Mugasha et al., 2013).

To estimate the amount of carbon stored in trees, forest inventory data (tree identification and measurements in plots) are converted into aboveground biomass (AGB) estimates with an allometric equation (Chave et al., 2004; Clark & Kellner, 2012), and AGB is then converted into carbon through estimates of carbon content in woody tissues (Thomas & Martin, 2012). Allometric equations are statistical models that estimate tree biomass from dendrometric characteristics, such as stem diameter (D, in cm) and total tree height (H, in m), and wood specific gravity (ρ, in g.cm^{-3}), the latter allowing converting a volume (~ D²H) into AGB (in kg). These equations are usually calibrated from destructive measurements, either on a single species or on a group of dominant species chosen to describe a vegetation type (Picard et al., 2012; Ribeiro et al., 2011). The choice of the allometric model is an important source of uncertainty in the biomass estimation process of tropical forests (Chave et al., 2004) that can contributes to 76% of the total error in tree AGB estimates in tropical Africa (Moundounga Mavouroulou et al., 2014; Picard et al., 2015). Similarly, the heterogeneity of environmental conditions from which individuals originate induces great error in generic allometric models and can be a source of sampling error propagation (Van Breugel et al., 2011).

During the laste decade, considerable efforts have been made in Africa to improve forest carbon estimates and specifically to develop biomass models, and notably in dense forests in Ghana (Henry et al., 2010), Cameroon (Djomo et al., 2010; Fayolle et al., 2013), Gabon (Ngomanda et al., 2014) and miombo woodlands (Mugasha et al., 2013; Ryan et al., 2011). Though general models for the global tropics (Chave et al., 2014) have been validated for Central Africa in a cross-site study (Fayolle et al., 2018), the drier formations in West Africa, such as the Sudanian drylands have been neglected due to their status as generally classified and/or sacred forests in which human interventions are prohibited (Gueulou et al., 2019). Allometric equations to estimate tree AGB were only developed for certain tree species isolated in savannas, most of which are of high socio-economic, cultural and ecological values that are used by local communities for multiple purposes including food, medicine, construction and fuelwood and/or for soil restoration through afforestation (Balima et al., 2020; Bayen et al., 2020; Chabi et al., 2016; Dimobe et al., 2018; Ganamé et al., 2020, 2021; Sawadogo et al., 2010). The protected forest relics in West Africa have yet never been sampled and tropical dry forest species represent only 9% of the global database on tree allometry and crown architecture (Jucker et al., 2022).

In Côte d'Ivoire, studies on the contribution of forests to carbon stocks and sequestration are also very recent and mostly focused on the wettest areas (Bakayoko et al., 2012; Lewis et al., 2013; Traoré et al., 2018). So far, apart from the recent work of Kouamé et al. (2022), who developed biomass equations for five savanna tree species in the Lamto Reserve, no study has yet addressed the development of biomass equations for forest relics in the Sudanian domain of Côte d'Ivoire. However, in these areas of great desertification threats, relics of sacred forests, classified forests and forests for scientific research still exist (Tiébré et al., 2016) and if these forests are well conserved, they can also constitute an important terrestrial carbon stocks and sinks (Pradhan et al., 2019; Qasim et al., 2016). In the absence of allometric equation specific to these dry forests, AGB estimation is often done using the pantropical models of Chave et al. (2005, 2014) that have yet not been properly tested. Whether pantropical equations are valid for estimating tree AGB or whether site-specific equations should be preferred is still an open question for dryland forest relics in northern Côte d'Ivoire and they carbon stored remains uncertain due to the lack of both appropriate allometric models and inventory data.

The aim of this study was to improve estimates of AGB stocks of dryland forest relics in Cote d'Ivoire using site-specific allometric models based on destructive data and newly acquired inventory data. The specific objectives were to (i) determine the dominant species of these dryland forest relics; (ii) develop local allometric equations for estimating total AGB and (iii) test the validity of existing allometric models, and (iv) characterize the stand structure (including carbon stock) of these dryland forest relics.

2. Materials and methods

2.1. Study sites

The study was conducted in three protected dryland forest relics in northern Côte d'Ivoire: the forest of the Lataha Forest Research Station, the sacred forest of Dolékaha and the classified forest of Korhogo (Figure 1). The study area is located between 9°20' and 9°40' N latitude and between 5°75' and 5°95' W longitude, in the sub-Sudanian sector of the Sudanian domain (Guillaumet & Adjanohoun, 1971). Annual rainfall over the last ten years (2010-2019) ranged from 886 mm.yr^{-1} to 1552 mm.yr^{-1} with an average of 1150 mm, for an average annual temperature of 27.7°C. The distribution of rainfall is unimodal with a rainy season from April to October (peak in September) and a dry season from November to March with no rainfall in January and December (Figure 1). The dry season is marked by the Harmattan, a dusty, dry and hot wind that lasts from three to five months. The vegetation is characterised by savanna formations (grassy, shrubby or tree savannas), relics of gallery forests, dense dry forests and open forests (Guillaumet & Adjanohoun, 1971). Among the three sites, the sacred forest of Dolékaha is a dense dry forest, that of Lataha is composed of a gallery forest and an open forest, and the part of the classified forest of Korhogo that was sampled in this study is a riparian forest (Figure 1, Supplementary File 1).

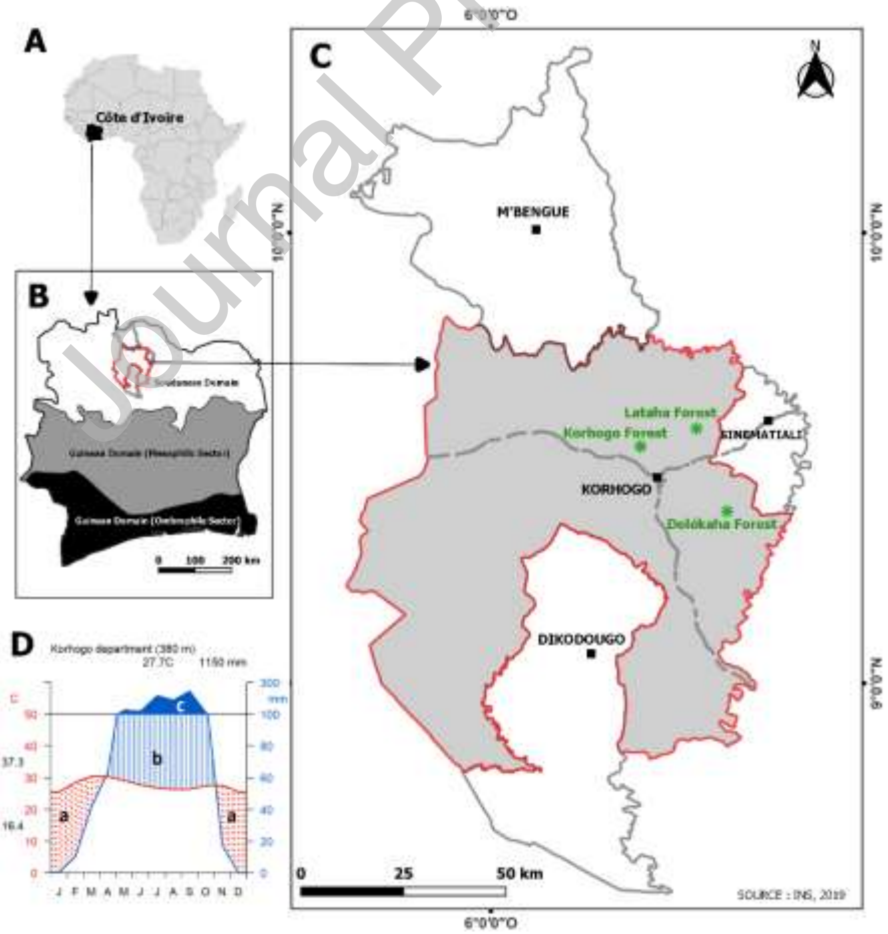


Figure 1. Location of the study area in Africa (A), in Côte d'Ivoire (B) according to the phytogeographic zones, and in the Korhogo department (C). The Walther-Lieth climatic diagram for the 2010-2019 period is also provided for the Korhogo department (D) and shows the dry season (a), the rainy season (b) and the period with major seasonal rainfall (c).

2.2. Forest inventory

To determine the dominant species and to overall characterize the stand structure in the three forest sites, an inventory based on the random selection of 25 × 25 m plots (625 m²) was adopted (Hawthorne & Jongkind, 2006). In these plots, all trees with a diameter at breast height DBH ≥ 5 cm were measured with a tape, and the total tree height was measured with a Laser telemeter. For trees with buttresses or aerial roots, the diameter was measured 30 cm above deformations. A reference specimen of each species was collected to confirm field identifications. In total, 41 plots corresponding to an area of 2.56 ha were inventoried in the Lataha forest (n=16 plots), in the sacred forest of Dolékaha (n=14) and in the Korhogo classified forest (n=11).

2.3. Destructive AGB data

A total of 34 trees belonging to seven out of the 10 most dominant species according to the inventory data were sampled, covering a range of 6-41 cm in diameter and of 8-19 m in height (Table 1). Information on the wood specific gravity of each species was extracted from the global wood density database (Zanne et al., 2009). Destructive sampling for AGB was restricted to the Lataha Forest because such measurements are not permitted in the Korhogo classified forest and in the Dolekaha sacred forest. Prior to the tree felling, the diameter at breast height (DBH) was measured with a tape. After felling, the total height (H) was also measured using a 50-meter tape, and the tree was divided into three compartments: the trunk, the branches, and the leaves. The fresh biomass of each compartment was measured in the field using a 500 kg scale. Samples (aliquots) of trunk, branches, and leaves were collected on each tree for the measurement of green/fresh mass with an electronic scale. The samples were then dried for one week at 105˚C for woody samples (from the trunk and branches) and for three days at 75˚C for leaf samples, for the measurement of the dry mass. The amount of dry matter was used to determine the dry mass from the green/fresh mass of the compartments measured in the field. This protocol was earlier developed for trees in moist forest (Fayolle et al., 2013; Henry et al., 2010; Ngomanda et al., 2014; Picard et al., 2012).

2.4. Data analysis

The inventory and destructive data were compiled with Excel spreadsheets, and data analysis and modelling were performed using version 4.0.3 of the R software (R core team 2020).

2.4.1. Dominant species

For each species in the inventory data we computed the Importance Value Index (IVI) of Curtis and McIntosh (1950) which combined the relative dominance (RDo, in terms of basal area), the relative density (RDe, in terms of stem number) and the relative frequency (Rf, in terms of plot presence). A species is considered ecologically dominant when its IVI is greater than 10 (Fobane et al., 2017) and this threshold was also retained for selecting dominant species for the development of mixed-species allometrics equations for estimating total aboveground biomass.

2.4.2. Allometric models

After preliminary visual exploration of the destructive data, we retained the linearized logarithmic form of the power function, that has been widely used to estimate tropical tree AGB in Africa (Djomo et al., 2016; Fayolle et al., 2013, 2018; Fonton et al., 2017; Henry et al., 2011; Ngomanda et al., 2014) and to describe plant allometry worldwide (Niklas, 1994). Tree AGB, the dependent variable, was related to three predictors: the trunk diameter at breast height (DBH), the total tree height (H) and the species wood specific gravity (ρ), and these predictors were considered individually or in combination (Table 2). The performance of the six models fitted was compared using the adjusted determination coefficient ($AdjR^2$), the residual standard error (RSE), and the Akaike information criterion (AIC), a criterion that penalizes the likelihood by the number of parameters (Burnham & Anderson, 2004). The residuals were visually examined to check for homogeneity of variance and normality (Djomo et al., 2016; Sileshi, 2014). The log-transformation, however, introduces a systematic bias when back-transforming the data, that was corrected using a correction factor, $CF = \exp(RSE^2/2)$ (Chave et al., 2005).

2.4.3. Prediction tests

The site-specific AGB models were compared to four published models developed for forests across the global tropics (Chave et al., 2014), and specifically for dry forests across the global tropics (Chave et al., 2005), in Africa (Djomo et al., 2016), and in Burkina Faso (Ganamé et al., 2021). The accuracy of predictions was assessed with the Root Mean Square Error

(*RMSE*) and the relative bias (*Bias%*). The *RMSE* (in kg) quantifies the magnitude (size) of the differences between the observed and predicted AGB. The *Bias%* measures the systematic deviation of model predictions from observed data (under- or over-estimation).

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

$$Bias\ (\%) = \frac{1}{N}\sum_{i=1}^{N}(AGB_{est,i} - AGB_{obs,i})/AGB_{obs,i} \quad (2)$$

where AGB_{est} and AGB_{obs} are the estimated and observed aboveground biomass for a tree i, respectively and N is the total number of trees. Paired t-tests were also used to test the null hypothesis of no difference between AGB_{est} and AGB_{obs}.

2.4.4. Stand structure

In addition to AGB, the stand structure of these dryland forest relics was also analysed with classical forest attributes including stem density, basal area, and Lorey's height, that were computed at the plot level for trees with a diameter ≥ 10 cm to be comparable with other studies. Mean and standard deviation of forest attributes are provided for the combined dataset and for each forest site separetely. Stem density and basal area respectively correspond to the number of stems and the sum of tree's cross-section in the plot, both returned at the scale of one hectare. Lorey's height corresponds to the average of tree height weighed by tree basal area. Tree AGB was estimated from our best local model and summed over all tree at the plot level to compute the AGB density per hectare (tDM.ha^{-1}).

3. Results

3.1. Overview of the data

In total 118 species belonging to 102 genera and 36 families were identified in the 41 plots inventoried (625 m² each, 2.56 ha in total). Ten predominant species, with an IVI greater than 10, all together contributed to 70.9% of the total basal area (Supplementary. File 2 and File 3). Among them, seven species present in the Lataha forest were selected for the destructive sampling and the development of mixed-species allometric equations.

A total of 34 trees belonging to these 7 out of the 10 most predominant species were destructively sampled and tree AGB ranged from 7.9 to 686.7 kg. The trunk biomass ranged from 6.9 to 217.7 kg, and that of branches from 0.72 to 563.3 kg, and that of leaves from 0.2 to 61 kg (Table 1). The highest proportion of dry biomass is observed in the branches (58.9%) and in the trunk (36.6%) while the leaves only contribute to 4.4% in average. The biomass allocation to the crown (branches and leaves) increased with the trunk diameter, from 30% in average for the [5-15[cm diameter class, and up to 70% for the [35-45[cm diameter class.

Table 1. Characteristics of the 34 trees destructively sampled in the dryland forest relics of northern Côte d'Ivoire. Species (botanical family), trunk diameter at breast height (DBH in cm), total tree height (H in m), wood specific gravity (ρ in $g.cm^{-3}$, not measured) and the biomass (kg) of the compartments (trunk, branches and leaves) and total aboveground biomass (AGB) are provided.

ID	DBH (cm)	H (m)	Trunk (kg)		Branches (kg)		Leaves (kg)		AGB (kg)
***Anthonotha crassifolia* (*Fabaceae*, n=7, ρ=0.8 $g.cm^{-3}$)**									
1	37.5	16	79.4	(11.8%)	563.3	(84.0%)	27.4	(4.1%)	670.2
2	11	11.2	34.8	(68.1%)	13.2	(25.8%)	3.12	(6.1%)	51.1
3	7.5	11	15.1	(82.1%)	2.3	(12.5%)	1	(5.4%)	18.4
4	28	13.5	133.4	(32.8%)	256	(63.0%)	17	(4.2%)	406.4
5	16	17	84.9	(71.8%)	30.6	(25.9%)	2.7	(2.3%)	118.3
6	18.5	13	90.8	(57.7%)	62.1	(39.5%)	4.5	(2.9%)	157.4
7	12	13	41.3	(62.4%)	21.4	(32.3%)	3.3	(5.0%)	66.2
***Berlinia grandiflora* (*Fabaceae*, n=4, ρ=0.62 $g.cm^{-3}$)**									
8	32	17.2	164.2	(47.3%)	167	(48.1%)	16.1	(4.6%)	347.4
9	14.5	13.7	58.3	(60.9%)	31.6	(33.0%)	5.6	(5.9%)	95.7
10	22	17.8	101.2	(54.0%)	80.8	(43.1%)	5.3	(2.8%)	187.3
11	11	11.7	30.2	(22.5%)	43.1	(32.1%)	61	(45.4%)	134.3
***Cola cordifolia* (*Malvaceae*, n=4, ρ= 0.5 $g.cm^{-3}$)**									
12	27.5	14	99.6	(66.4%)	43.9	(29.3%)	6.4	(4.3%)	150
13	23	12.5	79	(53.3%)	59.5	(40.2%)	9.6	(6.5%)	148.1
14	9.5	8.3	12	(66.7%)	3.8	(21.1%)	2.1	(11.7%)	18
15	10.8	9.7	15.8	(59.8%)	9	(34.1%)	1.5	(5.7%)	26.4
***Daniellia oliveri* (*Bignoniaceae*, n=5, ρ=0.4 $g.cm^{-3}$)**									
16	23	12.6	95.2	(59.2%)	61.6	(38.3%)	3.9	(2.4%)	160.7
17	13.5	11	29	(58.8%)	19.2	(38.9%)	1	(2.0%)	49.3
18	36	12	128.1	(28.1%)	299.2	(65.7%)	27.9	(6.1%)	455.4
19	33	12.4	31.2	(12.0%)	219.2	(84.1%)	10.2	(3.9%)	260.7
20	10	8.9	9.1	(50.3%)	8.4	(46.4%)	0.6	(3.3%)	18.1
***Diospyros mespiliformis* (*Ebenaceae*, n=4, ρ=0.7 $g.cm^{-3}$)**									
21	35	10.5	12.6	(6.3%)	177.4	(88.6%)	10.2	(5.1%)	200.2
22	6	9.3	9.2	(72.4%)	2.5	(19.7%)	1	(7.9%)	12.7
23	19	8	35	(25.5%)	95	(69.2%)	7	(5.1%)	137.2
24	13.5	10	33.5	(59.9%)	18.7	(33.5%)	3.6	(6.4%)	55.9
***Gmelina arborea* (*Lamiaceae*, n=5, ρ=0.4 $g.cm^{-3}$)**									
25	10.2	9.7	6.9	(87.3%)	0.7	(8.9%)	0.1	(1.3%)	7.9
26	41	17.2	217	(31.6%)	464.9	(67.7%)	4.7	(0.7%)	686.7
27	32	16.5	109.6	(64.0%)	61	(35.6%)	0.6	(0.4%)	171.3
28	20	19	78.1	(89.1%)	9.2	(10.5%)	0.3	(0.3%)	87.7
29	11.7	11.3	11.1	(88.8%)	1	(8.0%)	0.4	(3.2%)	12.5
***Isoberlinia doka* (*Fabaceae*, n=5, ρ=0.6 $g.cm^{-3}$)**									
30	20	13.3	100	(67.8%)	46.6	(31.6%)	0.8	(0.5%)	147.5
31	12	12.1	31.5	(68.6%)	13.4	(29.2%)	0.8	(1.7%)	45.9
32	27.5	11	90	(29.7%)	207.7	(68.5%)	5.5	(1.8%)	303.4
33	32	13	82.9	(16.7%)	398.2	(80.3%)	14.4	(2.9%)	495.6
34	11	10.8	25.4	(68.1%)	10.8	(29.0%)	1	(2.7%)	37.3

3.2. AGB models and prediction tests

We fitted six multi-species models (Table 2) and checked the residuals visually (Supplementary. File 4). According to AIC and RSE (lowest values) and adjusted R^2 (highest value), the model IV, $AGB= 0.0562(\rho D^2H)^{0.9749}$, was found to show the best performance for estimating total AGB. The models with two predictors (D and H), model II, $AGB=0.0709D^{1.9570}H^{0,6325}$ only slightly outperformed the model with only one predictor (D), model I, $AGB=0.2536D^{2.1113}$. As expected, we found that the six models fitted in this study provided accurate (low *RMSE* ~ 81 kg) and unbiased (*Bias%* < 8%) AGB estimates (Table 3). The models including three AGB predictors (D, H and ρ), namely models IV, V and VI showed the lowest *Bias%*, -3.89%, -2.71% and -3.38% respectively. Among the four published equations tested here, the best predictions were found for the equations of Djomo *et al.* (2016) and of Ganamé *et al.* (2021) established for dry forests in Africa and that both showed low errors (*RMSE* of 83.7 kg and 90.4 kg, respectively) and a slight underestimation (with a *%Bias* of -4.8 and -6.2%) though non-significant according to the paired t-tests (Table 3). In contrasts, the two pantropical equations (Chave et al. 2014, 2005) provided the largest errors (*RMSE* of 93.6 kg and 102 kg, respectively) and more importantly a systematic overestimation (*Bias%* > 20%) that was found significant according to the paired t-tests (Table 3).

Table 2. Allometric models for the prediction of tree aboveground biomass (AGB, in kg) from three predictors including stem diameter (D, in cm), total tree height (H, in m) and species wood gravity (ρ, in $g.cm^{-3}$). a, b, c are fitted parameters. Adjusted square regression coefficient ($AdjR^2$), residual standard error (RSE), Akaike information criterion (AIC), and the correction factor (CF) needed for back transformation of the log-log relationships are provided for each model. The best model (IV) and selected equation is shown in bold.

Model	**ln(a)**	**b**	**c**	**d**	**AdjR^2**	**RSE**	**AIC**	**CF**
I : ln AGB = lna + b ln D	-1.5024	2.1113			0.82	0.51	55.05	1.14
II : ln AGB = lna + b ln D + c ln H	-2.6452	1.9570	0.6325		0.83	0.51	55.21	1.13
III : ln AGB = lna + b ln(D^2H)	-3.14179	0.9335			0.83	0.50	53.65	1.13
IV : ln AGB= lna + b ln (ρD^2H)	**-2.95419**	**0.9749**			**0.89**	**0.40**	**38.91**	**1.08**
V : ln AGB = lna + b ln D + c ln H + dln ρ	-2.0198	2.0736	0.5391	1.3382	0.89	0.40	40.07	1.08
VI : ln AGB = lna + b ln (D^2H) +cln ρ	-2.74252	0.9713	1.3109		0.89	0.40	39.52	1.08

Table 3. Comparison of model accuracy between the allometric models fitted in this study (including correction factors) and previously published equations. The root mean squared error (*RMSE*, in kg), the relative bias (*Bias%*) and results (statistics and p-value) of paired t-tests between estimated and observed tree AGB are provided for all equations.

Models	**RMSE (kg)**	**Bias (%)**	**Paired t-test**	
			Statistic	***P***
This study				
Model I : $AGB=0.2536D^{2.1113}$	80.67	-6.70	0.85	0.4015
Model II : $AGB=0.0709\ D^{1.9570}\ H^{0,6325}$	76.98	-7.97	1.05	0.3022
Model III : $AGB=0.0488\ (D^2H)^{0.9335}$	79.12	-6.77	0.87	0.3887
Model IV : $AGB=0.0562(\rho D^2H)^{0.9749}$	76.62	-3.89	0.52	0.604
Model V : $AGB= 0.1432\ D^{2.0736}\ H^{0.5391}\ \rho^{1.3382}$	90	-2.71	0.32	0.7531
Model VI : $AGB= 0.0695\ (D^2H)^{0.9713}\ \rho^{1.3109}$	87.77	-3.38	0.40	0.6889
Published equations				
Djomo *et al*., (2016) : $AGB= 0.338D^{1.969}\ H^{0.295}\ \rho^{1.185}$	83.72	-4.80	0.55	0.5839
Ganamé *et al*., (2021) : $AGB= 0.0735D^{2.52}\ H^{0.22}\ \rho^{1.54}$	90.41	-6.19	0.63	0.5336
Chave *et al*., (2005) : $AGB=0.112(\rho D^2H)^{0.916}$	**93.64**	**23.66**	**-2.83**	**0.0078**
Chave *et al*., (2014) : $AGB=0.0673\ (\rho D^2H)^{0.976}$	**101.98**	**25.34**	**-2.77**	**0.0091**

3.3. Stand structure

For trees with a D ≥ 10 cm, the forest relics appeared relatively dense (Figure 2), with a mean stem density of 601 ± 204 $stems.ha^{-1}$ and basal area of 39.6 ± 17.8 $m^2.ha^{-1}$ across the three sites, for a relatively low canopy height (~13 m) and AGB (140 $t.ha^{-1}$). Strong structural variations were however identified across plots and sites, with higher basal area and AGB in Dolékaha and Korhogo, notably due to the presence of extremely large trees in a few plots leading to specifically dense stands locally (Figure 2). In contrast to stem density, both basal area and Lorey's height were found to be significantly correlated with plot level AGB and the relationship was the strongest with basal area.

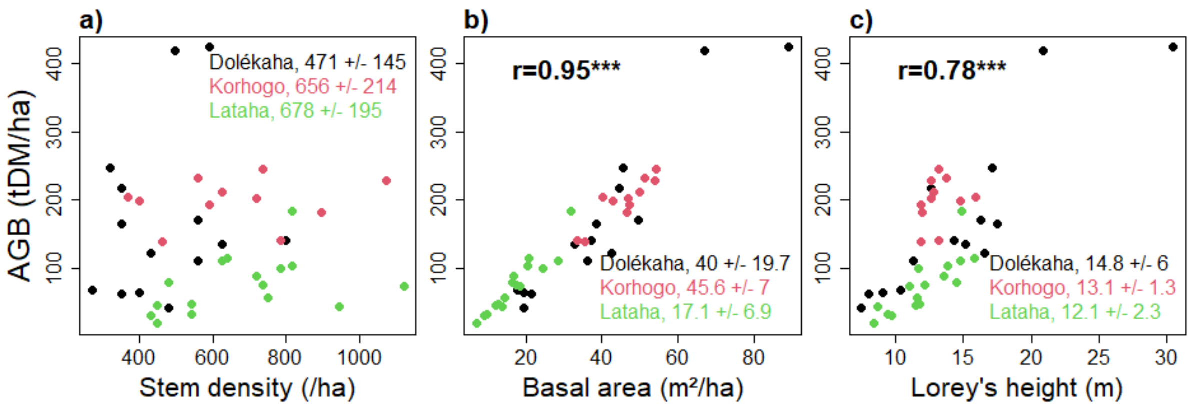


Figure 2. Relationship between aboveground biomass (AGB) at the plot level and forest attributes describing stand structure in the dryland forest relics of Côte d'Ivoire. Mean and standard error of stem density, basal area, and Lorey's height are given for the three sites according to the color code used for the plot color. The value of the Pearson's correlation coefficient (r) is given when significant, *** indicate $P<0.001$.

4. Discussion

4.1. Dominant species

In this study, inventory data from dryland forests relics provided information on tree species composition. The ten most dominant species included one exotic species, *Gmelina arborea* that spread in the area including these protected forests from experimental plots in the north of the country as elsewhere in Côte d'Ivoire. This species is now recognized by Louppe (2000) as part of the Ivorian forest landscape. The dominant species also inclued gregarious species characteritsics of West African forests and wooded savannas, *Anthonotha crassifolia, Isoberlinia doka* and *Daniellia oliveri* (Breteler, 2010; Guillaumet & Adjanohoun, 1971). These species are capable of regenerating easily in these areas and can develop a good resilience to dry climate and anthropogenic disturbances. As to *Berlinia grandifolia* and *Syzygium guineense* they are recognized as indicator species of Guinean, Sudanese and Sudanese gallery forests (Bouyer et al. 2005). Arbonnier (2004) also mentionned that *Diospyros mespiliformis* is found everywhere from Sahelo-Sudanese groves to Guinean forests and gallery forests in Africa. Finally, these dryland forest relics are also dominated by widely distributed species characteristics of semi-deciduous forests and dry forests such as *Ceiba pentandra* and *Antiaris toxicaria var. africana* (Dupuy (1998) and Adjanohoun (1964)). The dominant species (10 out of 118 inventoried species, 8% of species) contribute to a large share of the carbon stock (~ 70%) because they have the largest number of homogeneously distributed individuals and the largest number of large diameter individuals in the stand. The large contribution of dominant species to carbon stock is a general pattern. McNicol et al. (2018) showed that eight species out of the 50 inventoried in Miombo woodlands in southeast Tanzania store 80% of the carbon stock. Similarly, Bastin et al. (2015) showed that 1.5% of the dominant species account for over 50% of the AGB stock in several sites scattered in the dense forests of central Africa.

4.2. Biomass allocation and allometry

In the same line as the inventory data provided information on tree species composition for these dryland forest relics, the destructive sampling provided information on biomass allocation and allometry. The important quantity of AGB allocated to crown (63% in average) reflects the intrinsic development of the trees (architecture) in this phytogeographic zone, in comparison to the moist forest area where the biomass allocation to the crown is much lower with only 30% reported in Ghana (Henry et al., 2010), Gabon (Ngomanda et al., 2014) and across central Africa (Mankou et al., 2021), and where biomass allocation to the stem reflects investiment in height growth due to light competition. The highest proportion of AGB allocated to the branches compared to that allocated to the the trunk and leaves is common in savannas, and notably in the Sudanian and Sahelian areas (Balima et al., 2020, 2021; Bayen et al., 2020; Ganamé et al., 2021) though cross-continental variation in tree architecture has also been observed (Moncrieff et al., 2014). Interestingly, an increase of biomass allocation to crown with tree size was also retrieved here as earlier demonstrated for moist forest trees in central Africa (Mankou et al., 2021) and across the tropics (Ploton et al., 2016) and interpreted as a change in resource allocation during tree crown edification.

When we confronted our data to the pantropical equations of Chave et al. (2005) and of Chave et al. (2014), significant biases were identified, with an AGB overestimation by 23% and 25%, respectively. The validity in tropical Africa of the pantropical equations developed by Chave et al. (2005) for specific forest types (wet, moist, dry and mangrove forests) has been earlier debated because there were no trees from Africa in the training dataset. The equation for moist forest was found unbiased in Cameroon (Fayolle et al., 2013) while the equation for wet forest overestimated tree AGB by 40% in Gabon (Ngomanda et al. 2014). Although the subsequent pantropical equations of Chave et al. (2014) were fitted on a dataset containing 25% of trees from Africa, total aboveground biomass was found to be significantly overestimated here for trees sampled in dryland forest relics. Pantropical models were indeed developed on large dataset with a wide geographic distribution that did not account for site and forest type specificity. Other studies have shown that site-specific allometric models estimate forest biomass more accurately at the local scale (Djomo et al., 2016; Ganamé et al., 2021; Goussanou et al., 2016). Interestingly, the predictions of the models developed for African dry forests by Djomo et al. (2016) and Ganamé et al. (2021) both provided reliable AGB estimates. These results suggest a specific allometry for dry forest trees in Africa, since the data used to fit these models correspond to trees sampled in Côte d'Ivoire (the present study), Burkina Faso (Ganamé et al., 2021) and in several countries including Cameroon, Ghana, DR Congo, Gabon and Madagascar (Djomo et al., 2016) that are all subjected to the same climatic conditions, with an average annual rainfall of ~ 1,000 mm (from 840 mm to 1150 mm) and a dry season longer than five months (Boko-Koiadia et al., 2016; Djomo et al., 2016; Ganamé et al., 2021). The six equations developed in this study slightly underestimated biomass by 2.7% to 8%. These results are similar to those of Chave et al (2005), who showed that the error in estimating biomass is always of the order of 5%.

4.3. Stand structure

For the three study sites, the values of stem density (601 ± 204 stems.ha^{-1}) and basal area (39.6 ± 17.8 m².ha^{-1}) correspond to dense dry forest according to the thresholds proposed by Malaisse (1982, 30-40 m².ha^{-1}). These values of stem density and basal area are higher than that reported for other tropical dry forests with a total of of 311 ± 103 stems.ha^{-1} for a basal area of 10.8 ± 4.0 m².ha^{-1} in Venezuela (Feeley et al., 2005), 35 to 419 stems.ha^{-1} and 1.31 to 13.80 m².ha^{-1} in northern India (Sagar & Singh, 2006), 100.69 ± 40.02 stems.ha^{-1} and 5.1 ± 3.6 m^{2} ha^{-1} in southern India (Puttakame Gopalakrishna et al., 2015). The national forest inventory of Côte d'Ivoire carried out in 2021 also revealed lower values, with 389.1 ± 73 stems.ha^{-1} and 16.6 ± 3.0 m^{2}.ha^{-1} throughout the rural domain, classified forests and protected areas of the sub-Sudanese sector (Cuny et al., 2023). The high wood potential and large trees observed in our plots, compared with previous studies, can be explained by the low anthropic pressure exerted on these forest patches and also by the small size of the plots in this study (625 m^{2}) in contrast to the national inventory (5,000 m^{2}). In addition, the national inventory was also carried out in rural areas, where large-diameter trees are very rarely found, compared with this study, which was carried out only in classified and sacred forests, that are well protected by local communities, for whom these sites are sacred, and by the forestry administration and research structures, for whom these sites are also dedicated to biodiversity protection and research activities (Gueulou et al., 2019). In the Lataha site, the relatively young forest (protected since only 30 years) shows a greater abundance of small trees, and an overall less dense stand structure, in comparison with the sacred forests of Dolékaha and Korhogo, where the large trees have been preserved for long for adoration rituals. In this study, the above-ground biomass and carbon stocks were estimated at 141 ± 93 tDM.ha^{-1} and 71 ± 46 tC.ha^{-1}, respectively, which are within the upper range of the default values recommended by the GIEC (2006) for dense tropical dry forests (20 to 200 tDM.ha^{-1} and 10 to 100 tC.ha^{-1}, respectively). These estimates are also larger than the values of 53 ± 35 tC.ha^{-1} retrieved by Pan et al. (2013) for the world's tropical dry forests and of 29.7 tC.ha^{-1} retreived by Ryan et al. (2011) in Miombo woodlands in Mozambique but close to the 63.8 tC.ha^{-1} estimated for the forest of the sub-Sudanese and Sudanese sectors in Côte d'Ivoire by FAO and SEP-REDD+ (2017). These dry forest relics thus have a significant contribution to carbon stocks and sequestration in a landscape largely dominated by open vegetation. The higher quantity of biomass and carbon estimated here compared to these studies, is probably due to the high biomass of mature natural forests inventoried here, contrary to the works of these authors that included both intact and degraded forests. As earlier discussed, the small plot size can also influence the values (and variability) of forest attributes, and additional inventory data might be required.

5. Conclusions

This study identified ten dominant species, including *Gmelina arborea,* an exotic species that has spread into protected forests from experimental plots. The other dominant species are gregarious local species characteristic of West African forests and woody savannas. These dominant species represent 8% of the diversity but store more than 70% of the carbon stock. In addition to inventory data, our destructive sampling permitted to fit the first multispecies allometric equations for estimating tree AGB for the dryland forest relics of Côte d'Ivoire from tree diameter, total height and wood specific gravity. Pantropical models overestimate tree AGB by 20% while existing models for African dry forests provided reliable AGB estimates, suggesting a specific tree allometry for these trees. Finally, this study showed a relatively dense stand structure, in terms of stem density, basal area, and carbon stocks, in these protected and sacred forest relics.

Supplementary files

Supplementary. File1. Facies of the three forest relics studied

Supplementary. File2. Importance values of the species (IVI)

Supplementary. File3. Dominant species destructively sampled in the Lataha forest

Credit authorship contribution statement

Nina Gueulou : Writing-original draft, Investigation, Software, Formal analysis, Data curation ; Brahima Coulibaly : Conceptualization, Funding acquisition, Resources, Methodolgy, Project administration. Adeline Fayolle : Visualization, Methodology, Validation, Writing ; Noufou Doudjo Ouattara : Original draft preparation, Visualization, Resources, Writing – review ; Assandé Ahoba and Anatole Kanga N'Guessan : Original draft preparation, Visualization, Writing - review; Bakayoko Adama : Investigation, Project administration; Supervision

Declaration of Competing Interest

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

Acknowledgements

The biomass data collection was funded by the National Center for Agricultural Research in Côte d'Ivoire (CNRA, Forest and environment program operating fund 2020&2021). The authors give special thanks to this institution for their financial assistance. We extend our gratitude to the Forest Development Corporation of Côte d'Ivoire (SODEFOR) and to the populations of Dolékaha and Séhèlè villages for making the study sites available.

References

Adjanohoun, E. (1964). *Végétation des savanes et des rochers découverts en Côte d'Ivoire Centrale*. 177.

Alvarez, E., Duque, A., Saldarriaga, J., Cabrera, K., de Las Salas, G., del Valle, I., Lema, A., Moreno, F., Orrego, S., & Rodríguez, L. (2012). Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia. *Forest Ecology and Management*, *267*, 297–308.

Bakayoko, O., Assa, A. M., Coulibaly, B., & N'Guessan, K. A. (2012). Stockage de Carbone dans des peuplements de Cedrela Odorata et de Gmelina Arborea en Côte d'Ivoire. *European Journal of Scientific Research*, *75*(4), 490–501.

Balima, L. H., Kouamé, F. N. G., Bayen, P., Ganamé, M., Nacoulma, B. M. I., Thiombiano, A., & Soro, D. (2021). Influence of climate and forest attributes on aboveground carbon storage in Burkina Faso, West Africa. *Environmental Challenges*, *4*(April), 100123. https://doi.org/10.1016/j.envc.2021.100123

Balima, L. H., Nacoulma, B. M. I., Bayen, P., Dimobe, K., Kouamé, F. N., & Thiombiano, A. (2020). Aboveground biomass allometric equations and distribution of carbon stocks of the African oak (Afzelia africana Sm.) in Burkina Faso. *Journal of Forestry Research*, *31*(5), 1699–1711. https://doi.org/10.1007/s11676-019-00955-4

Bayen, P., Bognounou, F., Lykke, A. M., Ouédraogo, M., & Thiombiano, A. (2015). The use of biomass production and allometric models to estimate carbon sequestration of Jatropha curcas L. plantations in western Burkina Faso. *Environment, Development and Sustainability*, *18*(1), 143–156. https://doi.org/10.1007/s10668-015-9631-4

Bayen, P., Noulèkoun, F., Bognounou, F., Lykke, A. M., Djomo, A., Lamers, J. P. A., & Thiombiano, A. (2020). Models for estimating aboveground biomass of four dryland woody species in Burkina Faso, West Africa. *Journal of Arid Environments*, *180*(November), 104205. https://doi.org/10.1016/j.jaridenv.2020.104205

Boko-Koiadia, A., Cissé, G., Koné, B., & Séri, D. (2016). Variabilité Climatique Et Changements Dans L'environnement À Korhogo En Côte D'ivoire : Mythes Ou Réalité ? *European Scientific Journal, ESJ*, *12*(5), 158. https://doi.org/10.19044/esj.2016.v12n5p158

Bouyer, J., Guerrini, L., Cesar, J., De La Rocque, S., & Cuisance, D. (2005). A phyto-sociological analysis of the distribution of riverine tsetse flies in Burkina Faso. *Medical and Veterinary Entomology*, *19*(4), 372–378. https://doi.org/10.1111/j.1365-2915.2005.00584.x

Breteler, F. J. (2010). Revision of the African genus Anthonotha (Leguminosae, Caesalpinioideae). *Plant Ecology and Evolution*, *143*(1), 70–99. http://www.jstor.org/stable/41058269

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*(2), 261–304.

Chabi, A., Lautenbach, S., Orekan, V. O. A., & Kyei-Baffour, N. (2016). Allometric models and aboveground biomass stocks of a West African Sudan Savannah watershed in Benin. *Carbon Balance and Management*, *11*(1). https://doi.org/10.1186/s13021-016-0058-5

Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J. P., Nelson, B. W., Ogawa, H., Puig, H., Riéra, B., & Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, *145*(1), 87–99. https://doi.org/10.1007/s00442-005-0100-x

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., & Perez, R. (2004). Error propagation and sealing for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *359*(1443), 409–420. https://doi.org/10.1098/rstb.2003.1425

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrízar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., … Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, *20*(10), 3177–3190. https://doi.org/10.1111/gcb.12629

Clark, D. B., & Kellner, J. R. (2012). Tropical forest biomass estimation and the fallacy of misplaced concreteness. *Journal of Vegetation Science*, *23*(6), 1191–1196. https://doi.org/10.1111/j.1654-1103.2012.01471.x

Cuny, P., Plancheron, F., Bio, A., Kouakou, E., & Morneau, F. (2023). La forêt et la faune de Côte d'Ivoire dans une situation alarmante – Synthèse des résultats de l'Inventaire forestier et faunique national. *Bois & Forets Des Tropiques*, *355*, 47–72. https://doi.org/10.19182/bft2023.355.a36939

Curtis, J., & McIntosh, R. (1950). The Interrelations of Certain Analytic and Synthetic Phytosociological Characters Author (s): J . T . Curtis and R . P . McIntosh Published by : Ecological Society of America Stable URL : http://www.jstor.org/stable/1931497 . *Ecology*, *31*(3), 434–455.

Dimobe, K., Mensah, S., Goetze, D., Ouédraogo, A., Kuyah, S., Porembski, S., & Thiombiano, A. (2018). Aboveground biomass partitioning and additive models for Combretum glutinosum and Terminalia laxiflora in West Africa. *Biomass and Bioenergy*, *115*(November 2017), 151–159. https://doi.org/10.1016/j.biombioe.2018.04.022

Djomo, A. N., Ibrahima, A., Saborowski, J., & Gravenhorst, G. (2010). Allometric equations for biomass estimations in Cameroon and pan moist tropical equations including biomass data from Africa. *Forest Ecology and Management*, *260*(10), 1873–1885. https://doi.org/10.1016/j.foreco.2010.08.034

Djomo, A. N., Picard, N., Fayolle, A., Henry, M., Ngomanda, A., Ploton, P., McLellan, J., Saborowski, J., Adamou, I., & Lejeune, P. (2016). Tree allometry for estimation of carbon stocks in African tropical forests. *Forestry*, *89*(4), 446–455. https://doi.org/10.1093/forestry/cpw025

Dupuy, B. (1998). Bases pour une sylviculture en forêt dense tropicale humide africaine. *Serie FORAFRI, CIRAD*, *4*, 387.

FAO. (2010). Lignes directrices pour la gestion durabe des forêts en zones arides d'Afrique subsaharienne. *Document de Travail Sur Les Les Forêts et La Foresterie En Zones Arides*, *1*. www.fao.org/forestry

FAO et SEP-REDD. (2017). *Données forestières de base pour la REDD+ en Côte d'Ivoire. Inventaire de la biomasse forestière pour l'estimation des facteurs d'émission*. www.fao.org/publications

Fayolle, A., Doucet, J.-L., Gillet, J.-F., Bourland, N., & Lejeune, P. (2013). Tree allometry in Central Africa: Testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. *Forest Ecology and Management*, *305*, 29–37.

Fayolle, A., Ngomanda, A., Mbasi, M., Barbier, N., Bocko, Y., Boyemba, F., Couteron, P., Fonton, N., Kamdem, N., Katembo, J., Kondaoule, H. J., Loumeto, J., Maïdou, H. M., Mankou, G., Mengui, T., Mofack, G. I., Moundounga, C., Moundounga, Q., Nguimbous, L., … Medjibe, V. P. (2018). A regional allometry for the Congo basin forests based on the largest ever destructive sampling. *Forest Ecology and Management*, *430*(May), 228–240. https://doi.org/10.1016/j.foreco.2018.07.030

Feeley, K. J., Gillespie, T. W., & Terborgh, J. W. (2005). The utility of spectral indices from Landsat ETM+ for measuring the structure and composition of tropical dry forests. *Biotropica*, *37*(4), 508–519. https://doi.org/10.1111/j.1744-7429.2005.00069.x

Fobane, J. L., Onana, J. M., Zekeng, J. C., Biye, H. E., & Mbolo, A. M. M. (2017). Flora diversity and characterization of plant groups in Atlantic forests of Cameroon. *Journal of Biodiversity and Environmental Sciences*, *10*(5), 163–176.

Fonton, N. H., Medjibé, V., Djomo, A., & Kondaoulé, J. (2017). *Analyzing Accuracy of the Power Functions for Modeling Aboveground Biomass Prediction in Congo Basin Tropical Forests*. *d*(December). https://doi.org/10.4236/ojf.2017.74023

Ganamé, M., Bayen, P., Dimobe, K., Ouédraogo, I., & Thiombiano, A. (2020). Aboveground biomass allocation, additive biomass and carbon sequestration models for Pterocarpus erinaceus Poir. in Burkina Faso. *Heliyon*, *6*(4). https://doi.org/10.1016/j.heliyon.2020.e03805

Ganamé, M., Bayen, P., Ouédraogo, I., Balima, L. H., & Thiombiano, A. (2021). Allometric models for improving aboveground biomass estimates in West African savanna ecosystems. *Trees, Forests and People*, *4*(December 2020). https://doi.org/10.1016/j.tfp.2021.100077

Gibbs, H. K., Brown, S., Niles, J. O., & Foley, J. A. (2007). Monitoring and estimating tropical forest carbon stocks: Making REDD a reality. *Environmental Research Letters*, *2*(4). https://doi.org/10.1088/1748-9326/2/4/045023

GIEC. (2006). *Lignes directrices 2006 du GIEC pour les inventaires nationaux de gaz à effet de serre, Eggleston H.S., Buendia L., Miwa K., Ngara T. et Tanabe K. (eds). Publié : IGES, Japon*. http://www.ipcc-nggip.iges.or.jp

Goussanou, C. A., Guendehou, S., Assogbadjo, A. E., Kaire, M., Sinsin, B., & Cuni-Sanchez, A. (2016). Specific and generic stem biomass and volume models of tree species in a West African tropical semi-deciduous forest. *Silva Fennica*, *50*(2). https://doi.org/10.14214/sf.1474

Gueulou, N., Coulibaly, B., Ouattara, N. D., N'guessan, A. K., Ahoba, A., & Bakayoko, A. (2019). Modes de gestion et efficacité de conservation des reliques de forêts naturelles en zone tropicale sèche : cas du Département de Korhogo (Nord, Côte d'Ivoire). *International Journal of Biological and Chemical Sciences*, *13*(7), 3332–3346. https://doi.org/10.4314/ijbcs.v13i7.28

Guillaumet, J.-L., & Adjanohoun, E. (1971). La végétation de la Côte d'Ivoire. *Le Milieu Naturel de La Côte d'Ivoire*, *50*, 166–262.

Henry, M., Besnard, A., Asante, W. A., Eshun, J., Adu-Bredu, S., Valentini, R., Bernoux, M., & Saint-André, L. (2010). Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. *Forest Ecology and*

Management, *260*(8), 1375–1388. https://doi.org/10.1016/j.foreco.2010.07.040

Henry, M., Picard, N., Trotta, C., Manlay, R., Bernoux, M., Saint-andré, L., Henry, M., Picard, N., Trotta, C., Manlay, R., Valentini, R., Henry, M., Picard, N., Trotta, C., Manlay, R. J., Valentini, R., Bernoux, M., & Saint-andré, L. (2011). Estimating Tree Biomass of Sub-Saharan African Forests : a Review of Available Allometric Equations To cite this version : HAL Id : hal-02651041 Estimating Tree Biomass of Sub-Saharan African Forests : a Review of Available Allometric Equations. *Silva Fennica*, *45*, 477–596.

Jucker, T., Fischer, F., Chave, J., Coomes, D., Caspersen, J., Ali, A., Loubota Panzou, G. J., Feldpausch, T., Falster, D., Usoltsev, V., Adu-Bredu, S., Alves, L., Aminpour, M., Angoboy, I., Anten, N., Antin, C., Askari, Y., Avilés, R. M., Ayyappan, N., … Zavala, M. (2022). *Tallo database*. https://doi.org/10.5281/ZENODO.6637599

Koala, J., Sawadogo, L., Savadogo, P., Aynekulu, E., Heiskanen, J., & Saïd, M. (2017). Allometric equations for below-ground biomass of four key woody species in West African Savanna-woodlands. *Silva Fennica*, *51*(3). https://doi.org/10.14214/sf.1631

Kouamé, Y. A. G., Millan, M., N'Dri, A. B., Charles-Dominique, T., Konan, M., Bakayoko, A., & Gignoux, J. (2022). Multispecies allometric equations for shrubs and trees biomass prediction in a Guinean savanna (West Africa). *Silva Fennica*, *56*(2). https://doi.org/10.14214/SF.10617

Lewis, SL, Wheeler, CE, Mitchard, E. et al. (2019). *Restore natural forests to sequester carbon Online hed : Restoring natural forests is the best way to sequester carbon Plans to triple the area of plantations under the guise of ' forest restoration ' will not meet 1 . 5 degree climate goals ,*.

Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G., Van Der Heijden, G. M. F., Phillips, O. L., Affum-Baffoe, K., Baker, T. R., & Banin, L. (2013). Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1625), 20120295.

Loubota Panzou, G. J., Doucet, J. L., Loumeto, J. J., Biwole, A., Bauwens, S., & Fayolle, A. (2016). Biomasse et stocks de carbone des forêts tropicales africaines. *Biotechnology, Agronomy and Society and Environment*, *20*(4), 508–522.

Louppe, D. (2000). *Rapport de Mission en Côte d'Ivoire du 31 janvier au 13 février 2000*.

Mankou, G. S., Ligot, G., Loubota Panzou, G. J., Boyemba, F., Loumeto, J. J., Ngomanda, A., Obiang, D., Rossi, V., Sonke, B., Yongo, O. D., & Fayolle, A. (2021). Tropical tree allometry and crown allocation, and their relationship with species traits in central Africa. *Forest Ecology and Management*, *493*(April). https://doi.org/10.1016/j.foreco.2021.119262

Mbow, C., Verstraete, M. M., Sambou, B., Diaw, A. T., & Neufeldt, H. (2014). Allometric models for aboveground biomass in dry savanna trees of the Sudan and Sudan-Guinean ecosystems of Southern Senegal. *Journal of Forest Research*, *19*(3), 340–347. https://doi.org/10.1007/s10310-013-0414-1

MEA. (2005). Millennium Ecosystem Assessment, Ecosystems and Human Well-being: Synthesis. In *Island Press* (Vol. 4892, Issue 1). https://doi.org/10.11646/zootaxa.4892.1.1

Molto, Q. (2012). Estimation de biomasse en forêt tropicale humide Propagation des incertitudes dans la modélisation de la distribution spatiale de la biomasse en Guyane française. *Thèse/Université de Guyane*, 1–184.

Moncrieff, G. R., Lehmann, C. E. R., Schnitzler, J., Gambiza, J., Hiernaux, P., Ryan, C. M., Shackleton, C. M., Williams, R. J., & Higgins, S. I. (2014). Contrasting architecture of key African and Australian savanna tree taxa drives intercontinental structural divergence. *Global Ecology and Biogeography*, *23*(11), 1235–1244. https://doi.org/10.1111/geb.12205

Moundounga Mavouroulou, Q., Ngomanda, A., Lebamba, J., Laurier Engone Obiang, N., Gomat, H., Sidoine Mankou, G., Loumeto, J., Midoko Iponga, D., Kossi Ditsouga, F., Zinga Koumba, R., Henga Botsika Bobé, K., Lépengué, N., Mbatchi, B., & Picard, N. (2014). How to improve allometric equations to estimate forest biomass stocks? Some hints from a central African forest Domestication des espèces forestières fruitières View project Central African forest-savanna dynamics View project How to improve allometric equations to estimate forest biomass stocks? Some hints from a central African forest. *Article in Canadian Journal of Forest Research*. https://doi.org/10.1139/cjfr-2

Mugasha, W. A., Eid, T., Bollandsås, O. M., Malimbwi, R. E., Chamshama, S. A. O., Zahabu, E., & Katani, J. Z. (2013). Allometric models for prediction of above- and belowground biomass of trees in the miombo woodlands of Tanzania. *Forest Ecology and Management, 310*, 87–101. https://doi.org/10.1016/j.foreco.2013.08.003

Ngomanda, A., Engone Obiang, N. L., Lebamba, J., Moundounga Mavouroulou, Q., Gomat, H., Mankou, G. S., Loumeto, J., Midoko Iponga, D., Kossi Ditsouga, F., Zinga Koumba, R., Botsika Bobé, K. H., Mikala Okouyi, C., Nyangadouma, R., Lépengué, N., Mbatchi, B., & Picard, N. (2014). Site-specific versus pantropical allometric equations: Which option to estimate the biomass of a moist central African forest? *Forest Ecology and Management*, *312*, 1–9. https://doi.org/10.1016/j.foreco.2013.10.029

Niklas, K. J. (1994). *Plant allometry: the scaling of form and process. University of Chicago Press.* 1994.

Ouédraogo, S., Ouédraogo, O., Dimobe, K., Thiombiano, A., & Boussim, J. I. (2020). Prediction of aboveground biomass and carbon stock of Balanites aegyptaca, a multipurpose species in Burkina Faso. *Heliyon*, *6*(8). https://doi.org/10.1016/j.heliyon.2020.e04581

Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 593–622. https://doi.org/10.1146/annurev-ecolsys-110512-135914

Picard, N., Boyemba Bosela, F., & Rossi, V. (2015). Reducing the error in biomass estimates strongly depends on model selection. *Annals of Forest Science*, *72*(6), 811–823. https://doi.org/10.1007/s13595-014-0434-9

Picard, N., Saint-André, L., & Henry, M. (2012a). Manual for building tree volume and biomass allometric equations: from field measurement to prediction. *Manual for Building Tree Volume and Biomass Allometric Equations: From Field Measurement to Prediction, FAO; Food and Agricultural Organization of the United Nations*.

Picard, N., Saint-André, L., & Henry, M. (2012b). *Manuel de construction d'équations allométriques pour l'estimation du volume et la biomasse des arbres. De la mesure de terrain à la prédiction*. FAO; Food and Agricultural Organization of the United Nations.

Ploton, P., Barbier, N., Momo, S. T., Rejou-Mechain, M., Boyemba Bosela, F., Chuyong, G., Dauby, G., Droissart, V., Fayolle, A., Calisto Goodman, R., Henry, M., Guy Kamdem, N., Katembo Mukirania, J., Kenfack, D., Libalah, M., Ngomanda, A., Rossi, V., Sonke, B., Texier, N., … Pélissier, R. (2016). Closing a gap in tropical forest biomass estimation: Taking crown mass variation into account in pantropical allometries. *Biogeosciences*, *13*(5), 1571–1585. https://doi.org/10.5194/bg-13-1571-2016

Pradhan, A., Ormsby, A. A., & Behera, N. (2019). A comparative assessment of tree diversity, biomass and biomass carbon stock between a protected area and a sacred forest of Western Odisha, India. *Écoscience*, *26*(3), 195–204.

Puttakame Gopalakrishna, S., Leckson Kaonga, M., Kalegowda Somashekar, R., Satyanarayana Suresh, H., & Suresh, R. (2015). Tree diversity in the tropical dry forest of Bannerghatta National Park in Eastern Ghats, Southern India. *European Journal of Ecology*, *1*(2), 12–27. https://doi.org/10.1515/eje-2015-0013

Qasim, M., Porembski, S., Sattler, D., Stein, K., Thiombiano, A., & Lindner, A. (2016). Vegetation structure and carbon stocks of two protected areas within the South-Sudanian Savannas of Burkina Faso. *Environments - MDPI*, *3*(4), 1–16. https://doi.org/10.3390/environments3040025

Ribeiro et al. (2011). Impacts of biofuel in biodiversity hotspots. *Biodiversity Hotspots*, 277–293. https://doi.org/10.1007/978-3-642-20992-5

Ryan, C. M., Williams, M., & Grace, J. (2011). Above- and belowground carbon stocks in a miombo woodland landscape of mozambique. *Biotropica*, *43*(4), 423–432. https://doi.org/10.1111/j.1744-7429.2010.00713.x

Sagar, R., & Singh, J. S. (2006). Tree density, basal area and species diversity in a disturbed dry tropical forest of northern India: Implications for conservation. *Environmental Conservation*, *33*(3), 256–262. https://doi.org/10.1017/S0376892906003237

Sawadogo, L., Savadogo, P., Tiveau, D., Dayamba, S. D., Zida, D., Nouvellet, Y., Oden, P. C., & Guinko, S. (2010). Allometric prediction of above-ground biomass of eleven woody tree species in the Sudanian savanna-woodland of West Africa. *Journal of Forestry Research*, *21*(4), 475–481. https://doi.org/10.1007/s11676-010-0101-4

Sileshi, G. W. (2014). A critical review of forest biomass estimation models, common mistakes and corrective measures. *Forest Ecology and Management*, *329*, 237–254. https://doi.org/10.1016/j.foreco.2014.06.026

Soumah, F. S. (2018). *Les forêts sacrées de Guinée : intégration de l'écologie pour la conservation d'un patrimoine national*.

Thomas, S. C., & Martin, A. R. (2012). Carbon content of tree tissues: A synthesis. *Forests*, *3*(2), 332–352. https://doi.org/10.3390/f3020332

Tiébré et al. (2016). Caractérisation de la flore et de la végétation et potentiel de conservation de la biodiversité végétale en zone d'activités anthropiques dans le Nord-est de la Côte d'Ivoire. *Academia*, *17*(3), 9. http://www.ijias.issr-journals.org/%0ACaractérisation

Tiébré, M.-S., Vroh, B. T. A., Kouame, D., N'Da, K. D., & Yao, C.-Y. A. (2015). Effets d'un arbre exotique envahissant Hopea odorata Roxb.(Dipterocarpaceae) sur la diversité floristique et le stockage de carbone du Parc National du Banco en Côte d'Ivoire [Effects of exotic invasive tree Hopea odorata Roxb.(Dipterocarpaceae) on plant . *International Journal of Innovation and Applied Studies*, *10*(1), 207.

Traoré, S., Djomo, A. N., N'guessan, A. K., Coulibaly, B., Ahoba, A., Gnahoua, G. M., N'guessan, É. K., Adou Yao, C. Y., N'Dja, J. K., & Guédé, N. Z. (2018). Stand Structure, Allometric Equations, Biomass and Carbon Sequestration Capacity of <i>Acacia mangium</i> Wild. (Mimosaceae) in Côte d'Ivoire. *Open Journal of Forestry*, *08*(01), 42–60. https://doi.org/10.4236/ojf.2018.81004

Van Breugel, M., Ransijn, J., Craven, D., Bongers, F., & Hall, J. S. (2011). Estimating carbon stock in secondary forests: Decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management*, *262*(8), 1648–1657. https://doi.org/10.1016/j.foreco.2011.07.018

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., Miller, R. B., Swenson, N. G., Wiemann, M. C., & Chave, J. (2009). *Global wood density database. Dryad*.

Declaration of Competing Interest

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