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Mixed-Species Allometric Equations to Quantify Stem Volume and Tree Biomass in Dry Afromontane Forest of Ethiopia

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Abstract

Volume and biomass equations are essential tools to determine forest productivity and enable forest managers to make informed decisions. However, volume and biomass estimation equations are scarce for Afromontane forests in Africa in general and Ethiopia in particular. This limits our knowledge of the standing volume of wood, biomass, and carbon stock of the forests therein. In this study, we developed a new mixed-species volume and biomass equations for Afromontane forests and compared them with generic pantropical and local models. A total of 193 sampled trees from seven dominant tree species were used to develop the equations. Various volume and biomass equations were fitted using robust linear and nonlinear regression. Model comparison indicated that the best model to estimate stem volume was $\ln(v) = -9.909 + 0.954 * \ln(d^2 h)$, whereas the best model to estimate biomass was $\ln(b) = -2.983 + 0.949 * \ln(\rho d^2 h)$. These equations explained over 85% of the variations in the stem volume and biomass measurements. The mean density and basal area of trees in the forest with d ≥ 2 cm was 631.5 stems·ha⁻¹ and 24.4 m²·ha⁻¹. Based on the newly developed equations, the forest has on average 303.0 m³·ha⁻¹ standing volume of wood and 283.8 Mg·ha⁻¹ biomass stock. The newly developed allometric equations derived from this study can be used to accurately determine the stem volume, biomass, and carbon

storage in the Afromontane forests in Ethiopia and elsewhere with similar stand characteristics and ecological conditions. By contrast, the generic pan-tropical and other local models appear to provide biased estimates and are not suitable for dry Afromontane forests in Ethiopia. The estimated stem biomass and carbon stock in the Chilimo forest are comparable with the estimates from various tropical forests and woodlands elsewhere in Africa, indicating the importance of dry Afromontane forest for climate change mitigation.

Keywords

1. Introduction

Afromontane forests constitute a unique forest type occurring on high African mountains (White, 1983). They are mostly found in Ethiopia, Cameroon, and South Africa (White, 1983; Grimshaw, 2001; Gadow et al., 2016). Although they are widely separated, Afromontane forests share a similar mix of plant species (over 4000 species, of which ~3000 are endemic), which are often distinct from the surrounding lowland forests (White, 1983). Dry Afromontane forests are among the major natural forest types widely dispersed in the central, southeastern, eastern, northern, and southern highlands of Ethiopia (Friis et al., 2010, UN-REDD, 2017). This forest type has ecological significance, being the remnant forest in different parts of the country; it provides habitat for many endangered species and stores a large amount of carbon (Girma et al., 2014; UN-REDD, 2017; Gebeyehu et al., 2019). The forest also supports the livelihoods of many people by providing diverse forest products (Gobeze et al., 2009; Asfaw et al., 2013; Shiferaw et al., 2019). However, the potential of these forests has been impaired by severe anthropogenic disturbances, and the forests have been heavily deforested and degraded due to their location in areas suitable for settlement and agriculture (Lemenih & Bongers, 2011). Hence, these forests require management intervention, which could help to maintain their biodiversity, productivity, and sustainability (Teketay et al., 2010).

Sustainable forest management requires an accurate estimation of the important characteristics of the forest resources, i.e., stem density, basal area, the standing volume of wood, and biomass stock (Adekunle et al., 2013; Bettinger et al., 2016). This information is fundamental to determining the productivity of a forest and guiding forest management decisions (Husch et al., 2003; Akindele & LeMay, 2006; Adekunle et al., 2013). Quantifying the biomass stock of forests is also important for commercial uses (e.g., timber, fuel-wood, and fiber), for scientific studies of ecosystem productivity, energy, and nutrient flows, and for assessing the contribution of forests to the carbon cycle and climate change mitigation. Parresol (2001) stated that the biomass and volume of a tree are accurately estimated through regression analysis (allometric models). For this pur-

pose, the biomass and volume estimations of selected trees/shrubs were obtained through direct or indirect methods (i.e. tree harvesting, multiple height, and stem diameters measurements along the stem, weighing, and sub-sampling of tree components for laboratory-based moisture determination to convert fresh weight to dry weight) and related with one or more dimensions of a tree i.e. stem diameter and/or total height.

Stem volume and biomass assessment have global interest, especially in the context of the Kyoto Protocol rules and climate change agreements (Lindner & Karjalainen, 2007). Hence, developing countries involved with REDD+ (reducing emissions from deforestation and forest degradation) need to have a robust Measurement, Reporting, and Verification (MRV) system. Volume and biomass estimation models are a key element of the MRV system and enable us to properly assess the national wood, biomass, and carbon stocks. Despite this fact, information is scarce on stem wood volume and biomass stock in Afromontane forests in both Ethiopia and Africa in general; this is mainly due to the lack of locally developed biomass and volume estimation models. Developing a site-specific biomass model is a key element in the accurate estimation of forest biomass, carbon stock, and fluxes (Williams et al., 2008). Such information is gaining both economic and political currency in renewable energy development, carbon credit markets, and REDD + projects (Nath et al., 2019). Very few species-specific volume models (Pohjonen, 1991; Teshome, 2005; Berhe et al., 2013; Gereslassie et al., 2019; Tsega et al., 2019; Takenaka et al., 2020) and mixed and species-specific biomass models (Tesfaye et al., 2016; Solomon et al., 2017; Feyisa et al., 2018; Mokria et al., 2018; Abich et al., 2019; Daba & Soromessa, 2019; Tetemke et al., 2019) are available in Ethiopia. These models are developed either for single tree species or mixed species by using a very small number of trees and/or the sampling does not include the larger diameter size trees in the forest. Hence, precise estimates of the standing volume of wood and biomass stock are lacking in Ethiopia's various forests.

The limited availability of models in Ethiopia has led to the use of pantropical models, principally (Chave et al., 2014) and the general volume equation (v = d × h × f) where f = 0.5 (e.g., (Sisay et al., 2017)), to estimate tree biomass (Abere et al., 2017; Dibaba et al., 2019, Gebeyehu et al., 2019; Eshetu & Hailu, 2020) in different forests. The use of such a model often leads to biased biomass and volume estimates for particular species, forests, and sites because there are variations in wood density, tree allometry, form factor, and growthstage among species (Návar et al., 2002; Henry et al., 2011). Hence, it is vital to develop the site and species-specific models. However, given the great diversity of species and variability within species in tropical forests, various efforts have been made to develop mixed-species biomass and volume models (e.g., (Asrat et al., 2020a; Chave et al., 2014; Mugasha et al., 2016; Mokria et al., 2018)). However, very few efforts have been made in this aspect for Afromontane forests in Africa in general and Ethiopia in particular. As a result, our knowledge of the standing volume

of wood, biomass stocks, and carbon storage is limited for Afromontane forests. Therefore, the objective of this study was to develop mixed-species biomass and volume estimation model and accurately estimate the standing volume of wood, biomass, and carbon stock in the Chilimo dry Afromontane Forest in Central Ethiopia. In addition, we compared the predictive performance of our newly developed model with the previously developed pan tropical and other models. We believe that these models will be useful for conservation, REDD+ projects, and research on global environmental change in Afromontane forests across Africa.

2. Materials and Methods

2.1. Study Site Description

This study was conducted in the Chilimo forest, located 97 km west of Addis Ababa in central Ethiopia. It is geographically located at 38˚05'E to 38˚15'E and 9˚00'N to 10˚10'N longitude and latitude, at an altitudinal range of 2170 - 3054 m above sea level (Figure 1).

Chilimo forest currently covers a total area of 4500 ha. It is one of the few remnants of a dry Afromontane forest that once covered Ethiopia's Central Plateau. Soromessa & Kelbessa (2013) recorded 213 plant species in 83 families from this
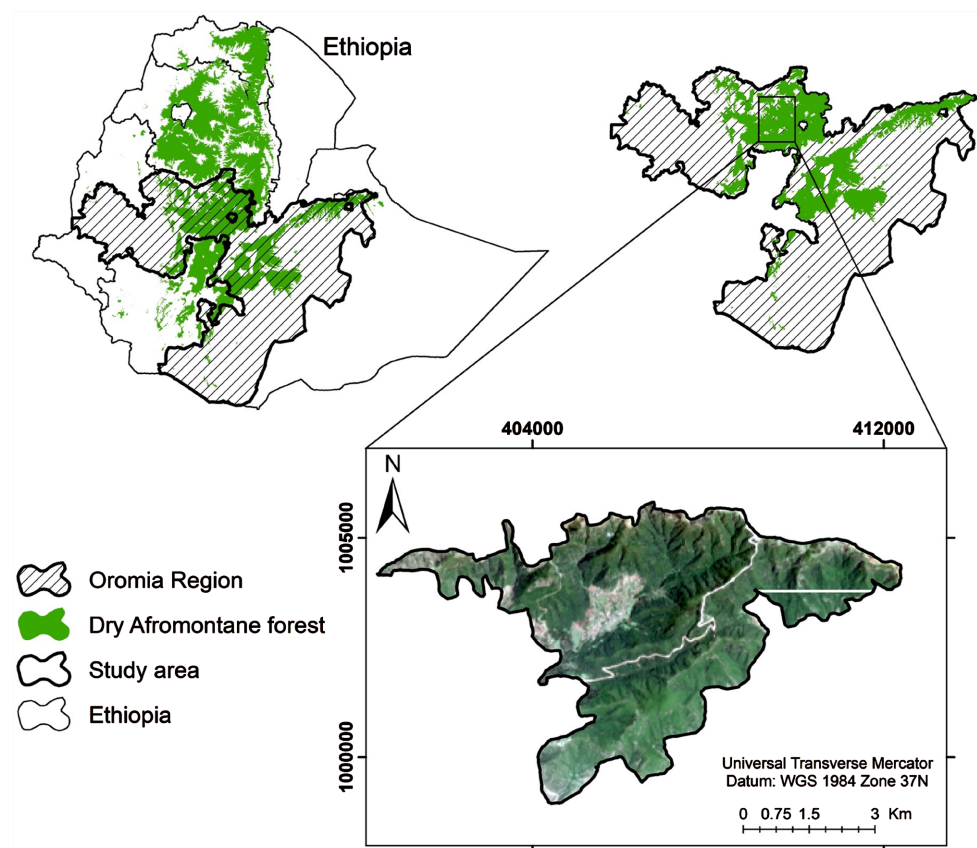
Figure 1. Map of the study area overlaid with the distribution map of dry Afromontane forests following Friis et al. (2010).

forest. The main species in the canopy layers are *Juniperus procera*, *Podocarpus falcatus*, *Prunus africana*, *Olea europaea* ssp. *cuspidata*, *Hagenia abyssinica*, *Apodytes dimidiata*, *Ficus spp.*, *Erythrina brucei*, and *Croton macrostachus* (Kassa et al., 2009; Soromessa & Kelbessa, 2013). In the past, the Chilimo forest was under state control. Since 1991, state control over the forest has weakened, and deforestation has increased significantly despite its designation as one of the National Forest Priority Areas (Kassa et al., 2009). Increasing timber extraction rates along with grazing and farming pressure radically reduced forest cover (Kassa et al., 2009). Currently, the forest is managed by local forest user groups organized as cooperatives under the participatory forest management schemes (Mohammed & Inoue, 2014).

2.2. Forest Inventory

We employed a systematic random sampling technique to collect vegetation data in February and March 2018. Overall, 161 sample plots (20 × 20 m) were established along the transect lines. The first transect was aligned parallel to the edge of the forest (20 m) and others were laid out systematically at 500 m intervals. The first plot was located randomly and the subsequent plots were established at 300 m intervals along the transect lines. The boundary of each plot was marked with pegs and/or plastic ropes. Then, the diameter at breast height (d) and the total height (h) of all trees with d ≥ 2.0 cm which falls within the plot boundary were measured using a diameter tape and Vertex IV ultrasonic hypsometer (Haglöf Sweden AB, Långsele, Sweden). A tree was judged to be within the plot when the center of the stem appeared to fall on or within the margins of the plot. Besides, the spatial location (latitude and longitude), elevation, and slope of each plot were measured using the Garmin GPS-72 receiver and Suunto Clinometer.

2.3. Tree Species Selection and Measurements

First, we selected seven dominant tree species (*Juniperus procera*, *Podocarpus falcatus*, *Allophylus abyssinicus*, *Olea africana* ssp. *cuspidata*, *Olinia rochetiana*, *Rhus glutinosa*, and *Scolopia theifolia*) based on the basal area information generated from the inventory data from the Chilimo forest. Second, representative sample trees were randomly chosen across the range of diameter sizes for the seven species among the fallen tree species during the asphalt road construction that passes through the Chilimo forest. Additional stem volume data were obtained from Tesfaye et al. (2016). The selected seven dominant tree species altogether contributed over 89% of the total basal area of the Chilimo forest.

A total of 194 trees were used to develop the stem volume and biomass model. The number of harvested trees was determined based on the relative abundance and diameter size distribution of each tree species. Hence, we sampled a larger number of trees from the abundant trees with a larger diameter size distribution

(e.g., *Juniperus procera* and *Podocarpus falcatus*) and a lower number of trees for the less abundant trees. Before felling, the diameters at the ground level, 0.3 m, 1.3 m, and the total height of the selected trees were measured. These measurements were used to calculate the stump volume (the part of the stem from ground level until 0.3 m). After felling, the stem was sectioned and the total length, and over bark diameters at the lower and upper part of each section were measured. The section volume was computed by using the Smalian formula whereas, the top section was computed using a cone formula (Burkhart & Tomé, 2012; West, 2015). The section volumes were summed up to estimate the total stem volume of each tree. The volume of branches and leaves was not considered in this study. The stem volume data were collected between February and March 2019. The wood densities (determined at 12% moisture content) of five tree species (*Allophylus abyssinicus*, *Olea Africana* ssp. *Cuspidata*, *Olinia rochetiana*, *Rhus glutinosa*, and *Scolopia theifolia*) recorded from the Chilimo forest were obtained from Tesfaye et al. (2016) and densities of *Juniperus procera* and *Podocarpus falcatus* were obtained from ICRAF's wood density database (Carsan et al., 2014). The stem biomass was calculated by multiplying the stem volume estimates by their basic wood densities following the procedures in Burkhart & Tomé (2012).

2.4. Model Development

The commonly used dendrometric variables i.e., diameter (d), height (h), and wood density (ρ) were used as independent predictor variables. We tested six volume and eight biomass equations (Table 1).

We selected the equations from the forestry literature based on their widespread use in Ethiopia and elsewhere (Berhe, 2009; Burkhart & Tomé, 2012; Picard et al., 2012; Mugasha et al., 2013; Gereslassie et al., 2019).

It must be noted that M1, M2, and M3 are the linear versions of the nonlinear volumes M4, M5, and M6, respectively. Similarly, among the biomass models, M1, M2, M3, and M4 are the linear versions of the nonlinear M5, M6, M7, and M8, respectively. Although the linear and nonlinear versions (e.g. M1 and M4 of the volume equations) are mathematically equivalent, they are not identical in the statistical sense (Parresol, 1999; Sileshi, 2014). As a result, the estimated parameters (e.g., slope) and biomass may slightly differ. Therefore, we compared the linear with the nonlinear versions because some authors use linear functions, while others apply nonlinear functions when developing biomass estimation models. We intended to see whether the linear functions significantly differ from their nonlinear versions in their performance.

Although 194 trees were initially sampled, one tree with a diameter of 98.0 cm consistently appeared as a leverage point across all models. Therefore, we excluded that tree from all analyses. Even then, we noted a variable number of outliers and leverage points depending on the model. Since the combined effect of outliers and leverage points can destabilize coefficients of models with multiple

Table 1. Volume and biomass models tested in this study.

Form	Models	Mathematical forms	References
Volume models			
Linear models	M1	$\ln(v) = \ln(\beta_0) + \beta_1 \ln(d) + \varepsilon$	Husch (1963)
	M2	$\ln(v) = \ln(\beta_0) + \beta_1 \ln(d^2 h) + \varepsilon$	Spurr (1952)
	M3	$\ln(v) = \ln(\beta_0) + \beta_1 \ln(d^2) + \beta_2 \ln(h) + \varepsilon$	Schumacher (1933)
Nonlinear models	M4	$v = \beta_0 * (d)^{\beta_1} * \varepsilon$	Husch (1963)
	M5	$v = \beta_0 * (d^2 h)^{\beta_1} * \varepsilon$	Spurr (1952)
	M6	$v = \beta_0 * (d^2)^{\beta_1} (h)^{\beta_2} * \varepsilon$	Schumacher (1933)
Biomass models			
Linear models	M7	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(d) + \varepsilon$	Husch (1963)
	M8	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(d^2 h) + \beta_2 \ln(\rho) + \varepsilon$	Spurr (1952)
	M9	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(d) + \beta_2 \ln(h) + \beta_3 \ln(\rho) + \varepsilon$	Schumacher (1933)
	M10	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(\rho d^2 h) + \varepsilon$	Chave et al. (2014)
Nonlinear models	M11	$b = \beta_0 * (d)^{\beta_1} * \varepsilon$	Husch (1963)
	M12	$b = \beta_0 * (d^2 h)^{\beta_1} (\rho)^{\beta_2} * \varepsilon$	Spurr (1952)
	M13	$b = \beta_0 * (\rho d^2 h)^{\beta_1} * \varepsilon$	Chave et al. (2014)
	M14	$b = \beta_0 * (d)^{\beta_1} (h)^{\beta_2} (\rho)^{\beta_3} * \varepsilon$	Schumacher (1933)

ln = natural logarithm, v = stem volume (m³), b = stem biomass (kg), h = total height (m), d = diameter at breast height (cm), and ρ = wood density (g cm³).

predictors, we used robust regression (Taskinen & Warton, 2013) in preference to ordinary least square (OLS) regression. The model fitting was done by *rlm* and *nlrob* function in the MASS and robust base package of R, respectively. These R functions fit models by iteratively re-weighted least squares (IRLS) method using the Tukey bisquare weighting method (Riazoshams et al., 2019). We compared the performance of the different models using model selection criteria and graphical analysis of residuals. Since linear models cannot be compared directly with nonlinear models, we conducted all model comparisons on the arithmetic scale. First, we back-transformed the predictions of linear models to original units to allow comparisons with our nonlinear models and other published equations. We used a correction factor (CF) to correct the systematic bias induced during the back-transformation of logarithmically transformed data (Chave et al., 2005; Sileshi, 2014). The CF is normally computed from the mean square of error (ε) as follows:

$$\text{CF} = \text{EXP}\left(\frac{\varepsilon^2}{2}\right) \tag{1}$$

Then we calculated various model selection criteria in the arithmetic domain to make the comparison of linear and nonlinear models straightforward. For this purpose, we chose the Nash and Sutcliffe efficiency factor (NSEF), the bias-corrected Akaike information criterion (AICc), the average systematic error (bias), and the root means square of error (RMSE). We did not include the R^2 due to its well-known limitations (Sileshi, 2014). Instead, we used the NSEF as its calculation is straightforward for both linear and nonlinear models. The NSEF formula is the same as the R^2 of linear regression but it is applied directly to the original biomass data and the predictions from any one of the models as follows:

$$\text{NSEF} = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum(y_i - \bar{y})^2} \tag{2}$$

where y_i is the observed (measured) value, $\hat{y}_i$ is the predicted value; $\bar{y}$ is the average of y_i. NSEF varies from $-\infty$ to 1; values close to 1 being the best while negative values indicate an unacceptable model performance.

Calculation of the AIC (Akaike, 1973) for models estimated using least square methods is tricky because AIC is originally formulated based on the negative log-likelihood from maximum likelihood estimation. Following (Gagné & Dayton, 2002; Chave et al., 2014), we calculated the AIC from the residual sum of squares (RSS) of the regression as follows:

$$\text{AIC} = n * \ln\left(\frac{\text{RSS}}{n}\right) + 2p \tag{3}$$

where n is the number of observations (sample size) and p is the number of model parameters. To correct for small sample sizes, we used the bias-corrected AIC (hereafter AIC_c) computed as:

$$\text{AIC}_c = \text{AIC} + \frac{2p(p+1)}{n-p-1} \tag{4}$$

Then, we computed the Akaike weights (AICw) from the AIC_c cohort of models as recommended by Johnson & Omland (2004). AICw indicates the probability that the model is the best among the set of candidate models, thus measuring the strength of evidence for each model. Therefore, we chose the model with AICw close to 1 as the best. For all models, the bias (%), MAPE (%), and RMSE (%) were calculated as follows in the arithmetic domain:

$$\text{Bias}(\%) = \frac{1}{R}\sum_{i=1}^{R}\frac{100}{n}\sum_{i=1}^{n}\frac{Y_i - \hat{Y}_i}{Y_i} \tag{5}$$

$$\text{MAPE}(\%) = \frac{1}{R}\sum_{i=1}^{R}\frac{100}{n}\sum_{i=1}^{n}\frac{\left|Y_i - \hat{Y}_i\right|}{Y_i} \tag{6}$$

$$\text{RMSE}(\%) = \frac{1}{R} \sum_{i=1}^{R} 100 \sqrt{\frac{1}{n} \sum_{i=1}^{n} \left(\frac{Y_i - \hat{Y}_i}{Y_i} \right)} \tag{7}$$

where R is the number of resampling (200), n is the number of trees per resampling r, and y_i and $\hat{y}_i$ are the observed and predicted biomass and volume values.

We also calculated a relative measure hereafter referred to as rRMSE% calculated as a ratio of RMSE to the mean of the predicted biomass and expressed in %, i.e., 100 * (RMSE/mean). This measure is sometimes called the coefficient of variation and is used for comparing models e.g., (Vonderach et al., 2018; Chianucci et al., 2020). The rRMSE % gives an estimate of the error in estimation as a percentage of the predicted mean biomass. Since the above criteria do not reveal problems inherent in the model specification (Sileshi, 2014), we conducted various model diagnostics including tests of normality, homoscedasticity of errors, and influence statistics (Table S1). We used the Shapiro-Wilk test to determine the normality of residuals. Test of normality and homogeneity alone are not adequate (Sileshi, 2014). Therefore, we conducted additional diagnostics to check whether certain observations have undue "influence" on the coefficients. There are two types of outliers, i.e. those in the response variable and outliers to the predictors are called leverage points (Taskinen & Warton, 2013). We used residual plots of standardized residuals to detect outliers against the explanatory variables to reveal patterns, and deemed values exceeding −2.0 or +2.0 as outliers that can cause serious heteroscedasticity. Since residual plots cannot reveal leverage points, we identified leverage points from the robust regression analysis (Table S1). We conducted a one-way analysis of variance (ANOVA) to test whether or not residuals from our best model vary with species. In linear models where two or more variables were included, we also checked the variance inflation factor (VIF) to assess the presence of multicollinearity between the predictor variables (Sileshi, 2014). In the case of nonlinear models, we checked for symmetry in estimated parameters using Hougaard's measure of skewness ($|g|$). It must be noted that nonlinear regression assumes that parameters are close to linear so that the uncertainty about the value of each parameter is symmetrical. A parameter with $g > 0.25$ is said to be noticeably skewed, and in such cases, alternative model parameterization is strongly advised (Hougaard, 1985).

2.5. Model Validation

In the analyses above, we have only examined the ability of various models to describe the data at hand, which is referred to as in-sample fit. This is sometimes confused with the predictive power of the model or its out-of-sample fit. However, models usually have a grossly inflated performance in-sample compared to their performance in follow-up studies (Ioannidis, 2008). The goodness of fit and model selection criteria also tend to better fit the sample data, especially when models are over-fitted (Sileshi, 2014). Therefore, we employed the Monte Carlo cross-validation technique to evaluate the biomass prediction performance of the models. The fits of the models were examined by randomly

splitting the data into two parts, with 70% for model development and 30% for model validation; this process was repeated 200 times. The commonly used model fit statistics (Equations (5)-(7)) were calculated during every repetition using the randomly selected data, and finally, the average values of the 200 repetitions were computed (Temesgen et al., 2014). A model that provides smaller values of these metrics was considered the best model. The final parameter estimates of the best model were obtained by fitting the model with the entire dataset. All of the statistical analyses were computed using the R software (R Core Team, 2013).

2.6. Comparison with Previously Published (Generic) Models

We compared the predictive performance of our biomass models with the previously published pan-tropical models and models from tropical dry forests in Africa (Table 2). We chose these models for comparison with our model because they are commonly used for biomass estimation in Ethiopia and elsewhere, see (Gebeyehu et al., 2019; Kendie et al., 2021; Siraj, 2019).

The usual criteria used for comparing local models have some limitations when comparing local with generic models. For example, R^2 is an inadequate criterion for comparing linear and nonlinear models because a nonlinear model does not have a true R^2 due to the absence of a true intercept. The RMSE is scale-dependent, and therefore, it does not help compare models in different formulations (e.g., linear vs. nonlinear). It is also hard to determine the magnitude of RMSE in the absence of a reference point. Hence, we used the rRMSE, MAPE (%), and NSEF (%) applied directly to the original data and the predictions from any one of the models.

2.7. Estimation of Stand-Level Basal Area, Volume, Biomass, and Carbon Stocks

The density (stem·ha^{-1}) and basal area (m^2·ha^{-1}) were calculated for each tree species. Each tree's stem volume and biomass were calculated using the newly developed volume (M2) and biomass model (M10) in this study. The belowground (root) biomass was estimated by using a 0.20% conversion factor of the

Table 2. Previously published models tested using our data set.

No	Mathematical forms	References
1.	$b = 0.112 * \left(\rho d^2 h \right)^{0.916}$	Chave et al. (2005)
2.	$b = 0.0673 * \left(\rho d^2 h \right)^{0.976}$	Chave et al. (2014)
4.	$b = 0.196 * \left(d \right)^{2.141} * \left(\rho \right)^{0.625}$	Tetemke et al. (2019)
3.	$\ln(b) = -1.134 + 1.969 * \ln(d) + 0.295 * \ln(h) + 1.185 * \ln(\rho)$	Djomo et al. (2016)

ln = natural logarithm, b = stem biomass (kg), h = total height (m), d = diameter at breast height (cm), and ρ = wood density (g cm^3).

stem biomass (MacDicken, 1997). The total biomass (the sum of the stem and root biomass) was converted into carbon by dividing the total biomass value by 2, following the procedures in Pearson et al. (2005).

3. Results

3.1. Harvested Tree Species

The 194 trees used here accounted for 7 dominant tree species accounting for 89% of the total basal area in the Chilimo forest (Table 3). The diameter, total height, and wood density ranged between 6.2 and 85.0 cm, 5.6 and 27.4 m, and 0.52 and 0.82 g·cm^{-3}, respectively. The majority of the tree species had diameters concentrated in a narrow range. For example, *Olea africana* ssp. *cuspidat*a, *Allophylus abyssinica*, *Olinia rochetiana*, *Rhus glutinosa*, and *Scolopia theifolia* had a diameter of less than 29 cm while *Juniperus procera* and *Podocarpus falcatus* had a diameter ranging between 11.6 and 85.0 cm. However, most of the tree species exhibited little variation in the wood density values (Table 3).

3.2. Volume Estimation Model

The parameter estimates, their corresponding standard errors, and the PRSE statistics of the evaluated volume models are given in Table 4. All parameters of the models were statistically significant at $\alpha = 0.001$ levels. The Monte-Carlo cross-validation statistics of the models are given in Table S4. Among the models, model 2 (M2) was the best model to predict the stem volume. This model produced the lowest RMSE, MAPE, and AICc and higher NSEF values. The observed and predicted stem biomass graphs using the evaluated models are shown in Figure S1. Among the models, M2 and M6 provided the closest prediction to the observed stem volume.

Table 3. Tree species used for model building and their wood density, diameter at breast height, and total height measurements.

No	Tree species	N	ρ	d (cm)		h (m)	
				Mean ± SD	Range	Mean ± SD	Range
1	Juniperus procera	89	0.58	34.3 ± 17.3	11.6 - 85.0	16.2 ± 5.3	6.8 - 27.4
2	Podocarpus falcatus	15	0.52	40.6 ± 15.4	20.0 - 64.0	19.2 ± 4.9	11 - 25.6
3	Olea africana	20	0.82	14.5 ± 5.9	6.3 - 28.8	10.6 ± 2.1	5.9 - 14.5
4	Allophylus abyssinicus	15	0.59	11.3 ± 3.9	6.4 - 21.3	10.6 ± 3.1	7.0 - 17.0
5	Olinia rochetiana	20	0.66	14.9 ± 6.7	6.2 - 27.5	12.6 ± 2.9	7.3 - 19.4
6	Rhus glutinosa	15	0.61	15.6 ± 4.9	9.0 - 23.5	11.3 ± 3.0	6.0 - 17.4
7	Scolopia theifolia	20	0.64	11.8 ± 4.1	6.4 - 22.0	8.2 ± 1.9	5.6 - 13.0

SD = standard deviation, N = number of sample trees, d = diameter at breast height (cm), h = total height (cm), ρ = wood density (g·cm^{-3}), and Range = minimum and maximum values.

Table 4. Parameter estimates, standard errors (in parenthesis), and PRSE statistics for the evaluated volume estimation models.
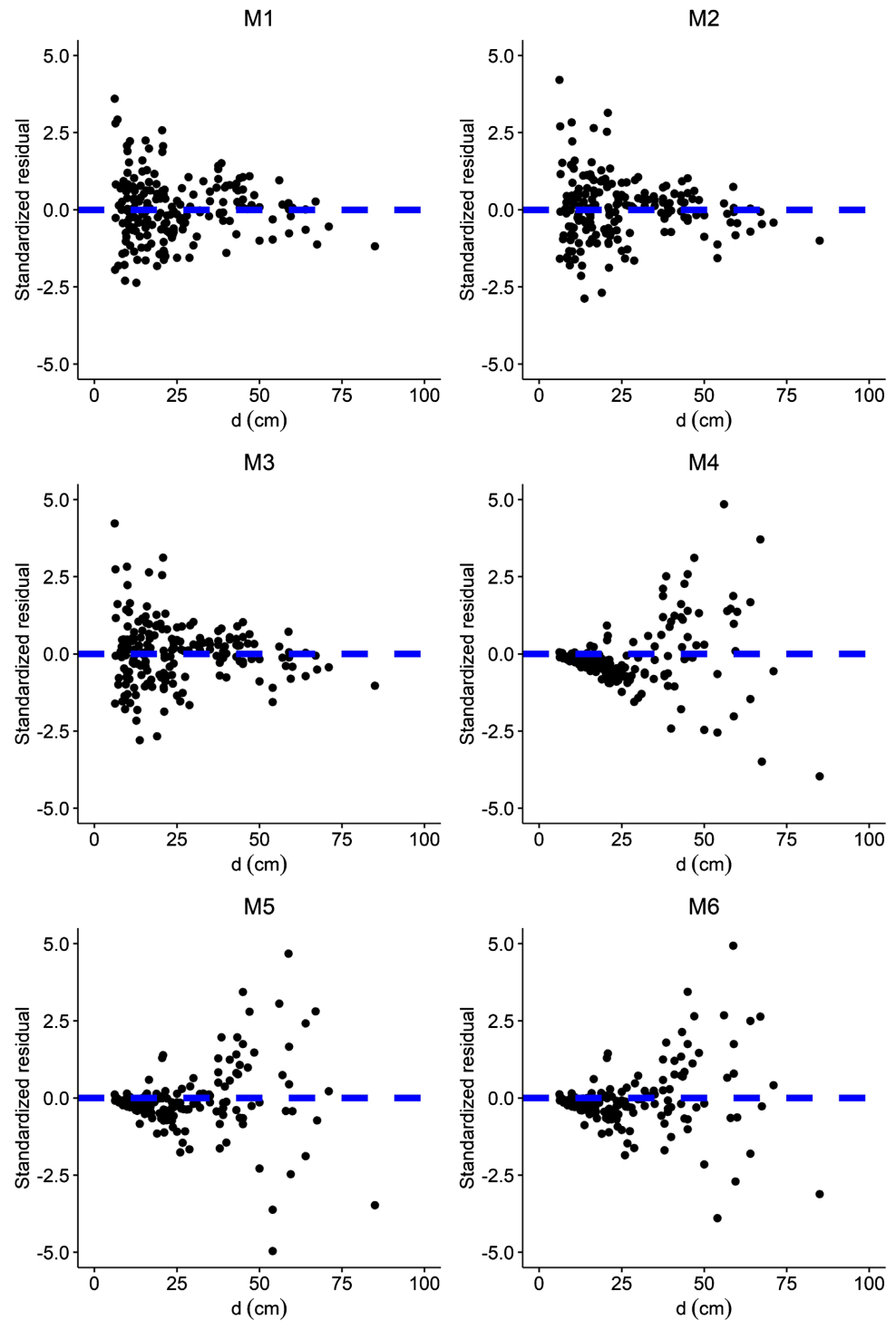
Models	Estimated parameters			PRSE		
	β_0	β_1	β_2	β_0	β_1	β_2
Linear models						
M1	−8.907 (−0.112)	2.385 (−0.036)		1.25	1.5	
M2	**−9.909** **(−0.095)**	**0.954** **(−0.011)**		**0.96**	**1.12**	
M3	−9.883 (−0.127)	0.962 (−0.026)	0.925 (−0.090)	1.29	2.72	9.7
Nonlinear models						
M4	0.0015 (0.000)	1.751 (−0.045)		18.15	2.55	
M5	0.0002 (0.000)	0.845 (−0.014)		15.09	1.6	
M6	0.0001 (0.000)	0.827 (−0.019)	0.939 (−0.068)	18.02	2.35	7.28

The best fit model is given in bold.

The residual graphs of the evaluated models are shown in Figure 2. The residuals of linear models were randomly scattered around zero lines for all fitted values, while the residuals of nonlinear models followed a funnel shape distribution indicating non-constant variance. Furthermore, the nonlinear models tended to have more outliers than the linear models and the parameter "β_0" in all nonlinear models was also significantly skewed (Table S1 and Table S2). Taking all these into consideration, we selected M2 rather than the non-linear models for volume estimation. ANOVA did not reveal significant variation with species in residuals from M2.

3.3. Stand Characteristics and Biomass Estimation at Chilimo Forest

The number of trees, basal area, and stem biomass of trees in the Chilimo dry Afromontane forest is presented in Table 5. The average standing volume of wood was 303.0 m³·ha⁻¹. Overall, *Podocarpus falcatus* (43.5%), *Juniperus procera* (38.1%), *Schefflera volkensii* (7.5%), and *Schefflera abyssinica* (2.2%) were the tree species that exhibited the largest stem volume wood. Each of these species also comprised 49.1%, 39.3%, 6.2%, and 2.1% of the total stem biomass. The measured stem biomass values were highly variable across the plots, with an average value of 283.8 Mg·ha⁻¹. The estimated carbon stocks also varied between 15.3 and 989.4 Mg·ha⁻¹, with a mean value of 170.3 Mg·ha⁻¹ in the Chilimo forest.

Figure 2. Residual graphs of the evaluated volume models.

3.4. Biomass Estimation Model

The parameter estimates, their corresponding standard errors, and the PRSE statistics of the evaluated models are given in Table 6. All parameters of the nonlinear models were significantly different from zero (p < 0.001) except parameters β_2 and β_3 of M8 and M9, which were not. The goodness-of-fit statistics based on

Table 5. Summary of forest inventory results, estimated stem volume (M2), biomass (M10), and carbon stocks in the Chilimo dry Afromontane forest.

| Stand characteristics	Unit	Mean	Minimum	Maximum	SD
Stand density	stems·ha^{-1}	631.5	25.0	2600.0	455.3
Basal area	m^2·ha^{-1}	24.4	1.5	100.9	15.1
Stem volume in the forest	m^3 ha^{-1}	303.0	7.5	1592.0	312.8
Stem biomass	Mg·ha^{-1}	283.8	25.5	1649.0	298.9
Belowground biomass	Mg·ha^{-1}	56.8	5.1	329.8	59.8
Total biomass	Mg·ha^{-1}	340.6	30.63	1978.8	358.7
Carbon stock	Mg·ha^{-1}	170.3	15.3	989.4	179.4

Table 6. Parameter estimates, standard errors (in parentheses), and PRSE statistics for the evaluated biomass models.

Models	Estimated parameters				PRSE			
	β_0	β_1	β_2	β_3	β_0	β_1	β_2	β_3
Linear models								
M7	−2.238 (−0.107)	2.301 (−0.034)			4.8	1.5		
M8	−3.127 (−0.093)	0.929 (−0.011)	0.278* (−0.155)		3	1.2	55.9	
M9	−3.142 (−0.123)	1.847 (−0.051)	0.945 (−0.083)	0.274* (−0.157)	3.9	2.8	8.8	57.2
M10	**−2.983 (−0.092)**	**0.949 (−0.011)**			**3.1**	**1.2**		
Nonlinear models								
M11	0.913 (−0.162)	1.744 (−0.044)			17.8	2.5		
M12	0.123 (−0.020)	0.847 (−0.014)	0.593 (−0.185)		16.6	1.6	31.2	
M13	0.176 (−0.045)	1.355 (−0.048)	1.067 (−0.100)	0.107 (−0.266)	14.2	1.6	25.8	3.5
M14	0.138 (−0.020)	0.849 (−0.013)			9.4	248.6		

*Indicates non-significant coefficients at α = 0.05. The best fit model is given in bold.

cross-validation of the evaluated models are given in Table S4. The cross-validation statistics indicated that M9 from the linear models and M12 from the nonlinear models were the best for biomass estimation. However, the PRSE statistics have

shown that some of the parameters of M8, M9, M12, M13, and M14 had PRSE > 25%. The observed and predicted stem biomass graphs using the evaluated models are shown in Figure 3.
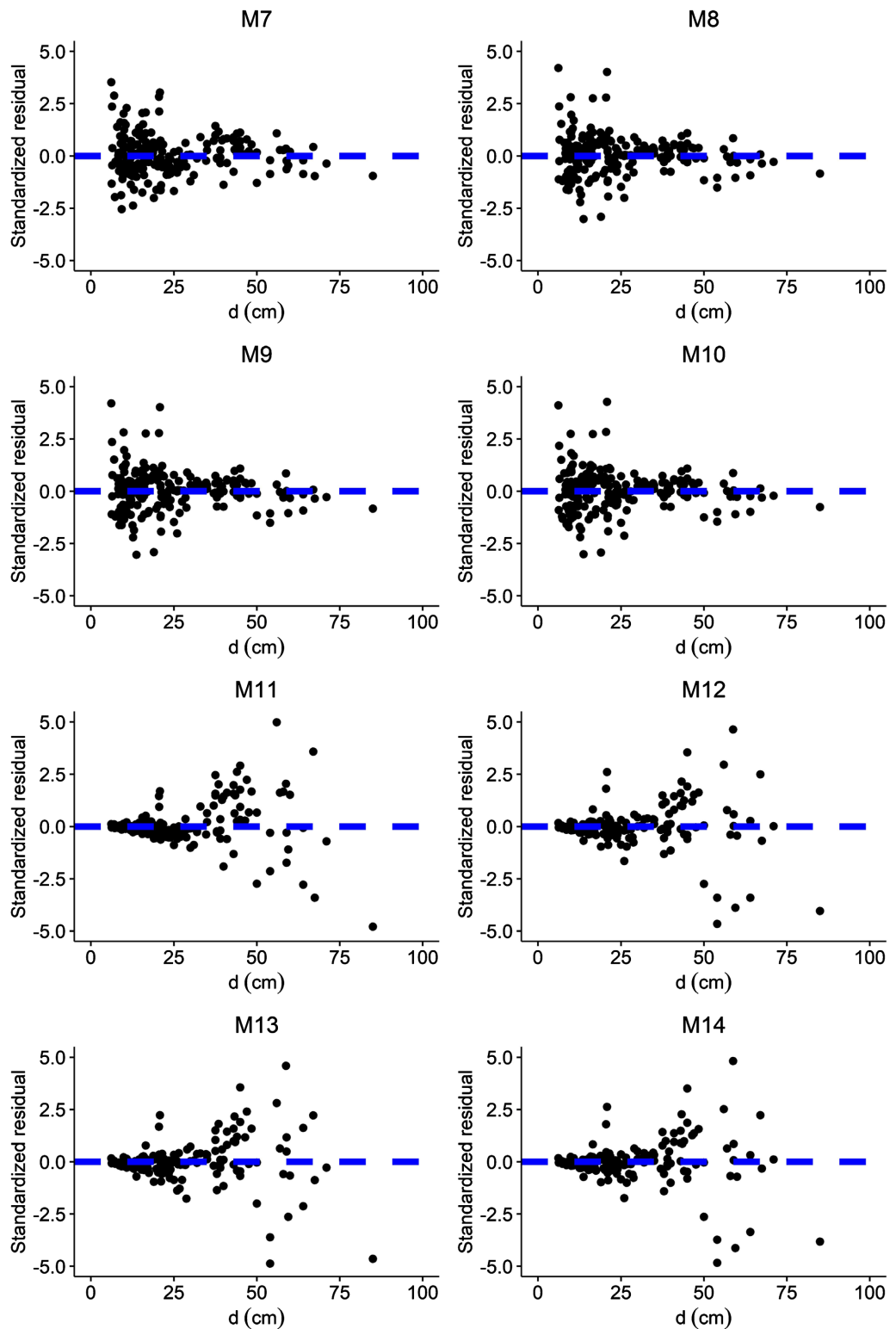

Figure 3. Residual graphs of the evaluated biomass models.

Visual analysis of the graphs shows that except for M7 and M11, the remaining models overestimated the stem biomass (**Figure S2**). However, M10 provides the closest stem biomass prediction to the remaining biomass models.

The residual graphs of the evaluated models are shown in **Figure 3**. The residuals of linear models were randomly scattered around zero lines for all fitted values, while the residuals of nonlinear models followed a funnel shape distribution indicating non-constant variance. Furthermore, the parameter "β_0" in all nonlinear models was significantly skewed, and the nonlinear models tended to have more outliers than the linear models (**Table S1** and **Table S2**). Moreover, the assumption of multicollinearity was not violated, since none of the explanatory variables of the evaluated models showed a VIF value higher than 5. Taking all these into consideration, we selected M10 as the best model for stem biomass estimation.

3.5. Comparison of Our Models with Published Biomass Models

The stem biomass prediction and the associated fit statistics of the evaluated models are given in **Table S5**. The models by Chave et al. (2005, 2014) systematically overestimated stem biomass, especially for trees with $d > 25$ cm (**Figure 4**), which is evidenced by systematically declining residuals (**Figure 5**). Conversely, the model developed by Tetemke et al. (2019) was less accurate and severely underestimated the stem biomass. Our best model (M10) and the model developed by Djomo showed the highest prediction performance (**Table S5** and **Figure 4**). However, the model by Djomo et al. (2016) was developed for small-diameter trees ($d < 32$ cm) and is not consistent for larger trees. This indicated that
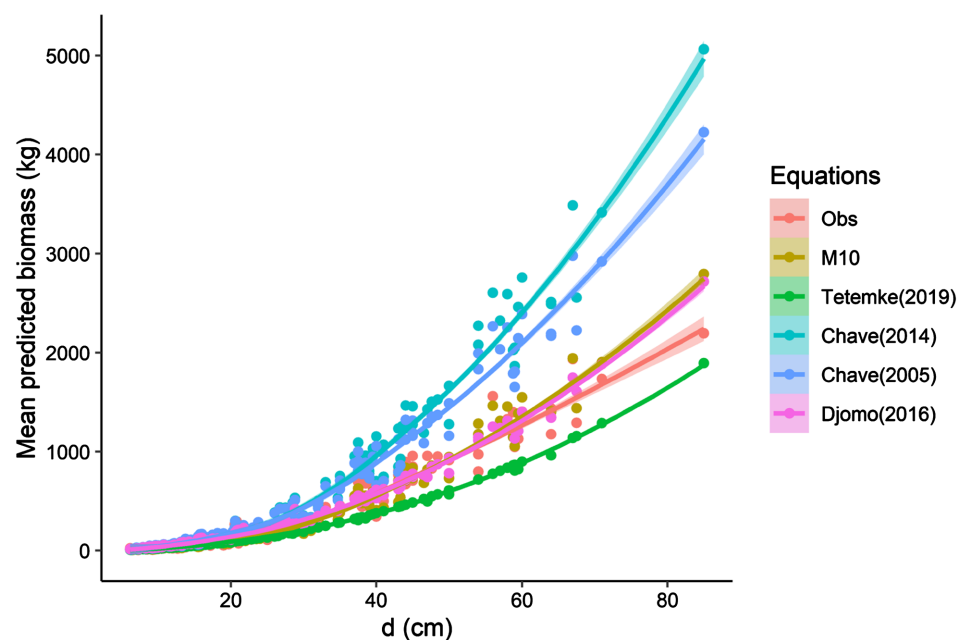
Figure 4. Comparison of biomass prediction performance by our best model and previously published biomass models. The dots in different colors represent the biomass prediction by each model and the lines represent the best fit line.
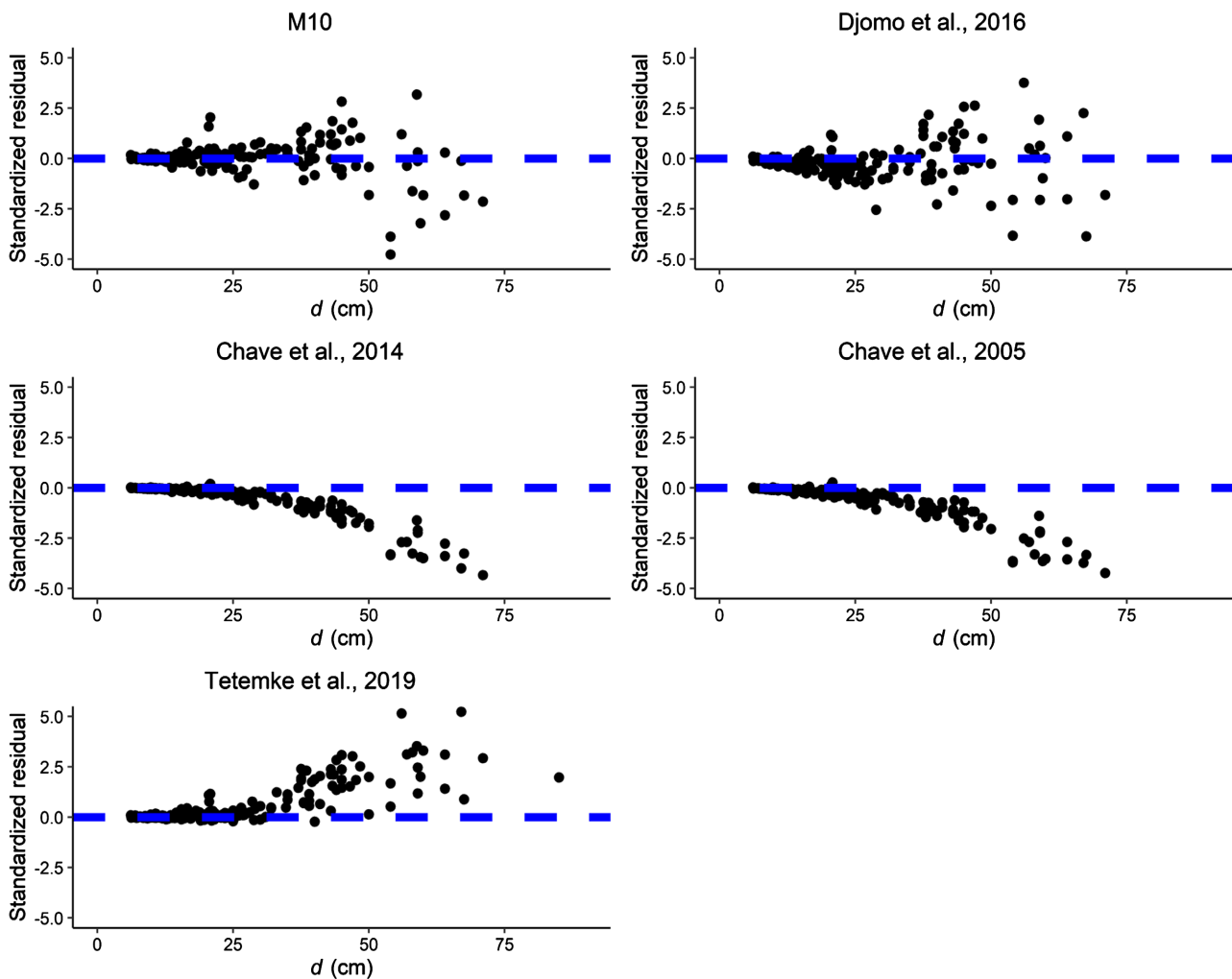
Figure 5. Comparison of the residuals plots of our best models with the generic biomass models using our dataset.

our best model (M10) is the most appropriate model to accurately estimate the stem biomass of trees.

4. Discussions

Very few studies have attempted to develop stem volume equations in Ethiopia (Pohjonen, 1991; Teshome, 2005; Berhe et al., 2013; Gereslassie et al., 2019; Tsega et al., 2019; Takenaka et al., 2020). In this study, we developed mixed-species allometric equations using 193 individuals from seven dominant tree species from the Chilimo forest in central Ethiopia. The selected trees contributed over 89% of the total basal area of the forest. The number and diameter size range of the sampled trees used in the present study were relatively higher than in previous biomass model development efforts in Ethiopia. For instance, Tetemke et al. (2019) used 86 trees and developed a mixed-species model for dry Afromontane forests in Northern Ethiopia. Similarly, Mokria et al. (2018) and Asrat et al. (2020a) sampled 84 and 63 trees and developed biomass models for exclosures and dry Afromontane forests in north-western and south-central Ethiopia, re-

spectively.

The evaluated volume models exhibited varied stem volume prediction performance (Table S4). The dbh-only model had the highest RMSE and MAPE and the lowest NSEF values, both in the linear and nonlinear forms. This indicates that diameter alone is not a sufficient predictor for stem volume estimation. The addition of height improved the prediction performance of the model by reducing the RMSE and MAPE by 11% and 5%, respectively. This is consistent with the findings of (e.g., (Chave et al., 2005; Mate et al., 2015; Goussanou et al., 2016)), who reported that the inclusion of height improved the predictive performance of a model. On the contrary, various studies (e.g., (Asrat et al., 2020b; Segura & Kanninen, 2005; Mugasha et al., 2016)) have argued that the dbh-only model outperformed a volume model with height and dbh. This is mainly attributed to the difficulty of height measurement in a closed canopy tropical forest due to the complex crown form and stand condition (Sharma & Parton, 2007). In this study, the combined variable model (M2), which incorporates diameter and height, becomes the best volume model. The predictor variables of this model explained over 95% of the variances in the stem volume. Similarly, Pohjonen (1991) reported that a combined variable model (d and h) provided the best stem volume prediction with lower error (10% - 12%) for the *Juniperus procera* tree from the Menagesha Suba forest in Ethiopia. A combined variable function has been considered the most appropriate and preferred function for predicting the total stem volume of trees (Burkhart & Tomé, 2012). This is because the stem form of a tree is better explained by a combination of height and diameter than by height or diameter, alone (e.g. (Husch et al., 2003)).

Very few tree volume estimation models have been found in Ethiopia (Pohjonen, 1991; Teshome, 2005; Gereslassie et al., 2019; Tsega et al., 2019; Takenaka et al., 2020). Most of the existing models were developed for single tree species mainly from pure plantation stands of Cupressus lusitanica, Juniperus procera, and Eucalyptus globulus. This study reported a mixed-species volume model developed using 193 individuals from seven tree species from the Chilimo dry Afromontane forest. The newly developed mixed-species volume model will help to accurately estimate the standing volume of wood and ensure sustainable management efforts in dry Afromontane forests in Ethiopia. Generally, there is a high demand for wood in Ethiopia, and the country is currently importing a large amount of wood to satisfy national demand. This enables the country to allocate a large amount of hard currency to import processed wood (MEFCC, 2018). However, there is a huge amount of wood in the natural forests that can satisfy the increasing wood demand in Ethiopia (MEFCC, 2018). Accurate estimation of the standing volume of wood from the natural forests in Ethiopia is constrained by the lack of site-specific volume models. Using our newly developed stem volume model, we noted that on average, 303.0 m³·ha⁻¹ volume of wood is found in the Chilimo forest. The observed volume of wood is higher than the volume estimated from dry Afromontane forests in the Amhara region (Sisay et

al., 2017), Miombo woodlands in Tanzania (Luoga et al., 2002), moist tropical forests in Nigeria (Lowe, 1997), and closed tropical broadleaf forests (Brown et al., 1989) (Table S3). This implies that a large amount of wood is available in the Chilimo forest, which can be used under a sustainable forest management scheme. Additionally, the domestic wood production from the Afromontane forest will enable the country to save the hard currency allocated to import wood and use it for other purposes. However, care should be taken to enhance the regeneration of the harvested trees, minimize damage during harvesting, and develop locally applied logging regulations (i.e., determine minimum felling diameter, annual allowable cut, and minimum impact harvesting techniques) before allowing logging from Chilimo forest. The observed variation in stand volume might be related to the differences in the stocking, basal area, tree allometry, and disturbance level among the forests. In our study, volume data is derived from the main stem of trees (branch wood volume is not accounted for), whereas in the other studies, the total volume of trees was reported. The mean density (631.5 stems·ha^{-1}) and basal area (24.4 m^2·ha^{-1}) in our study area were higher than the findings from Afromontane forests in the Amhara region (580 stems·ha^{-1}) and Miombo woodlands in Tanzania (347.6 stems·ha^{-1} and 9.8 m^2·ha^{-1}). On the other hand, the Chilimo forest is one of the community-managed forests, and most trees are concentrated in the lower and medium diameter size class (97% are < 60 cm diameter class), which indicates that the forest is regenerating and recovering from the past disturbances. It is well known that undisturbed forests with many trees accumulate more volume than disturbed forests.

Biomass models are usually developed by adopting direct and indirect methods. The direct method involves felling trees and weighting, whereas the indirect method requires species-specific volume, wood density, and BEF information (Picard et al., 2015). It is well known that tree biomass can be accurately determined by the direct weighting method. However, this method is time-consuming and expensive (Husch et al., 2003). In this study, we determined the stem biomass by multiplying each tree's volume and the respective wood density following the procedures in Burkhart & Tomé (2012). This is mainly related to the shortage of time to harvest and collect the data from the study area. It is quite obvious that uncertainty in stem biomass estimation might occur for such computations compared to the direct weighting method. Despite this fact, the biomass model based on dbh alone has shown lower efficiency compared with multiple covariate models (Table 5). A model with one predictor variable (dbh-based model) has shown poor prediction performance as evidenced by larger RMSE (37%) and MAPE (24%) values (Table S4). The addition of height and wood density improved the biomass prediction performance of the model by reducing the RMSE by 9% and MAPE by 5%. This indicates that height and wood density enabled the capture of more variability in stem biomass from the sampled trees (Chave et al., 2014). Although the cross-validation statistics show that M9 and M12 are the best models, the PRSE statistics revealed that some pa-

rameters of M8, M9, M12, M13, and M14 had PRSE > 25%, and parameters β_2 and β_3 of M8 and M9 were not significantly different from zero. In line with this, Sileshi (2014) indicated that a coefficient estimate of a model is unreliable if PRSE is greater than 25%. Hence, these models cannot be reliably used for biomass prediction purposes. Accordingly, we selected the combined variable model (M10) which comprised diameter (d), height (h), and wood density (ρ) for biomass estimation. This model explained over 96% of the variation in the stem biomass measurements. This is consistent with various studies e.g., (Chave et al., 2014) which reported that a combined variable model provided better biomass prediction than the other models.

The biomass estimated in this study (340.6 Mg·ha^{-1}) was less than the biomass estimates from the South African Mistbelt forest (Mensah et al., 2016) and closed-canopy tropical forests in 12 countries in Africa (Lewis et al., 2013). However, it was comparatively higher than the estimates from the moist Afromontane forest in Ethiopia (Wood et al., 2019), the tropical rain forest in Costa Rica (Clark & Clark, 2000), the Montane forest in Congo (Imani et al., 2017), and Mata Atlantic forest in Brazil (Alves et al., 2010) (Table S3). Similarly, the carbon stock (170.3 Mg C·ha^{-1}) estimates in this study were higher than the estimates from the humid forest in Congo (Xu et al., 2017) and Montane forest in Tanzania (Willcock et al., 2014), but lower than the estimates from moist Afromontane forest in Ethiopia (Mewded & Lemessa, 2020), South African Mistbelt forest (Mensah et al., 2016), tropical rainforest in Gabon (Goïta et al., 2019), Brazilian Amazonia forest (Lima et al., 2012), and Montane rainforest (Munishi & Shear, 2004) in Tanzania. The observed variation might be related to the difference in the models used to estimate the biomass, the disturbance level, the species composition, and the differences in the number of larger diameter trees, which constituted a significant amount of biomass as evidenced by the findings in moist forests across the tropics (Slik et al., 2013). Differences in biomass estimates for dry and moist tropical forests have been attributed to the use of different allometric equation forms (e.g., (Poorter et al., 2016)). The forest structure also showed a larger number of trees in the lower and middle diameter classes, which indicates that the forest was in a growth stage. Overall, the Chilimo forest had a substantial amount of estimated stem biomass and carbon stocks compared with the estimates from other tropical forests in Africa, which reveals the importance of dry Afromontane forests for climate change mitigation through carbon sequestration.

Compared with our newly developed model, the mixed-species equation developed by (Tetemke et al., 2019) severely underestimated the stem biomass of trees in the present study (Table S5). On the other hand, the generic pan-tropical models consistently overestimated the stem biomass of trees above $d \geq 30$ cm (Table S5 and Figure 5). Given the importance of large trees in the carbon budget, the biomass in large trees must be accurately estimated. However, the generic pan-tropical models were not able to predict biomass for the larger trees; this implies that the generic pan-tropical models are inferior to our mod-

els. This is consistent with the previous studies that reported that the model tended to overestimate tree biomass compared with locally developed models (Djomo et al., 2010; Van Breugel et al., 2011; Ngomanda et al., 2014). The possible explanation could be the difference in wood density range, tree allometry (diameter and height range), tree species composition, site quality, and climatic condition, which affect the efficiency of the compared models. For example, the database used to develop the model in (Chave et al., 2014) showed that the tree species had a wood density ranging between 0.09 and 1.12 g·cm^3, a diameter between 5 and 122 cm, and a total height between 1.2 and 70.7 m, whereas in this study, the database comprised relatively lower wood density values ranging between 0.52 and 0.82 g·cm^3, a diameter between 6.2 and 85.0 cm, and total height between 5.6 and 27.4 m. These variations could be the possible source of the uncertainty among the models used to accurately predict the stem biomass of trees. Despite this fact, the Chave equation (Chave et al., 2014) remains the commonly used model, submitted to the UNFCC and various local studies, for calculating the biomass and CO_2 emission levels from Ethiopian forests (Girma et al., 2014; Girma et al., 2014; UN-REDD, 2017; Solomon et al., 2018; Gebeyehu et al., 2019; Siraj, 2019). In this study, we noted that the newly developed mixed-species model could accurately estimate the stem biomass compared to the frequently used pan-tropical and local models. Hence, we recommend the use of these models in the Chilimo dry Afromontane forest as well as other similar Afromontane forests elsewhere. However, caution should be taken to not use these models in a forest comprising different tree species, tree diameter size ranges, and climatic conditions than those in the dry Afromontane Forest considered in this study.

This study presents a new approach to estimating the stem volume and biomass from the Chilimo dry Afromontane forest; we consider this an important decision support tool for the management of forests in Ethiopia. This approach enables the government or forest owners to obtain accurate information on the stand-level standing stock of wood, stem wood biomass and make utilization plans. However, this study has some limitations that a subsequent study could improve. Due to the short data collection period (as a result of road construction), we could not collect the branch and foliage data and did not use the direct weighting method to estimate the biomass of tree components. Furthermore, wood density information did not include bark density, which could be a possible source of bias in biomass estimation. Hence, we recommend including this critical component of the tree and updating the equations in future efforts.

5. Conclusion

The lack of a biomass and volume equation is a major bottleneck hindering the national carbon stock estimation endeavors and management of natural forests in Ethiopia. The newly developed mixed-species equations can be used to accurately quantify the standing volume of wood and biomass stock and enable forest managers to develop appropriate management strategies for dry Afromontane

forests. This study demonstrated that a combined variable model that includes diameter, height, and wood density was the best model for stem biomass and volume estimation. The frequently used pan-tropical models systematically over-estimated stem biomass for larger trees and should not be used for biomass estimation in the present study area. This study also suggested that the Chilimo Afromontane forest has a substantial amount of biomass and carbon stocks compared with the estimates from other tropical forests in Africa. This high-lights the importance of the Afromontane forest for climate change mitigation and the carbon market. Considering the limitations of this study, we recommend further research, as well as developing tapper and height-diameter equations for trees from Dry Afromontane forests.

Acknowledgments

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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Supplementary Materials

Table S1. Model diagnostics: significance (*P*) of Shapiro-Wilk test (PSW), outliers (%), leverage points (%).

Equations	Code	Mathematical form	PSW	Outliers (%)	Leverage (%)
Volume	M1	$\ln(v) = \ln(\beta_0) + \beta_1 \ln(d) + \varepsilon$	0.8177	1.03	1.03
	M2	$\ln(v) = \ln(\beta_0) + \beta_1 \ln(d^2 h) + \varepsilon$	0.0184	2.58	1.03
	M3	$\ln(v) = \ln(\beta_0) + \beta_1 \ln(d^2) + \beta_2 \ln(h) + \varepsilon$	0.0750	2.58	1.55
	M4	$v = \beta_0 * (d)^{\beta_1} * \varepsilon$	<0.0001	5.15	
	M5	$v = \beta_0 * (d^2 h)^{\beta_1} * \varepsilon$	<0.0001	2.58	
	M6	$v = \beta_0 * (d^2)^{\beta_1} (h)^{\beta_2} * \varepsilon$	<0.0001	2.58	
Biomass	M7	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(d) + \varepsilon$	0.6697	1.55	1.03
	M8	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(d^2 h) + \beta_2 \ln(\rho) + \varepsilon$	0.0917	4.12	18.04
	M9	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(d) + \beta_2 \ln(h) + \beta_3 \ln(\rho) + \varepsilon$	0.0194	3.61	13.92
	M10	$\ln(b) = \ln(\beta_0) + \beta_1 \ln(\rho d^2 h) + \varepsilon$	0.0690	2.58	1.03
	M11	$b = \beta_0 * (d)^{\beta_1}$	<0.0001	4.64	
	M12	$b = \beta_0 * (d^2 h)^{\beta_1} (\rho)^{\beta_2}$	<0.0001	2.06	
	M13	$b = \beta_0 * (\rho d^2 h)^{\beta_1}$	<0.0001	2.06	
	M14	$b = \beta_0 * (d)^{\beta_1} (h)^{\beta_2} (\rho)^{\beta_3}$	<0.0001	5.15	
	Chave2005		NA	4.64	
	Chave2014		NA	3.61	
	Djomo2016		NA	1.55	
	Tetemke2018		NA	6.19	

Table S2. Skewness in the nonlinear parameter estimates. Values in bold are considerably skewed according to Hougaard's measure of skewness (|g|).

Models	Parameter	Estimate	95% Confidence limits		Skewness (|g|).
			Lower	Upper	
Volume					
M4	β_0	0.0006	0.0004	0.0008	0.460
	β_1	2.0028	1.9186	2.0870	0.046
M5	β_0	0.0002	0.0001	0.0002	0.403
	β_1	0.8459	0.8194	0.8723	0.040

Continued

M6	β_0	0.0001	0.0001	0.0002	0.476
	β_1	0.8277	0.7897	0.8656	0.005
	β_2	0.9334	0.7996	1.0673	0.020
Biomass					
M11	β_0	0.3718	0.2467	0.4970	0.457
	β_1	1.9830	1.8992	2.0667	0.047
M12	β_0	0.1298	0.0880	0.1716	0.428
	β_1	0.8453	0.8185	0.8722	0.033
	β_2	0.6588	0.2948	1.0227	−0.008
M13	β_0	0.1403	0.1012	0.1795	0.381
	β_1	0.8478	0.8213	0.8742	0.039
M14	β_0	0.1173	0.0743	0.1602	0.491
	β_1	1.6583	1.5817	1.7349	0.003
	β_2	0.9246	0.7884	1.0608	0.018
	β_3	0.6828	0.3165	1.0492	−0.006

Table S3. Comparison of the estimated stem volume ($m^3 \cdot ha^{-1}$), biomass ($Mg \cdot ha^{-1}$), and carbon stock ($Mg \cdot ha^{-1}$) in the Chilimo forest with other tropical forests.

Variables	Site	Mean	References
Volume	Afromontane forest Ethiopia	28.9 - 92.4	Sisay et al., 2017
	Miombo woodlands in Tanzania	47.0	Luoga et al., 2002
	Closed tropical broadleaf forest	22.5 - 122.3	Brown et al., 1989
	Dense forests in India	469.4	Chhabra et al.,2002
	Moist tropical forest in Nigeria	220.0	Lowe 1997
Biomass	Rain forest in Costa Rica	186.0	Clark and Clark 2000
	Brazilian Atlantic forest	263.0	Alves et al., 2010
	Montane forest in Congo	290.0	Imani et al., 2017
	Closed-canopy forests in Africa	395.7	Lewis et al., 2013
	Central Amazonia forest	327.8	Castilho et al., 2006
	South African Mistbelt forest	358.1	Mensah et al., 2016
Carbon	Humid forest in Congo	139.9	Xu et al., 2017
	Montane forest in Tanzania	130.0	Wilcock et al., 2014
	Primary forest in Indonesia	175.0	Stas 2014
	South African Mistbelt forest	179.0	Mensah et al., 2016
	Tropical rainforest in Gabon	223.0	Goïta et al., 2019
	Brazilian Amazonia forest	253.0	Lima et al., 2012
	Moist Afromontane forest Ethiopia	384.4	Mewded and Lemessa 2019
	Montane rainforest in Tanzania	427.0	Munishi and Shear 2004

Table S4. Model comparison and selection based on Monte-Carlo cross-validation statistics.

Models	No	Bias (Kg)	RMSE (%)	MAPE (%)	NSEF (%)	AICc	AICw	CF
Volume models								
Linear	M1	0.006	39.046	23.929	92.183	−380.1	0.0	1.004
	M2	−0.008	27.883	18.988	95.985	−473.8	1.0	1.001
	M3	−0.007	28.285	19.125	95.862	−469.5	0.2	1.001
Nonlinear	M4	−0.005	38.104	29.721	92.609	−598.9	0.0	NA
	M5	−0.004	24.007	25.887	97.086	−627.6	1.0	NA
	M6	−0.004	24.045	25.751	97.058	−607.7	0.0	NA
Biomass models								
Linear	M7	6.058	36.556	23.753	92.985	1807.0	0.0	1.003
	M8	−2.153	26.243	18.389	96.310	1692.7	0.0	1.001
	M9	−2.185	26.344	18.654	96.285	1683.6	1.0	1.001
	M10	−2.831	27.110	18.895	96.050	1699.4	0.0	1.001
Nonlinear	M11	2.302	36.001	29.302	93.190	1421.9	0.0	NA
	M12	−1.361	23.820	22.357	96.998	1273.6	0.6	NA
	M13	−2.160	23.947	24.686	96.970	1280.5	0.4	NA
	M14	−1.859	24.144	22.471	96.894	1313.1	0.0	NA

Note: figures in bold represent the best fit volume and biomass models.

Table S5. Comparison of stem biomass prediction by our best model and previously published generic pan-tropical biomass models using our dataset.

Types	Models	Observed (kg)	Predicted (Kg)	Bias (%)	rRMSE (%)	MAPE (%)
Our best model	M10	294.87	299.01	−1.38	27.16	18.72
Generic models	Chave et al. (2005)	294.87	473.32	−37.70	70.39	73.77
	Chave et al. (2014)	294.87	517.21	−42.99	86.71	70.45
	Djomo et al. (2016)	294.87	315.32	−6.49	26.87	42.75
	Tetemke et al. (2018)	294.87	207.54	42.08	84.86	26.34
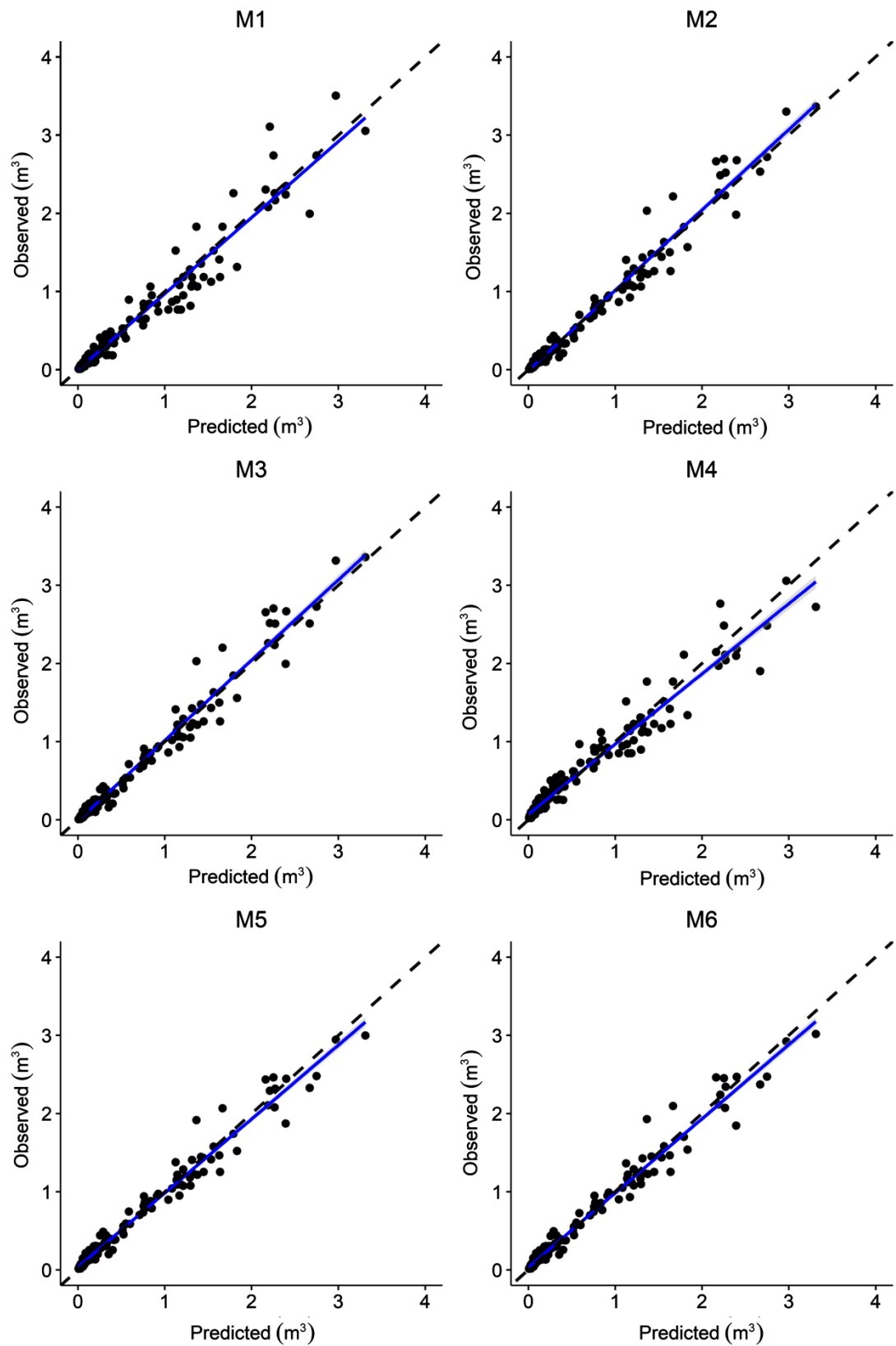
Figure S1. The observed (the full circle) against predicted (the solid blue line) stem volume graphs for the evaluated models. The dashed line represents the 1:1 line (i.e., a perfect fit between the observed and predicted).
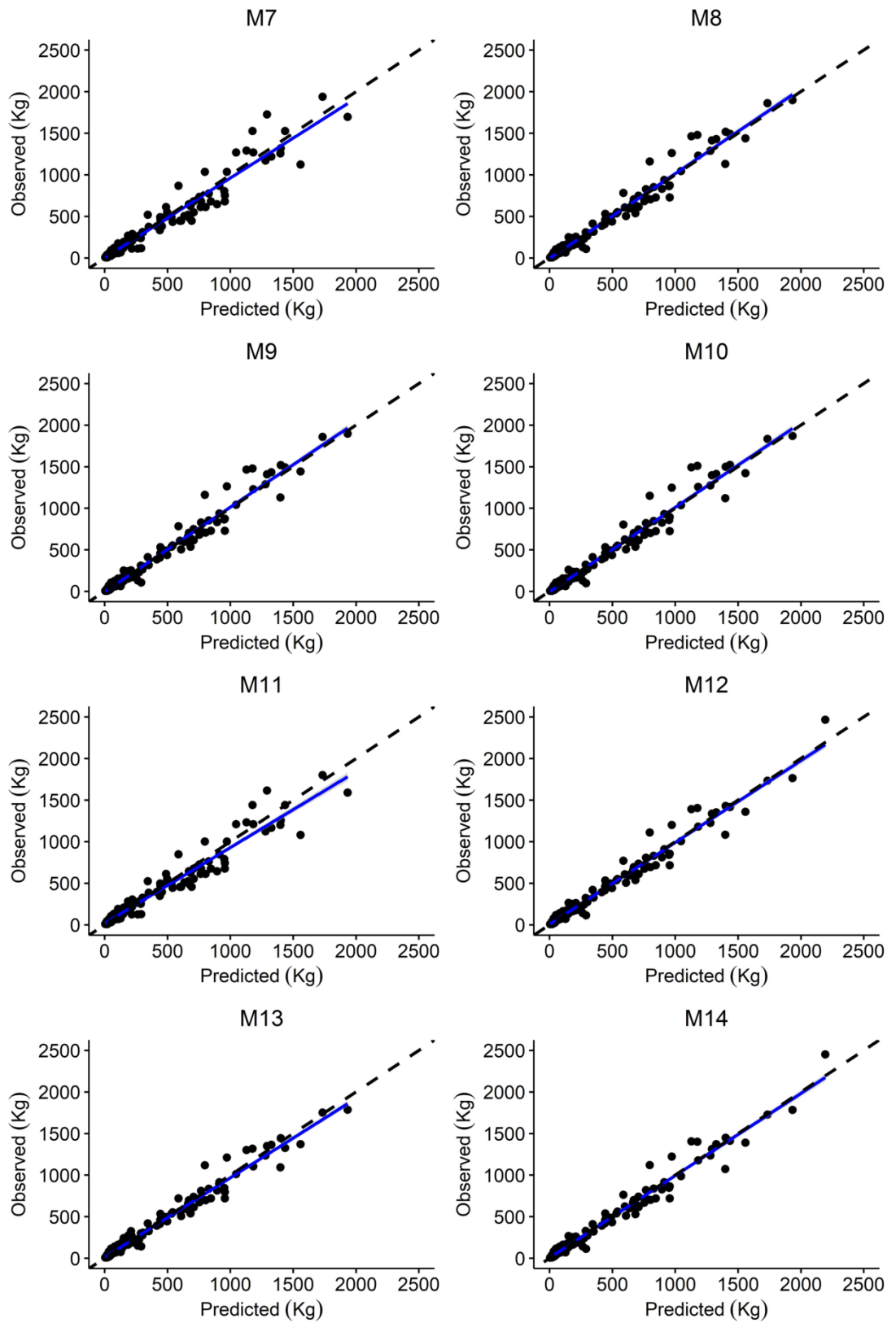
Figure S2. The observed stem biomass (the full circles) and predicted values (solid blue line) using the evaluated biomass models. The dashed line represents the 1:1 line (i.e., a perfect fit between observed and predicted).