

Species specifc and multi‑species allometric models for estimating aboveground biomass of native perennial plant species grown in the agricultural landscape of Central Ethiopia

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Abstract Agroforestry plays a significant role in climate change mitigation and thus bufers the pressure on forest resources. However, owing to the lack of accurate biomass models, the contribution of these systems towards carbon storage remains poorly understood, which makes it difficult to implement climate change mitigation initiatives. Besides, most of the biomass predictions for trees grown in agricultural lands rely on the models developed for natural forests. This study therefore aimed to develop species-specifc and multi-species allometric equations

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for predicting the aboveground biomass (AGB) of native perennial plant species in the agricultural landscape of central Ethiopia. Ninety-fve individuals representing six perennial plant species with diameter at breast height ranging from 3.5 to 65 cm were destructively harvested. Diameter at breast height (*DBH*), total height (*ht*), wood bulk density (*wbd*), and crown diameter (*cd*) were used as predictors of the AGB. The study found that *DBH* was the best single predictor of AGB for *Oldeania alpina* and *Faidherbia albida*, with options for other species. Multiple variable models combining *DBH-ht* exhibited the highest predictive capacity for AGB in *Erythrina brucei, Albizia schimperiana,* and *Croton macrostachyus,* whereas the combination of *DBH*–*cd* and *DBH*–*ht*– *wbd*–*cd* best predicted the AGB of *Acacia abyssinica* and mixed species, respectively. Species-specifc and mixed-species models showed the best predictive capacity for AGB compared to other frequently used regional and pan-tropical models. The fndings of the study suggest that mixed-species AGB models will be used when species-specifc allometric models are not available at a given site.

Keywords Agroforestry systems · Biomass prediction · Dendrometric variables · Destructive sampling

Introduction

Climate change is one of the most pressing global environmental issues of the twenty-frst century (Liu et al. [2018](#page-16-0)). Deforestation and forest degradation are two major anthropogenic drivers of increased greenhouse gas (GHG) emissions (Kaisa et al. [2017;](#page-15-0) Bayen et al. [2020](#page-14-0)). The current global greenhouse gas emissions are estimated to be 10 Pg $(1 \text{ Pg} = 1012 \text{ kg})$ of carbon (C) per year (Amundson and Biardeau [2018](#page-14-1)). Climate change, in turn, affects many developing countries that rely on climate-sensitive sectors like rainfall-dependent and traditional agricultural practices (Matewos [2019](#page-16-1)). For instance, it increased species extinction (Trisos et al. [2020\)](#page-17-0), food shortages (Ayinu et al. [2022\)](#page-14-2), disease outbreaks (Orke and Li [2022\)](#page-16-2), and reduced crop yields (Ginbo [2022\)](#page-15-1).

Agroforestry systems are among the land uses that have been suggested as a global solution to increase the effectiveness of land use while minimizing negative environmental effects and economic risks for farmers (Mey and Gore [2021](#page-16-3)). The system is suggested to synergize climate change adaptation and mitigation (Dhyani et al. [2020](#page-15-2)), and recognized as a GHG mitigation strategy under the Kyoto Protocol (Semere et al. [2022](#page-17-1)). Agroforestry systems cover over one billion ha, supporting about 560 million people in developing countries (Shi et al. [2018\)](#page-17-2). The systems sequester 1.1–2.2 Pg C annually over a 50-year period globally (Dixon [1995\)](#page-15-3). Besides, the conversion of 630 million hectares of unproductive cropland and grassland to agroforestry could add about 586,000 Mg C per year by 2040 (Verchot et al. [2007\)](#page-17-3).

Smallholder farmers in Ethiopia have also developed site-specifc agroforestry practices that have high potential for climate change mitigation. Homegardens, parklands, and woodlots are among the most common agroforestry practices in the country for a long time (Tsedeke et al. [2021\)](#page-17-4). In the central part of Ethiopia, where this study was conducted, the local people have been engaged in various agroforestry practices. The majority of the smallholder farmers in the study region integrate trees with crops for shade, soil improvement, and fuelwood. They also commonly maintain a variety of perennial plant species in and around their homegardens and woodlots for a range of products and services.

Due to a lack of appropriate biomass estimation models, the Ethiopian National Forest Monitoring and Assessment Program did not take into account trees in agricultural landscapes when assessing carbon stocks in the past. Also various researchers adopted pantropical generalized biomass equations developed for natural forests (e.g., Chave et al. [2014\)](#page-14-3) to calculate the carbon stock of trees in agricultural landscapes (e.g., Gebremeskel et al. [2021;](#page-15-4) Chemeda et al. [2022](#page-14-4)). Biomass models developed for natural forests may not be suitable for agrofor-estry (Tumwebaze et al. [2013\)](#page-17-5), because tree allometry varies with tree architecture and silvicultural management (Zhang et al. [2020](#page-17-6)). Moreover, the application of existing pantropical biomass equations derived from a large dataset may not assure optimal precision of biomass estimation at small scales due to site- and species-specifc characteristics (Ngomanda et al. [2014](#page-16-4); Djomo et al. [2016;](#page-15-5) Paul et al. [2016](#page-16-5)). In that case, species-specific allometric equations may be more efective in determining the biomass and carbon stocks of the species than regional and pantropical equations (Mahmood et al. [2020a,](#page-16-6) [b\)](#page-16-7).

To date, only a few allometric models for predicting biomass in Ethiopian agroforestry have been developed for *Cofea arabica* and *Ensete vetricosum* (Negash et al. [2013a,](#page-16-8) [b](#page-16-9)) and trees scattered on rangeland (Feyisa et al. [2018\)](#page-15-6). A recent review of biomass models by Sebrala et al. [\(2022](#page-17-7)) found out that the allometric biomass equation for native tree and shrub species has received very little attention in Ethiopia. This has made carbon accounting very difficult for several perennial plant species in agroforestry systems nationally (Rosenstock et al. [2019\)](#page-17-8).

So, it was hypothesized that the derived speciesspecifc and mixed species AGB allometric model of native perennial plant species growing in agricultural landscape can give an accurate estimation compared to the frequently used pantropical and regional allometric models. Thus, the present study aimed at (1) developing species-specifc and mixed species allometric biomass models for estimating AGB of native perennial plant species in agricultural landscapes as well as (2) evaluating the performance of some previously developed pantropical and regional models for estimating AGB in agricultural landscapes.

Materials and methods

Study site description

The study was conducted on the smallholder agricultural landscape in Toke Kutaye, Dire Enchini, and Liban Jawi districts of West Shewa zone, which is located in Central Ethiopia (Fig. [1](#page-2-0)). West Shewa is geographically located between 8° 17′ and 9° 56′ N and 37° 17′ and 38° 45′ E. The zone has three agroecological zones namely; highland (Dega) ranging from an elevation of 2000 m to 3500 masl, midland (Woina dega) from 1600 to 2000 masl; and lowland (Qola) below 1600 masl. The mean annual rainfall and monthly temperature were 1569 mm and 22 °C, respectively. A range of soil types are found, but the dominant soil types are vertisols and loams. Rain-fed agriculture with a mixed farming system consisting of annual crop production and livestock rearing is the major livelihood source for inhabitants in the study area. The most commonly grown crops in the area include barley (*Hordeum vulgare*), teff (*Eragrostis teff*), wheat (*Triticum aestivum*), maize (*Zea mays*), and enset (*Ensete ventricosum*). Livestock production involves mixtures of indigenous and crossbred cattle raised under semi-zero

grazing systems. The smallholder farmers also use a variety of agroforestry systems, such as home gardens, parklands, and woodlots. Homegardens are multi-story techniques that mimic the structure and species diversity of a forest, including a variety of trees, annual crops, enset, highland bamboo, and other species (Eyasu et al. [2020](#page-15-7)). Another sort of agroforestry practice is parkland, which make up a signifcant portion of the land use in the eastern and northern parts of Ethiopia (Endale et al. [2016;](#page-15-8) Woldu et al. [2020](#page-17-9)). Parklands are made of carefully selected trees and shrubs from the forest that have been cleared for cropping, and their regeneration is is assisted in the agricultural landscape (Tadesse et al. [2019\)](#page-17-10). Woodlots are another typical agroforestry practices in which tree species are planted on productive or degraded areas in order to provide fuel wood and construction materials (Manaye et al. [2021\)](#page-16-10).

Fig. 1 Map of the study area

Sampling and biomass determination

Data were collected through two phase sampling. For the frst phase, forest inventories were performed using a total of 243 sample plots. Accordingly, 81 $(20 \times 20 \text{ m})$ quadrats were laid in homegardens and 81 (10×10 m) quadrats in woodlots. In contrast, 81 $(100 \times 50 \text{ m})$ quadrats were used in parklands. Visual estimation was used to divide farms into grid points, and then random selection was done to place the quadrat. On the sampled plots, trees were measured for their diameter at breast height (*DBH*), total height (*ht*), the average crown's diameter (*cd*), and the species type identifed. A caliper or diameter tape was used to measure tree diameters, while tree height was measured using a hypsometer. Additionally, the maximum and minimum crown diameters were measured with a measuring tape in order to determine the average crown diameter (*cd*).

For the second phase, six perennial plant species, namely: *Acacia abyssinica* Hochst.*, Croton macrostachyus* Del.*, Faidherbia albida* Del.*, Albizia schimperiana* Oliv.*, Erythrina brucei* Schweinf.*,* and *Oldeania alpina* (K. Schum), were chosen for destructive sampling based on forest inventory result that consider their importance value index (IVI) (Pothong et al. [2022\)](#page-16-11) (Supplementary material 1). To maintain representativeness of the sample (Moussa and Mahamane 2018) and minimize errors caused by the predominance of one diameter class over another (Sileshi [2014\)](#page-17-11), individual trees were stratifed into seven *DBH* classes and proportionally chosen over these diameter classes (Supplementary material 2). The inclusion of an unequal number of small-diameter trees compared to large-diameter trees in the sampling increases heteroscedacity (Sileshi [2014](#page-17-11)). However*, Oldeania alpina* culms were categorized into three age classes: age class 1, one- and two-year-old culms; age class 2, three- and four-year-old culms; and age class 3, fveand six-year-old culms (Abebe et al. [2023](#page-14-5)) using the culm's morphological features (Embaye et al. [2005](#page-15-9)). Besides, during destructive sampling, efforts were made in the selection to represent altitudinal variation (Asrat et al. [2020a](#page-14-6)). A total of 95 perennial plant individuals (13 for each species) were randomly chosen from *DBH* classes to minimize the cost and negative ecosystem impacts of harvesting large number of trees (Duncanson et al. [2015\)](#page-15-10). However, for *Oldeania alpina*, 30 individuals were chosen from age

classes since 30–50 sample culms are recommended to develop site-specifc allometric models (Huy and Long [2019\)](#page-15-11). Before felling the perennial plant, ecological information such as slope, altitude, and coordinates were all recorded. Moreover, dendrometric variables including the diameter at breast height (*DBH*), the diameter of the stump's height (*dsh*), the total height (*ht*), and the average crown's diameter (*cd*) (Tesfaye et al. [2016](#page-17-12)), and the age of *Oldeania alpina*, were recorded for each perennial plant species (Table [1](#page-4-0)).

Once the measurements were done, the selected trees were felled (at 0.3 m above the ground level) and processed accordingly. Following the removal of branches and leaves, the felled trees were divided into distinct biomass components, such as stems, branches (large branches with mid-diameter ≥ 10 cm, medium branches size with mid-diameter < 10 cm and > 5 cm and small branches with mid-diameter≤5 cm and≥2 cm) and leaves. Stem refers to the main shoot from the ground to the top of apical meristems up to 2 cm in diameter for highland bamboo. The cut-of diameter of the stems of other trees was set at 2.5 cm because this is the minimum size used for commercial purposes in many areas where wood fuel is scarce (Giday et al. [2013\)](#page-15-12). The remaining part was considered as branch biomass. The leaves' part contained all twigs, branches<2 cm, fowers, fruits, seeds, and leaves. Each component was weighed separately in the feld for its fresh weight using a hanging balance. For each tree, three disks were taken from the stem and branches (large, medium, and small). For determining the leaves' dry weight, 250-g aliquots of each tree's leaves were obtained (Daba and Soromessa [2019\)](#page-14-7). The sub-samples were placed in an airtight plastic bag and brought to a laboratory, where the green volumes were determined using the water displacement method (Liu et al. [2023\)](#page-16-13) after the bark was removed. Disks that were too large for the volumetric devices were immersed in a larger container, and the green volume was calculated based on the volume of water displaced from the container (Tetemke et al. [2019\)](#page-17-13). The wood's bulk density (*wbd*) for each disk was determined as the ratio of oven-dry mass to green volume. Then, the stem and branch subsamples were dried at 105 °C, while the leaves and twigs subsamples were dried in an oven at 70 °C for 48 h. After drying, the three subsamples were averaged within each component.

Species name	$\mathbf n$	DBH (cm)	ht(m)	cd(m)	wbd (g/cm^3)	Total dry biomass (Kg)		
		Mean (ranges)	Mean (ranges)	Mean (ranges)	Mean (ranges)	Mean (ranges)		
Oldeania alpina	10	$5.48(3.5-7.4)$	$10.04(8-13)$	$2.37(1.6-2.8)$		$0.42(0.37-0.55)$ $9.39(4.75-13.85)$		
	10	$7.55(4.6-10)$	$11.4(9.2-13.5)$	$2.48(1.7-3)$		$0.45(0.30-0.54)$ 11.17 $(6.66-17.42)$		
	10	$6.79(5-8.1)$	$12.08(10.7-13.3)$	$2.33(1.5-2.8)$		$0.45(0.33-0.58)$ 14.22 $(8.27-19.67)$		
Faidherbia albida	13	38.54 (8.00-65.00)	$7.62(4.40 - 11.00)$	$4.45(1.90 - 6.20)$		$0.71(0.54 - 0.99)$ 914.99 (32.08 - 2194.29)		
Acacia abyssinica	13	32.50 (11.50–52.00)	$5.68(4.00 - 8.00)$	$6.73(4.10-10.50)$		$0.67(0.48-0.87)$ 630.88 (71.80 - 1382.13)		
Erythrina brucei	13	42.67 (9.80-59.00)	$10.97(5.20 - 16.00)$	$4.42(2.88 - 6.10)$	$0.60(0.41-0.76)$	607.19 (53.91-1062.73)		
Albizia schimperiana	13	46.50 (7.00-65.00)	$11.79(3.00-15.60)$	$5.32(2.00 - 7.00)$		$0.77(0.52-0.89)$ 1015.12 (21.84-1723.57)		
Croton macrostachyus	13	41.54 (17.00-61.00)	$12.92(7.20 - 16.30)$	$9.82(4.00-14.00)$		$0.56(0.41-0.80)$ 647.94 (139.61-1153.38)		
Mixed-species	65	40.35 (7.00–65.00)	$9.80(3.00-16.30)$	$6.15(1.90 - 14.00)$	$0.66(0.41-0.99)$	763.23 (21.84–2194.29)		

Table 1 Statistical summary for biometric variables and aboveground biomass of the sampled perennial plant species in agricultural landscapes of central Ethiopia

Where; *DBH*: diameter at breast height (cm); *ht*: height (m); *wbd*: wood density (g/cm3); *cd*: average crown diameter (m); *n*: number of observations

The biomass of each tree section (stem, branch, and leaf) was determined by multiplying the total fresh weight of the section by the respective ratio of oven dry weight to fresh weight. The stump, (i.e., the portion of the stem up to 30 cm above the ground) was also considered component of the merchantable stem section for all trees. We computed the stump volume (V) using the formula $V = \pi d^2L$, where π is 3.14, d is the stump mid-diameter in m, and L is the length of each stump in m (Magdaline et al. [2020](#page-16-14)). Later, the biomass of the stump was calculated using volume and wood basic density. The total dry weights of the stem, branch, and tied bundle of twigs and leaves were as added up to determine the tree's total aboveground biomass.

Data analysis

All the data analysis and graphical representation in this study were performed using the R programming language (R Core Team [2020\)](#page-16-15). Multicollinearity among independent variables was tested by applying the variance infation factor (VIF) using the "car" package, (Zhao et al. [2019](#page-17-14); Rahman et al. [2021\)](#page-16-16), and no multicollinearity was found among the independent variables included (VIF < 2.56) (Table 3). Pearson correlation tests were applied to determine the degree of relationship between AGB and dendrometric parameters (Moussa and Mahamane [2018](#page-16-12)). We therefore, tested weighted nonlinear least squares regression by using the 'nls' function in the R software because it performed better than log-linear models (Huynh et al. [2021\)](#page-15-13). Weighted non-linear was used to account for heteroscedasticity in residuals (Huy et al. $2019a$). Huynh et al. (2022) (2022) showed that weighted non-linear models also had a lower Furnival's Index (FI) than log-linear models. Moreover, the variance is assumed to be proportional to the square of the mean of the biomass in this study, as recommended by Aabeyir et al. [\(2020\)](#page-14-8). When the Q-ratio (i.e., the ratio between the parameter estimates of *DBH* and parameter estimates of *ht*, in a separate variable model) is equal to 2.0 (between 1.5 and 2.5), it is common to include $(DBH)^2 \times ht$ as a single input in the regression to address collinearity problems (Dutcă et al. [2019](#page-15-16)). Due to the low collinearity between *DBH* and *ht* in this study and the fact that similar biomass models previously developed in Ethiopia produced Q-ratios outside the range of 1.5–2.5 (Tetemke et al. [2019](#page-17-13); Asrat et al. [2020b\)](#page-14-9), a separate predictor approach was adopted for modeling.

Accordingly, eight biomass models (Eqs. $1-8$ $1-8$) using non-linear regression equations were tested for multispecies models while the four models without the wbd were ftted/tested for species-specifc cases. *DBH* is the most frequently used variable for predicting biomass. Other variables, such as *ht, wbd*, and average crown diameter (*cd*), have also often been combined with *DBH* in allometric models in previous studies (Asrat et al. [2020b](#page-14-9); Dao et al. [2021\)](#page-15-17). Because adding *ht* as a predictor variable to *DBH* accounts for variation in AGB among trees with the same diameter value

(Mensah et al. [2016](#page-16-17)) and reduces relative error (Muku-ralinda et al. [2021\)](#page-16-18). Wood density also affects how much biomass is allocated to wood and foliage because trees with low wood densities devote more resources to photosynthetic processes that promote the development of foliage (King et al. [2006](#page-16-19)). Moreover, including average crown diameter (cd) also improved predictions compared to using a single variable alone (Dimobe et al. [2019](#page-15-18); Flores-Hernández et al. [2020;](#page-15-19) Romero et al. [2022\)](#page-16-20). The following general nonlinear model forms for prediction of biomass were ftted:

$$
Model1: Y = a \times (DBH)^b
$$
 (1)

Model2 : $Y = a \times (DBH)^{b} \times (ht)^{c}$ (2)

Model3 : $Y = a \times (DBH)^{b} \times (cd)^{c}$ (3)

Model4 : $Y = a \times (DBH)^{b} \times (wbd)^{c}$ (4)

$$
Model5: Y = a \times (DBH)^{b} \times (ht)^{c} \times (wbd)^{d}
$$
 (5)

Model6 : $Y = a \times (DBH)^b \times (ht)^c \times (cd)^d$ (6)

$$
Model7: Y = a \times (DBH)^{b} \times (wbd)^{c} \times (cd)^{d}
$$
 (7)

$$
Model8: Y = a \times (DBH)^{b} \times (ht)^{c} \times (wbd)^{d} \times (cd)^{e} \quad (8)
$$

where *Y* represents the biomass of the a tree, *a, b, c, d* and *e* are the estimated parameters of the fitted models, *DBH* is the diameter at breast height (cm), *ht* is the tree height (m), *cd* is average crown diameter (m), and *wbd* is the wood density (gcm⁻³) of a given tree.

Model evaluation, selection, and comparison

Four ft statistics were combined to choose the best candidate models: AIC (Akaike Information Criterion); pseudo-R²; RMSE (Root Mean Square Error); and MAE (mean absolute error) (Ubuy et al. [2018b](#page-17-15); Asrat et al. [2020b](#page-14-9)). The best models have a high pseudo- R^2 and the lowest AIC, RMSE, and MAE calculated using the *caret* function in the R software.

For the cross validation of the equations, the root mean square error (RMSE) and mean prediction error (MPE) were computed using the leave one out cross variation (LOOCV) approach. This approach leaves one observation for validation and the remaining *n*−1 observations for training the model. The excluded observation is predicted, and the error is calculated. The procedure is repeated n time until every observation has been left out and predicted. The RMSE and MPE are computed using the *n* errors. These statistical parameters were calculated as follows:

RMSE =
$$
\sqrt{\text{MSE}} = \sqrt{\frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{n}}
$$
,
RMSE% = $\frac{\text{RMSE}}{\overline{Y}} \times 100$ (9)

$$
MPE = \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)}{n}, MPE\% = \frac{MPE}{\overline{Y}} \times 100 \quad (10)
$$

$$
AIC = n \log \left(\frac{\sum_{i=1}^{n} (\hat{y}_i - y_i)^2}{n} \right) + 2p
$$
 (11)

Pseudo - R² = 1 -
$$
\frac{SSR}{CSST} = 1 - \frac{SSR}{\sum_{i=1}^{n} (yi - \overline{Y})^2}
$$
 (12)

where *SSR* is the sum of squared residuals, *CSST* is the corrected sum of squares $(\sum y \cdot \bar{Y})^2$, *p* is the number of parameters in the model, *yi* is the observed AGB, \hat{y}_i is predicted AGB, *n* is the total number of observations, and \overline{Y} is mean of observed AGB. With the use of our dataset, we compared several previously developed species-specifc and generic models for aboveground biomass in agroforestry and natural forests (Table [2](#page-6-0)). First, some species-specifc models from Ethiopia (Giday et al. [2013](#page-15-12); Mulatu and Fetene [2013;](#page-16-21) Abebe et al. [2023\)](#page-14-5) and Niger (Moussa and Mahamane [2018](#page-16-12)) were tested. Then three relevant generic models from the natural forests of Ethiopia (Ubuy et al. [2018b](#page-17-15); Tetemke et al. [2019](#page-17-13); Asrat et al. [2020b\)](#page-14-9) and other sub-Saharan African countries (Kuyah et al. [2012](#page-16-22)), as well as the pan-tropical model developed by Chave et al. ([2014\)](#page-14-3) were tested. The model developed by Chave et al. ([2014\)](#page-14-3) was chosen since it is extensively used in tropical regions. Three generic models for natural forests that were developed using multiple variables as in the current study were employed because there was a lack of a general and species-specifc model for trees in agricultural landscapes, and there is high possibilities that such

Model type	Expression	Age n		dbh/dsh range (cm) References	
General multispecies (pan- tropical)	$AGB = 0.0673 \times (DBH2 \times ht \times$ $wbd)^{0.976}$			4004 5.0 - 180.0	Chave et al. (2014)
General multispecies (Kenya)	$AGB = 0.225 \times (DBH)^{2.341} \times$ $(wbd)^{0.73}$		72	$3.0 - 102.0$	Kuyah et al. (2012)
General multispecies (Ethiopia)	$AGB = 0.21765 \times (DBH)^{1.77660}$ \times (ht) ^{0.33242} \times (crw) ^{0.65575} \times $(wbd)^{1.07739}$		63	$7.0 - 106.5$	Asrat et al. $(2020b)$
General multispecies (Ethiopia)	$AGB = 0.217 \times (DSH)^{1.8428} \times$ $(ht)^{0.3361} \times (wbd)^{0.2963}$		305	$2.5 - 29.5$	Ubuy et al. $(2018b)$
General multispecies (Ethiopia)	$AGB = 0.350 \times (DBH)^{1.864} \times$ $(cra)^{0.171} \times (wbd)^{0.485}$		86	$2.9 - 45.2$	Tetemke et al. (2019)
Species-specific (Niger)	$AGB = 0.06457 \times (DBH)^{2.4629}$		20	5.73 - 65.92	Moussa and Mahamane (2018)
Species- specific (Ethiopia)	$AGB = 0.02977 \times (DSH)^{2.827}$		39	$2.54 - 28.6$	Giday et al. (2013)
Species-specific (Ethiopia)	$AGB = 0.259 \times (DBH)^{2.098}$	$1 - 2$			Abebe et al. (2023)
	$AGB = 0.139 \times (DBH)^{2.577}$	$3 - 4$			

Table 2 Previously published species-specifc and mixed species biomass allometric model tested using the data set from this study

cra: Crown area (m^2) , crw: crown width (m) , ht; tree height (m) , DBH: diameater at breast height (cm) , DSH: Diameter at stump height (cm), and wbd: wood bulk density $(g/cm³)$

AGB = $0.165 \times (DBH)^{2.487}$ 5–6 42 3.0–7.1 Species-specific (Ethiopia) $AGB = exp(0.172 \times DBH)$ 1–2 Mulatu and Fetene ([2013\)](#page-16-21)

> $AGB = exp(0.289 \times DBH)$ 3–4 $AGB = exp(0.30 \times DBH)$ 5–6

models will be used. These models were developed by Tetemke et al. (2019) (2019) , Ubuy et al. $(2018b)$ $(2018b)$, and Asrat et al. ([2020b\)](#page-14-9) using samples of trees from Ethiopia. The models developed by Giday et al. ([2013\)](#page-15-12) for *Acacia abyssinica* and by Abebe et al. ([2023\)](#page-14-5) and Mulatu and Fetene ([2013\)](#page-16-21) for *Oldeania alpina* were the most useful ones we found in the literature utilizing samples of trees from Ethiopia. The generic models developed by Kuyah et al. [\(2012](#page-16-22)) and speciesspecifc ones developed by Moussa and Mahamane [\(2018](#page-16-12)) for *Faidherbia albida* were also the most pertinent ones we discovered in the literature because they were developed for tree species that were grown on agricultural landscapes. To look for signifcant diferences between observed and predicted biomass levels, the paired t-test was employed.

Results

Species-specifc and mixed-species allometric equations to estimate AGB

The aboveground biomass (AGB) model using only *DBH* as the predictor variable (Model 1) performed best for two of the species (*Faidherbia albida* and *Oldeania alpina*) and was optional for other species (Table [3](#page-7-0)). The ftting statistics of this model (Model 1) were typically good, with pseudo- R^2 varying between 85 and 99% across all species and mixed species. Moreover, the model developed for *Faidherbia albida* had the highest pseudo- R^2 (0.99), the lowest RMSE (59.3), and the lowest AIC (138.77) with a significant $(p<0.01)$ regression model. This model somewhat underpredicted the aboveground biomass for *Faidherbia albida* and 1–2-year-old highland bamboo (*Oldeania alpina*) by 0.57% and 0.3%, respectively. However, it overpredicted the aboveground biomass for 3–4, and 5–6-year-old highland bamboo (*Oldeania alpina*) by 0.15% and 0.05%, respectively.

For *Erythrina brucei* and *Albizia schimperiana,* a multiple-variable model that included *DBH* and *ht* (model 2) was shown to have a lower AIC than the models using *DBH* as the single variable (model 1), but they had a comparable pseudo- R^2 . Adding *ht* to *DBH* (Model 2) as a compound variable was also the best-performing model that signifcantly improved the statistical fts for AGB of *Croton macrostachyus*

Table 3 List of fitted above round biomass (AGB) allometric models for studied perennial plant species and mixed-species in agricultural landscapes of central Ethiopia **Table 3** List of ftted aboveground biomass (AGB) allometric models for studied perennial plant species and mixed-species in agricultural landscapes of central Ethiopia

(AIC), and Variance Infation Factor (VIF)

when compared to the model based on *DBH* as a single predictor.

An allometric model including *DBH* and *cd* (Model 3) as predictors ftted well with our data for the prediction of AGB with a high pseudo- R^2 (0.99) and low AIC (135.94) and RMSE (40.8) for *Acacia abyssinica*. The model that takes into account *DBH* and *ht* resulted in an improved pseudo- R^2 , but had a higher AIC and RMSE compared with model 3 (Table [3](#page-7-0)). A multiple-variable model (Model 8) that includes *DBH, ht, wbd*, and *cd* had the highest pseudo-R2 value (0.95) and the lowest AIC (780.03) for mixed species that developed by using the full dataset (excluding *Oldeania alpina*). Hence, Model 8 was selected as the best-ft allometric biomass model for the prediction of the AGB for mixed species.

Performance of the present models compared to previously published models

The best-ft model of *Oldeania alpina* showed the lowest value for the percentage of residual mean square error (RMSE kg) and model prediction error (MPE%) compared to the species-specifc allometric biomass models (Mulatu and Fetene [2013](#page-16-21); Abebe et al. [2023\)](#page-14-5). The paired t-test indicated that our bestft AGB model and observed aboveground biomass were statistically identical for this species (Table [4](#page-9-0)). The graphical presentation of the 1:1 line also supported that our best-ft AGB model for *Oldeania alpina* was similar to the observed AGB (Fig. [2](#page-12-0)). The biomass model of Mulatu and Fetene [\(2013](#page-16-21)) signifcantly overpredicted the AGB for 1–2, 3–4, and 5–6 years old highland bamboo, while the biomass model of Abebe et al. (2021) signifcantly underpredicted the AGB for 1–2, 3–4 and 5–6 years old highland bamboo (Table [4](#page-9-0)).

The residual mean square error (RMSE%) and model prediction error percentage (MPE%) values of these best-ft models showed high precision of predictability for *Faidherbia albida* and *Acacia abyssinica* over species-specifc models developed by Moussa and Mahamane ([2018\)](#page-16-12) and Giday et al. [\(2013](#page-15-12)), respectively, and generic models (Kuyah et al. [2012;](#page-16-22) Chave et al. [2014](#page-14-3); Ubuy et al. [2018b](#page-17-15); Tetemke et al. [2019;](#page-17-13) Asrat et al. [2020b\)](#page-14-9). Nevertheless, among the generic models, the equation developed by Asrat et al. ([2020b\)](#page-14-9) for AGB based on 63 trees with dbh≥5 cm in the Dry Afromontane forests of southcentral Ethiopia ranked 2nd lowest in RMSE (%) and MPE (%) for these two species. The paired t-test differences between the observed and predicted AGB were not statistically signifcant for those two species. The scatter plot diagram also depicted the points close to the line of best ft which confrms that the models provided a good ft to the data for both *Faidherbia albida* and *Acacia abyssinica* (Fig. [2](#page-12-0)). However, the generic models of Chave et al. ([2014\)](#page-14-3), Ubuy et al. [\(2018b](#page-17-15)), Asrat et al. [\(2020b](#page-14-9)), and Tetemke et al. [\(2019](#page-17-13)) signifcantly overpredicted the AGB, but the biomass of the two species was signifcantly under-estimated by Kuyah et al. ([2012\)](#page-16-22). Species-specific models developed by Moussa and Mahamane ([2018\)](#page-16-12) for *Faidherbia albida* signifcantly overpredicted the AGB, while Giday et al. [\(2013](#page-15-12)) underpredicted biomass for *Acacia abyssinica.*

The best-ranked models of *Erythrina brucei* (Model 2) *and Albizia schimperiana* (Model 4) showed the lowest RMSE (%) and MPE (%) com-pared to the generic models (Kuyah et al. [2012;](#page-16-22) Chave et al. [2014;](#page-14-3) Ubuy et al. [2018b](#page-17-15); Tetemke et al. [2019;](#page-17-13) Asrat et al. [2020b](#page-14-9)). The observed biomass of *Erythrina brucei* and *Albizia schimperiana* was not signifcantly diferent from the biomass predicted by our allometric models (*p*>0.05). However, it was signifcantly diferent from the biomass predicted from the allometric models developed by Kuyah et al. [\(2012](#page-16-22)), Chave et al. ([2014\)](#page-14-3), Asrat et al. [\(2020b](#page-14-9)), and Tetemke et al. [\(2019](#page-17-13)). The allometric models developed by Ubuy et al. ([2018b\)](#page-17-15) and Tetemke et al. [\(2019](#page-17-13)) overpredicted the AGB for those two species. In contrast, when the allometric models developed by Kuyah et al. (2012) (2012) , Chave et al. (2014) (2014) , and Asrat et al. [\(2020b](#page-14-9)) were applied, the biomass was underpredicted as indicated by the higher MPE value (Table [4](#page-9-0)).

Our best-ft model (Model 5), overpredicted the AGB of *Croton macrostachyus* by 0.08%, a small value when compared with other equations that have been generated to predict aboveground biomass in Ethiopia and tropical forests in general (Table [4](#page-9-0)). The results became more conspicuous in the graphical presentation of the goodness of ft 1:1 line, indicating the capability of our best-ft model 5 to predict the AGB accurately and precisely (Fig. [2](#page-12-0)). Application of these previously developed models to our dataset underpredicted or overpredicted

Table 4 Comparison of species-specifc and mixed species model with previously published allometric models

Species	Age (year)	Model reference	Mean observed AGB (kg)	Mean pre-	RMSE		MPE	
				dicted AGB (kg)	$\%$	kg	$\%$	kg
Oldeania alpina	$1 - 2$	Current study	9.39	9.42 ns	8.63	0.81	-0.34	0.03
		Abebe et al. (2023)		$10.06*$	64.1	6.02	-39.2	3.68
		Mulatu and Fetene (2013)		2.66***	41.4	3.89	38.6	3.62
	$3 - 4$	Current study	11.17	11.15 ns	5.28	0.59	0.15	0.02
		Abebe et al. 2023		28.06***	179	19.96	-151	16.9
		Mulatu and Fetene (2013)		9.96***	9.96	13.8	1.54	10.9
	$5 - 6$	Current study	14.22	14.21 ns	2.46	0.35	0.05	0.01
		Abebe et al. 2023		27.53***	49.4	7.03	-43	6.11
		Mulatu and Fetene (2013)		$10.91***$	10.9	44.5	6.38	43
Acacia abyssinica		Current study	630.88	633.05 ns	6.44	40.82	-0.34	2.15
		Kuyah et al. (2012)		740.71*	31	195	-17	110
		Chave et al. (2014)		283.47***	66.4	419	55.1	347
		Asrat et al. $(2020b)$		555.25*	20.8	131	12	75.6
		Ubuy et al. $(2018b)$		281.47***	69.2	437	55.4	349
		Giday et al.(2013)		952.35*	77.8	491	-51	322
		Tetemke et al. (2019)		296.42***	65.3	412	53	334
Albizia schimperiana		Current study	1015.12	1016.46 ns	3.97	73.83	-0.13	1.32
		Kuyah et al. (2012)		1794.21***	89	903	-77	779
		Chave et al. (2014)		1304.6**	42	427	-29	290
		Asrat et al.(2020b)		1234.13*	32.6	331	-22	219
		Ubuy et al. (2018b)		649.53***	41.9	425	36	366
		Tetemke et al. (2019)		548.4***	52.4	532	46	467
Faidherbia albida		Current study	914.99	909.81 ns	6.49	59.3	0.57	5.22
		Kuyah et al. (2012)		1319.1*	68.3	625	-44	404
		Chave et al. (2014)		642.95**	38.7	354	29.7	272
		Asrat et al.(2020b)		752.06*	27.2	249	17.8	163
		Ubuy et al. (2018b)		439.39**	69.6	637	52	476
		Moussa and Mahamane (2018)		721.81***	25.1	230	21.1	193
		Tetemke et al. (2019)		413.14**	71.1	651	54.9	502
Erythrina brucei		Current study	607.19	598.75 ns	10.9	65.9	1.39	8.44
		Kuyah et al. (2012)		1193.3***	115	699	-97	586
		Chave et al. (2014)		806.54*	54.2	329	-33	199
		Asrat et al. (2020b)		687.41*	24.3	148	-13	80.2
		Ubuy et al. $(2018b)$		501.89***	20.3	123	17.3	105
		Tetemke et al. (2019)		379.42***	42.9	261	37.5	228
Croton macrostachyus		Current study	647.94	647.41 ns	6.34	41.11	0.08	0.52
		Kuyah et al. (2012)		992.82***	66.4	430	-53	345
		Chave et al. (2014)		728.3*	19	123	12.4	80.3
		Asrat et al.(2020b)		982.5*	20.9	135	-14	88.1
		Ubuy et al. (2018b)		494.68***	27	175	-49	319
		Tetemke et al. (2019)		382.6***	47.7	309	41	265

Table 4 (continued)

ns=Nonsignifcant model parameter estimates (*p*>0.05); *, ****, and ***** signifcant at *p*<0.05, *p*<0.01 and *p*<0.001, respectively

according to the models generated for each region. For example, equations developed by Kuyah et al. [\(2012\)](#page-16-22); Asrat et al. [\(2020b\)](#page-14-9); and Ubuy et al. [\(2018b\)](#page-17-15) signifcantly underpredicted biomass. In contrast, when the allometric models developed by Tetemke et al. ([2019\)](#page-17-13); and Chave et al. ([2014](#page-14-3)) were applied, the biomass was signifcantly overpredicted by 40.95% and 12.40%, respectively (Table [4](#page-9-0)).

The residual mean square error (RMSE%) and the model prediction error (MPE%) of the best-ft model (model 8) for mixed-species were lower than those of generic (Asrat et al. [2020b](#page-14-9); Kuyah et al. [2012](#page-16-22); Tetemke et al. [2019\)](#page-17-13) models. Nevertheless, among the generic models, Asrat et al. [\(2020b\)](#page-14-9) ranked the 2nd lowest RMSE (%) and MPE (%) (Table [4\)](#page-9-0). The 1:1 line shown in Fig. [2](#page-12-0) indicates that the closer the values are to the 1–1 line, the lower the bias of the prediction. The biomass predicted by Chave et al. [\(2014\)](#page-14-3) was comparable with observed AGB. However, the biomass model of Ubuy et al. [\(2018b\)](#page-17-15) and Tetemke et al. [\(2019\)](#page-17-13) signifcantly overpredicted the AGB, while biomass model of Kuyah et al. (2012) (2012) (2012) and Asrat et al. $(2020b)$ $(2020b)$ significantly underpredicted the biomass (Table [4](#page-9-0)).

Discussion

Species-specifc and mixed-species allometric models to predict AGB

Power allometric models were used to predict the AGB of six native perennial plant species grown on agricultural landscape in central Ethiopia. These type of models are preferred over polynomial and logarithmic equations because they are commonly used, simple, and practical for predicting the biomass of many woody species (Ou and Boussim [2020\)](#page-16-23). Our speciesspecifc biomass models outperformed over mixedspecies models. This is consistent with the fndings of Nyamukuru et al. [\(2023](#page-16-24)). Similarly, multiple-variable models performed better than single-variable models in both species-specifc and multi-species models. Our results are in agreement with those of Nyamukuru et al. [\(2023](#page-16-24)) for trees and shrubs biomass estimation in the African savanna ecosystems who found that multiple-variables models performed better than single variable models.

For *Oldeania alpina*, the most accurate allometric biomass model used *DBH* as the only explanatory variable. This is in line with fnding of Inoue et al. ([2019\)](#page-15-20) that *DBH* to be the most accurate predictor to explain the biomass variability for square bamboo in western Japan. A study carried out in the Bobiri forest reserve in Ghana also showed that *DBH* alone explains variations in the biomass distributions among biomass components, age classes, and total biomass of bamboo (Amoah et al. [2019\)](#page-14-10). Similar to that, a study in southwestern Ethiopia on *Oldeania alpina* (Yebeyen et al. [2022](#page-17-17); Abebe et al. [2023\)](#page-14-5) supported the notion that allometric models based solely on *DBH* would increase the value of the predicted biomass. In this study, adding tree height to equations for highland bamboo did not improve the model's performance. This showed that biomass equations using the *DBH* variable are easy and take less time to measure. Dense highland bamboo woodlots in the study area can also cover bamboo plants tree tops, making

Fig. 2 The relationship between the observed and the pre-◂dicted AGB for six studied species and mixed-species model. The dashed line represents the 1:1 line or reference line, whereas the black solid line represents the ftted line

it challenging to measure heights in the feld. Similar to this, Nfornkah et al. [\(2021](#page-16-25)) also revealed that the dense culms of bamboo made it hard to measure height nondestructively, making the use of the height variable model for bamboo problematic from the start. Roxburgh et al. ([2015\)](#page-17-18) and Mensah et al. ([2017\)](#page-16-26) also found that the inclusion of tree height did not result any signifcant improvements over the simple power model, proving that species affects how much extra predictors would enhance biomass models.

The allometric models developed with *DBH* as an explanatory variable were also the best performing models that provide a best prediction of AGB for *Faidherbia albida*. For this species, AGB estimates using *DBH* alone led to lower AIC and RMSE and increased accuracy. This agrees with authors (Beedy et al. [2016;](#page-14-11) Moussa and Mahamane [2018](#page-16-12)), who revealed *DBH* is the accurate predictor of AGB of *Faidherbia albida* in Malawi and Niger, respectively. The fndings suggest that *DBH* change substantially accounts for the variability of tree biomass in agricultural landscape. The facts that tree diameter is the simplest variable to measure in the feld and had a signifcant correlation with AGB. For ease of model application and validation, it is advised to use fewer explanatory variables (Sileshi [2014](#page-17-11)). Additionally, we found that compared to using *DBH* alone, adding tree height data did not signifcantly improve biomass prediction. It is also related to *Faidherbia albida* trees' tendency to branching, which leads to more radial development than apical growth. The insignifcant improvement of height on AGB prediction could also be due to the process of pollarding and prunning branches in parkland agroforestry at intervals of three to four years to increase light availability for understory crops. Moreover, this study found that the inclusion of crown diameter did not improve the model ft for *Faidherbia albida.* The size of the tree afects the strength of the association between crown diameter and AGB; it is weaker in trees with small crowns (Dimobe et al. [2018](#page-15-21)). *Faidherbia albida* has a less variable geometry of the canopy, possibly due to the inherent plasticity of its canopy to interplant disturbances from pollarding and prunning branches in parkland agroforestry.The fndings of this study show that models with multiple variables (*DBH* and *ht*) had better predictive ability for AGB in *Albizia schimperiana, Croton macrostachyus*, and *Erythrina brucei* than the *DBH* alone model. Including tree height as a predictor variable in AGB models is usually recommended as it can improve model ft, robustness, increased efficiency, and lower model prediction error for fruit tree species in Bangladesh than the commonly used pantropical and regional models (Saha et al. [2021](#page-17-19)). Many researchers believe that including height in models will lessen model site specifcity (Dutcă et al. [2018](#page-15-22); Dutcă [2019](#page-15-23)).

Recently, crown dimensions are essential for improving tree biomass estimates and simplifying AGB estimation (Tetemke et al. [2019](#page-17-13); Loubota Panzou et al. 2021 ; Jucker et al. 2022). In this study, combing *cd* with *DB*H improved model ft by 3% and reduced the relative error by 5.4% for AGB of *Acacia abyssinica*. This could be because the branching patterns of the studied tree species shared approximately 40% of the total AGB. This result is in line with recent study on tree allometry in the dry afromontane forest of Ethiopia where crown width improved model's prediction (Asrat et al. [2020b](#page-14-9)). Similar fndings were made by Dao et al. [\(2021](#page-15-17)) for *Mangifera indica* in parklands of the Sudanian zone of Burkina Faso.

The fndings indicate that, for mixed species, the predictor variables may account for 85–95% of the variance in the dependent variable. For mixed species, *DBH* alone as a single predictor explained over 85% of the variation in AGB and had a relative error of 19.52%. However, adding tree height as an additional predictor reduced the relative error for AGB by 3.01% and improved model ft by 5% for mixed species. Similar observations have been reported on species equations (Mukuralinda et al. [2021](#page-16-18); Mensah et al. [2017\)](#page-16-26) and regional mixed-species equations (Teshome et al. [2022\)](#page-17-20) that tree height data improves biomass prediction when compared to equations that use DBH as the only predictor variable.

However, the inclusion of crown diameter did not improve the ft of the model for mixed species. This suggests that the correlation between crown diameter and AGB is size-dependent, with the association being weaker in smaller-crowned trees. The characteristics of pooled tree data may be used to determine tree allometry. For instance, *Faidherbia albida* has a less variable geometry of the canopy, probably as a result of disturbances from pollarding and prunning branches at intervals of three to four years, which lower the AGB prediction of crown diameter in mixed species. A similar trend was observed in Burkina Faso (Mukuralinda et al. [2021\)](#page-16-18) where the inclusion of crown diameter did not improve the model fts for *Terminalia laxifora*.Some studies indicate that using wood bulk density as an independent variable in allometric models can signifcantly increase the accuracy of the biomass model in tropical forests (Huy et al. [2019b\)](#page-15-25), whereas other studies found that doing so had no significant effect on the model's performance (Zhao et al. [2019;](#page-17-14) Mahmood et al. [2020a](#page-16-6)). The complexity of feld data gathering and reliance on additional laboratory analysis prevent wood bulk density from being utilized frequently. Some researchers rely on datasets like the Global Wood Density Database (Khan et al. [2020\)](#page-16-28). Also, Ethiopia's Forest Reference Level report for the REDD + implementation used the wood density database rather than directly determining this statistic (Ubuy et al. $2018a$). This signifies the importance of inclusion of basic wood density to be included in biomass models as an explanatory variable, which also helps lower model uncertainty (Mukuralinda et al. [2021](#page-16-18)).

Our results show that the addition of *wbd* to *DBH* alone (model 4) reduced the relative error for AGB by 6.28% and improved model ft by 7% for mixed species. Other studies recommend wood density as an additional predictor variable that can be used to improve biomass prediction(Mukuralinda et al. [2021](#page-16-18); Zhu et al. [2021](#page-15-26); Ganamé et al. 2021). Moreover, the model 5 with three predictors (*DBH, ht*, and *wbd*) reduced the relative error for AGB by 7.85% and improved model ft by 10% for mixed species. Similar observation has been reported in species-specifc model (Daba and Soromessa [2019;](#page-14-7) Abich et al. [2021\)](#page-14-12) and mixed-species equations (Ganamé et al. [2021\)](#page-15-26) where inclusion of *DBH, ht,* and *wbd* data improves biomass prediction when compared to equations that use DBH as the only predictor variable.

Multiple variables models combining *DBH, ht, wbd*, and *cd* as predictors reduced the relative error for AGB by 8.4%, improved model ft by 10%, and perform the best ftness among all of the models for mixed species. Our results agree with reports on regional mixed-species equations (Asrat et al. [2020b](#page-14-9); Tetemke et al. [2019\)](#page-17-13) that *DBH, ht, wbd*, and *cd* data improve biomass prediction when compared to other models for mixed species. This may be due to the fact that pooling biomass data to develop mixed species models increases the sample size and results in stable regression parameters and variance estimates (Xiang et al. [2016\)](#page-17-22). Moreover, multiple-predictor models were more effective than single-predictor models (Smith et al. [2021\)](#page-17-23). Our fnding is most likely due to the diferent morphologies of the studied species, meaning that the inclusion *of DBH, ht, wbd, and cd* accounted for variation in the AGB induced by diference in tree architectures.

Performance of the present models compared to previously published models

Generally, the models developed for this study performed better and had a smaller residual mean square error (RMSE%) and the model prediction error (MPE%) since there were more sampled trees in the study. Applying allometric equations with small sample numbers will lead to a bias of up to 70% (Duncanson et al. 2015). In the current study, we employed 95 destructively sampled perennial plant individuals to develop biomass models. Taking into account Ethiopia's restrictions on destructive sampling and the costs associated with biomass assessment in general, the number of sample trees used in this study was greater than previously reported general and species-specifc models. Furthermore, the inclusion of a large tree in the sample for this study may improve the precision of the biomass prediction. In contrast to the current models, which were built for trees on agricultural landscape, many of the earlier models were developed for natural forests, with the exception of Moussa and Mahamane [\(2018](#page-16-12)) and Kuyah et al. [\(2012](#page-16-22)). Because tree biomass allometric models vary by site (Ducey [2012](#page-15-27)). The allometry of trees is a result of the interaction between endogenous growth processes and exogenous constraints exerted by the environment. The interactions between individuals change tree architectures, including canopy area, branching, and stem form, which determine biomass allocation (Yang et al. [2019](#page-17-24)). Moreover, characteristics of species and their silvicultural management may be an explanation for the lower prediction of regional and pan-tropical generic allometric models when they are applied to the existing data.

Conclusion

This study has developed species-specifc and multispecies biomass allometric models to provide accurate estimates of AGB for native perennial plant species in the agricultural landscape of central Ethiopia. The models with only *DBH* as a predictor were the best single predictors of AGB for *Oldeania alpina* and *Faidherbia albida*, and options for other species. Multiple variable models combining *DBH-ht* exhibited the highest predictive capacity for AGB in *Erythrina brucei, Albizia schimperiana,* and *Croton macrostachyus,* whereas the combination of *DBH-cd* and *DBH*-*ht-wbd-cd* best predicted the AGB of *Acacia abyssinica* and mixed species, respectively. Species-specifc and mixed-species models showed the best predictive capacity for AGB compared to other frequently used regional and pan-tropical models. The fndings of the study suggest that mixed-species AGB models will be used when species-specifc allometric models are not available at a given site. The allometric models can be used as the basis for reporting and verifying biomass and carbon stocks in the agricultural landscape for carbon crediting schemes such as $REDD+$ and CDM. However, caution must be taken when applying the models to other datasets since their applicability is limited to the range of *DBH*, land use type, and biophysical conditions of the study area.

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Author contributions G.D. designed the study, conducted feld and laboratory work. M.N. and L.B. searched research fund. G.D., M.N., Z.A., and L.B. analyzed the data and wrote the manuscript. M.N., Z.A., and L.B. supervised work.

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Declarations

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