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Research paper

## Aboveground biomass partitioning and additive models for *Combretum glutinosum* and *Terminalia laxiflora* in West Africa

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## ABSTRACT

Accurate estimates of aboveground biomass (AGB) strongly depend on the suitability and precision of allometric models. Although additive allometric equations are expected to reduce uncertainties due to additivity property between biomass of tree components, methods for developing biomass equations do not comply with the additivity property. This study aimed to evaluate biomass allocation patterns within tree components, and to develop additive allometric equations for *Combretum glutinosum* and *Terminalia laxiflora* in West Africa. Sixty trees were destructively sampled and measured for stem, branch and leaf biomass in Sudanian savannas of Burkina Faso. Biomass allocation to stem, branch and leaf was assessed by calculating the biomass fractions for each component. Bivariate relationships between biomass fraction and diameter at breast height (dbh) were further examined. For each biomass component we tested three non-linear allometric equations based on dbh alone, and dbh in combination with height and/or crown diameter as independent variables. Seemingly Unrelated Regressions were used to fit a system of additive biomass allometric equations. Branch biomass accounted for between 60 and 70% of the AGB. Branch mass fraction increased with increasing stem diameter while a reverse trend was observed for leaf and stem mass fractions. The decline in the mass fraction was more pronounced for the leaf than the stem. Additive biomass models developed for the two species exhibited good model fit and performance, with explained variance of 68–89%. The models developed in this study provide a robust estimation of tree biomass components and can be used in Sudanian savannas of West Africa.

## 1. Introduction

Reliable, accurate and cost effective methods for estimating tree biomass are required in order to determine geographic distribution of carbon stocks, understand changes in carbon stocks due to land use change, and to quantify feats of global initiatives that address climate change such as REDD+ (Reducing Emissions from Deforestation and forest Degradation in developing countries plus conservation of forest carbon stocks, sustainable management of forest and enhancement of forest carbon stocks). Carbon estimates are primarily derived from assessments of biomass. Biomass estimates are specifically essential for understanding the role of forests as carbon sinks or sources, and for sustainable forest management [1,2]. Aboveground biomass (AGB) is a useful measure for comparing structural and functional attributes of

forest and savanna ecosystems across a wide range of environmental conditions [3] and can serve as an indicator for the distribution and abundance of vegetation above the ground [4]. Current estimates of biomass stocks for the Sudanian savanna range are highly variable, and range between 21.32 Mg/ha [5] and 46 Mg/ha [6]. Some of the variations in the estimates can be attributed to the method chosen for biomass estimation [7–9]. Inconsistencies in biomass estimates can lead to varied conclusions and a fragmented understanding of the role of Sudanian savanna ecosystem in climate change and development.

The most accurate and direct method of estimating tree biomass is destructive sampling [10]. Also known as harvest method, it involves harvesting all the trees in a known area and measuring the weights of the wood and foliage components [11]. Destructive sampling is limited to small areas or small tree sample sizes; it is not recommended on

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endangered tree species or in protected areas [12], and cannot be used for repeated measurement over time [13]. Studies show that destructive sampling is time consuming, strenuous, expensive and labour intensive [14,15]. To circumvent these limitations, non-destructive methods such as use of allometric biomass equations (hereafter called allometric equations) have been developed. Once developed, allometric equations can be used to assess biomass on large scale and allow follow up measurements. Allometric equations form the basis for converting non-destructively obtained data, for example from ground-based inventory or from remote sensing to biomass [16]. The equations can be applied to dendrometric parameters of trees such as diameter at breast height (DBH), height, crown diameter (CD) and wood density in forest inventory data; or to indirectly measured (remotely sensed) parameters that are correlated to biomass, such as crown metrics, forest density or leaf area index to obtain biomass density. The role of allometric equations in determining the potential of forests and other ecosystems for climate protection underscores the need to develop robust equations that allow accurate quantification of biomass.

There is a general lack of allometric models suitable for biomass estimation in West African Sudanian savanna ecosystems. This presents a major problem since the region lack species specific models for most important local tree species [17,18]. Recent studies have reported allometric models that are specific to African ecosystems, for example afrotemperate and moist central African forest [7,12], agroforests [14,19,20] and other vegetation types [21,22]. Only a limited number of studies have focused on dryland environments; for example Sawadogo et al. [23] in Burkina Faso, Chabi et al. [6] in Benin and Trendenick et al. [24] in Mali. Biomass models from these studies are commonly used across neighboring countries. Because of limited number of species-specific or site-specific allometric equations, estimation of biomass in this region largely relies on general purpose equations cited in Brown [11], Chave et al. [25], and Chave et al. [26]. It is difficult to obtain accurate biomass estimates with such approach. The Sudanian savanna vegetation is highly heterogeneous; tree cover and structure is greatly influenced by environmental variability and anthropogenic disturbances. This limits the use general purpose equations such as Brown [11] developed using data from savanna ecosystems of South America and dry forests of India, as well as regional equations that have not been validated. A major limitation to development of allometric equations in dryland regions relates to difficulties in obtaining measured field data in these species-rich ecosystems [25]. Data for development of allometric equations primarily come from destructive sampling; although few studies have tried to develop allometric equations from non-destructive measurements [27,28].

The value of the allometric model depends on empirical data used. This determines how accurate a given model estimates AGB for a particular vegetation [8,9]. There is mounting evidence that application of models not suitable to the target environment and species results in large systematic deviations from observed data [4,14]. Studies have tried to correct such uncertainties by varying the number of predictor variables in the equations. The majority of studies develop allometric equations that use dbh [4,23,29] as the lone predictor variable. Other tree parameters that have been investigated as the main predictor variables include basal diameter [14], total tree height [4], CD or crown area [30–32] and wood density [12,26]. Allometric equations with dbh alone are commonly used because of the ease of measuring diameter with high accuracy. However, allometric equations that includes height and/or wood density as additional predictor variables have been published [5,33]; integrating height and wood density in biomass assessment can improve the predictive abilities of equations as well as their appropriateness to different locations [7,25,26,32,34], although the improvement can be species-sensitive [12]. The challenges of using allometric equations with multiple predictors include inability to accurately measure parameters such as CD and height [30], lack of (or variable) wood density data for most tree species, and to ill-understood relationships between the many variables [8].

Allometric equations that account for the additive property of biomass components are scarce [35–37]. Additive allometric equations reduce uncertainties due to additive property between biomass components. Unlike additive allometric equations, non-additive allometric equations fit the biomass data of total, sub-total and components separately [38]. Consequently, the sum of predictions from allometric equations of components may not be equal to the model prediction from the total biomass model. Previous studies have reported the importance of accounting for biomass additivity [39,40]; the system developed should ensure that the sum of the predictions for the tree components obtained from allometric equations of stem, branches and leaves equals the prediction for the whole tree [35,41]. Three methods are used to achieve additivity in a set of nonlinear models: adjustment in proportion (AP), ordinary least square with separating regression (OLSSR) and seemingly unrelated regression (SUR) [35,42]. SUR is commonly used to fit the system of additive allometric equations [37,38,43] because it ensures high efficiency of additivity and has strong ability to account for correlations among the components [20,35,41].

The vegetation of the Sudanian zone of Burkina Faso is dominated by species of Combretaceae, especially individuals of *Combretum glutinosum* and *Terminalia laxiflora* [44]. These species are well-known for their socio-economic and ecological importance [45]. So far, there are no validated specific allometric equations for estimating the above-ground biomass for these species in Burkina Faso. As a result, the role of these species in climate change mitigation through carbon sequestration is poorly understood and is either underestimated or overestimated depending on the allometric equation chosen for biomass estimation. To fill this gap, this study aims to evaluate biomass allocation patterns within tree components and develop additive allometric equations for *Combretum glutinosum* and *Terminalia laxiflora*. The specific objectives of this study were to (1) assess, within sampled trees, the patterns of biomass allocation and variation of component mass fractions according to tree diameter; (2) evaluate the performance of species-specific allometric equations developed to estimate stem, branch, leaf biomass of *Combretum glutinosum* and *Terminalia laxiflora*; (3) determine the system of additive allometric equations that best predicts the total aboveground biomass of the two studied species.

## 2. Material and methods

### 2.1. Study area

The study was conducted in three experimental sites located in Dano watershed, Total Wildlife Reserve of Bontioli and Nazinga Game Ranch in Burkina Faso, West Africa (Fig. 1). These sites are located in the southern Sudanian agro-ecological zone of Burkina Faso across a flat area with an average altitude of 300 m. They are situated within the Sudanian regional centre of endemism [46,47]. The widespread vegetation types in the study area are tree and shrub savannas with a grass layer dominated by the annual grasses such as *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilger) C.E. Hubbard, as well as the perennials such as *Andropogon gayanus* Kunth. and *Andropogon asciodis* C.B.Cl. The climate is tropical with a unimodal rainy season, lasting for about 6 months from May to October. The mean annual rainfall for 30 year period (1983–2013) is  $879.15 \pm 149.44$  mm for Dano,  $1062.78 \pm 147.99$  mm for Bontioli and  $996.3 \pm 172.53$  mm for Nazinga. The temperature ranges from 16 to 32 °C in December–January and 26–40 °C in March–April. The most frequently encountered soils are Lixisols [48].

### 2.2. Description of tree species

*Combretum glutinosum* Perr. ex DC. is a fairly fast-growing deciduous shrub species with a maximum height of 12 m (Photo 1), widely spread across the Sahel from Senegal to Cameroon and eastwards to the Sudan

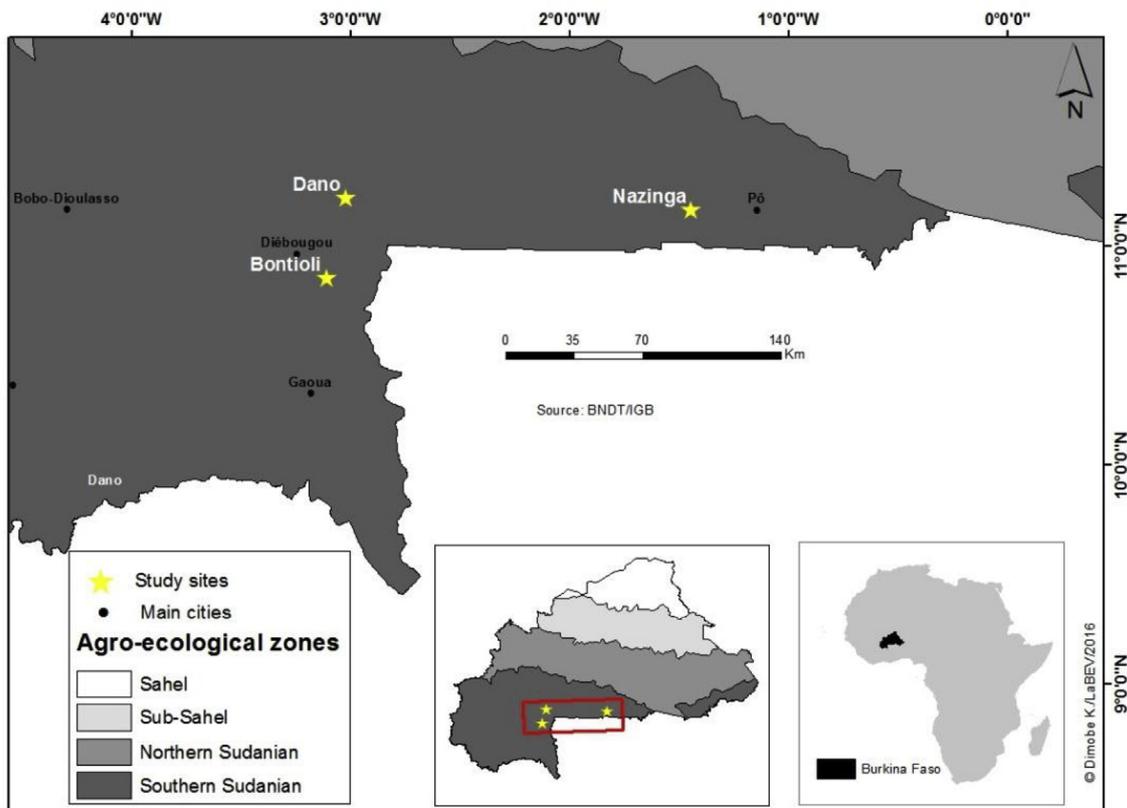


Fig. 1. Location of the study sites in West Africa. The insets denote the map of Burkina Faso and Burkina Faso in Africa.

[49]. It is found in savanna and open woodland with an annual rainfall of 200–900 mm [50]. The species is tolerant to arid conditions, and is resilient to fire [51]. It grows in open clusters or in pure associations, on sandy or degraded soils, and can sprouts during the dry season [49]. *C. glutinosum* has a twisted trunk that is low branching and an open but rounded crown. The tree is primarily used for medicine and dye; its wood is used in construction, fencing, general carpentry and as a source

of fuelwood.

*Terminalia laxiflora* Engl. & Diels is a deciduous small tree with up to 15 m height (Photo 2). It is widely distributed in sub-Saharan Africa, occurring in Senegal and Gambia eastward to western Ethiopia and Uganda, and southward to north-eastern DR Congo [52]. The species is widely distributed in deciduous woodland and bushy grassland. It has been reported in Burkina Faso in areas receiving between 750 and

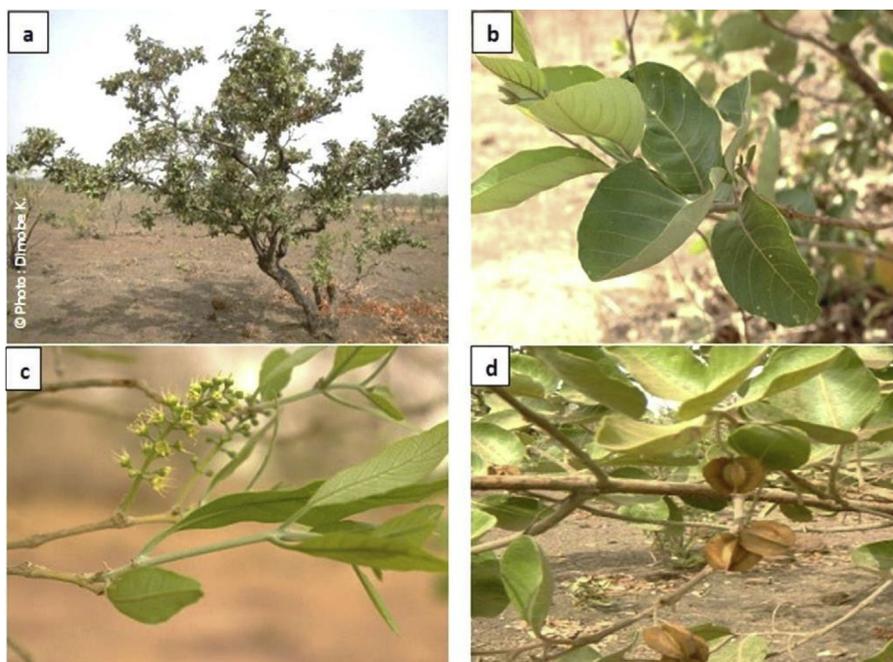


Photo 1. Specimen of the tree (a), leaves (b), blooming flowers (c) and fruits (d) of *Combretum glutinosum* in Dano watershed, Burkina Faso.

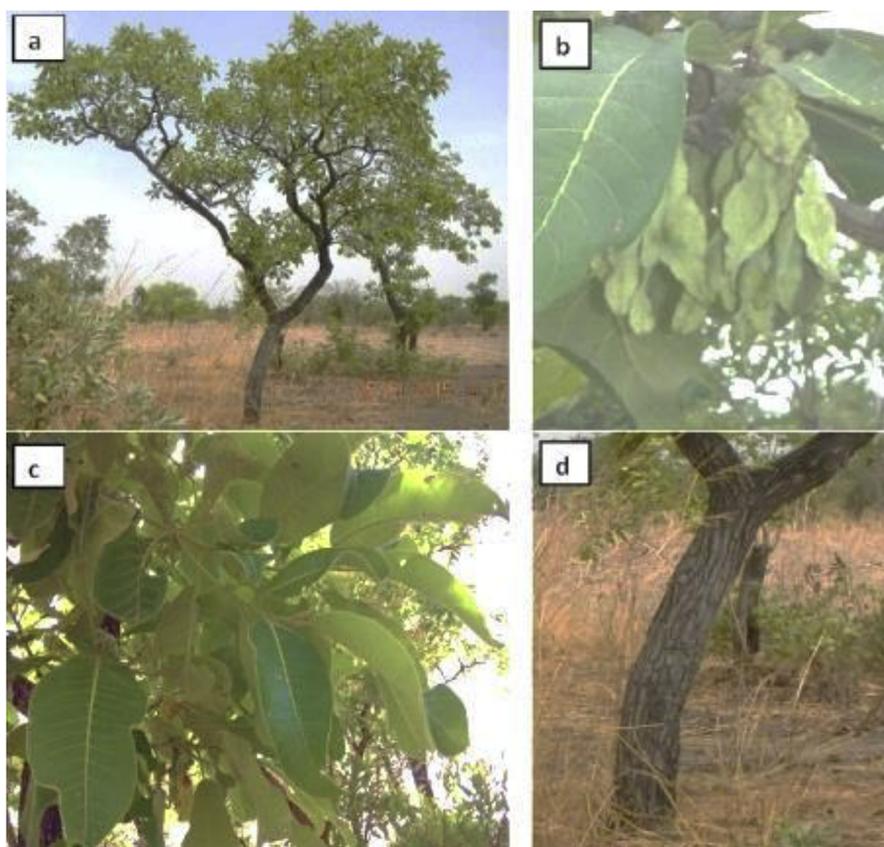


Photo 2. Specimen of the tree (a), fruits (b), leaves (c), and trunk (d) of *Terminalia laxiflora* in Nazinga Game Ranch, Burkina Faso.

1000 mm of rainfall per year [51], where it is mainly used for timber. *T. laxiflora* has a thick, corky bark that makes it fire-resistant.

### 2.3. Biomass sampling

Measurements of dbh, total tree height and CD, and field observations were conducted from April to May 2015. Ten individual trees for each of the two species were harvested at each of the three study sites, giving a total of sixty trees for measurements of biomass and subsequent development of allometric equations (Table 1). Total tree height, dbh, basal diameter and CD were measured for all individual trees of *C. glutinosum* and *T. laxiflora* prior to the harvesting. The CD of each tree was measured twice (cross-wise), along the east–west direction and the north–south direction in order to avoid bias [53]. Crown diameter and dbh were measured with a tape graduated in cm. Total tree height was measured from the base of the trunk to the tip of the tree using a clinometer. Diameter at breast height was measured with a diameter tape held tight and horizontal to the stem axis. For trees forking below 1.3 m, the diameter of all ramifications was measured

and the quadratic mean diameter (root-mean-squared) was calculated as the square root of the sum of squares of dbh of individual stems.

Trees selected for sampling were cut at the base using a chain saw. The branches were removed from the stem (main trunk of the tree from the base to the tip along the most straight bough) and were cut into weighable sections. All foliar material was separated from branches and collected into bags to facilitate weighing. The fresh weights of stem, branches and leaves for each individual tree were separately determined in the field using a 100 kg scale balance. Small samples of leaves, stem and branches were obtained, and their green weight determined using a 5 kg electronic balance (precision 0.5 g). The samples of branches and stem were taken as a pie or cylinder discs of 5 cm thickness depending on the size (diameter) of the trunk or branch. The fresh weight of each disc was recorded in the field immediately after harvesting the trees.

The discs and leaf samples were transported to the laboratory where they were oven dried to a constant weight at 105 °C (samples of branches and stems) or 75 °C (samples of leaves). The dry weight of the samples was recorded immediately after removal from the oven. The

Table 1  
Statistical summary of sampled tree characteristics and biomass data.

Site	DBH (cm)		Height (m)		CD (m)		Aboveground tree biomass (kg)			
	Mean	Range	Mean	Range	Mean	Range	Stem	Branch	Leaves	Aboveground
<b><i>C. glutinosum</i></b>										
Dano	6.98 ± 2.18	5–11.7	3.82 ± 0.86	2.87–5.4	3.04 ± 0.37	2.51–3.6	4.56 ± 3.66	13.23 ± 7.84	1.71 ± 0.95	19.50 ± 11.41
Bontioli	7.14 ± 1.61	5.6–10.4	3.60 ± 0.64	2.7–4.83	2.58 ± 0.55	1.57–3.39	3.11 ± 2.30	10.86 ± 6.62	2.20 ± 1.25	16.17 ± 9.54
Nazinga	7.24 ± 2.78	5–13.2	4.33 ± 1.37	2.9–7.35	3.10 ± 0.99	1.84–5.34	3.95 ± 4.06	14.64 ± 13.92	2.18 ± 1.32	20.78 ± 18.86
<b><i>T. laxiflora</i></b>										
Dano	11.89 ± 3.29	7.5–18.1	5.94 ± 1.27	3.97–7.84	4.25 ± 1.24	2.46–6.85	12.41 ± 7.85	37.58 ± 53.49	4.14 ± 3.14	54.13 ± 57.91
Bontioli	11.83 ± 6.86	7.00–24.8	6.32 ± 1.92	3.84–9.30	4.14 ± 1.88	2.38–7.37	18.30 ± 26.05	53.41 ± 74.02	6.46 ± 7.42	78.18 ± 105.64
Nazinga	10.38 ± 8.66	6.3–34.7	5.84 ± 2.24	4.02–11.7	4.02 ± 3.08	2.65–12.65	13.93 ± 32.08	71.40 ± 197.03	5.50 ± 11.13	90.83 ± 240.19

sample dry weight was divided by corresponding green weight to obtain the dry-to-green weight ratio for each tree component (stem, branches and leaves). The dry weight (biomass) of each component was obtained by multiplying the dry-to-green weight ratio by the green weight of the respective tree component. Total aboveground biomass of the tree was computed as the sum of all component weights in kilograms.

2.4. Data analysis

Biomass allocation to stem, branch and leaf was assessed by calculating for each component the biomass fractions, i.e. component biomass divided by total aboveground biomass. Bivariate relationships between biomass fraction and tree diameter were further examined for each biomass component and the study species. The relationship between biomass (of stems, branches, leaves and aboveground) and predictors variables (dbh and height) was first explored graphically to identify outliers and the nature of correlation. Allometric equations were generated for stem, branch, foliage and aboveground components based on three non-linear models (equations (1)–(3)) with dbh, height (h) and CD as independent variables: equation (1), dbh as the lone predictor variable; equation (2), dbh fitted with height; and equation (3), dbh fitted with height and crown diameter as additional predictor variables. The three sets of equation for component biomass (wi) were fitted as follows:

$$\ln(W_i) = \ln(a) + b \cdot \ln(dbh) \tag{1}$$

$$\ln(W_i) = \ln(a) + b \cdot \ln(dbh^2 \times h) \tag{2}$$

$$\ln(W_i) = \ln(a) + b \cdot \ln(dbh^2 \times h) + c \cdot \ln(Cd) \tag{3}$$

Diameter at breast height and height were used as combined predictor variable to account for variation of height for the same value of diameter while solving collinearity issue in linear regression [4]. Seemingly Unrelated Regressions were used to fit the system of allometric equations (each biomass component and total aboveground biomass) to realize the additivity property between tree biomass components, achieved through constraint on equation parameters [41]. The utility in applying the SUR method is that it allows for fitting simultaneously the biomass equations, thus accounts for correlations between regressions residuals. The system of additive allometric equations for the tree biomass components was built for equations (1)–(3) separately, as described in the following formulas.

For equation (1):

$$\ln(W_s) = \ln(\alpha_s) + \beta_s \cdot \ln(dbh) \tag{1.1}$$

$$\ln(W_b) = \ln(\alpha_b) + \beta_b \cdot \ln(dbh) \tag{1.2}$$

$$\ln(W_l) = \ln(\alpha_l) + \beta_l \cdot \ln(dbh) \tag{1.3}$$

$$W_t = \alpha_s \cdot dbh^{\beta_s} \cdot cf_s + \alpha_b \cdot dbh^{\beta_b} \cdot cf_b + \alpha_l \cdot dbh^{\beta_l} \cdot cf_l \tag{1.4}$$

Where  $W_s$ ,  $W_b$ ,  $W_l$  and  $W_t$  are the stem, branch, leaf and aboveground biomass, respectively;  $\alpha_i$  and  $\beta_i$  are the regression coefficients and  $cf_i$  the correction factor associated with these regressions.

For equation (2):

$$\ln(W_s) = \ln(\alpha_s) + \beta_s \cdot \ln(dbh^2 \times h) \tag{2.1}$$

$$\ln(W_b) = \ln(\alpha_b) + \beta_b \cdot \ln(dbh^2 \times h) \tag{2.2}$$

$$\ln(W_l) = \ln(\alpha_l) + \beta_l \cdot \ln(dbh^2 \times h) \tag{2.3}$$

$$W_t = \alpha_s \cdot (dbh^2 \times h)^{\beta_s} \cdot cf_s + \alpha_b \cdot (dbh^2 \times h)^{\beta_b} \cdot cf_b + \alpha_l \cdot (dbh^2 \times h)^{\beta_l} \cdot cf_l \tag{2.4}$$

For equation (3):

$$\ln(W_s) = \ln(\alpha_s) + \beta_s \cdot \ln(dbh^2 \times h) + \gamma_s \cdot \ln(Cd) \tag{3.1}$$

$$\ln(W_b) = \ln(\alpha_b) + \beta_b \cdot \ln(dbh^2 \times h) + \gamma_b \cdot \ln(Cd) \tag{3.2}$$

$$\ln(W_l) = \ln(\alpha_l) + \beta_l \cdot \ln(dbh^2 \times h) + \gamma_l \cdot \ln(Cd) \tag{3.3}$$

$$W_t = \alpha_s \cdot (dbh^2 \times h)^{\beta_s} \cdot Cd^{\gamma_s} \cdot cf_s + \alpha_b \cdot (dbh^2 \times h)^{\beta_b} \cdot Cd^{\gamma_b} \cdot cf_b + \alpha_l \cdot (dbh^2 \times h)^{\beta_l} \cdot Cd^{\gamma_l} \cdot cf_l \tag{3.4}$$

The correction factors (CF) in these equations were used to correct the bias introduced due to back-transformation of the log-transformed response variable into the original scale. The following formula was applied:

$$CF = \exp\left(\frac{RSE^2}{2}\right) \tag{4}$$

Where RSE is the standard error of residuals obtained from the regression.

The performance of the models was evaluated by looking at the statistical fits (the proportion of variance explained  $R^2$ , the root mean squared error RMSE, and the mean absolute deviation MAD) [12]. The significance of the estimated parameters at  $p < 0.05$  was also considered. The best additive model for each species was selected by combining the best model for each biomass component. Allometric equations with highest  $R^2$ , and lowest RMSE and MAD values were considered as the best fitting. We tested for significant deviations between the predicted values and observed values of AGB, using paired t-test. Graphical analyses of predicted vs. observed values of AGB were plotted for each species using the best set of additive allometric equations. Heteroscedastic behavior was checked for the selected models by graphically analyzing the trend in the relative error of estimation (estimated value minus observed value divided by observed value). We also compared the performance of the selected SUR AGB models against fitted Ordinary Least Squares (OLS) AGB models (see Supplementary Information) by computing the relative error of estimation, and found nonsignificant differences between the two methods (Supplementary Information).

3. Results

The two species exhibited greater biomass allocation to branches (between 60 and 70% of the total biomass), compared to stem and leaf (Fig. 2). Despite the marked difference in diameter range of the two species, the leaf and stem mass fractions decreased with increasing tree diameter. The decline in the mass fraction was more pronounced for the leaf than the stem; a reverse trend (increasing mass fraction-diameter lines) was observed for the branch component (Fig. 3). These results suggest that as tree size increases, more biomass is allocated to the woody structure (especially branch) at the expense of the foliage.

The non-linear trend in observed values of height and AGB as function of dbh is presented in Fig. 4. The results of the additive

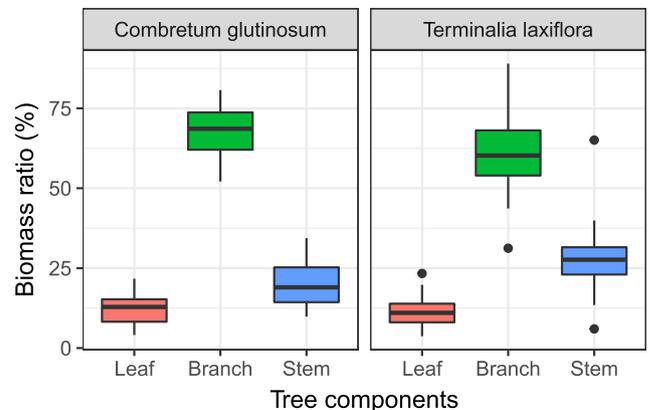


Fig. 2. Partitioning of aboveground biomass (biomass ratio) in the stem, branch and leaf component in *C. glutinosum* and *T. laxiflora*.

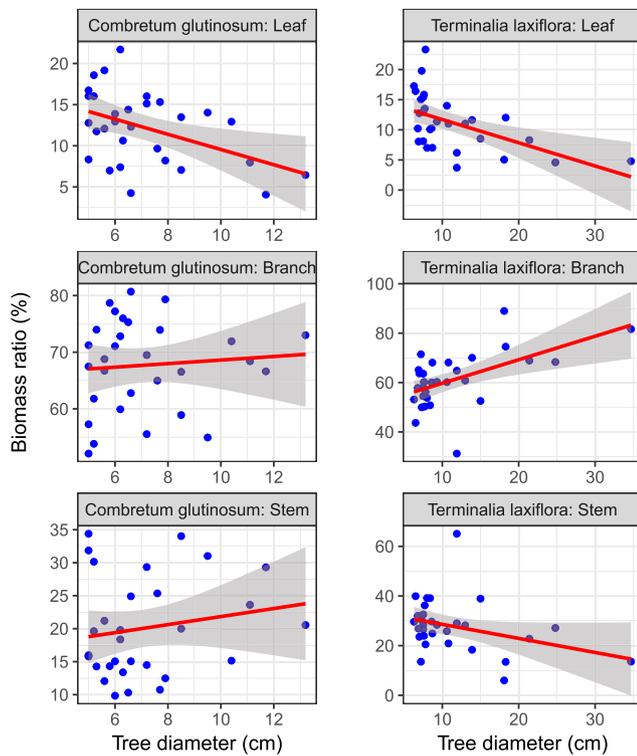


Fig. 3. Variation of tree component mass fraction according to diameter at breast height for *C. glutinosum* and *T. laxiflora*.

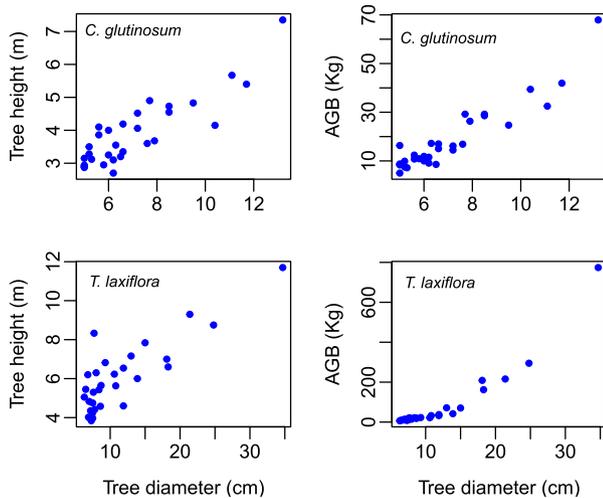


Fig. 4. The relationship between diameter at breast height, and (a) total tree height; (b) aboveground biomass for *C. glutinosum* and *T. laxiflora*.

biomass equations for both species are summarized in Table 2. For *C. glutinosum*, RMSE and MAD values ranged from 0.421 to 0.427 and from 0.327 to 335, respectively, while and  $R^2$  ranged from 41.3% to 43.1% for leaf biomass; the leaf component was best predicted when using the square of dbh and height ( $dbh^2 \cdot h$ ) as predictor. Similarly, stem biomass was better predicted when using  $dbh^2 \cdot h$ , which had lower RMSE (0.409) and higher  $R^2$  (69.71%) values. Branch biomass equations on the contrary, showed less error when both  $dbh^2 \cdot h$  and crown diameter were included in the model; the corresponding RMSE, MAD and  $R^2$  values were 0.280, 0.199 and 81.53%, respectively. Equations with dbh as the only predictor showed the best fit leaf and branch biomasses for *T. laxiflora* while equation with  $dbh^2 \cdot h$  was most suitable for stem biomass (Table 2). Adding crown diameter as predictor did not significantly improve the goodness-of-fit for *T. laxiflora*.

Allometric equations considered most appropriate are presented in Table 3. The additive AGB equation was obtained by combining the best allometric equation of each biomass component. For *C. glutinosum*, the additive allometric equation was  $AGB = e^{-2.01}(dbh^2h)^{0.49} + e^{-1.55}(dbh^2h)^{0.59}(Cd)^{0.79} + e^{-3.22}(dbh^2h)^{0.83}$  with 69% of explained variance. Using this model, we found no significant deviations between the predicted values and observed values of AGB ( $t = -0.269$ ,  $p$ -value = 0.789 for *C. glutinosum*; and  $t = 0.986$ ,  $p$ -value = 0.332 for *T. laxiflora*). The plot of observed versus predicted AGB coincided with the linear trend of  $y = x$ , with relatively constant error with increasing dbh (Fig. 5). The variance explained was comparatively higher for *T. laxiflora* (89%), and the additive allometric equation was  $AGB = e^{-3.51}(dbh)^{1.99} + e^{-3.67}(dbh)^{2.82} + e^{-3.70}(dbh^2h)^{0.89}$ . Fig. 5 also showed linear trend of 1:1 for the scatter plot of observed and predicted AGB values based on the selected additive model.

#### 4. Discussion

Variation in biomass allocation among tree components is usually observed when comparing species, trees of different ages and individuals [54]. The results of this study showed that the branch biomass had the greatest portion of AGB for *C. glutinosum* and *T. laxiflora*. However, several studies reported that tree stem/trunk is the component which represents the greatest portion of total biomass [55,56]. The decrease of leaf and stem mass fractions with increasing stem diameter observed in this study can be explained by the fact that, as trees get larger, the production of leaf biomass per unit of branch wood mass decreases [57]. This result is consistent with findings on *Celtis africana*, *Combretum kraussii*, *Croton sylvaticus*, *Syzygium gerrardii*, *Trichilia dregeana*, *Xymalos monospora* [57] in South African mistbelt forests and *Casuarina equisetifolia* [56] in a tropical forest of Hainan Island in China. According to King [58], the reduction in leaf biomass production results from declining production of branch biomass when branches get older. Our results also suggest that as tree size increases, relatively less biomass is allocated to stem compared to branches plus foliage, probably because more resources are invested into height growth for competition for aboveground resources such as light. Trees with more biomass in branches have a competitive advantage that allows them to out-compete neighbors by growing in height and expanding crown area to shade out competitors. The increase in branch mass fraction with increasing tree diameter means that when the trees get older, new branches come out and behave like younger trees. A similar trend was observed in *Eucalyptus* spp, though *Eucalyptus* spp invests high biomass proportion in stems compared to branches and leaves [59].

Additivity in biomass has been recognized as a desirable characteristic of a system of models to predict biomass of tree components [20,35,43]. According to Riofrío et al. [20], the use of the SUR method to fit the system of equations ensures the additive property. This study did not evaluate the performance of the SUR method against others, and thus limited the discussion to the fitted allometric equations. Several studies reported that tree diameter is the best predictor of biomass [60–62], generally explaining more than 75% of biomass variability. However, in this study, the use of stem diameter (dbh) as only predictor did not provide accurate estimates of biomass component fractions in *C. glutinosum*. This suggests that improvement of model fits through incorporation of additional dendrometric parameters is case-sensitive, as reported in a recent study by Mensah et al. [12].

Inclusion of tree height as additional predictor improved the equations for stem biomass for both *C. glutinosum* (above) and *T. laxiflora*, but only equation for leaf biomass for *C. glutinosum*. Similar observation has been reported in china [63], where introduction of tree total height in the model provided a good fit for the biomass data of all tree components. Allometric equations that include height as additional predictor variable have wider application in tropical forests [33]. This is critical in tropical dry forests where trees are shorter and branch ramification is often lower than 1.3 m height [60]. Using allometric

**Table 2**

Regression coefficients with goodness-of-fit statistics of the additive biomass allometric equations for the leaf, branch, and stem components of *C. glutinosum* and *T. laxiflora* using seemingly unrelated regression.

Equation	Predictors	Components	Regression coefficients			Performance criteria		
			ln(α)	β	γ	RMSE	MAD	R <sup>2</sup>
<i>C. glutinosum</i>								
1	dbh	Leaf	-2.04*** ± 0.56	1.35** ± 0.29		0.426	0.335	41.62
2	dbh <sup>2</sup> *h	Leaf	<b>-2.01*** ± 0.54</b>	<b>0.49*** ± 0.10</b>		<b>0.421</b>	<b>0.328</b>	<b>43.13</b>
3	dbh <sup>2</sup> *h; CD	Leaf	-1.99** ± 0.55	0.46** ± 0.14	0.16 <sup>ns</sup> ± 0.45	0.427	0.327	41.28
1	dbh	Branch	-1.70*** ± 0.42	2.10*** ± 0.21		0.315	0.239	76.64
2	dbh <sup>2</sup> *h	Branch	-1.60*** ± 0.40	0.76*** ± 0.08		0.313	0.224	77.03
3	dbh <sup>2</sup> *h; CD	Branch	<b>-1.55*** ± 0.36</b>	<b>0.58*** ± 0.09</b>	<b>0.83** ± 0.29</b>	<b>0.280</b>	<b>0.199</b>	<b>81.53</b>
1	dbh	Stem	-3.32*** ± 0.55	2.28*** ± 0.28		0.416	0.325	68.79
2	dbh <sup>2</sup> *h	Stem	<b>-3.23*** ± 0.53</b>	<b>0.83*** ± 0.10</b>		<b>0.409</b>	<b>0.309</b>	<b>69.71</b>
3	dbh <sup>2</sup> *h; CD	Stem	-3.19*** ± 0.53	0.73*** ± 0.13	0.46 <sup>ns</sup> ± 0.43	0.409	0.303	69.87
<i>T. laxiflora</i>								
1	dbh	Leaf	<b>-3.52*** ± 0.42</b>	<b>1.99*** ± 0.18</b>		<b>0.423</b>	<b>0.302</b>	<b>81.19</b>
2	dbh <sup>2</sup> *h	Leaf	-3.94*** ± 0.47	0.79*** ± 0.07		0.435	0.303	80.03
3	dbh <sup>2</sup> *h; CD	Leaf	-2.79*** ± 0.67	0.32 <sup>ns</sup> ± 0.22	1.38* ± 0.61	0.407	0.281	82.59
1	dbh	Branch	<b>-3.68*** ± 0.34</b>	<b>2.82*** ± 0.14</b>		<b>0.340</b>	<b>0.250</b>	<b>93.08</b>
2	dbh <sup>2</sup> *h	Branch	-4.22*** ± 0.43	1.11*** ± 0.07		0.399	0.311	90.49
3	dbh <sup>2</sup> *h; CD	Branch	-2.91*** ± 0.58	0.57** ± 0.19	1.58** ± 0.53	0.352	0.262	92.59
1	dbh	Stem	-3.10*** ± 0.38	2.21*** ± 0.16		0.380	0.294	86.82
2	dbh <sup>2</sup> *h	Stem	<b>-3.69*** ± 0.36</b>	<b>0.89*** ± 0.06</b>		<b>0.335</b>	<b>0.272</b>	<b>89.77</b>
3	dbh <sup>2</sup> *h; CD	Stem	-3.74*** ± 0.56	0.91*** ± 0.18	-0.05 <sup>ns</sup> ± 0.51	0.341	0.273	89.39

α, β, and γ are allometric coefficients, while RMSE, MAD and R<sup>2</sup> are the root mean square error, Mean Absolute Deviation and coefficient of determination used as measures of fit.

Bold values are indicative of the final selected models for each biomass component.

**Table 3**

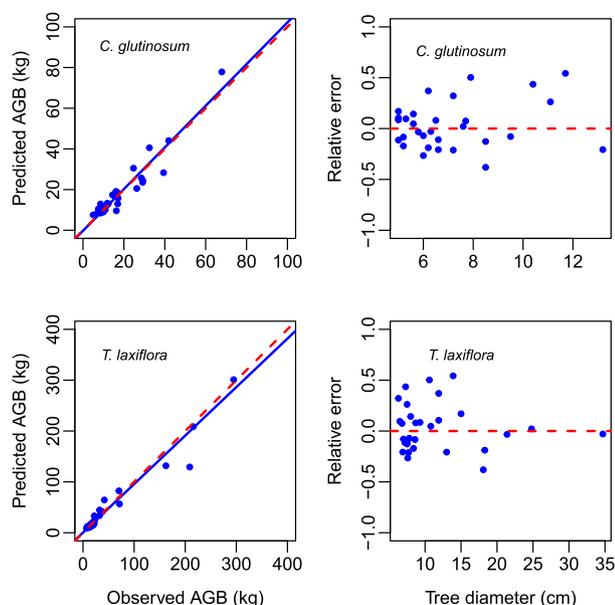
Selected biomass equation simultaneously fitted using seemingly unrelated regression for *C. glutinosum* and *T. laxiflora* species. CF is the correction factor for the equations.

Components	Biomass equations	RMSE	MAD	R <sup>2</sup>	CF
<i>C. glutinosum</i>					
Leaf	ln (Leaf biomass) = -2.01 + 0.49ln (dbh <sup>2</sup> h)	0.421	0.328	43.13	1.09
Branch	ln (Branch biomass) = -1.55 + 0.59ln (dbh <sup>2</sup> h) + 0.79ln (CD)	0.28	0.199	81.52	1.04
Stem	ln (Stem biomass) = -3.22 + 0.83ln (dbh <sup>2</sup> h)	0.409	0.309	69.71	1.09
AGB	ABG = e <sup>-2.01</sup> (dbh <sup>2</sup> h) <sup>0.49</sup> + e <sup>-1.55</sup> (dbh <sup>2</sup> h) <sup>0.59</sup> (CD) <sup>0.79</sup> + e <sup>-3.22</sup> (dbh <sup>2</sup> h) <sup>0.83</sup>	0.362	3.164	68.54	
<i>T. laxiflora</i>					
Leaf	ln (Leaf biomass) = -3.51 + 1.99ln (dbh)	0.423	0.302	81.19	1.09
Branch	ln (Branch biomass) = -3.67 + 2.82ln (dbh)	0.34	0.250	93.08	1.04
Stem	ln (Stem biomass) = -3.70 + 0.89ln (dbh <sup>2</sup> h)	0.334	0.272	89.77	1.06
AGB	ABG = e <sup>-3.51</sup> (dbh) <sup>1.99</sup> + e <sup>-3.67</sup> (dbh) <sup>2.82</sup> + e <sup>-3.70</sup> (dbh <sup>2</sup> h) <sup>0.89</sup>	0.356	8.819	89.44	

equations based on the dbh alone in tropical dry forests leads to over-estimating the number of tree stems and the biomass. Studies show that carbon estimates across the tropics can be overestimated, for example by between 13% [33] and 24% [64] if height is ignored. Other studies recommend wood density, crown diameter, and site as additional predictor variables that can be used to improve biomass prediction [7,25,26,32,34]. This study found that inclusion of crown diameter reduced the RMSE of branch biomass estimates (from 0.315 to 0.280) and improved the goodness of fit (from 76.64 to 81.53) for *C. glutinosum*. However, inclusion of crown diameter did not improve the model fits for *T. laxiflora*. This probably reveals that crown diameter may not be not be good predictor of AGB in *T. laxiflora* that of *C. glutinosum*. The strength of relationship between crown diameter and aboveground biomass depends on the size of the tree; being weak in trees with small crowns [30]. Trees such as *T. laxiflora* have less variable geometry of the canopy, possibly due to inherent plasticity of its

canopy to interplant competition or disturbances.

The study has developed new allometric equations, which are lacking for estimation of biomass for *T. laxiflora* in West Africa. Previous studies have developed allometric equations for *C. glutinosum* in West Africa in Senegal and Burkina Faso [23,61]. Our findings on *C. glutinosum* revealed that the biomass of components and AGB are better predicted by the combination of two or three predictors as a single variable. The models tested to estimate the relationships between biomass and explanatory variables are of the log-log form, which have been shown to predict the biomass of shrub and tree species with high accuracy [65,66]. Chave et al. [25] pointed out that biological data are heteroskedastics and that it is necessary to log-transform the variables to comply with the conditions of normality and homoscedasticity. The models developed for *C. glutinosum* in this study used dbh, crown diameter and height as predictors. In contrast, Mbow et al. [61] developed cubic models using only dbh and height in separate equations.



**Fig. 5.** Scatter plots for (a) predicted and observed values of aboveground biomass (AGB), and (b) relative error in AGB predictions based on the selected AGB additive model for and diameter at breast height for *C. glutinosum* (above) and *T. laxiflora* (below).

Sawadogo et al. [23] used basal diameter and the dbh as single variable in a linear model, although tree biomass does not generally scale in a similar proportion with dendrometric parameters. The variance explained in our model was 87.44% compared to 85.2% obtained by Sawadogo et al. [23]. The sample size per species in this study (30 individuals) is lower than those of Mbow et al. [61] and Sawadogo et al. [23] who used 39 and 103 individuals, respectively. It is also important to note that for *C. glutinosum* stem diameter ranged from 5 to 13.2 cm while Mbow et al. [61] used individuals with dbh varying from 5.1 to 27.1 cm. The differences observed between allometric equations developed in this study and existing allometric equations [23,61] could be explained by differences in sites, range of dbh, number of individuals, and management. The influence of site on growth and accumulation of tree biomass could be seen through soil effects (nutrient availability, soil moisture and soil structure) on primary production.

## 5. Conclusion

*C. glutinosum* and *T. laxiflora* species allocate more biomass in branches, as a possible mechanism to give the plant a competitive advantage, being able to expand crown area to shade out competitors. Diameter at breast height alone is a good predictor of biomass in branches, while stem requires inclusion of height to improve biomass predictions. The biomass models developed in this study can be applied to other Sudanian savanna ecosystems of West Africa, provided that tree growth parameters of dbh, height and crown area fall within similar ranges to those of the sampled population. The applicability of these additive equations is therefore restricted to the dbh ranges covered by trees used in this study (5–34.70 cm), which represents only a section of the ontogeny of these species.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.biombioe.2018.04.022>.

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