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Aboveground and belowground tree biomass and carbon stocks in the miombo woodlands of the Copperbelt in Zambia

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ABSTRACT

Globally, belowground biomass (BGB) accounts for 20–26% of total biomass, and as such it is an important carbon (C) pool for many vegetation types. However, large uncertainty exists for belowground biomass C compared to aboveground stocks. Using data from 108 destructively harvested trees belonging to 36 miombo species, we estimated root to shoot ratios, and developed models for estimation of aboveground biomass (AGB), BGB and total biomass C stocks in the Copperbelt province of Zambia. We also validated our models using independent datasets from elsewhere in Zambia and Malawi. The C fractions in wood ranged between 51.9 and 58.9%, which was higher than the IPCC default value. The root to shoot ratio was found to be 0.303. The analysis also demonstrated isometric scaling of BGB with AGB. According to cross-validation results, the model that incorporated wood density (ρ), diameter at breast height (D) and total stem height (H) formulated as $AGB = 0.093(\rho D^2 H)^{0.97} * 1.08$ outperformed existing models developed for the miombo woodlands in Zambia. The best model for BGB was $BGB = 0.476(AGB)^{0.88} * 1.126$. Using the top-ranked models, the stand-level AGB stocks were estimated at 222.2 Mg ha^{-1} , while BGB stocks were estimated at 52.4 Mg ha^{-1} . Aboveground and belowground C stocks were 125.3 Mg ha^{-1} and 29.5 Mg ha^{-1} , respectively. Total biomass C stocks were estimated at 152.1 Mg ha^{-1} or $558.3 \text{ Mg ha}^{-1} \text{ CO}_2$ equivalent sequestered in tree biomass. These estimates may be used as baseline data for future carbon management and for emerging payment for ecosystem services projects in miombo woodlands.

KEYWORDS

Allometry; bootstrapping; carbon stocks; cross-validation; isometric scaling

Highlights

- We developed models for aboveground (AGB) and belowground (BGB) biomass of miombo trees
- The best AGB model consisted of tree diameter, height and wood density
- BGB was isometrically related to AGB
- We estimated carbon stocks at 125.3 Mg ha^{-1} in AGB and 29.5 Mg ha^{-1} in BGB
- Our models outperformed earlier models developed for miombo woodlands in Zambia

1. Introduction

The living biomass of the world's forests contains more than 40% of the global terrestrial carbon (C) stocks [1]. Globally, belowground biomass (BGB) is estimated to account for 20–26% of the total biomass, and as such it is an important C pool for many vegetation types and land-use systems.

However, belowground stocks are poorly estimated and hence the potential of tropical forests to mitigate climate change remains a major source of uncertainty [2]. Therefore, accurate estimation of belowground biomass is a critical component of many applications, especially in quantifying C stocks, sequestration rates [2, 3] and the global C cycle [4]. The amount of biomass and C stocks distributed in different tree components is dependent upon a number of factors such as tree species, floristic composition and growth strategies within a climatic zone [5], tree size and density [6] and geographic location [7]. Additionally, multiple human induced pressures and demographic and land-use changes [8, 9] have been reported to influence the amount of biomass and C stock.

Miombo woodlands represent large and dynamic vegetation landscapes across southern Africa (Figure 1a) that play a critical role as reservoirs of biomass and C stocks [10]. Thus, they are

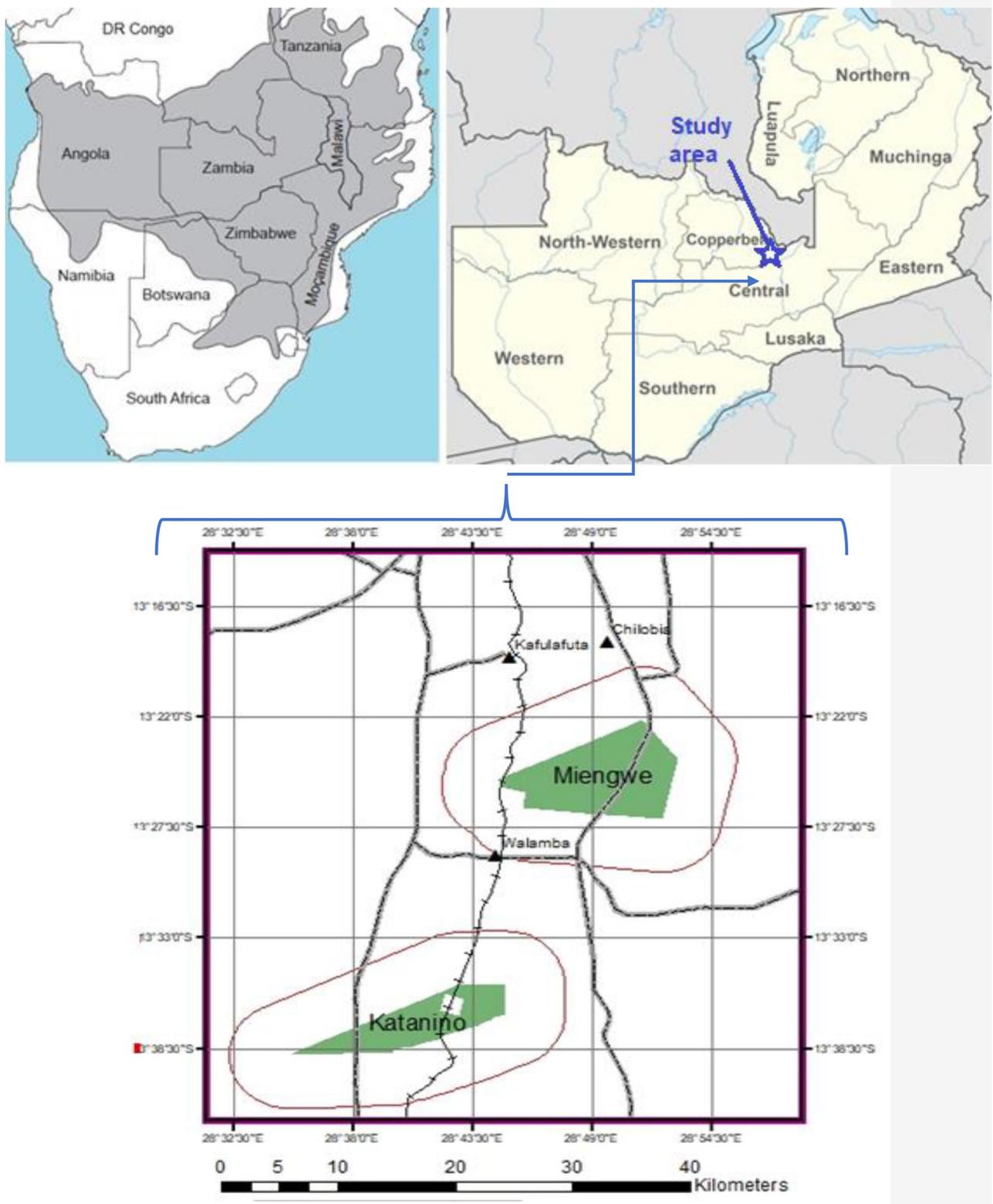


Figure 1. Coverage of the miombo woodlands [22] and the location of the study areas.

considered an important element in the global climate change mitigation [11], and hence present significant prospects for execution of emerging C credit market mechanisms such as Reduced Emissions from Deforestation and Forest Degradation (REDD+) strategies and policies [12, 13]. Furthermore, there is heightened interest in understanding the capability of the miombo woodlands to sequester C [14]. However, the key

to successful execution of REDD+ lies on development of accurate C estimation models.

Miombo woodlands are characterised by high heterogeneity [15] and diversity of tree species. For example, there are approximately 8,500 species of higher plants (of which 54% are endemic) in the miombo woodlands [16], making them one of the world's high biodiversity hotspots [17]. Due to the diversity of tree species and heterogeneity of

Table 1. Estimates of tree density, basal area, diameter, height, wood density, root to shoot ratio, plant C content, AGB, BGB and C stocks for the study area.

Variables	Range	Mean	95% CL [†]
Tree density (trees ha ⁻¹)	103-684	508.9	481.6-537.4
Basal area (m ² ha ⁻¹)	0.9-136.3	23.6	18.9-27.9
Diameter (cm)	5-52.2	22.2	20.2-24.2
Total height (m)	4.2-22.8	12.8	11.9-13.6
Wood density (g cm ⁻³)	0.42-0.86	0.61	0.60-0.63
Root to shoot ratio	0.15-0.82	0.30	0.21-0.40
C content (%)	51.9-57.6	56.4	56.2-56.6
Measured AGB (kg tree ⁻¹)	7.8-2374.4	440.0	330.8-537.8
Modelled AGB (kg tree ⁻¹)	5.5-2405.2	446.3	346.5-537.2
Measured BGB (kg tree ⁻¹)	2.8-246.8	53.5	21.6-78.8
Modelled BGB (kg tree ⁻¹)	6.0-196.6	54.7	27.8-78.3
Measured AGB (Mg ha ⁻¹)	4.1-1511.6	217.1	160.8-268.4
Best estimate of AGB (Mg ha ⁻¹) [‡]	2.4-1295.1	222.2	168.9-269.4
Best estimate of BGB (Mg ha ⁻¹)	1.7-317.5	52.4	40.2-63.3
Best estimate of AGBC (Mg ha ⁻¹)	1.4-730.5	125.3	95.1-152.7
Best estimate of BGBC (Mg ha ⁻¹)	0.9-179.1	29.5	22.8-35.6

[†]The 95% CL were produced using 9999 bootstrap replicates.

[‡]The best estimate is the value derived using the best model.

environments, the applicability of species-specific models is limited and their accuracy is questionable in miombo woodlands.

Globally, patterns of distribution of AGB in terrestrial ecosystems are well understood. On the other hand, large uncertainty exists for belowground biomass C [2]. For example, Robinson [2] showed that the forest inventory-based estimates of root C account for only 60%, indicating on average 40% underestimation of the root C pool across forest types. This uncertainty is caused mainly by incomplete sampling of roots and mass loss during sample storage and preparation [2]. Excavations of root systems of trees is not only difficulty but also expensive. This creates not only information gaps on the belowground contribution but also renders the models inapplicable to new sites [18].

The majority of studies in Zambian miombo woodlands have focused on species-specific aboveground biomass models [14, 19], many of which used generic pan-tropical models [20]. Information is scant on belowground biomass and C storage in the miombo woodlands especially for the Copperbelt region. Therefore, the main objectives of this study were (i) to develop and validate models for estimating AGB and BGB of the miombo tree species and (ii) to estimate total biomass and C stock in the Copperbelt region of Zambia. We hypothesized that BGB can be accurately estimated using allometric models involving diameter (D) at breast height and AGB.

2. Materials and methods

2.1. Study area

The study was conducted in Katanino and Miengwe forest reserves located in Masaiti District

(Figure 1). The two sites were chosen for two main reasons, namely, (i) increasing land-cover changes due to anthropogenic pressure over the last 32 years [21] and (ii) absence of information on aboveground and belowground biomass and C stocks for the area. The forest reserves are located approximately 90 km, south of Ndola town along the Ndola – Kapiri-Mposhi road. Katanino forest reserve lies between 13° 25' 00" and 13° 45' 00"S and 28° 25' 00" and 28° 40' 00"E at an altitude of 1200 m. The forest covers an estimated area of 4,532 hectares [21]. Miengwe Forest reserve lies between latitude 13° 24' 05"S and longitude 28° 49' 00"E, with a gross area of 8, 094 hectares.

The forest areas occur on Katanga rock system. The area receives rainfall averaging 1200 mm per annum and experiences three seasons; hot dry (September-November), rainy season (December–March) and cold dry season (April-August) [22]. The most common soil type is the residual lateritic soil comprising mostly silty clays to silty sands. The major vegetation of the study areas is wet miombo. It is a single tree-storey woodland with a light, closed canopy miombo woodlands, characterised by the dominance of Papilionaceae and Fabaceae, especially of the genera *Brachystegia* (*B. spiciformis*, *B. longifolia*), *Julbernardia* (*J. globiflora*, *J. paniculata*), and *Isoberlinia angolensis*.

2.2. Sampling method

For each study site, grid system based on X and Y coordinates of 250 m by 250 m quadrants were superimposed on the vegetation map to give the potential number of grid intersection points from which sampling points were randomly selected by the first author. A total of 112 circular sample plots of 20 m radius (92 in Miengwe and 20 in Katanino) were generated. Prior to undertaking destructive sampling, data from a total of 112 sample plots were analysed to define vegetation communities using TWINSpan for Windows version 23 [23]. TWINSpan analysis is a numerical method for constructing a classification of sample plots and uses this classification to obtain a classification of species according to their ecological preferences, allowing the determination of homogenous plant community groups [16, 23]. A total of 18 homogenous clusters yielding 63 sample plots were obtained. Based on the vegetation data from the 63 sample plots, we conducted an excel-based simple random sampling method to select tree species from each representative cluster for

destructive sampling. A total of 108 individual trees (95 at Miengwe and 13 in Katanino) belonging to 36 species (Supplementary Table S1) across a range of trunk diameters (5–52 cm) (Table 1) were randomly selected and harvested. Total height (H) of the sample trees ranged between 4.2 and 22.8 m (Supplementary Figure S1), while diameter (D) at breast height ranged between 5 and 52.2 cm (Table 1). We then estimated basal area as the sum of cross-sectional area measured at breast height (1.3 m) of all trees in a stand (in $\text{m}^2 \text{ha}^{-1}$). Accordingly, the stem basal area for the study sites was estimated at $23.6 \text{m}^2 \text{ha}^{-1}$ (Table 1). Tree density was estimated from a total of 63 plots by complete enumeration. Accordingly, density was estimated at 508 trees ha^{-1} (Table 1).

All the selected trees were identified to the species level, their diameters (D) were measured at breast height in cm) and total tree height (in m). The diameters were determined over-bark to the nearest 0.1 cm, with the diameter tape held horizontally and tightly at the stem. Total tree height of felled trees was measured using 50 metres measuring tape. The total number of trees destructively harvested is much higher than what Kachamba *et al* [11] ($n = 74$ trees) used for developing aboveground and belowground biomass models. The sample size is also twice the minimum number of 50 trees [24].

The selected trees were cut at the base approximately 15 cm aboveground using a chainsaw, and separated into trunk (from stump at 20 cm aboveground to the first point where the first branches start), branches (all portions of the tree above the defined bole stem up to a minimum diameter of 2.5 cm) and twigs and leaves (all branches with diameter below 2.5 cm). All felled trees were cut into segments of 1.0–1.5 m lengths and weighed for fresh weight using a solar powered digital END-T3 flatbed weighing indicator (model YH-T3 multifunctional weighing indicator) with 600 kg capacity and a precision of 0.01 kg. In order to account for loss in form of sawdust during cross-cutting of billets, all diameters at points of cross-cutting were measured to calculate the cumulative losses. Sub-samples of wood discs and twigs and leaves were obtained and their fresh weights determined using a 6000 g capacity precision balance (Model THB 6000) (precision 0.001 g).

For determination of belowground biomass, the entire root system of individual trees was excavated manually. The first step of excavation involved clearing the topsoil around the tree base to expose all roots initiating from the root crown.

The roots were classified as root crown, main roots (all roots branching from the root crown) and side roots (roots branching from the side roots). All roots were followed until they tapered to ≤ 2 mm in diameter. In all, 18 of the destructively harvested individuals (representing 13 trees species) were excavated to provide data on root biomass and determination of root:shoot ratio.

Fresh samples of three discs were taken from trunk base, larger branches and small branches to account for possible variation in wood density. The discs were oven dried and, submerged in water for 48 h to reach saturation point prior to undertaking volume measurements [25]. Due to the irregular nature of sample discs, volume was determined by water displacement method [19] using graduated cylinders. Sample volume was taken as the amount of water displaced. The sample specimens were then oven-dried to a constant weight at 105°C (for samples of stems and branches) [26] and 60.5°C (twigs and leaves) for 48 h at the Zambia Forestry College Laboratory and subsequently weighed using a precision scale to 0.001 g. The sub-sample dry and fresh weights were used to determine the tree specific dry to fresh weights ratios (DF-ratios) which were used to convert measured fresh tree mass in the field to dry weight biomass [27]. The average wood density (g cm^{-3}) per sample tree was calculated as oven-dry divided by volume at saturation point [4].

Oven-dried sample components (stem, branch and twigs and leaves) of each of the harvested trees were ground into fine powder for analysing the C fractions at the Mt Makuru Agriculture Research Institute. The fine powder was then sieved through 1 mm sieve. The percentage of C for each sample was determined using loss on ignition method adopted from Ullah and Al-Amin [28]. In this method oven-dried ground powder samples (1.0 g) were put in pre-weighted crucibles which were ignited in the muffle furnace at 550°C for 2:30 hrs. The crucibles were cooled slowly in the furnace after which they were weighted with ash. The ash and organic carbon percentages were calculated according to Bezezew *et al.*, [29] (Eqs 1).

$$\text{Ash (\%)} = \frac{W3 - W1}{W2 - W1} \times 100 \quad (1)$$

$\text{C (\%)} = (100 - \% \text{Ash}) \times 0.58$ (considering 58% carbon in ash-free litter material) where C is the organic carbon [29]; W1 the weight of crucibles; W2 the weight of oven dried ground samples crucibles; W3 is the weight of ash + crucibles.

2.3. Statistical analysis

2.3.1. Development of models

Allometric relationships between D, H and ρ and tree biomass (AGB and BGB) were tested by fitting linear regression equations [24]. Before fitting equations, each variable was transformed into natural logarithm (ln) to ensure linearity, normality and homoscedasticity [24]. The allometric parameters were estimated using ordinary least square (OLS) regression. Empirical slopes (b) of the allometric relationships were compared with theoretical values, and differences were declared significant when the 95% confidence limits (CL) of the empirical estimates do not encompass theoretical values.

Several mathematical forms have been applied in developing models [30, 31]. In this study, the following general model formulations were chosen for aboveground biomass (AGB) and belowground biomass (BGB) used as independent variables and diameter (D) at breast height in cm, total tree height (H in m) and wood density (ρ in g cm^{-3}) as the dependent variables.

Models for AGB

$$\text{Model 1: } \ln(\text{AGB}) = \ln(a) + b \ln(D) + \varepsilon \quad (2)$$

$$\begin{aligned} \text{Model 2: } \ln(\text{AGB}) \\ = \ln(a) + b \ln(D) + c \ln(\rho) + \varepsilon \end{aligned} \quad (3)$$

$$\begin{aligned} \text{Model 3: } \ln(\text{AGB}) \\ = \ln(a) + b \ln(D) + c \ln(H) + \varepsilon \end{aligned} \quad (4)$$

$$\begin{aligned} \text{Model 4: } \ln(\text{AGB}) \\ = \ln(a) + b \ln(D) + c \ln(H) \\ + d \ln(\rho) + \varepsilon \end{aligned} \quad (5)$$

$$\text{Model 5: } \ln(\text{AGB}) = \ln(a) + b \ln(\rho D^2 H) + \varepsilon \quad (6)$$

Models for BGB

$$\text{Model 6: } \ln(\text{BGB}) = \ln(a) + b \ln(D) + \varepsilon \quad (7)$$

$$\text{Model 7: } \ln(\text{BGB}) = \ln(a) + b \ln(D) + c \ln(\rho) + \varepsilon \quad (8)$$

$$\begin{aligned} \text{Model 8: } \ln(\text{BGB}) \\ = \ln(a) + b \ln(D) + c \ln(H) + \varepsilon \end{aligned} \quad (9)$$

$$\begin{aligned} \text{Model 9: } \ln(\text{BGB}) \\ = \ln(a) + b \ln(\text{AGB}) + \varepsilon \end{aligned} \quad (10)$$

$$\begin{aligned} \text{Model 10: } \ln(\text{BGB}) \\ = \ln(a) + b \ln(\rho D^2 H) + \varepsilon \end{aligned} \quad (11)$$

where AGB = total aboveground biomass (kg/tree); BGB = belowground biomass; D = diameter at breast height; H = tree height. Variables a, b, c, and d, are model parameters. "ln" is the natural logarithm and ε is a random error with a mean = 0 and variance = $V\varepsilon$.

Model 9 was included in the comparison because of the empirical allometric relationship observed between BGB and AGB [32, 33]. Models 1–10 were then compared with the following existing models developed for AGB in a dry miombo woodland in Zambia [28, 34] and BGB in Malawi [11].

Aboveground biomass

$$\text{Chidumayo (2013a) } \text{AGB} = 0.045(D)^{2.765} \quad (12)$$

$$\text{Chidumayo (2014) } \text{AGB} = 0.0799(D)^{2.535} \quad (13)$$

Belowground biomass

$$\begin{aligned} \text{Chidumayo (2014) } \ln(\text{BGB}) \\ = -1.944 + 2.171 * \ln(D) \end{aligned} \quad (13)$$

$$\text{Kachamba et al (2016) } \text{BGB} = 0.285(D)^{1.993} \quad (14)$$

Chidumayo's and Kachamba *et al.* models were chosen because they were developed and tested for similar miombo woodland sites, and therefore are more relevant than the generic pan-tropical models such those published by [30].

2.3.2. Model selection and validation

There are a number of model selection criteria in the literature [25]. In this study, we chose the root mean square of error (RMSE), the mean percentage error (MPE), Akaike Information Criterion (AIC) and Akaike Information Criterion weights (AICw) [25]. The model having the highest R^2 , lowest RMSE, AIC and highest AICw was selected as the best model for the data. The AICw represents the relative likelihood of a model given the data. A model whose AICw approaches 1 is said to be unambiguously supported by the data [32]. The mean percentage error (MPE%), sometimes referred to as relative error or error of prediction [25] was calculated as:

$$\text{MPE\%} = \frac{100}{n} \times \sum_{i=1}^n \left[\frac{y_p - y_0}{y_0} \right] \quad (15)$$

where n is the number of trees, y_p is the predicted biomass from model, y_0 is the observed biomass in field measurements.

The RMSE, which is a function of both bias and precision, is a measure of accuracy of predictions [35]. When computing RMSE and MPE%, the

predicted values were back-transformed to the original unit after correction for regression error. Upon back-transformation, all predicted values were multiplied by a correction factor (CF) calculated as $CF = \exp(1/2MSE)^2$. This was necessary to minimise the systematic bias introduced during the back transformation of log-transformed values [36].

The steps taken above only assess the ability of a model to describe the data at hand (or *in-sample fit*). However, models usually have a grossly inflated performance *in-sample* compared to their performance in follow-up studies, a phenomenon known as the *winner's curse* [37, 38] in the statistics literature. Therefore, our focus here was to assess the predictive power (*out-of-sample fit*) of our top-ranked model. Therefore, we validated our AGB and BGB models using two independent datasets. The first dataset consisted of 141 measurements of AGB, D, H and ρ from Zambia, which we obtained from the supplementary online material of Chave *et al.* [30]. We used this dataset to validate our top-ranked AGB model by regressing the measured AGB against the AGB predicted by our top ranked model, Chidumayo's model and an empirical model derived from the data as prescribed in Sileshi [25]. The second dataset consisted of 41 AGB and corresponding BGB measurements of miombo woodland trees from Malawi in Kachamba *et al.* [11].

We also cross-validated our AGB and BGB models using the K-fold cross-validation method. This method takes K replicate samples of the data, each one using (K-1)/K of the data to build the model and the remaining 1/K of the data to test the model. We undertook the cross-validation with macros written in the SAS system and the procedure PROC SURVEYSELECT to generate the samples and the PROC REG to fit our model and generate cross-validation criteria. We used the R^2 , RMSE and the mean absolute error (MAE), two of the popular measures of model performance in cross-validation, to compare the different models. In the arithmetic scale, the RMSE is more sensitive to occasional large errors as the squaring process gives disproportionate weight to very large errors. Therefore, we did all cross-validation on the log-transformed data because we did not want large errors to be significantly more penalized than small ones. MAE measures the average prediction error in a set of predictions, without considering the direction of errors.

2.3.3. Quantifying aboveground and belowground carbon at stand level

First, the best fit model was applied to the pooled inventory data to estimate AGB or BGB at the tree level [39]. Then the biomass estimates were converted to C stock using the mean tree C % value of 56.4%. Since wood density was only determined for the destructively sampled trees, the missing wood density values were filled using average genus wood density values [40]. Lastly, tree biomass and C stocks were calculated for the stand level (in $Mg\ ha^{-1}$) by multiplying the AGB (kg per tree) by the tree density per ha^{-1} and dividing by 1000. The amount of CO_2 equivalent sequestered in the total tree biomass was estimated by multiplying the sum of AGBC and BGBC by the CO_2 to C ratio of 3.67 [41].

Finally, we estimated the 95% confidence intervals (CIs) using bootstrapping. Traditionally, CIs are obtained from a parametric estimator of the standard errors (SE) of a statistic, and then the lower and upper 95% CIs are obtained by adding $\pm SE$ multiplied by 1.96, which is the critical value of the t distribution [42]. This calculation assumes that the estimator is approximately normally distributed. Bootstrapping was proposed as a non-parametric alternative for determining the SE of any statistic [43]. Bootstrapping involves drawing independent samples from the data and calculating the target statistic on each draw. It then uses the resulting empirical distribution to obtain an estimate of the SE. The advantage of bootstrapping is that the estimated CIs are robust when the underlying population value doesn't conform to the traditional assumptions of normality and asymptotic theory used to derive the SE [43]. Therefore, we obtained the 95% CIs of tree density, basal area, diameter, height, wood density, root to shoot ratio, plant C content, AGB and BGB using 1999 bootstrap replicates. We used 95% CIs because they provide the uncertainty around estimated values. For the model predicted AGB and BGB, we also calculated a relative measure of error hereafter referred to as RMSE% calculated as a ratio of RMSE to the mean of the predicted biomass and expressed in %, i.e. $100*(RMSE/mean)$. The RMSE% gives an estimate of the error in estimation as a percentage of the predicted mean biomass [44].

We estimated total tree biomass by combining AGB and BGB in a simultaneous equation. To guarantee the additivity property of the tree biomass equations, we used nonlinear seemingly unrelated regression (NSUR) [44, 45] implemented *via* the

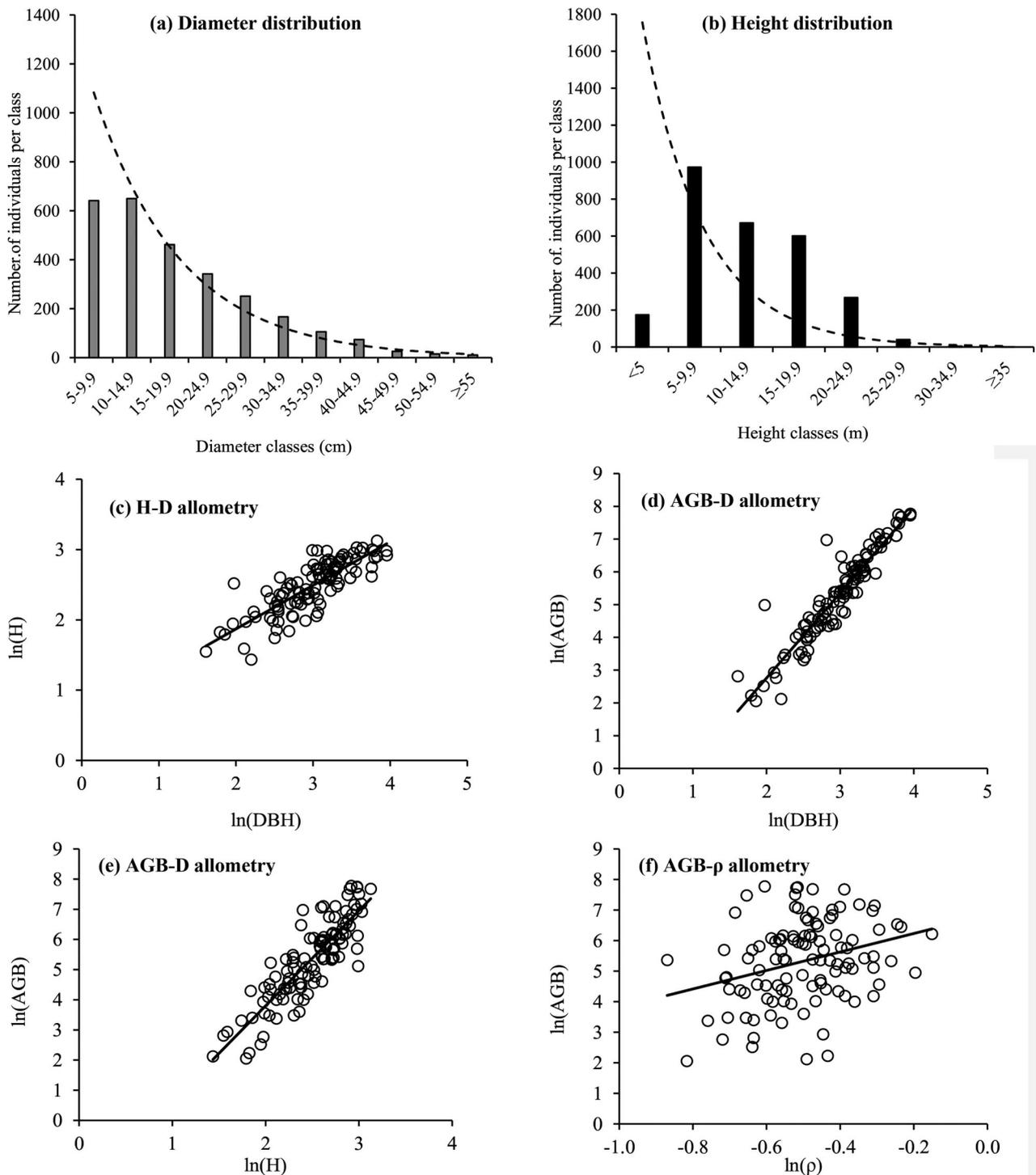


Figure 2. Diameter and height distribution (a & b) and the relationships between stem height and diameter at breast height (c), diameter and aboveground biomass (AGB) (d), AGB biomass and stem height (e) and AGB biomass and wood density (f) in the logarithmic domain. The dashed line in (a) and (b) represent the inverse J-shaped trend in size distribution following an exponential function.

MODEL procedure of the SAS system. This simultaneous equation incorporated models 5 and 9.

3. Results

3.1. Population structure and size distribution

Populations of the sampled vegetation all exhibited an inverse-J shape of size structure for both diameter and height, with proportionally highest frequency of

small plants (in the diameter class 5–9.9 cm) relative to the larger ones. This signifies that the vegetation in the study sites is stable and that the young plants are ready to replace older ones. There are no significant differences in species composition between the Katanino and Miengwe forest reserves as both belong to the wet miombo. With 12 and 10 individuals, *Julbernardia paniculata* and *Brachystegia longifolia* were the most dominant species in the sample trees, followed by *Isoberlinia angolensis* and *Brachystegia*

Table 2. Parameter estimates and cross-validation criteria for comparing the various models tested for above- and below-ground tree biomass in the miombo woodlands of the Copperbelt in Zambia.

No	Model	Parameter estimates				CF	Cross-validation criteria		
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>		R ² (%)	RMSE	MAE
	ln(ABG) =								
1	$\ln(a)+b\ln(D)$	-2.42 ± 0.28	2.59 ± 0.09			1.12	95.0	0.438	0.301
2	$\ln(a)+b\ln(D)+c \ln(\rho)$	-1.71 ± 0.35	2.53 ± 0.09	1.06 ± 0.33		1.11	94.9	0.444	0.301
3	$\ln(a)+b\ln(D)+c \ln(H)$	-3.10 ± 0.27	1.93 ± 0.14	1.07 ± 0.18		1.09	95.5	0.418	0.266
4	$\ln(a)+b\ln(D)+c\ln(H)+d\ln(\rho)$	-2.49 ± 0.34	1.92 ± 0.14	1.00 ± 0.18	0.84 ± 0.29	1.08	95.7	0.409	0.263
5	$\ln(a)+b\ln(\rho D^2 H)$	-2.38 ± 0.23	0.97 ± 0.03			1.08	96.4	0.370	0.255
	ln(BGB) =								
6	$\ln(a)+b\ln(D)$	-3.63 ± 0.85	2.52 ± 0.30			1.14	89.9	0.544	0.456
7	$\ln(a)+b\ln(D)+c\ln(\rho)$	-3.55 ± 1.16	2.51 ± 0.32	0.12 ± 1.08		1.15	88.8	0.570	0.483
8	$\ln(a)+b\ln(D)+c\ln(H)$	-3.85 ± 0.92	2.24 ± 0.47	0.43 ± 0.57		1.14	87.2	0.596	0.463
9	$\ln(a)+b\ln(AGB)$	-0.74 ± 0.49	0.88 ± 0.10			1.13	91.6	0.496	0.414
10	$\ln(a)+b\ln(\rho D^2 H)$	-3.30 ± 0.82	0.90 ± 0.11			1.14	88.8	0.562	0.443

Figures in parentheses represent standard errors of parameters.

Figures in bold face represent the top-ranked model.

spiciformis (Supplementary Table S1). A total of 15 species (41.2% of the sampled species) were represented by only one individual, while 4 species were represented by 2 individuals (Supplementary Table S1). The diameter and basal area distribution of the sample trees revealed an inverse J-shaped size class distribution (Figure 2a and b). The most dominant species (*J. paniculate*) was represented in all size classes (Supplementary Figure S1) although the sample size is small to make conclusions about its size frequency distribution.

3.2. Allometric scaling between variables

Figure 2 presents the allometric scaling relationships between H, D and AGB. The empirical slope (*b*) of the H-D scaling ($b = 0.63$; CL: 0.55–0.71) was not significantly different from theoretical value of 0.67. The empirical slope of the AGB-D scaling ($b = 2.59$; CL: 2.41–2.77) was also not significantly different from the theoretical values of 2.75. AGB isometrically scaled with H, and the empirical slope ($b = 3.15$; CL: 2.81–3.50) was not significantly different from the theoretical slope ($b = 3$) under geometric similarity. Similarly, the empirical slope of the BGB-AGB scaling ($b = 0.88$; CL: 0.68–1.07) was not significantly different from the theoretical value of 1 for isometric scaling of belowground biomass with aboveground biomass.

3.3. Wood density and carbon content

Estimated wood density was in the range of 0.42 and 0.86 g cm⁻³ with a mean of 0.61 g cm⁻³ (Table 1). The highest values were recorded in *Dalbergiella nysae* (0.82 g cm⁻³) followed by *Erythrophleum africanum* (0.79 g cm⁻³) and *Combretum collinum* (0.77 g cm⁻³), while the lowest was in *Ficus capensis* (0.30 g cm⁻³). The C content of the woody tree components was in the

range of 51.9 and 58.9% with a mean of 56.4% (Table 1). Species-specific variation in C concentration was also observed in individual tree species (data not shown).

3.4. The root: shoot ratios

The mean root to shoot ratio of the 18 individuals excavated was 0.30 (95% CL: 0.21–0.40 (Table 1). Significant correlation could not be established between stem diameter and root to shoot ratio although a trend in decrease was noted with increase in stem diameter.

3.5. Estimation of AGB and BGB

Parameters estimates of the various models tested for AGB and BGB are summarized in Table 2. Among the AGB models compared, in terms of AIC, Model 5 had the highest support by the data (Table 2). In terms of RMSE, this model also performed better than the two existing models developed by Chidumayo for miombo woodland trees (Table 3). Chidumayo's models tended to have larger margins of error (%RSE = 40–60%) in the diameter ranges above 10 cm, while our models tended to have <40% error, decreasing with increase in tree diameter (Figure 4c). The existing models systematically underestimated AGB across D ranges (Figure 3a). For the validation dataset from Zambia, our best AGB model (i.e. Model 5) was also better than the empirical model and Chidumayo's model as indicated by the higher R² and lower RMSE and AICc criteria.

In the BGB validation data from Malawi, our best model (Model 9) was better than the empirical model, but inferior to Chidumayo's and Kachamba *et al.* models in terms of AICc. Our model tended to underestimate BGB by 36%, while Kachamba *et al.* model overestimated BGB by 20%

Table 3. Models expressed in the arithmetic domain and compared using the estimated biomass (in kg tree⁻¹) root mean-square of error (RMSE in kg tree⁻¹), RMSE expressed as a percentage of the mean (%RMSE) and mean percentage error (MPE in %).

	Model No	Model form	Biomass	RMSE	%RMSE	MPE	
AGB	1	$AGB = 0.088(D)^{2.59} * 1.12$	448.1	171.5	38.3	20.8	
	2	$AGB = 0.180(D)^{2.53} * \rho^{1.06} * 1.11$	442.3	165.7	37.5	19.8	
	3	$AGB = 0.045(D)^{1.93} * (H)^{1.07} * 1.09$	442.1	152.2	34.4	16.6	
	4	$AGB = 0.083(D)^{1.92} * (H)^{0.999} * (\rho)^{0.84} * 1.08$	428.5	167.0	39.0	13.5	
	5	$AGB = 0.093(\rho D^2 H)^{0.97} * 1.08$	446.3	166.1	37.2	17.8	
	Chidumayo1	$AGB = 0.0446(D)^{2.765}$	372.9	186.9	50.1	-7.9	
	Chidumayo2	$AGB = 0.0799(D)^{2.535}$	319.5	248.2	77.7	-12.2	
BGB	6	$BGB = 0.026(D)^{2.52} * 1.14$	54.2	19.8	36.5	34.6	
	7	$BGB = 0.029(D)^{2.51} * (\rho)^{1.32} * 1.15$	57.9	19.3	33.4	26.0	
	8	$BGB = 0.021(D)^{2.24} * (H)^{0.43} * 1.14$	53.9	19.9	36.9	24.5	
	9	$BGB = 0.476(AGB)^{0.88} * 1.13$	54.7	18.5	33.9	23.9	
	10	$BGB = 0.037(\rho D^2 H)^{0.90} * 1.14$	52.8	22.0	41.7	24.1	
		Chidumayo	$BGB = 0.143 * (D)^{2.171}$	87.9	42.7	48.6	132.9
		Kachamba <i>et al.</i>	$AGB = 0.285(D)^{1.993}$	100.6	55.5	55.1	186.0

(Table 4). However, Chidumayo's and Kachamba *et al.* models tended to systematically overestimate BGB (Figure 4b). All models had large errors of prediction (%RMSE > 40%) of BGB for trees with diameter <10 cm. While our models tended to have <30% error in the diameter ranges of 10–20 cm, the errors with Chidumayo's and Kachamba *et al.* models were > 40% of BGB (Figure 4d).

3.6. AGB, BGB and C stocks

We estimated the stand-level AGB, BGB and C stocks for the pooled inventory data using our top ranked model (Table 1). Our best estimate of AGB was 222.2 Mg ha⁻¹ was very close to our value of 217.1 Mg ha⁻¹ calculated from the measured trees (Table 1). Accordingly, the C stocks in AGB were estimated at 125.3 Mg C ha⁻¹. BGB was isometrically related to AGB, and the best model: $BGB = 0.476(AGB)^{0.88} * 1.126$ was applied to estimate BGB stocks. Accordingly, the estimated BGB stocks were 52.4 Mg ha⁻¹ which translated into BGB C stocks of 29.5 Mg C ha⁻¹ (Table 1). Using NSUR total tree biomass was estimated at 270.1 Mg ha⁻¹ (95% CL: 207.4–328.7 Mg ha⁻¹) giving C stocks estimated at 152.1 Mg ha⁻¹ (95% CL: 115.9–184.1 Mg ha⁻¹). In terms of the amount of CO₂ sequestered in tree biomass, this translates to 558.3 Mg ha⁻¹ CO₂ eq.

4. Discussion

The miombo is often known to be dominated by a few species. On the study site *J. paniculata* and *B. longifolia*, *I. angolensis* and *Brachystegia spiciformis* were the most dominant species. These are also the species ranked high in terms of the Importance Values Index in miombo woodlands in the Copper Belt [46]. The size distribution of the sampled tree species conformed to the classical

inverse J-shaped curve, where a large number of young trees continue to regenerate under the canopies of fewer large and mature trees. The inverse J-shaped curve is an indication of a steady and self-maintaining population, in which young trees will steadily replace the older trees. Kalaba *et al.* [46] cite a number of other studies in the Miombo woodlands that have reported similar size class distributions. The ability of the Miombo species to regenerate from coppices regrowth and root suckers [46] also indicates potential for woodland recovery after disturbances. The fact that the most dominant species (*J. paniculata*) is represented in all size classes means that it is likely to maintain its population without significant shift in carbon management.

Although tropical forests hold a great potential for C storage in tree biomass, quantifying their contribution to C storage has been challenging because of the difficulty in estimating BGB. This study has provided evidence for isometric scaling of BGB with AGB in miombo woodland species consistent with allometric theory [32, 33]. This provides opportunities for estimating BGB directly from AGB using allometric models, and avoid the need for root excavation. When estimating tree biomass, wood density is an important variable which is central to the accounting of C sequestration in forests. However, wood density may depend on a range of intrinsic or environmental factors such as species, age, climate, geographical location [31]. In this study, we have demonstrated variability in wood density. The average wood density found in this study is within the range of values (0.58–0.67 g cm⁻³) reported for trees in other parts of Africa [30, 31].

Plant C content is one of the most important traits, and it is critical for assessing global C cycle [47]. Usually, a default value of 50% is used when converting biomass into C estimates [48]. Our 95%

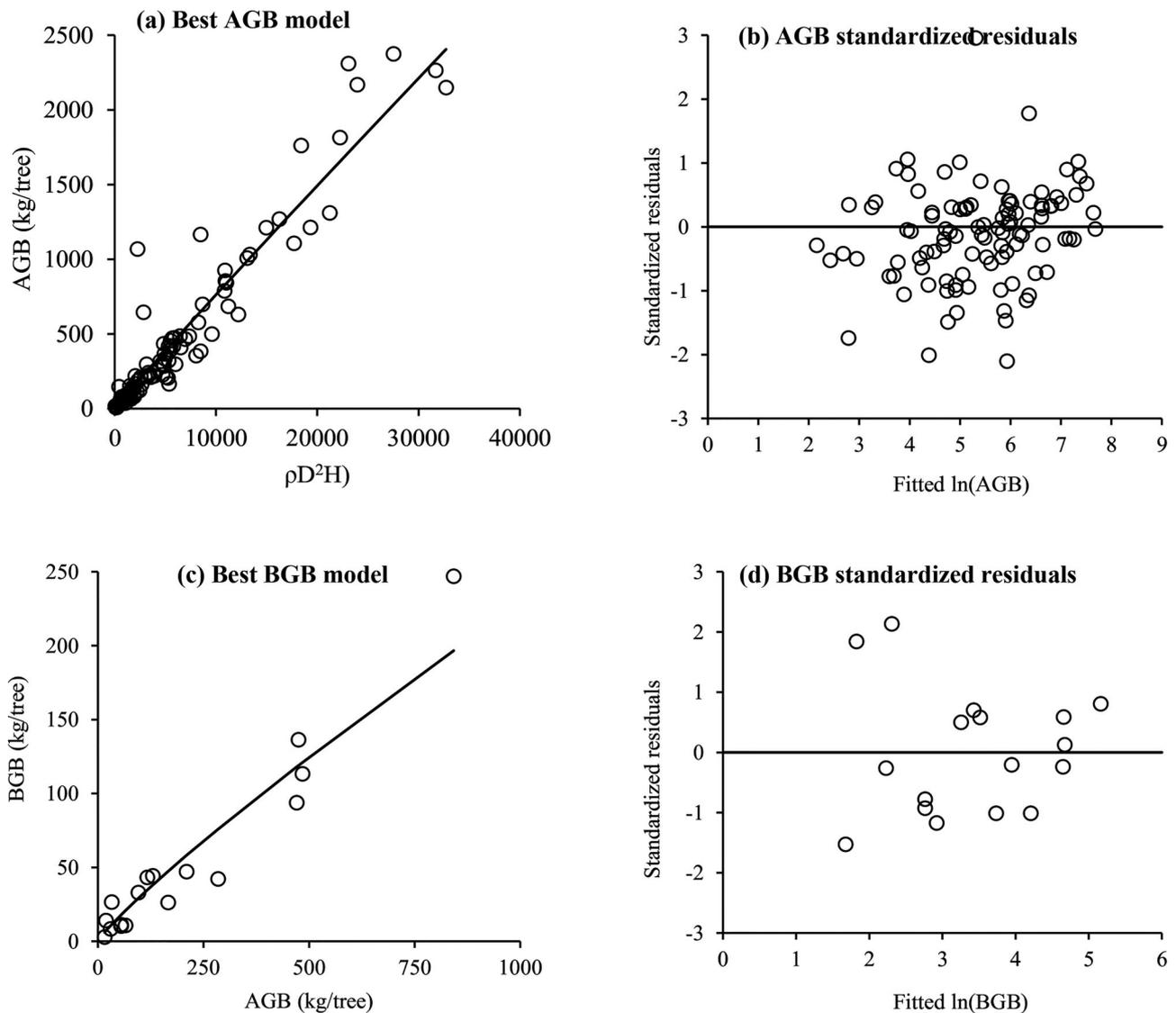


Figure 3. Top-ranked aboveground biomass (AGB) and belowground biomass (BGB) models and the distribution of the standardized residuals. The Shapiro-Wilk test for normality of residuals for the AGB model was significant ($p < 0.001$), while for the BGB model it was not significant ($p = 0.3858$).

CL (51.9–58.9%) indicates that the C content is much higher than this default value and values reported in other studies. Ngoma *et al.* [19] reported a range of 34–53% for the Zambezi teak forest in Western Zambia. At global level, values of 45–47.9% [49], 47–49% [47] and 48.4–51% [50] have been reported. We have demonstrated here significant variability in C concentrations. Therefore, using the default value of 50% as biomass C conversion factor may ignore the high variability in C content [51] and hence lead to biased estimates of C stocks.

The mean root to shoot ratios of the 18 excavated individual trees was within the range of values (0.25–0.75) reported in miombo woodlands of Tanzania [52] and Central Africa [53]. However, our values are much lower than values reported in other studies; for example, 0.38–0.62 in Zambia [19], 0.40–0.60 in Tanzania, [13], 0.42–0.58 in Mozambique, [54] and 0.25–0.9 in Malawi [11].

Studies elsewhere attributed the difference in root to shoot ratios differences in tree roots architecture, tree species, soil depths, sampling methods and soil characteristics [53]. With regard to root sampling methods, our study involved complete excavation of the entire root system of target tree species whereas, other researchers [11, 13, 28] undertook root sampling.

Of the five models tested in this study, the model that included diameter, height and wood density as predictors provided the best *out-of-sample* fit. Our results are consistent with [54] and [4] who observed that incorporation of these variables resulted in the lowest uncertainty. In the validation using independent samples, this model also outperformed earlier models [28, 34] developed for miombo woodlands. The model by Chidumayo generally tended to underestimate AGB. This is partly due to the omission of the correction factor in the models by Chidumayo [28, 34]. Inclusion of

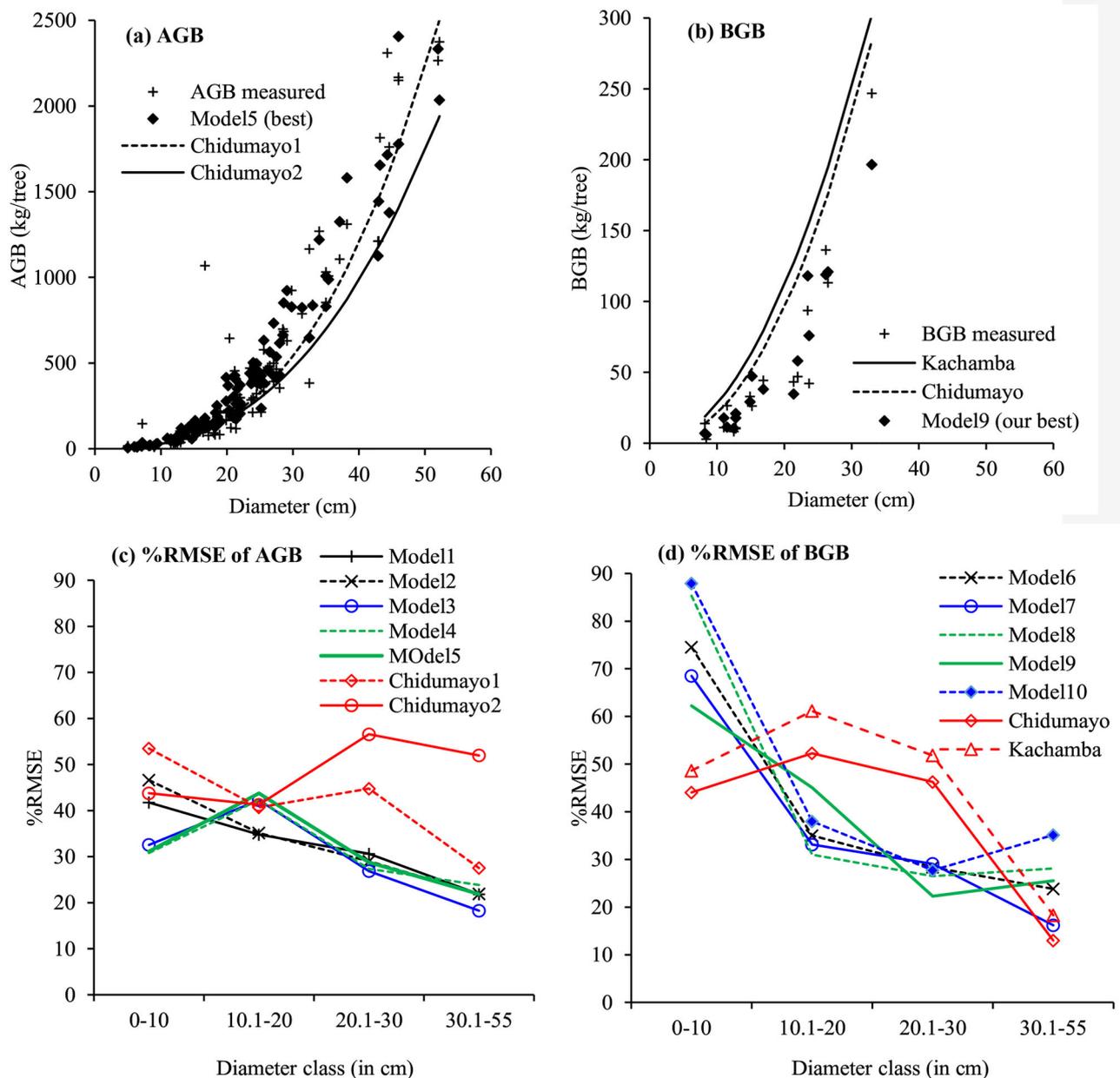


Figure 4. Comparison of predictions by our best model with existing models of aboveground biomass (AGB) and belowground biomass (BGB) proposed by Chidumayo and Kachemba for miombo woodland trees (a and b) and the error of prediction (RMSE) expressed as a percentage of the mean (c) of AGB and BGB.

Table 4. Performance of our best model in comparison to existing models in independent validation datasets from Zambia and Malawi.

Variable	Validation data	Model	R ²	MPE	RMSE	AICc
AGB (N = 141)	Zambia	Our best (Model 5)	0.953	18.3	27.8	941.6
	Zambia	Chidumayo's	0.926	-14.1	34.8	1005.4
BGB (N = 41)	Malawi	Our best (Model 9)	0.939	-36.7	166.3	423.9
	Malawi	Chidumayo's	0.945	8.7	158.8	420.1
	Malawi	Kachemba's	0.953	20.3	145.7	413.1

the correction factor is a requisite when back-transforming data because its omission leads to a downward bias in predicted values [55].

Our results confirm that models formulated in the form of our Model 5 provide an acceptable approximation of AGB in the miombo woodland species. This model was also found to be superior in our data as well as the validation dataset from

Zambia. Our results are consistent with other studies which demonstrated that multi-species allometric models using a combination of pD^2H as identical predictor variables result in accurate aboveground biomass estimation [30]. However, Kachamba *et al.* [11], in their study of Malawian miombo noted that inclusion of ρ as independent variable did not improve biomass prediction. This

may be attributed to fact that wood density values were not obtained from their study sites but extracted from the global wood density database. Therefore, we recommend that our Model 5 be used for estimation of AGB in preference to the model proposed by Chidumayo *et al.* [28].

Our best BGB model was the one where AGB was used as the only predictor. This is consistent with earlier global analyses that show isometric scaling between aboveground and belowground dry biomass across phyletically and ecologically diverse species [32]. Allometric theory also predicts that AGB and BGB scale is in a near isometric manner across diverse forest-types, regardless of vegetation composition [32, 33]. This implies that once AGB is accurately quantified, BGB can be estimated from AGB more accurately than using other dendrometric measurements such as height and stem diameter. Our model was also superior to existing BGB models proposed by Chidumayo [34] and Kachamba *et al.* [11] for miombo woodland species. The existing models tended to overestimate BGB relative to our model across all diameter sizes (Figure 3).

Our basal area estimate of $23.6 \text{ m}^2 \text{ ha}^{-1}$ (95% CL: $18.9\text{--}27.9 \text{ m}^2 \text{ ha}^{-1}$) is within the values reported for the miombo [56–58]. According to a comprehensive review earlier studies in the miombo woodlands by Frost [56] most stands have basal area of $7\text{--}22 \text{ m}^2 \text{ ha}^{-1}$. Higher values ($59\text{--}117 \text{ m}^2 \text{ ha}^{-1}$) have also been recorded in small plots in Zambia [56]. Stand basal area provides an index of both the harvestable volume, aboveground woody biomass and carbon stocks since it integrates the effect of both the number and size of trees [56, 59].

Our estimates of AGB (222.2 Mg ha^{-1}) are higher than values reported in other studies in the miombo. In Zambia, Kalaba *et al.* [20] reported 79.2 Mg ha^{-1} AGB and $39.6 \text{ Mg C ha}^{-1}$, while Chidumayo [28] reported an average of 123.4 Mg ha^{-1} AGB for old growth miombo woodlands. In a study covering six Southern African countries, Tamene *et al.* [59], reported 119.9 Mg ha^{-1} and $56.4 \text{ Mg C ha}^{-1}$. The differences in estimated AGB and C stock is probably due to differences in ecological and anthropogenic factors. Our estimates of total biomass C storage ($152.1 \text{ Mg C ha}^{-1}$) are larger than those reported in other Miombo woodlands (e.g. Refs. [60, 61]). Our C stocks are relatively lower than estimates from, for example, South Africa's Mistbelt forests (358.1 Mg ha^{-1} and $179.0 \text{ Mg C ha}^{-1}$) [40], the average C density for

Africa (119 Mg C ha^{-1} reported in Campbell *et al.* [62] or estimates from tropical rainforests of Africa (202 Mg C ha^{-1} [63] and above 350 Mg C ha^{-1} [12]). The results underscore the need to account for stand characteristics and species variability in order to accurately measure C stocks and stock changes and comply with good practice guidance as provided for by the IPCC [64]. A key step to achieving this level of accuracy is to classify vegetation into homogeneous plant communities so as to capture representative characteristics and traits of vegetation befitting multi-species modelling. The results of this study have implications for the implementation of mechanisms such as REDD+, the nationally determined contribution (NDC) and other policies for the reduction of emissions. Zambia is a pilot country under the REDD+ initiative, and the miombo woodland is a target of REDD+ projects [65]. Our study provides empirical evidence on C storage in miombo woodlands in Zambia and neighbouring countries. Zambia's NDCs includes both mitigation and adaptation targets. A significant portion of the mitigation program aims to reduce emissions from land-use, land-use change and forestry by implementing forest enhancement [GRZ, [66]]. In that endeavour, our models could be used for monitoring progress in REDD+ projects and implementation of the NDC. Our estimates of C stocks may also be used as baseline data for future carbon management as well as monitoring progress under the NDC of Zambia. Our C estimates also highlight that up to 125 Mg C ha^{-1} can be lost if a mature miombo woodland in the study area were to be cleared for other projects.

5. Conclusions

Using the top-ranked models, the stand-level AGB, BGB and C stocks in miombo woodlands of Copperbelt in Zambia are comparable to values reported in other tropical forests of Africa. The most important conclusion from this analysis is that the best-model to quantify belowground biomass is an allometric model using AGB alone as a predictor variable. The analyses also demonstrated that more accurate estimates of AGB can be found using $\rho D^2 H$ than all other models. The estimated total biomass and C stock values are comparable with values reported from other dry tropical forests in Africa. This provides evidence of the woodland's potential to sequester CO_2 . Due to the need for prioritising CO_2 mitigation actions, it is important

to consider the C storage potential of miombo woodlands in conservation and landscape management planning. The results also have implications for the implementation of emission reduction mechanisms and policies in Zambia.

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Disclosure statement

The authors declare no conflict of interest.

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