SILVA FENNICA

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Multispecies allometric equations for shrubs and trees biomass prediction in a Guinean savanna (West Africa)

Highlights

- New allometric equations were developed for predicting aboveground and belowground biomass (AGB and BGB) of trees and multi-stemmed shrubs in the Guinean savannas based on field measurements, providing information for West African mesic savannas and filling a critical knowledge gap.
- AGB and BGB of trees were better predicted from the quantity $\rho D_b^2 H$ (with ρ the specific wood density in g cm^{-3}, D_b the stem basal diameter in cm, and H the tree height in m).
- Obtaining accurate estimates of AGB and BGB in multi-stemmed shrubs required additional consideration of the total number of stems.
- The root/shoot biomass ratio decreased with increasing of the stem size (measured by D_b) for trees but remains relatively unchanged for shrubs.

Abstract

Currently, tools to predict the aboveground and belowground biomass (AGB and BGB) of woody species in Guinean savannas (and the data to calibrate them) are still lacking. Multispecies allometric equations calibrated from direct measurements can provide accurate estimates of plant biomass in local ecosystems and can be used to extrapolate local estimates of carbon stocks to the biome scale. We developed multispecies models to estimate AGB and BGB of trees and multi-stemmed shrubs in a Guinean savanna of Côte d'Ivoire. The five dominant species of the area were included in the study. We sampled a total of 100 trees and 90 shrubs destructively by harvesting their biometric data (basal stem diameter D_b, total stem height H, stump area S_S, as well as total number of stems n for shrubs), and then measured their dry AGB and BGB. We fitted log-log linear models to predict AGB and BGB from the biometric measurements. The most relevant model for predicting AGB in trees was fitted as follows: AGB = 0.0471 $(\rho D_b^2 H)^{0.915}$ (with AGB in kg and $\rho D_b^2 H$ in g cm^{-1} m). This model had a bias of 19%, while a reference model for comparison (fitted from tree measurements in a similar savanna ecosystem, Ifo et al. 2018) overestimated the AGB of trees of our test savannas by 132%. The BGB of trees was also better predicted from $\rho D_b^2 H$ as follows: BGB = 0.0125 $(\rho D_b^2 H)^{0.6899}$ (BGB in kg and $\rho D_b^2 H$ in g cm^{-1} m), with 6% bias, while the reference model had about 3% bias. In shrubs, AGB and BGB were better predicted from $\rho D_b^2 H$ together with the total number of stems (n). The best fitted allometric equation for predicting AGB in shrubs was as follows: AGB = 0.0191 $(\rho D_b^2 H)^{0.6227} n^{0.9271}$. This model had about 1.5% bias, while the reference model overestimated the AGB of shrubs of Lamto savannas by about 79%. The equation for predicting BGB of shrubs is: BGB = 0.0228 $(\rho D_b^2 H)^{0.7205} n^{0.992}$ that overestimated the BGB of the shrubs of Lamto savannas with about 3%

bias, while the reference model underestimated the BGB by about 14%. The reference model misses an important feature of fire-prone savannas, namely the strong imbalance of the BGB/AGB ratio between trees and multi-stemmed shrubs, which our models predict. The allometric equations we developed here are therefore relevant for C stocks inventories in trees and shrubs communities of Guinean savannas.

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1 Introduction

An accurate assessment of carbon (C) stocks and dynamics in savanna ecosystems is currently required for a better estimate of C balance in Africa (Ciais et al. 2011; Ifo et al. 2018). The African continent is extensively covered by savannas (Murphy et al. 2016), a biome in which woody and grassy plants coexist with varying relative abundance. Despite their lower density and smaller size compared to forests trees, savanna trees account for a significant contribution to the C budget of Africa (Delmas et al. 1991; Grace et al. 2006). Unfortunately, very little field data is available in African savannas and even more dramatically in the wet savannas, despite their large spatial extent. The total cover of the Guinean savannas is estimated to be about 600 million ha of land from western Senegal to eastern Nigeria, of which only ~10% is used for agriculture (Nyerges and Green 2000; World Bank 2009; Dinerstein et al. 2017), suggesting a high but undervalued carbon sequestration potential in this region. It is well established that both aboveground biomass (AGB) and belowground biomass (BGB) of savanna trees are significant contributors to the C sink, and should thereby be accurately estimated to calculate C balance (Loiola et al. 2015; Koala et al. 2017; Ifo et al. 2018). Currently, data is critically needed in tropical ecosystems (including forests and savannas), calling for developing new methods alleviating the practical challenges associated to digging out root systems; most current estimates of net primary productivity of woody plants and associated C stocks are derived from variables describing the aboveground compartment only (Yuen et al. 2013; Koala et al. 2017; Paul et al. 2019; Zhou et al. 2020). Estimating the BGB is a key step in refining tropical savanna models as a significant carbon stock is found belowground (Jackson et al. 1996; Mokany et al. 2006).

Allometric equations are necessary for estimating C stocks in vegetations around the world, as direct destructive measurements cannot be used at large scales (Addo-Danso et al. 2016; Ouédraogo et al. 2020). Initial destructive measurements in the field are however required to provide robust models (Picard et al. 2012). Allometric equations are statistical models estimating the tree biomass from their biometric characteristics, such as stem diameter or total tree height (Picard et al. 2012; Maulana et al. 2016). These equations are usually calibrated from field measurements on either a single species or a group of species chosen to describe a vegetation type (Ribeiro et al. 2011; Picard et al. 2012). The accuracy of the models always depends both upon the number of measurements

per species and upon the range of environmental conditions from which individuals are sourced (Picard et al. 2012; Colgan 2013; Chave et al. 2014). For instance, landscape heterogeneity (not explicitly accounted for) induces larger error in allometric models and can be a source of sampling error propagation (van Breugel et al. 2011; Picard et al. 2012; Mbow et al. 2014). If significant information about the above- and belowground stocks of C is available in the dry sub-Saharan savannas, additional efforts are urgently needed to describe the wet savannas (i.e., Guinean savannas). These two types of savannas are controlled by very contrasted environmental drivers: drought and herbivory in dry savannas, fire and plant competition in wet savannas (Osborne et al. 2018). These separate drivers selected species with distinct suites of traits (Maurin et al. 2014; Charles-Dominique et al. 2016; Osborne et al. 2018; Kindermann et al. 2022), and could impact strongly the investment in belowground parts that is on average higher in fire dominated places (Frost et al. 1986; Gignoux et al. 1997; Tomlinson et al. 2012; Fidelis et al. 2013; February et al. 2019).

In West African dry savannas (Sudanian savannas), several multispecies allometric equations are available to estimate both AGB and BGB of savanna trees (Sawadogo et al. 2010; Chabi et al. 2016; Koala et al. 2017; Dimobe et al. 2018; Bayen et al. 2020; Ganamé et al. 2021). The situation is different in West African wet savannas (Guinean savannas) as very few equations have been proposed (like Ifo et al. 2018) and the estimation of tree biomass in this region commonly uses general pantropical equations (Djagbletey et al. 2018; Amara et al. 2019; Atsri et al. 2020), notably the equation suggested by Chave et al. (2014). While Guinean and Sudanian savannas host similar species, the overall communities are disjoint and carbon allocation strategies and biomass distribution in plants (AGB vs. BGB) is likely to differ as these two systems experience distinct fire and precipitation regimes (Tomlinson et al. 2012; Osborne et al. 2018). This implies that models should be informed by data sourced for each phytogeographic zone. A recent global analysis (Qi et al. 2019) highlighted the important variations of the root/shoot biomass ratio (RSR) across biomes and vegetation types, according to environmental variables including temperature, rainfall, plant height, shoot biomass, latitude, all differing between Guinean and Sudanian savannas. In tropical savannas, fire and herbivory induce rapid changes in vegetation structure affecting the ratio between above- and belowground tree parts (Frost et al. 1986; Sankaran et al. 2005; Staver et al. 2009; Tomlinson et al. 2012; Scogings and Sankaran 2019). In wet savannas, fire is recognized as the main factor controlling the growth dynamic of woody plants (Sankaran et al. 2005; Bond 2008; Staver et al. 2011; N'Dri et al. 2022) and should promote a higher RSR compared to dry savannas (Gignoux et al. 2006; Tomlinson et al. 2012; Pausas et al. 2018; Wigley et al. 2019; Le Stradic et al. 2021). Last, large-scale models have been developed for woody plants assuming they are all trees, while most individuals composing a savanna stand can be developing as shrubs, with several small diameter stems (Zizka et al. 2014). Both trees and shrubs are abundant in savannas and usually have long life-spans of comparable magnitude (Bond and Midgley 2001; Gignoux et al. 2006; N'Dri et al. 2014; Gaillard et al. 2018). The pantropical allometric equation proposed by Chave et al. (2014): first, is not designed to accurately describe shrubs that could have very different RSR from trees (Qi et al. 2019); second, implies recording their diameter at breast height (dbh) that is not practical for multi-stemmed shrubs (Tietema 1993; Paul et al. 2017; Magarik et al. 2019; Kindermann et al. 2022) because a majority are shorter than 1.3 m or too branched at this height. These problems affecting plant biomass estimations are amplified in savannas by the fire action. Indeed, frequent fires in savannas favor shrubs with large underground storage organs, by repeatedly killing their aboveground parts in earlier growth stages. This situation leads to a mismatch between AGB and BGB compared to an undisturbed case (Gignoux et al. 1997; Tomlinson et al. 2012; Swemmer and Ward 2019).

In this study, we measured aboveground and belowground biomass of the five dominant woody species of the savanna of the Lamto Scientific Reserve (Côte d'Ivoire) corresponding to a

typical Guinean savanna (Menaut and Abbadie 2006). We then measured a few easy to record variables and tested how they could be used to estimate AGB and BGB for these species. Therefore, we propose multispecies allometric models for West African Guinean savannas, predicting total AGB and BGB of trees and shrubs. We calibrated our models using destructive sampling carried out on nine plots located in three different savanna physiognomies (open shrubby savanna, dense shrubby savanna, tall woody savanna) and the predictions of the allometric equations fitted here were compared to those of existing equations for a similar savanna ecosystem.

2 Material and methods

2.1 Study area and sampling sites

The study was carried out from 2017 to 2020 at the Lamto Scientific Reserve (LSR). LSR is located in the middle Côte d'Ivoire (6°13′–6°25′N and 5°15′–4°97′W) and belongs to the Pre-forest sector of the Guinean domain (Fig. 1) and to the Guinean forest-savanna mosaic ecoregion (Olson et al. 2001). In the LSR area, fire has been held responsible for the presence of savannas where climate should be able to sustain rainforests (Monnier 1968). Adjanohoun (1964) defines Guinean savannas as "stretches of tall grass enclosed in dense forests or between these and open forests− they are scattered with trees and palms− they contain relict patches of dense forest and are crossed by numerous gallery forests− without fire they develop into dense semi-deciduous forests". Over the 20-year period from 1998 to 2017, the average annual temperature and precipitation of LSR region were 28.5 °C and 1218 mm respectively. Rainfall periods are: a long rainy season from February to November, usually interrupted by a short dry season in August and a dry season from December to January. Temperatures are fairly constant between 27 and 29 °C throughout the year (Tiemoko et al. 2020).
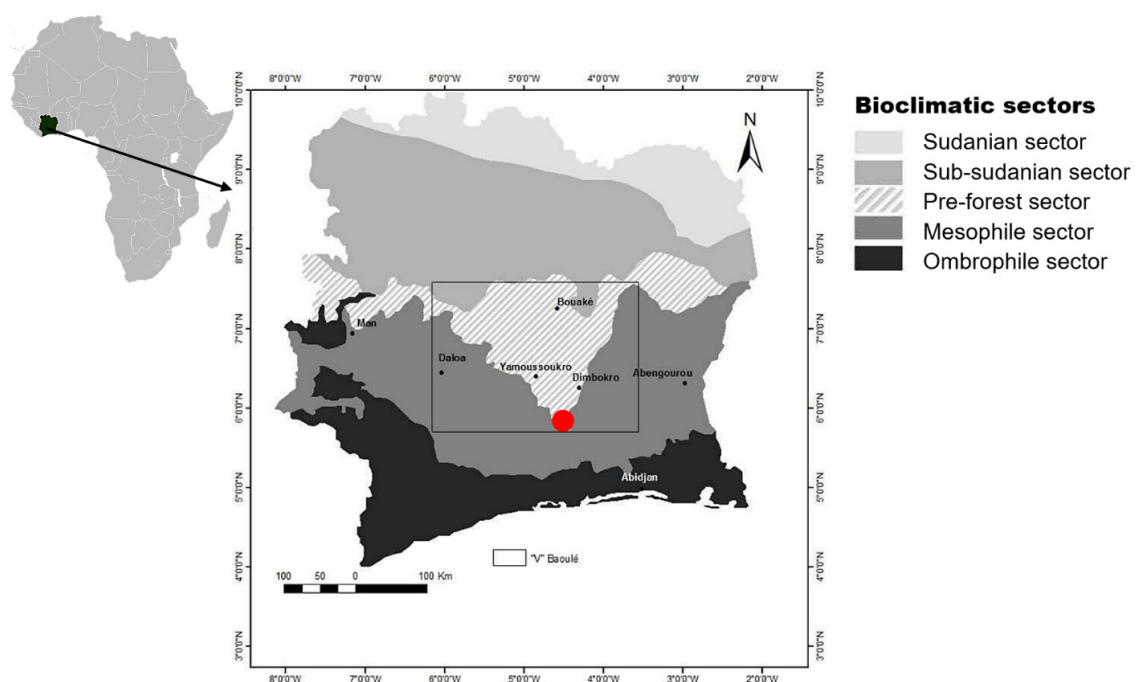
Fig. 1. Location of the study site: Lamto Scientific Reserve (in solid red circle), in Côte d'Ivoire.

LSR is about 80% Guinean savannas, with variable tree densities (Menaut and Abbadie 2006), the 20% remaining consist in gallery forests and forest islands. Thanks to the high-water availability, the savanna of LSR supports the development of a dense, diversified and tall grass layer, that can overtop the shrubs layer (Menaut and Abbadie 2006; Koffi et al. 2019). The total net primary production of the vegetation, including the aboveground and belowground net primary production of herbaceous and woody plants, were estimated to be 22–43 t ha^{-1} yr^{-1} of dry matter. The woody vegetation contributes at most 20% to this production (Menaut and César 1979; Menaut and Abbadie 2006). Three facies of savanna can be distinguished based on the cover of the woody and herbaceous species (Menaut and Abbadie 2006): a grassy savanna, dominated by the perennial grass *Loudetia simplex* (Nees) C.E.Hubb. (Poaceae) (woody cover < 7%) − a shrubby savanna, dominated by *Andropogonaceae* of the genera *Andropogon* L. and *Hyparrhenia* Andersson ex E.Fourn. (7% < woody cover < 62%) − and a woody savanna, with a discontinuous herbaceous layer and a very dense shrub layer (woody cover > 62%). When drying up, the grass layer provides abundant fuel for fires burning annually through the reserve, usually in mid-January. In the Lamto savannas, and generally in all the wet savanna ecosystems, regular burning of vegetation exerts a stabilizing effect on the habitat by preventing massive tree invasion (Monnier 1968; Menaut and Abbadie 2006; N'Dri et al. 2022).

Our study was conducted within three savanna physiognomies of the Lamto savannas (Supplementary file S1: Fig. 1, available at https://doi.org/10.14214/sf.10617): an open shrubby savanna, a dense shrubby savanna and a woody savanna. Sampling sites consisted of nine 0.5-hectare plots (50 m × 100 m) pre-established in 2016, with three plots representative of each savanna physiognomy (Suppl. file S1: Fig. 2).

2.2 Species of the study

We considered the most abundant woody species of the Lamto savannas. The woody layer of Lamto savannas is composed of about 90% of adult trees of the following four species: *Bridelia ferruginea* Benth. (Phyllanthaceae), *Crossopteryx febrifuga* (Afzel. ex G.Don) Benth. (Rubiaceae), *Cussonia arborea* Hochst. ex A.Rich. (Araliaceae), and *Piliostigma thonningii* (Schum.) Milne-Redh. (Fabaceae) (Menaut and Abbadie 2006). *Annona senegalensis* Pers. (Annonaceae) is also an abundant species but only in the shrub layer. According to Adjanohoun (1964), these five species belong to the *Brachiaria Brachylopha* Stapf (Poaceae) association and are native to the Sudano-Zambezian region before being acclimatized to humid conditions. Among these species, *C. arborea* and *C. febrifuga* grow only as single-stemmed trees from young to adult stages, whereas *P. thonningii* and *B. ferruginea* exist as single-stemmed trees or multi-stemmed shrubs, and *A. senegalensis* maintains a shrubby growth form in both young and old developmental stages (Monnier 1968; Menaut 1971). Photos of some specimens of each species are presented in Suppl. file S1: Fig. 3.

2.3 Sampling design

A total of 190 individuals among the five dominant species were collected − 90 of which were multi-stemmed shrubs and 100 were single stemmed trees (Table 1). The sampled shrubs were divided into three classes, based on the number of stems: 3–5 stems, 6–10 stems, and >10 stems. Trees were sampled in three classes of the stem basal diameter (D_b): $D_b < 10$ cm, 10 cm $\leq D_b \leq 15$ cm and $D_b > 15$ cm. Considering that the length of lateral roots of some woody plants can reach more than 20 m in the Lamto savannas (Monnier 1968), we distributed the total number of individuals to be sampled evenly among the nine study plots, with 10 shrubs per plot and 11 or 12 trees per

Table 1. Sampling criteria and number of trees and shrubs sampled per species. Among the five dominant woody species of LSR's savanna, two (*Crossopteryx febrifuga* and *Cussonia arborea*) grow only in a typical single-stemmed tree, two (*Piliostigma thonningii* and *Bridelia ferruginea*) grow both as a single-stemmed tree or as a multi-stemmed shrub and one (*Annona senegalensis*) grows exclusively as a shrub.

Species	Shrubs		Trees		Total
	n	*N*	D_b (cm)	*N*	
A. senegalensis	3–5	15	-	-	30
A. senegalensis	6–10	10	-	-	
A. senegalensis	>10	5	-	-	
B. Ferruginea	3–5	15	<10	10	55
B. Ferruginea	6–10	10	10–15	10	
B. Ferruginea	>10	5	>15	5	
C. Febrifuga	-	-	<10	10	25
C. Febrifuga	-	-	10–15	10	
C. Febrifuga	-	-	>15	5	
C. arborea	-	-	<10	10	25
C. arborea	-	-	10–15	10	
C. arborea	-	-	>15	5	
P. thonningii	3–5	15	<10	10	55
P. thonningii	6–10	10	10–15	10	
P. thonningii	>10	5	>15	5	
Total		90		100	*N* = 190

n: number of stems per individual; *N*: number of samples; D_b: stem basal diameter.

plot. We sampled in such a way as to obtain samples of each species in the three studied savanna physiognomies. On each sampling site, the distance between two sampled individuals was kept to ~15–20 m.

2.4 Measurement of dendrometric parameters of trees and shrubs

For trees, the total height of individuals (*H*) was measured using interlocking graduated stakes reaching a total height of 12 m. The basal diameter (D_b, diameter above the aerial part of the stump) was directly measured for small-sized stems ($D_b \leq 5$ cm), using a caliper. For the individuals with basal diameter greater than 5 cm, we first measured the stem basal circumference also above the aerial part of the stump using a measuring tape, and then converted the circumference to diameter.

For shrubs, the total number of stems (*n*) for one individual was determined. We measured the individual's maximum height (*H*), which corresponds to the height of the tallest stem, and the height (h_i) and basal diameter (d_i) of each stem ($i = 1…n$). We also estimated an equivalent basal diameter (D_b) for each individual multi-stemmed shrub from the sum of cross-sectional areas at the base of all the stems, according to the Eq. 1.

$$D_b = \sqrt{\frac{4\sum_{i=1}^{n} S_{b,i}}{\pi}}$$

(1)

where $S_{b,i}$ corresponds to the cross-sectional area at the base of each stem *i* ($i = 1…n$).

For each tree and shrub sampled, the total circumference of the stump (C_S) was measured (see Suppl. file S1: Fig. 4) and was used to estimate the corresponding surface area of the stump (S_S) according to Eq. 2.

$$S_S = C_S{}^2 / (4\pi) \tag{2}$$

2.5 Excavation and root removal

From the plant base, we exposed the main roots and the proximal parts of each lateral root in the first soil horizons by digging soil using a pickaxe, a daba (a kind of hoe with a short handle) and a machete. Each root was then excavated from its insertion zone towards its distal end. Fine roots (diameter < 2 mm, Jackson et al. 1996) were not sampled.

2.6 Determination of the dry biomass for each plant compartment

The aboveground part of each sample was cut at ground level and then divided into compartments: trunk, branches and leaves for large trees (D_b > 10 cm); main stem, twigs and leaves for smaller trees (D_b < 10 cm) and shrubs. Similarly, the belowground compartment of each sample was removed from the soil and divided into taproot and lateral roots. The stump was counted as a component of the belowground compartment.

The carbon mass represents about 40–50%, on average, of a plant's dry biomass (Martin and Thomas 2011; Ma et al. 2018). To obtain the total dry biomass of samples in our study, the total fresh biomass of each component of the aboveground compartment (the trunk, large branches plus twigs and leaves for trees, and the stems including twigs and leaves for shrubs) was weighed after felling the stems and digging up the roots. The total fresh biomass (B_f) of above- and belowground components of large trees were obtained in the field to the nearest 25 g. The fresh biomass of shrubs components and that of all subsamples were obtained in the laboratory to the nearest 0.1 g. Five fresh subsamples of each sample were collected and weighed to obtain their fresh mass (b_f), together totaling about 0.2–1 kg of stems (including twigs) for shrubs, 1–5 kg of trunk, 0.5–1 kg of branches plus twigs and 0.5–1 kg of stump for trees, 0.1–0.5 kg of leaves and 0.1–1 kg of roots (including tap root and lateral roots) for all the samples. All the subsamples were then oven-dried. The woody parts (trunk/stem, branches and twigs, roots) were dried at 105 °C and the leaves were dried at 75 °C, until a constant dry biomass (b_d) was obtained after 3 to 5 days of drying. After drying the subsamples, the average water content (WC) of each sample of the different aboveground and belowground components was estimated using Eq. 3. The total dry biomass (B_d) of each aboveground and belowground component was thus deduced from Eq. 4, and then the total dry mass of the aboveground and belowground compartments (AGB and BGB) of each sample was estimated by summing all the B_d of their different components.

$$WC = \left(\frac{b_f - b_d}{b_f} \right) 100 \tag{3}$$

$$B_d = \frac{100 - WC}{100} B_f \tag{4}$$

where WC (%) is the water content of one sub-sample; b_f and b_d are respectively the fresh biomass and dry biomass of each sub-sample of the sample of the aboveground and belowground components of plants; B_f and B_d (kg) are respectively the total fresh biomass and total dry biomass of each sample.

2.7 Statistical analysis, development and evaluation of the allometric equations

All the statistical analysis and graphics were performed using the version 4.0.2 of the R software (R core team 2020). Data were recorded in spreadsheets attached as Suppl. file S2, which metadata are in Suppl. file S3. The Suppl. file S4 includes all R-codes used to perform statistical tests and graphics.

Merging data of all the tree species together, the variation of the total aboveground biomass (AGB), the total belowground biomass (BGB) and the root/shoot biomass ratio (RSR) of trees were studied in relation to the different classes of the basal diameter (D_b), using one-way ANOVA and Tukey's HSD (honestly significant difference) tests. We similarly evaluated the variation of AGB, BGB and RSR of shrubs according to different classes of the total number of stems (n) and different classes of the equivalent basal diameter of stems (D_b) using ANOVA or Student's t-test. Differences in RSR between growth forms were tested using the Student's t-test.

The reference model we retained to predict AGB and BGB after preliminary graphical exploration is the linearized logarithmic form of the power function: the allometric equations were fitted using log-log linear models relating AGB or BGB to the one or several predictors. All the variables measured in the field were considered as potential predictors or independent variables: the total number of stems (n), the stem basal diameter (D_b, in cm) corresponding to the equivalent basal diameter of stems for multi-stemmed shrubs, the stem total height (H, in m) corresponding to the stem maximum height for multi-stemmed shrubs and the surface area of the stump (S_S, in cm^2). We used also, as explanatory variable, a proxy for plant biomass (w, in g cm^{-1} m) corresponding to the product $\rho D_b^2 H$, where the term $D_b^2 H$ represents a proxy of the stem volume V ($V = \alpha D_b^2 H$, with e.g., $\alpha = \pi/12$ for a cone and $\alpha = \pi/4$ for a cylinder, and most stem tapers with intermediate α values); ρ is the wood specific density (in g cm^{-3}). For multi-stemmed shrubs $D_b^2 H$ was estimated for each individual from the basal diameter (d_i) and the height (h_i) of each stem (i) according the Eq. 5.

$$D_b^2 H = \sum_{i=1}^{n} d_i^2 h_i \tag{5}$$

The wood density values considered in this study represent the averages obtained from wood density values provided by the following studies or databases: N'Dri et al. (2018a), Ifo et al. (2018), Aabeyir et al. (2020), the Global wood density database (Zanne et al. 2009), the African Wood Density Database (Carsan et al. 2012). N'Dri et al. (2018a) study was achieved on tree samples of the LSR and provides a species-specific value for *Bridelia ferruginea*, *Crossopteryx febrifuga*, *Cussonia arborea* and *Piliostigma thonningii*. Ifo et al. (2018) also provide a species-specific value, for *Annona senegalensis*, *B. ferruginea* and *C. febrifuga*. Aabeyir et al. (2020) provide a species-specific value for *C. febrifuga* and *P. thonningii*. A genus-level average value was extracted from the African Wood Density Database for *C. arborea*, while the Global wood density database provides a species-specific value for *C. febrifuga* and allowed us to compute a genus-level average value for *A. senegalensis*, *B. ferruginea* and *C. arborea*.

We initially checked for multicollinearity between the independent variables (n, D_b, H, w and S_S) by determining the variance inflation factor (VIF, Belsley 1980) associated with each variable in the regression models of AGB and BGB. The VIF was computed according the Eq. 6. It represents the score of a given independent variable highlighting the degree to which other independent variables explain this variable. In this study, we considered an independent variable as non-collinear to other(s) when the VIF value was not exceeding 10 (Midi and Bagheri 2010).

$$VIF_j = \frac{1}{1 - R_j^2} \tag{6}$$

where VIF_j is the variance inflation factor for the jth predictor and can take on values from unity to infinity.

After removing the predictors with a VIF value > 10, all the remaining independent variables were used in a first full model, and then we investigated for the best models for predicting AGB and BGB by eliminating some of the predictors using stepwise selection (Zhang 2016). The criteria for evaluating the performance of the models were the p-value of each independent variable, the model simplicity (i.e., with fewer predictors), the adjusted coefficient of determination (Adj. R^2) and the Akaike information criterion (AIC). The validation assumptions of the models were tested by examining the residuals versus fitted values to check for homogeneity of variance and the normality of residuals (Suppl. file S3).

The logarithmic transformation of data induces a bias in the biomass estimation when reverting to the initial variables (Baskerville 1972). A correction of AGB and BGB estimates was therefore necessary and consisted of multiplying the estimated biomass by a correction factor (CF) calculated as (Sprugel 1983, Eq. 7):

$$CF = \exp\left(\frac{RSE^2}{2}\right) \tag{7}$$

where CF is the correction factor and RSE is the residual standard error of the regression.

In the next step, we tested whether the relation between AGB or BGB and the quantitative independent variables retained in the final model differed significantly (P-value < 0.05) according to growth form and species as categorical explanatory variables, using analysis of covariance (ANCOVA). ANCOVA combines linear regression and ANOVA and tests if the slopes of the interactions between the different terms of the categorical variable and of a given quantitative variable are different from each other (Crawley 2013). With regards to the growth form, when the interactions were significant, we fitted separate models for trees and shrubs individually. In the case of non-significant interactions, a single prediction model for both trees and shrubs would be better. We also examined for differences in regression parameters between the different species.

Finally, the AGB and BGB prediction models fitted in this study were compared to those of Ifo et al. (2018) fitted from tree measurements in the savanna of the Plateau Batéké (Congo) by using basal diameter as a predictor instead of dbh (equation 3 for AGB and equation 5 for BGB in their study). Three of the studied species in our study were part of the Ifo et al. (2018) study, namely *Annona senegalensis*, *Bridelia ferruginea* and *Crossopteryx febrifuga*. Models were compared on the basis of the model bias. The model bias is a measure of systematic deviation of model predictions from observed data (Chave et al. 2014; Aabeyir et al. 2020) and was computed from Eq. 8.

$$Bias = 100\left[\frac{\sum_{i=1}^{N}\left(B_{est,i} - B_{obs,i}\right)}{\sum_{i=1}^{N}\left(B_{obs,i}\right)}\right] \tag{8}$$

where $B_{obs,i}$ is the observed biomass of the ith sample, $B_{est,i}$ is the predicted biomass of the ith sample, N is the number of samples.

3 Results

3.1 Distribution of dendrometric parameters and variation of aboveground biomass, belowground biomass and root/shoot biomass ratio

The total height (H) of the samples of single-stemmed trees ranged from 0.75 to 7.5 m, with an average value of 3.43 m. The basal diameter (D_b) of stems ranged from 2 to 59 cm, with an average value of 14 cm. The stump surface area (S_S) ranged from 3 cm^2 to 3555 cm^2 (average 313 cm^2). The shrubs had between 3 and 23 stems, and maximum heights (H) ranged from 0.75 to 2.5 m. The equivalent basal diameter (D_b) of the stems of shrubs ranged from 2 to 9 cm, while the stump surface area ranged from 25 to 2477 cm^2.

RSR significantly differed between growth forms, either considering all species ($P < 0.001$, Fig. 2A), or considering separately those species that present both growth forms ($P < 0.001$ for each species, Fig. 2B). Overall, the mean RSR of shrubs (estimated at 1.8 ± 0.7) was higher than that of trees (estimated at 0.9 ± 0.72) (Fig. 2A). The total aboveground dry biomass (AGB) ranged from 0.1 to 139.23 kg (average 18.8) in trees and from 0.1 to 5.16 kg (average = 0.85) in shrubs (Fig. 3). The total belowground dry biomass (BGB) ranged from 0.12 to 71.71 kg (average 9.98) in trees and from 0.11 to 9.21 kg (average 1.62) in shrubs (Fig. 3). The RSR was significantly higher in smaller trees ($D_b < 10$ cm) compared to larger trees ($D_b > 10$ cm) (one-way ANOVA, $F_{(2,97)} = 21.49$, $P < 0.001$, Fig. 3C): it was greater than 1 (BGB > AGB) in smaller trees and less than 1 (BGB < AGB) in larger trees. In shrubs, the RSR did not vary significantly with the individual number of stems nor with D_b (one-way ANOVA, $P > 0.05$). As in small trees with $D_b < 10$ cm, the RSR was generally greater than 1 (BGB > AGB) in shrubs, regardless of their D_b and number of stems (Fig. 3F).
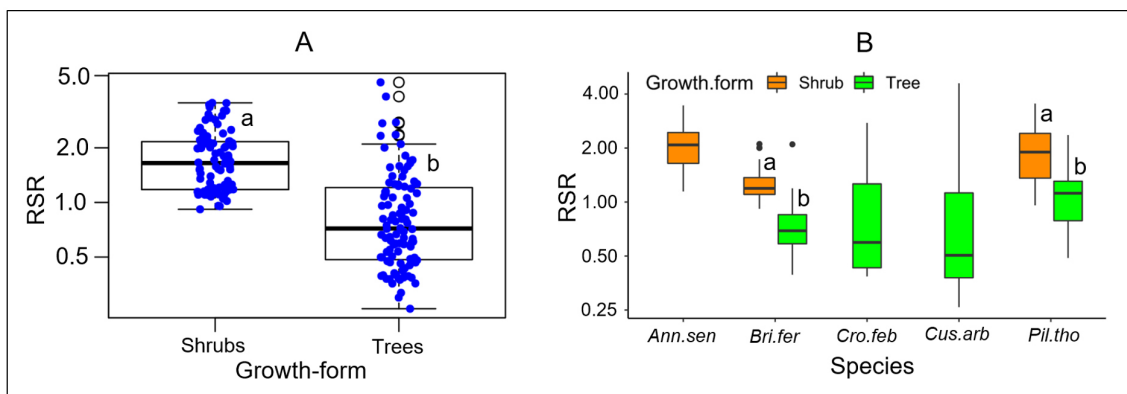
Fig. 2. Distribution of the root/shoot biomass ratio (RSR) according to its growth form. In Panel A, species are pooled according to their growth form; specific values are shown in panel B. The different box colors in panel B correspond to different growth forms. The lower-case letters next to box plots indicate, when different, groups of significantly different values at the 95% threshold according to Student's t-test. At intraspecific level (panel B), comparison of RSR between growth forms was done only for species including both growth forms (tree and shrub). Plant species: Ann.sen (*Annona senegalensis*); Bri.fer (*Bridelia ferruginea*); Cro.fer (*Crossopteryx febrifuga*); Cus.arb (*Cussonia arborea*); Pil.tho (*Piliostigma thonningii*).
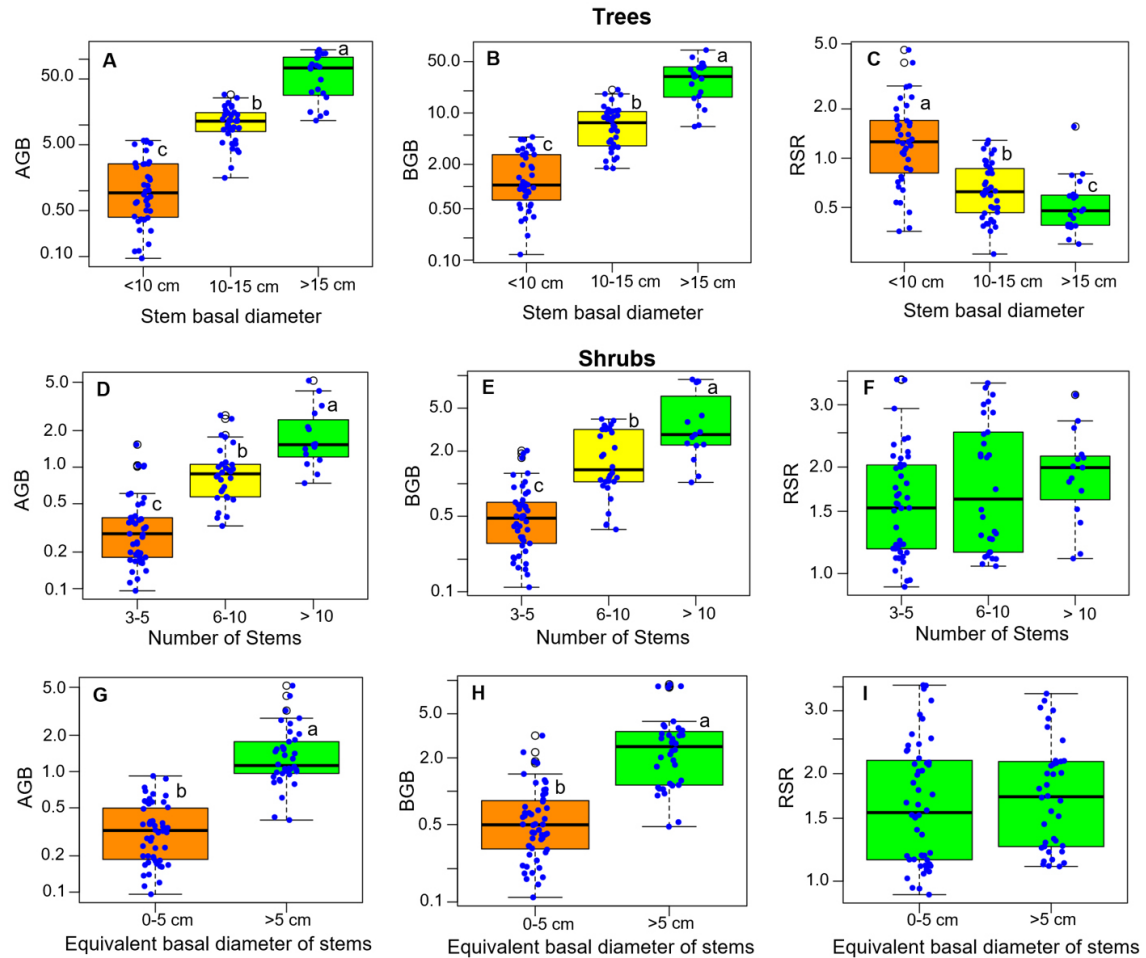
Fig. 3. Distribution of the total above- and belowground biomass (AGB and BGB) and of the root/shoot biomass ratio (RSR) according to classes of basal diameter, number of stems and stem equivalent basal diameter for shrubs. The box colors and lower-case letters next to box plots indicate, when different, groups of significantly different values at the 95% threshold according to Tukey's HSD post-hoc test by class of each variable (panels 3A–3E) or to Student's t-test (panels 3G–3I).

3.2 Allometric equations for predicting AGB and BGB

Except for the variable D_b with associated VIF = 11.25, all the other independent variables had VIF < 10 and were included in the full starting model for stepwise regression. At conventional level, only effects of variables w (proxy for stem biomass computed from stem volume, $w = \rho D_b^2 H$) and n (total number of stems) were found to be statistically significant ($P < 0.05$) for predicting AGB and BGB considering by both tree and shrub measurements. After application of the stepwise selection procedure (Suppl. file S5: Text 1 and Text 2), the final models predicted AGB and BGB from w and n, with Adj-R^2 = 0.91 and AIC = 309 for the AGB prediction model, and Adj-R^2 = 0.83 and AIC = 352 for the BGB prediction model. However, on the one hand, the ANCOVA test (Table 2) showed strong interaction between w and the growth form in the AGB prediction model. On the other hand, the interaction between n and the growth form seemed to be trivial since all trees had $n = 1$ stem, while n strongly varied in shrubs. In the BGB prediction model, the interaction between the w and the growth form was not significant, but the model was also affected by the difference in dispersion of n values between trees and shrubs. In addition, analysis of the data distribution

Table 2. Effects of growth form, w ($\rho D_b^2 H$ in g cm^{-1} m) and n (total number of stems) and their interaction on the estimation of the aboveground and belowground biomass (AGB and BGB) in Lamto trees and shrubs. For trees, D_b (cm) corresponds to the stem basal diameter and H (m) represents the total height in the term $\rho D_b^2 H$. For shrubs, the term $D_b^2 H$ corresponds to the sum of $d_i^2 h_i$ ($i = 1…n$) of the n stems, where d_i (cm) and h_i (m) are respectively the basal diameter and the total height of each stem. ρ (g cm^{-3}) is the woody specific density.

Dependent variables	Source of variation	Mean Sq	F value	P value
ln(AGB)	Growth form	242.31	1021.72	<0.001***
	ln(w)	332.04	1400.05	<0.001***
	ln(n)	11.07	46.68	<0.001***
	Growth form: ln(w)	2.55	10.74	<0.01**
ln(BGB)	Growth form	107.24	356.31	<0.001***
	ln(w)	214.84	713.83	<0.001***
	ln(n)	23.10	76.75	<0.001***
	Growth form: ln(w)	0.03	0.09	>0.05

showed that trees reach a much larger aerial volume ($D_b^2 H$) than shrubs – the average aerial volume of the sampled trees was about 151.1 dm^3 (min = 0.265; max = 1909.165), which is about 42 times larger than that of the shrubs, which was 3.6 dm^3 (min = 0.609; max = 12.902). For these reasons, we finally fitted separate models for predicting AGB and BGB for trees and shrubs.

In trees, AGB and BGB were better predicted from w (Table 3). The results of ANCOVA tests revealed significant interaction ($P<0.001$) between w and species (Suppl. file S5: Table 1), resulting in the variation of regression coefficients and the goodness of AGB and BGB prediction models between species (Table 4). Regardless to the AGB prediction model, Adj-R^2 significantly increased in *Crossopteryx febrifuga* and *Piliostigma thonningii* (0.96 and 0.94 respectively), while Adj-R^2 decreased in *Bridelia ferruginea* and *Cussonia arborea* (0.86 and 0.87 respectively;

Table 3. Regression parameters of the fitted allometric models for predicting above- and belowground biomass (AGB and BGB in kg) of trees and shrubs measured in the Guinean savanna of Lamto Scientific Reserve. Variable w corresponds to the product $\rho D_b^2 H$ (g cm^{-1} m) and variable n represents the total number of stems. For trees, D_b (cm) corresponds to the stem basal diameter and H (m) represents the total height in the term $\rho D_b^2 H$. For shrubs, the term $D_b^2 H$ corresponds to the sum of $d_i^2 h_i$ ($i = 1…n$) of the n stems, where d_i (cm) and h_i (m) are respectively the basal diameter and the total height of each stem. ρ (g cm^{-3}) is the woody specific density. Values in brackets = standard error (se) of the estimated value; Adj-R2 = Adjusted R square; AIC = Akaike information criterion; CF = Correction factor due to logarithmic transformation; a, b and c are constants and represent the regression coefficients of the models.

Model		Regression coefficients			Adj-R2	AIC	CF
		a (se)	b (se)	c (se)			
Trees	ln(AGB) = a + b ln(w)	–3.2191 (0.18) ***	0.9150 (0.03) ***	-	0.90	176.19	1.1780
	ln(BGB) = a + b ln(w)	–2.2527 (0.18) ***	0.6899 (0.03) ***	-	0.82	181	1.1875
Shrubs	ln(AGB) = a + b ln(w) + c ln(n)	–4.0272 (0.17) ***	0.6227 (0.06) ***	0.9271 (0.09) ***	0.84	80.27	1.0699
	ln(BGB) = a + b ln (w) + c ln(n)	–3.9059 (0.23) ***	0.7205 (0.09) ***	0.9920 (0.13) ***	0.77	136.56	1.1347

Table 4. Difference between species of the regression parameters of the fitted allometric models for predicting above- and belowground biomass (AGB and BGB in kg) of trees and shrubs measured in the Lamto Scientific Reserve. Variable w corresponds to the product $\rho D_b^2 H$ (g cm^{-1} m) and variable n represents the total number of stems. For trees, D_b (cm) corresponds to the stem basal diameter and H (m) represents the total height in the term $\rho D_b^2 H$. For shrubs, the term $D_b^2 H$ corresponds to the sum of $d_i^2 h_i$ ($i = 1…n$) of the n stems, where d_i (cm) and h_i (m) are respectively the basal diameter and the total height of each stem. ρ (g cm^{-3}) is the woody specific density. Values in brackets = standard error (se) of the estimated value; Adj-R2 = Adjusted R square; CF = Correction factor due to logarithmic transformation; a, b and c are constants and represent the regression coefficients of the models.

Growth form	Model for biomass prediction	Species	Regression coefficients			Adj-R2	CF
			a (se)	b (se)	c (se)		
Trees	ln(AGB) = a + b ln(w)	B. ferruginea	−1.9674 (0.32) ***	0.7226 (0.06) ***	-	0.86	1.0822
		C. febrifuga	−4.1332 (0.24) ***	0.1000 (0.04) ***	-	0.96	1.1059
		C. arborea	−3.2339 (0.39) ***	0.9374 (0.07) **	-	0.87	1.2743
		P. thonningii	−3.1290 (0.28) ***	0.9167 (0.05) ***	-	0.94	1.0293
	ln(BGB) = a + b ln(w)	B. ferruginea	−1.7230 (0.38) ***	0.6116 (0.07) ***	-	0.76	1.1176
		C. febrifuga	−3.0946 (0.18) ***	0.7650 (0.03) ***	-	0.97	1.0564
		C. arborea	−1.8752 (0.40) ***	0.5928 (0.08) **	-	0.71	1.2989
		P. thonningii	−2.1070 (0.26) ***	0.7361 (0.05) ***	-	0.91	1.0678
Shrubs	ln(AGB) = a + b ln(w) + c ln(n)	A. senegalensis	−4.4805 (0.20) ***	0.8738 (0.10) ***	0.8865 (0.12) ***	0.94	1.0264
		B. ferruginea	−3.3522 (0.24) ***	0.7027 (0.07) ***	0.5083 (0.12) ***	0.86	1.0463
		P. thonningii	−4.2124 (0.20) ***	0.1112 (0.13) >0.05	1.7147 (0.17) ***	0.94	1.0293
	ln(BGB) = a + b ln (w) + c ln(n)	A. senegalensis	−4.5151 (0.37) ***	1.0006 (0.19) ***	1.0992 (0.22) ***	0.86	1.0954
		B. ferruginea	−3.4570 (0.29) ***	0.8295 (0.08) ***	0.5008 (0.14) **	0.84	1.0718
		P. thonningii	−3.8090 (0.37) ***	0.3054 (0.24) >0.05	1.5140 (0.30) ***	0.84	1.0989

Table 4). The same pattern was found for the BGB prediction model; Adj-R^2 significantly increased in *C. febrifuga* and *P. thonningii* (0.97 and 0.91 respectively) and decreased in *B. ferruginea* and *C. arborea* (0.76 and 0.71 respectively; Table 4). Ultimately, AGB was predicted in trees according to Eq. 9 and BGB was predicted following Eq. 10, including the bias correction factor (Eq. 7). Fig. 4A and Fig. 4B show the graphical representation of the two models respectively, and the normal probability plot and other quantile distributions that allowed us to validate the assumptions of each model are provided in Suppl. file S5: Fig. 1 and Suppl. file S5: Fig. 2 respectively.

$$AGB = 4.71 \times 10^{-2} \left(w \right)^{0.915} \tag{9}$$
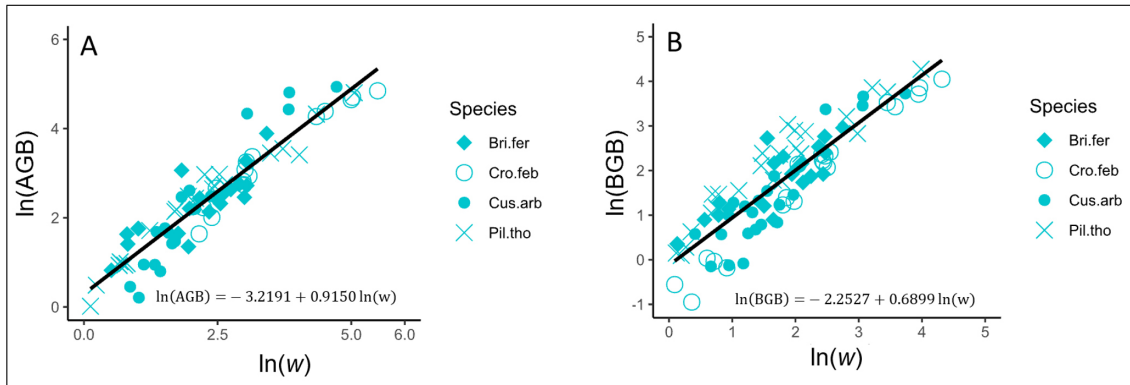
Fig. 4. Fits of the best models predicting the above- and belowground biomass (AGB and BGB) of trees in the savanna of the Lamto Scientific Reserve: A) Fit of the best model predicting AGB in trees; B) Fit of the best model predicting BGB in trees. AGB and BGB are well predicted from the variable w (g cm^{-1} m) = $\rho D_b^2 H$, where D_b (cm) and H (m) represent the stem basal diameter and the stem total height, respectively; ρ (g cm^{-3}) is the woody specific density. Tree species are shown with different symbols.

$$BGB = 1.25 \times 10^{-1} \left(w\right)^{0.6899} \tag{10}$$

with AGB and BGB in kg and $w = \rho D_b^2 H$ in g cm^{-1} m.

In shrubs, AGB and BGB were better predicted using both w and n in the prediction models (Table 3). Given two shrubs with the same aerial volume but different numbers of stems, the one with the greater number of stems is expected to have the greater BGB (Fig. 5B). As a result, in species growing both as multi-stemmed shrubs and single-stemmed trees, individuals growing in shrubby growth form have potentially higher BGB than young trees with same aerial size. The results of ANCOVA tests (Suppl.file S5: Table 1) revealed significant interaction ($P<0.001$) between species and w ($P<0.05$) and between species and n ($P<0.01$); therefore, regression coefficients and the goodness of AGB and BGB prediction models varied between species (Table 4). Overall, the Adj-R^2 of both AGB and BGB prediction models increased at the specific level. For AGB prediction model, we found the same value of Adj-R^2=0.94 in *Annona senegalensis* and *Pili-*
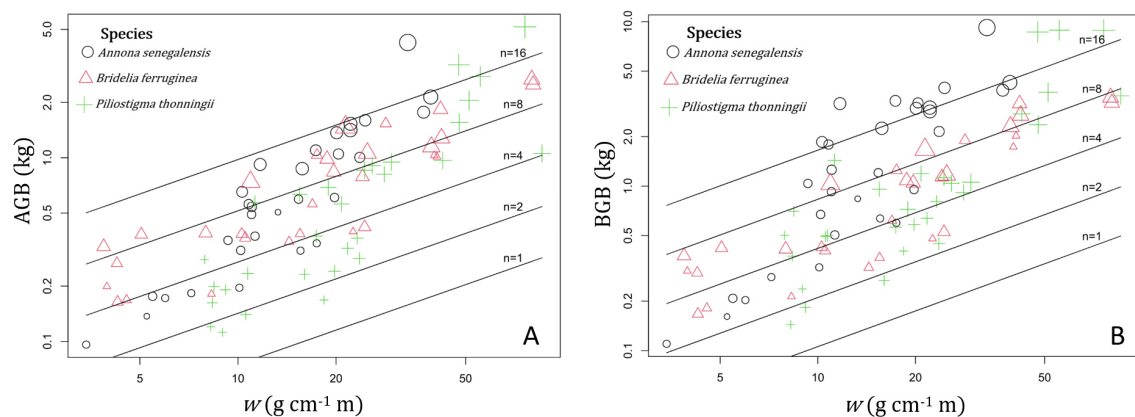
Fig. 5. Variation of the aboveground biomass (AGB) and belowground biomass (BGB) of shrubs according to the variable $w = \rho D_b^2 H$ and the total number of stems (n). In the term $\rho D_b^2 H$, ρ (g cm^{-3}) is the woody specific density and the term $D_b^2 H$ corresponds to the sum of $d_i^2 h_i$ ($i = 1...n$) of the n stems (with d_i = basal diameter in cm and h_i = total height of each stem in m). The different symbols and color of data points correspond to the different shrub species, and the size of points is proportional to log(n).

ostigma thonningii, while in *Bridelia ferruginea*, the Adj-R2 reached 0.86 (Table 4). With respect to the BGB prediction model, the Adj-R^2 reached 0.84 in *B. ferruginea* and *P. thonningii*, and was 0.86 in *A. senegalensis* (Table 4). Ultimately, AGB was predicted in shrubs following Eq. 11 and BGB was predicted according to Eq. 12. Fig. 5A and Fig. 5B show the graphical representation of the two models respectively. The normal probability plot and other quantile distributions that allowed us to validate the assumptions of each model are provided in Suppl. file S5: Fig. 3 and Suppl. file S5: Fig. 4 respectively.

$$AGB = 1.91 \times 10^{-2} (w)^{0.6227} (n)^{0.9271} \tag{11}$$

$$BGB = 2.28 \times 10^{-2} (w)^{0.7205} (n)^{0.992} \tag{12}$$

with AGB and BGB in kg, $w = \rho D_b{}^2 H$ in g cm^{-1} m and n = total number of stems in individual shrub.

3.3 Comparison with others allometric equations fitted for Guinean savanna trees

The AGB prediction model of Ifo et al. (2018) – fitted from tree measurements in the Guinean savanna of the Plateau Batéké (Congo) using basal diameter as a predictor instead of dbh – overestimated the AGB of trees measured in Lamto savannas with a 133% bias. This bias is very high compared to the 19% overestimation with the allometric equation fitted in our study (Table 5). Using the shrub dataset, Ifo et al. equation overestimated the AGB by about 79%, against 1.5% overestimation with our equation. Conversely, the BGB prediction model of Ifo et al. (2018) better predicted the BGB of Lamto savannas trees with only 2.7% overestimation, compared to the allometric equation we fitted in this study that overestimated the BGB by 6%. But the Ifo et al. (2018) model underestimated the BGB of shrubs of Lamto savannas by 14%, while our equation overestimated the BGB of shrubs by only 2.7% (Table 5).

Table 5. Comparison of model accuracy between the allometric models fitted to trees and shrubs measurements of the savanna of Lamto Scientific Reserve and the allometric equations adjusted by Ifo et al. (2018) from trees measurements in the savanna of the Plateau Batéké in Congo basin. The variable w corresponds to the product $\rho D_b{}^2 H$ (g cm^{-1} m), where D_b (cm) and H (m) respectively represent the stem basal diameter and the total height in trees; and in shrubs the term $D_b{}^2 H$ corresponds to the sum of $d_i{}^2 h_i$ ($i = 1…n$) of the n stems (d_i = basal diameter in cm; h_i = total height of each stem in m). ρ (g cm^{-3}) is the woody specific density. Written alone, D_b (cm) corresponds to the stem basal diameter for trees and to the equivalent basal diameter of stems for shrubs (see Eq. 1 for detail relative to the measure of the equivalent basal diameter in shrubs).

| | Models fitted in this study | | Ifo et al. (2018) models | |
	Trees	Shrubs	Trees	Shrubs
Model	AGB = 4.71 10^{-2} $(w)^{0.9150}$	AGB = 1.91 10^{-2} $(w)^{0.6227}$ $(n)^{0.9271}$	AGB = 9.31 10^{-2} $(w)^{0.9135}$	
Model bias (%)	19.04	1.48	132.48	78.76
Model	BGB = 1.25 10^{-1} $(w)^{0.6899}$	BGB = 2.28 10^{-2} $(w)^{0.7205}$ $(n)^{0.9920}$	BGB = 12.58 10^{-2} $(\rho D_b{}^2)^{0.8640}$	
Model bias (%)	6.04	2.70	2.65	−14.05

4   Discussion

We developed multi-species allometric equations to predict the total aboveground biomass (AGB) and the total belowground biomass (BGB) of trees and shrubs in the Guinean savannas. Our study was carried out in a Guinean savanna of Côte d'Ivoire and considered the dominant woody species of this biome, *i.e.*, *Crossopteryx febrifuga*, *Piliostigma thonningii*, *Cussonia arborea*, *Bridelia ferruginea* and *Annona senegalensis* (Menaut and César 1979). The notion of dominant species in a given ecosystem generally refers to a large population size or the size of individuals of some species, usually observed/measured at aboveground level. However, the dominance concept can also be applied to species or individuals with significant belowground proportions (Ottaviani et al. 2020), as it is the case for shrubs in savanna ecosystems. Neglecting shrub biomass in woody biomass measurements in savannas may therefore lead to a relatively large underestimation of C stocks in this biome, contributing to uncertainties in the carbon balance of Africa. For example, in the shrubby savannas of Lamto, where we conducted this study, the average tree density can be estimated at 380/ha (30% of total woody density) and the average shrub density at 900/ha (70% of woody density), based on floristic inventories (N'Dri et al., unpublished data) conducted on nine 0.5-ha plots described by N'Dri et al. (2018b). Considering these proportions and the average of directly measured AGB and BGB of trees and shrubs, we found that shrubs represent about 10% of the total AGB and more importantly, 27% of the total BGB. Ignoring the shrub biomass would therefore represent a significant underestimation of the total woody biomass in Lamto savannas. Another source of underestimation of woody biomass in savannas is the use of a default root/shoot biomass ratio (RSR) – as indicated in the 2006 IPCC Guidelines for national greenhouse gas inventories (Eggleston et al. 2006) – for estimating the BGB of trees. For example, in Côte d'Ivoire, the default RSR used in the implementation of REDD+ is 1/5, i.e., BGB = 0.2 AGB. According to our predictions, the average BGB of trees in the Lamto savannas is about 6 t ha^{-1} of dry matter. While applying the IPCC default RSR, the BGB would be estimated to about 2.3 t ha^{-1}, i.e., about 160% underestimated. The use of allometric equations developed in this study could therefore contribute to the enhancement of tree BGB measurements in Guinean savannas, which is a requirement to get financial compensation related to REDD+ and others C sequestration activities in these environments (Picard et al. 2012).

Among several explanatory variables we tested, $w = \rho D_b^2 H$ was found to be the most relevant for better prediction of AGB and BGB of trees in the Lamto savannas. Our results support the suggestion of Chave et al. (2014) who proposed a single allometric model for estimating AGB of tropical trees using the combined variable $\rho D^2 H$ as unique predictor when wood specific gravity (ρ), trunk diameter (D) and total tree height (H) are available. Indeed, from the exploration of a very large database consisting of direct measurements of over 4000 trees from 58 sites, Chave et al. (2014) found that the AGB of tropical trees was reliably predicted by $\rho D^2 H$, regardless of the vegetation type, the provenance, and the environmental factors. This finding was very relevant and is helpful in the context of regionalization or extrapolation of allometric equations for estimating tree biomass and carbon stocks at broader scales (Picard et al. 2012). Although Chave et al. (2014) analysis focused on the AGB of tropical forest trees – excluding trees with dbh < 5 cm – our results showed that the AGB and the BGB of the Lamto savannas trees are also better estimated (Adj-$R^2 = 0.90$ and 0.82 respectively) using $w = \rho D^2 H$ as the single predictive variable. Ifo et al. (2018) and Aabeyir et al. (2020) also highlighted the accuracy of estimates of the AGB of trees using $\rho D^2 H$ as single predictor, respectively in the Central African and West African wet savannas. The power of $\rho D^2 H$ for predicting tree biomass, especially for estimating the AGB, is due to its being a good proxy of tree biomass. Indeed, $\rho D^2 H$ describes a minimal model where the trunk/stem is considered as an integrative compartment of all the mechanical and functional constraints of the

tree, while being massive and having a fairly simple shape (between cylinder and cone). We can therefore assume that the trunk/stem volume, calculated from a realistic hypothesis about its shape (the square of the diameter times the height), is a good predictor of the AGB of trees (Crow and Schlaegel 1988). However, the use of the basal diameter rather than the diameter at breast height (dbh) – that is widely used for biomass prediction in forest trees – is more reliable for predicting tree biomass in West African savannas (Sawadogo et al. 2010; Amadou 2020; Ouédraogo et al. 2020). The base of the stem represents the best part for measuring accurately stem diameter in savanna trees, as higher up stems are generally deformed due to regular fire damage. Also, dbh is an unpractical measure for multi-stemmed shrubs (Tietema 1993; Paul et al. 2017; Magarik et al. 2019; Kindermann et al. 2022) since a majority reaches stem heights shorter than 1.3 m and can total a large number of stems (more than 20 in our case).

The use of the pantropical allometric equation of Chave et al. (2014) often mis-estimated the biomass of savanna trees at the local scale, i.e., at site-specific or species-specific levels (Chabi et al. 2016; Beirne et al. 2019; Ganamé et al. 2021). This has been attributed, on the one hand, to the difference in size between the local and the pantropical databases, and on the other hand, to the fact that the pantropical equation was fitted from data of many sites (58 sites) and numerous species with different ecological characteristics (Djomo et al. 2010; Fayolle et al. 2013; Henry et al. 2013; Chave et al. 2014; Goussanou et al. 2016; Beirne et al. 2019). If we agree that using $\rho D^2 H$ as single predictor leads to more accurate estimates of the AGB of tropical trees, then the regression of AGB by $\rho D^2 H$ should be readjusted for savanna trees using specific field data and at a given spatial scale (Ifo et al. 2018). If tree species used to fit allometric equations share the same growing conditions and functional traits, we expect (i) regression parameters of AGB on $\rho D^2 H$ to be good and specific for the growing environment, and (ii) AGB (and BGB) estimates from $\rho D^2 H$ to be more accurate (van Breugel et al. 2011; Picard et al. 2012; Mbow et al. 2014). To generalize, we believe that the pantropical approach would be more interesting and consensual if applied to each specific biome by harvesting data from different sites with the same ecological drivers. In this regard, the multispecies allometric models provided here may be relevant for the Guinean savanna ecoregion or the wet savanna ecoregion, where trees have similar physiognomy and functional traits (Osborne et al. 2018). In wet savannas, the high frequency of fire has led trees species to develop common functional traits such as: high ability to regrow rapidly after fire, high growth rate of bark between two successive fire episodes, shade intolerance, low specific leaf area, and high RSR at young ontogenic stages (Gignoux et al. 1997; Bond et al. 2008; Dantas and Pausas 2013; Parr et al. 2014; Charles-Dominique et al. 2015).

According to Chave et al. (2014), the environmental variability results mainly in variation in height-diameter allometries of trees across the vegetation types they studied (i.e., tropical wet, dry and moist forests). Concerning savanna ecosystems, several studies have pointed out that frequent fires can affect the architecture and the growth form of woody species (Hoffmann and Solbrig 2003; Mlambo and Mapaure 2006; Zizka et al. 2014; Moncrieff et al. 2014; Stevens 2021; Clarke et al. 2021). For example, some savanna species such as *Bridelia ferruginea* and *Piliostigma thonningii* we studied here grow as both single-stemmed trees and multi-stemmed shrubs, due to the variability of fire effects on stems in the early growth stages. The construction of a single stem versus multiple stems may suggest two different strategies of carbon investment in the AGB (Higgins et al. 2007; Sheffer et al. 2014; Götmark et al. 2016; Yang et al. 2020) that can result in a variation of the height-diameter allometries among and within species.

According to our results, the height-diameter relationship varied according to the growth form and species (Suppl. file S5: Table 2), and the inclusion of stem number (n) as a secondary predictive variable associated with $\rho D_b^2 H$ improved the allometric models for predicting AGB and BGB in both trees and shrubs communities of Lamto savannas (Table 2). In the single allometric

model proposed by Chave et al. (2014) all trees were assumed to have a single stem, hence the form factor (defined as the ratio between AGB and $\rho D_b^2 H$) varied weakly across vegetation types. If the variation in the total number of stems (n) between vegetation types was considerable, as would be the case by taking into account both tree and shrub vegetations, it is logical to assume that the form factor would be dependent on n and would differ across vegetation types and according to the species or the growth form. All the trees harvested in our study had a single stem while n varied from 3 to 23 in shrubs. Although the number of stems was implicitly accounted for the $D_b^2 H$ calculation in shrubs by summing the $d_b^2 h$ of all the individual stems, the variable n nevertheless significantly contributed to improve AGB and BGB prediction when data of trees and shrubs were taken together or by using only the dataset on shrubs. In addition, the variance inflator factor (VIF) associated with the variable n indicated no collinearity with the other variables. The number of stems was also identified by Lufafa et al. (2009) as a good predictor of BGB in some shrub communities of Senegal. We think that the association of w with n can be explored as a way to extend the pantropical model of Chave et al. (2014) to savannas and other biomes where multi-stemmed shrubs are abundant.

On the one hand, we noted a relative similarity in BGB estimates of trees between the prediction from our equation and the prediction of the Ifo et al. (2018) equation (Table 5), although the two models are fitted with different predictors: $\rho D_b^2 H$ in our study and ρD_b for Ifo et al. (2018). Existence of collinearity between D_b and $\rho D_b^2 H$ can justify the fact that both variables ρD_b and $\rho D_b^2 H$ have same significant effects on BGB variation. However, since the stem height-diameter relationship for a same species or a group of species can differ across savanna environments depending on specific environmental conditions (e.g., fire frequency, presence or not of large herbivores, tree-grass competition), the use of $\rho D_b^2 H$ rather than ρD_b as predictor of trees biomass seems to be more appropriate. On the other hand, our results showed a major gap in the AGB estimates between the prediction made from the allometric equation we developed and the prediction from the reference model (Table 5). This gap could be explained by the differences between the specific wood densities used in each study. For the common species of both studies, namely *Bridelia ferruginea* and *Crossopteryx febrifuga*, the specific wood densities were larger in our study: 0.64 versus 0.61 for *B. ferruginea* and 0.724 versus 0.579 for *C. febrifuga*. Concerning the other species, only *Cussonia arborea* had a smaller wood density than the species studied in Ifo et al. (2018) (Suppl. file S5: Table 3). The difference in wood specific densities may induce relative overestimation or underestimation of AGB at the individual-level or species-level, which would affect the global AGB estimates at the stand-level. Another reason that could explain the gap in AGB estimation between our equation and the Ifo et al. equation is the difference of the $D_b^2 H$/AGB ratio between samples. Our investigations showed that for the same tree species and the same $D_b^2 H$ value, the AGB measured for the Ifo et al. (2018) samples were relatively larger (Fig. 6) although the wood
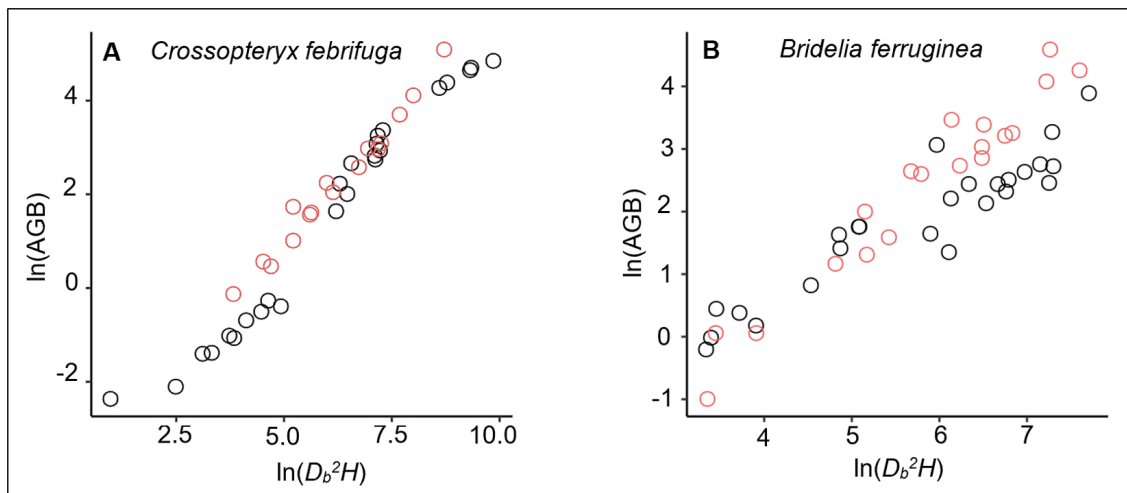
Fig. 6. Relationships between the aboveground biomass (AGB) and aboveground volume ($D_b{}^2H$) for: A) 41 *Crossopteryx febrifuga* trees and B) 44 *Bridelia ferruginea* trees. The black dots correspond to data measured in Lamto savannas, while the red dots represent the measured data in Ifo et al. (2018) study. The Ifo et al. data used here were extracted from the figure 4a of their study showing a plot of the aboveground biomass versus wood density times tree height times square diameter at the base for 88 trees from five species measured in the savannas of the Plateau Batéké in Congo. We extracted only data related to *Crossopteryx febrifuga* and *Bridelia ferruginea* (16 trees and 19 trees respectively); and $D_b{}^2H$ were inferred from $\rho D_b{}^2H$ values.

specific densities we used in our study were higher. In the Lamto savannas, the $D_b{}^2H$/AGB ratio of trees can be substantially affected for some species, notably for *C. febrifuga* (much less for *B. ferruginea* and *P. thonningii*), due to the interaction between fire and termites that causes progressive hollowing of the tree trunk (N'Dri et al. 2011, 2014). This phenomenon is generally observed in large trees ($D_b > 10$ cm), that represented 60% of our trees sample. However, biomass losses due to the hollowing of tree trunks were not directly quantified in this study. In order to achieve realistic and reliable estimates, Kindermann et al. (2022) emphasized the need to account for biomass losses due to disturbance when estimating of the AGB of woody plants in disturbance-prone ecosystems. Indeed, it is difficult to sample undamaged and/or regularly shaped adult trees in disturbance-prone ecosystems such as savannas, since the tree growth cycles and aboveground architecture are continuously affected by disturbance (Archibald and Bond 2003; Moncrieff et al. 2011; Hempson et al. 2020).

Because we used an expanded range of sizes for trees and shrubs, the allometric equations developed here can be easily adapted to other data. The range of root/shoot biomass ratio (RSR) in our sample (0.36–4.6) is roughly similar to the range reported for shrublands (including savannas) by Mokany et al. (2006) (i.e., 0.335–4.250). This similarity may be explained by the inclusion of a fairly wide range of sample sizes, from very small individuals (basal diameter < 5 cm) to large individuals (basal diameter reaching more than 50 cm). According to our results, RSR is not constant in trees and decreases with aerial size (i.e., with age), while RSR does not vary in shrubs over time. This highlights two major points: (i) the size of the aerial part of shrubs depends directly on the size of root reserves, hence on the total size of the root system. Previous studies such as Schutz et al. (2009) and Zhu et al. (2012) have shown that shrubs life-history, notably the resprouting ability, is correlated to root reserves, after analyzing carbohydrate concentrations and pool size in the root system of numerous individuals. The dependence of the aerial part of shrubs on the root system is explained here by a non-significant variation of RSR over time. (ii) in trees, the aboveground compartment can survive fire without the need for large root reserves (Vesk 2006), thanks to its size and bark thickness (Bond and Midgley 2001; Charles-Dominique et al. 2016; Osborne et al. 2018). Contrary to shrubs, belowground biomass has ceased to be critical for survival to fire.

5   Conclusion

This study provides the first database on biomass allometry of trees and shrubs for the Guinean savannas, filling a critical knowledge gap. It also provides new multi-specific allometric models for estimating total aboveground biomass (AGB) and total belowground biomass (BGB) of trees and shrubs in Guinean savannas. Given the relevance of the results and the quality of the sample and sampling methods, the allometric equations developed are recommended for biomass estimation in this ecoregion and can be tested in other Guinean savannas outside of the Lamto Reserve. In particular, the results of this study will help to improve the Forest Reference Level (FRL) in the framework of the REDD+ mechanism (Reduction of Greenhouse Gas Emissions from Deforestation and Forest Degradation) application in Côte d'Ivoire.

Our work can be improved if additional efforts for data collection are completed in other Guinean savannas. This may be useful for refining the equations fitted here and should take into account: (i) the difference in traits between trees and shrubs, (ii) biomass allocation patterns in species in relation to the developmental stage of individuals, (iii) biomass losses due to disturbance: for example, the dynamics of hollowing of trees due to fire-termites interaction that affect the volume-biomass ratio.

Supplementary files

S1.pdf: Studied facies, vegetation map of the Lamto Scientific Reserve, aboveground and belowground parts of some specimens of study species and measurement of the stump circumference (C_S) used to estimate the stump surface area (S_S) in samples,
S2.xls: Data recorded in spreadsheets,
S3.pdf: Metadata of data recorded in S2,
S4.R: R code,
S5.pdf: Models selection process and relation between variables, regression table and quantiles distributions in the fitted models for predicting AGB and BGB in trees and shrubs,
available at https://doi.org/10.14214/sf.10617.

Funding

Acknowledgements

Declaration of openness of data and code

All the data are submitted with the present manuscript. Upon acceptance, we authorize the publisher to archive the data in an online library for any interested reader to access.

Authors contribution

Y.A.G.K, J.G, A.B.N and A.B. designed the study. Y.A.G.K, M.M, M.K, T.C.-D. and J.G. conducted the field experimentations in Lamto savannas and Y.A.G.K and M.K collected the data. Y.A.G.K., T.C.-D, J.G., M.M. and A.B.N wrote the manuscript. Y.A.G.K and J.G. produced all the figures. All authors analyzed and interpreted the data, contributed to the refinement of the manuscript in its successive versions and approved the final version.

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