Research Article

Allometric Models for Estimating Tree Volume and Aboveground Biomass in Lowland Forests of Tanzania

Wilson Ancelm Mugasha, 1 Ezekiel Edward Mwakalukwa, 2 Emmanuel Luoga, 3 Rogers Ernest Malimbwi, 3 Eliakimu Zahabu, 3 Dos Santos Silayo, 4 Gael Sola, 5 Philippe Crete, 5 Matieu Henry, 3 and Almas Kashindye 6

1 Tanzania Forestry Research Institute (TAFORI), P.O. Box 1854, Morogoro, Tanzania
2 Department of Forest Biology, Sokoine University of Agriculture, P.O. Box 3010, Morogoro, Tanzania
3 Department of Forest Mensuration and Management, Sokoine University of Agriculture, P.O. Box 3013, Morogoro, Tanzania
4 Department of Forest Engineering, Sokoine University of Agriculture, P.O. Box 3012, Morogoro, Tanzania
5 UN-REDD Programme, Food and Agriculture Organization of the United Nations (FAO), Viale delle Terme di Caracalla, 00153 Rome, Italy
6 Forest Training Institute, Olmotonyi, P.O. Box 943, Arusha, Tanzania

Correspondence should be addressed to Wilson Ancelm Mugasha; wilmugasha@gmail.com

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Models to assist management of lowland forests in Tanzania are in most cases lacking. Using a sample of 60 trees which were destructively harvested from both dry and wet lowland forests of Dindili in Morogoro Region (30 trees) and Rondo in Lindi Region (30 trees), respectively, this study developed site specific and general models for estimating total tree volume and aboveground biomass. Specifically the study developed (i) height-diameter (htdbh) models for trees found in the two sites, (ii) total, merchantable, and branches volume models, and (iii) total and sectional aboveground biomass models of trees found in the two study sites. The findings show that site specific htdbh model appears to be suitable in estimating tree height since the tree allometry was found to differ significantly between studied forests. The developed general volume models yielded unbiased mean prediction error and hence can adequately be applied to estimate tree volume in dry and wet lowland forests in Tanzania. General aboveground biomass model appears to yield biased estimates; hence, it is not suitable when accurate results are required. In this case, site specific biomass allometric models are recommended. Biomass allometric models which include basic wood density are highly recommended for improved estimates accuracy when such information is available.

1. Introduction

In Tanzania, lowland forests are located close to the Indian Ocean, and occasionally further inland up to the base of the Eastern Arc Mountains below 1000 m above sea level, often embedded within larger areas of miombo woodlands and Montane/humid forests [1]. The total area covered by lowland forest in Tanzania is estimated to be about 1.7 mil. ha [2]. Depending on the magnitude of precipitation, lowland forests may be categorised into dry (<1000 mm) and wet (>1000 mm) [3]. In the northern part of Tanzania, the lowland forest strips are very thin but as one moves south, the strips expand further to the inland. Based on the National Forest Resource Monitoring and Assessment (NAFORMA) classification, of the eight land cover types, the lowland forest belongs to “forest” cover [2]. Other lands classified in these cover types include humid Montane, Mangrove, and plantations.

Lowland forest supports the livelihood of thousands of people directly (fuel wood, food, medicine, and construction materials) and indirectly by offering environmental services which include biodiversity, catchment values, and carbon
sequestration. The latter has recently received global attention due to climate mitigation function they offer [4]. However, there is uncertainty of the quantities of carbon stocks in the lowland forests in Tanzania since no local biomass allometric model is available.

Volume models which are able to quantify merchantable tree volume and total volume are also required when trees are warranted for commercial purposes. Timber licensing and pricing system in Tanzania based on volume estimation [5] requires also that tree-sectional volume models are developed. Such models will aid in obtaining accurate quantitative information on the amount of wood for specific uses, that is, saw timber and fuel wood. To date there are no total or tree sectional volume estimation models for lowland forest of Tanzania. Preferred trees species for timber in the lowland forests include Pterocarpus angolensis, Afzelia quanzensis, and Sterculia quinqueloba [6]. However, due to diminishing rate of these tree species and large demand of timber, lesser known timber tree species has been exploited [7, 8]. Therefore, this necessitates the need to develop multispecies volume models other than for only known timber tree species [9]. Though not common in the scientific literature, many multispecies volume models have been developed and can be found in the international allometric equations database GlobAllomeTree [10].

The need for quantification of carbon stocks for different forest types is also relevant for the emerging carbon credit market mechanism such as Reducing Emission from Deforestation and Forest Degradation (REDD). This requires that appropriate allometric models specific for a given forest type are in place [11, 12]. Allometric models use the easy to measure individual tree parameters such as diameter at breast height (dbh) and total tree height (ht) from forest inventories to estimate volume and AGB. Another important explanatory variable for biomass estimating allometric model is wood basic density (WD) which is determined from wood samples in laboratory as a ratio of dry mass to the green volume [13]. Literature lists these variables according to their importance as dbh, WD, and ht in explaining tree biomass variations and dbh and ht for tree volume [12, 13]. Among the three explanatory variables, tree dbh and ht have been often used as only explanatory variables to develop biomass allometric models because they are readily available compared to WD which results in overall poor estimation of AGB [14, 15] especially for forests where WD of trees varies considerably [12, 13]. This calls for the need of developing biomass allometric models which integrate WD in estimating tree biomass.

Conventionally, forest inventories measure dbh of all trees in each plot but often few are randomly selected and measured for ht for development of simple and local ht-dbh models that are used to estimate ht of trees not measured in the field [16, 17]. This implies that biomass allometric model, in practice, requires local ht-dbh models for ht estimation. Although Mugasha et al. [18] recently developed ht-dbh models for four main forest types including lowland forest, none of the sites were selected from the lowland forests in the coast. Furthermore, due to large variations in ht from one forest to another as a function of climate and other environmental factors, it is imperative that a local ht-dbh model is developed to improve the tree volume or biomass estimates [19, 20].

It is against this background that this study entails develop site specific and general models for estimating total tree volume and aboveground biomass. Specifically the study aims to develop and compare (i) height-diameter (ht-dbh) models for trees found in the two sites, (ii) total, merchantable, and branches volume models, and (iii) total and sectional aboveground biomass models of trees found in the two study sites.

2. Material and Methods

2.1. Study Sites Description. The study area covered two forest reserves, namely, Rondo forest reserve located in Lindi Region and Dindili forest reserve located in Morogoro Region in Tanzania (Figure 1). Rondo forest reserve is located along the coast of Indian Ocean (39.08'E, 10.04'S) 46 km from the Indian Ocean shores in Lindi Region (Figure 1). The area of the forest is about 14 060 ha and it is managed by the government. The forest is described as lowland forest (wet) and situated at the top of the plateau in a relatively flat terrain between 465 and 885 m above sea level. The average annual rainfall is 1 215 mm and the mean annual temperature is between 15 and 31°C. Dindili forest reserve is located in the inland (37.87'E, 6.70'S) about 117 km away from the Indian ocean shores. The forest is situated about 50 km east west of Morogoro municipality, the administrative capital of Morogoro Region. The area of the forest is 1 009.9 ha and it is managed by the government as a catchment forest. The forest is described as lowland forest (dry) and situated at the ridge top of a mountain between 465 and 765 m above sea level. The average annual rainfall is 1 000 mm and the mean annual temperature is between 21 and 26°C.

2.2. Field Sampling. This study implemented a nested 1ha plot design. This was necessary to capture as much as possible the large trees which are normally excluded when a small concentric circular sample plot design is used [22].

For each study sites, the following plot design was implemented:

(i) two 1 ha plots (100 × 100 m) where all trees greater or equal to dbh of 50 cm were measured for dbh and ht,

(ii) one 0.5 ha plot (50 × 100 m) nested in (i) above where all trees with dbh greater or equal to 20 cm and less than dbh of 50 cm were measured for dbh and at least 25% of the trees were selected randomly and measured for ht,

(iii) one 0.1 ha plot (50 × 20 m) nested in (ii) above where all trees with dbh less than 20 cm and greater or equal to dbh of 5 cm were measured for dbh and at least 10% of trees were measured for ht.

The measured trees were marked with paint to ensure that no measurement repetition was made. Total number of sample trees measured for both dbh and ht were 153 and 322 for Dindili and Rondo forests, respectively.
2.3. Selection and Destructive Sampling of Sample Trees. To secure an appropriate distribution of sample trees with regard to tree sizes and tree species, information collected from sample plot inventories was used. The tree size, species distribution, and dominance/abundance of species from forest inventory information were used for the selection of sample trees to be used in volume and biomass modelling. A total of 30 trees were selected from each site to represent typical size and species distributions for each tree species (Table 1). Prior to the destructive procedure, all sample trees were recorded for species name, while dbh were measured with calipers or a diameter tape and ht measured using Suunto hypsometer. Trees were further divided into five major sections, namely,

(i) buttress (if any),
(ii) bole stem (merchantable section),
(iii) branches including tops (up to a minimum diameter of 2.5 cm),
(iv) twigs with diameter less than 2.5 cm,
(v) leaves.

Table 1: Selection and Destructive Sampling of Sample Trees corresponding to tree size distribution in each plot.

| Diameter class (cm) | Trees ha$^{-1}$ | Trees felled | Total number of trees felled |
|---------------------|-----------------|--------------|----------------------------|
|                     | Rondo | Dindili | Rondo | Dindili | All |
| 5–15                | 540   | 435     | 3     | 5       | 8   |
| 15–25               | 169   | 128     | 7     | 1       | 8   |
| 25–35               | 74    | 59      | 1     | 6       | 7   |
| 35–45               | 41    | 26      | 2     | 4       | 6   |
| 45–55               | 23    | 17      | 2     | 4       | 6   |
| 55–65               | 12.5  | 8       | 0     | 6       | 6   |
| 65–75               | 8.5   | 1       | 3     | 2       | 5   |
| 75–85               | 2.5   | 0       | 3     | 2       | 5   |
| 85–100              | 2     | 0       | 5     | 0       | 5   |
| 100                 | 2     | 0       | 4     | 0       | 4   |
| Total               | 874.5 | 674     | 30    | 30      | 60  |
For small trees with dbh < 10 cm, no merchantable stem part was considered. For trees with dbh ≥ 10 cm no specific minimum diameters were set to distinguish between merchantable stem biomass and branch biomass. However, the decision between these ranges was based on subjective judgment of the researchers and districts forest department personnel experience on the total length of the stem that can be used to produce timber. All leaves were separated from twigs and weighed separately.

Stems and branches were trimmed and crosscut into manageable billets ranging from 1 to 2.5 m in length and then weighed for green weight. In addition, the length and the mid-diameter of billets were measured for the purpose of estimating tree volume. At least two small wood samples of 2 cm thick from the tree core to the outside excluding bark were extracted from stem sections (depending on the stem length) and three samples from branches and weighed immediately in the field. Twigs were tied into separate bundles and weighed in the field and the green weights of each were recorded. Small wood samples from each bundle were extracted, labelled, and measured for green weight in the field. Leaves were collected in bundles, weighted in the field and small sample (small bunch of leaves), extracted, and weighed. Samples from all components were sent to the laboratory in order to determine dry to green weight ratio and WD.

2.4. Laboratory Measurements. In the laboratory all stems, branches, twigs, and leaves subsamples collected from the field were oven dried at 103 ± 2°C to constant weight. Dried samples were weighed and the biomass ratios for each pile of stems, branches, and twigs components were computed as the ratio of oven-dry weight to green weight. Green volumes of the sample disks/wood samples were obtained after soaking the disks/wood samples in water for at least four days until all disks are saturated. Using the water displacement method, the volume of each disk/wood sample was determined [23]. Wood basic density (WD, g cm\(^{-3}\)) for each disk/wood sample was determined as the ratio of dry weight (g) to green volume (cm\(^3\)).

2.5. Data Preparation. Components biomass was estimated as the product of dry to green ratio and total green weight (kg) of the respective tree component. The total biomass for each tree was obtained as the sum of stump, stem, branches, twigs, and leaves component tree biomass. Huber’s formula [24] was applied to compute billet volume. Volume of tree merchantable stem and branches was obtained by summing the volumes of the billets of the respective sections for that particular tree. Total tree volume was finally obtained through summation of stem and branches component volume. The resulting dataset was used for developing volume and biomass models.

2.6. Data Analysis

2.6.1. Height-Diameter Models Development. Five nonlinear model forms outlined below were used to model ht for the sample tree measured for both ht and dbh during the forest inventory exercise. Their characteristics, that is, flexibility and shape, are well documented in the literature [25]:

\[
ht = 1.3 + a \times [1 - \exp(-b \times \text{dbh})]^c
\]

(see [26]),

\[
ht = 1.3 + a \times \left[ \exp\left(\frac{-b}{(\text{dbh} + c)}\right) \right]
\]

(see [27]),

\[
ht = 1.3 + a \times \left[ \exp(-b \times \exp(-c \times \text{dbh})) \right]
\]

(see [28]),

\[
ht = 1.3 + \left[ \frac{\text{dbh}^2}{a + b \times \text{dbh} + c \times \text{dbh}^2} \right]
\]

(see [29]),

\[
ht = 1.3 + \left[ \frac{a}{\exp(-b \times \exp(-c \times \text{dbh}))} \right]
\]

(see [30]).

2.6.2. Volume and Biomass Models Development. Prior to the analysis, dependent variables (volume and biomass) were plotted against each of the explanatory variables to examine the range and shape of the functional relationship and to assess the heterogeneity of the variance. The following general nonlinear model forms for prediction of volume and biomass were fitted:

\[
Y = a \times \text{dbh}^b,
\]

(6)

\[
Y = a + b \times \text{dbh}^3,
\]

(7)

\[
Y = a \times \text{dbh}^b \times \text{ht}^c,
\]

(8)

\[
Y = a \times \left( \text{ht} \times \text{dbh}^2 \right)^b,
\]

(9)

\[
Y^1 = a \times \left( \text{WD} \times \text{dbh}^2 \times \text{ht} \right)^b,
\]

(10)

where \(Y\) is the volume (m\(^3\) tree\(^{-1}\)) or biomass (kg tree\(^{-1}\)); WD is wood basic density (g cm\(^{-3}\)); \(a, b,\) and \(c\) are model parameters to be estimated. WD (in model (10)) was not used as a predictor in modelling tree volume.

The NLP procedure (Nonlinear Programming) in SAS software [31] was used to fit the models parameters. The procedure fits both model parameters and variance parameters (Variance = \(n^2 \times \text{dbh}^{2m}\)), where \(n\) and \(m\) are parameters to be estimated) simultaneously by applying maximum likelihood regression approach. This type of procedure was used due to its flexibility to work with equations forms and its recognized robustness over nonlinear models with additive error and log transformed models [32]. A broad range of initial values for the model and variance parameters were used to ensure
an optimal solution to the Root Mean Square Error (RMSE) minimization. Selection of our final models was based on high adjusted $R^2$, low RMSE, and finally low Akaike Information Criterion (AIC). The selected biomass and volume models were evaluated by computing prediction error and model efficiency [13, 33] as follows:

$$\text{MPE} = \left(\frac{100}{n}\right) \times \left[\frac{\sum (\hat{y} - y)}{y} \right] \% \quad (11)$$

$$\text{EF} = 1 - \left[\frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2}\right], \quad (12)$$

where MPE is prediction error, EF is model efficiency, $y_i$ is observed volume or biomass, $\hat{y}_i$ is predicted volume or biomass, $\bar{y}$ is the mean of observed volume or biomass, and $n$ is the number of trees.

In addition, the generic biomass model developed by Chave et al. [12] for tropical forest, volume model for miombo woodlands [9], biomass and volume models developed for montane/humid forests [21, 34], and ht-dbh model for lowland forests in Tanzania were also tested to the modelling data.

3. Results

3.1. Height-Diameter Models. Parameter estimates and model performance criteria for ht-dbh models are presented in Table 2. For Dindili, model (4) performed better in terms of $R^2$ (68%), RMSE (2.65 m), and smaller AIC than other fitted models while for Rondo model (3) performed better with $R^2$ (61%), RMSE (2.89 m), and smaller AIC than other fitted models (result for other poor performing models not shown). When all data sets were fitted to develop a general model, model (3) performed better than other models. However, general ht-dbh model had larger RMSE (around 3 m) and lower $R^2$ (0.57) than site specific models. Trees found in Rondo forest were found to be relatively taller than those in Dindili forest at a given dbh (Figure 2). Height-diameter model developed by Mugasha et al. [18] overestimated and underestimated trees smaller and larger than dbh of about 40 cm, respectively, in Rondo while in Dindili, the model overestimated ht of trees larger than dbh of about 14 cm (Figure 2). Equations (13) represent the selected site specific and general ht-dbh models:

$$\text{ht (Dindili)} = 1.3 + \left[\frac{\text{dbh}^2}{0.4239 + 0.8893 \times \text{dbh} + 0.0398 \times \text{dbh}^2}\right],$$

$$\text{ht (Rondo)} = 1.3 \times \left[\frac{22.8525}{\exp(-1.9824 \times \exp(-0.0888 \times \text{dbh}))}\right],$$

$$\text{ht (General)} = 1.3 \times \left[\frac{21.2679}{\exp(-2.1776 \times \exp(-0.0993 \times \text{dbh}))}\right]. \quad (13)$$

3.2. Total, Stem, and Branch Tree Volume Models. Parameter estimates and model performance criteria for total tree volume and tree sections are presented in Table 3. By fitting the four alternative volume models to entire data set, over 92% and 73% of the variations of total and sectional tree volume, respectively, were explained. Based on AIC, model (7) was the best performing one for models with only dbh and model (8) for models with both dbh and ht. Although model (8) outperformed model (7), the performance differences were quite insignificant. As expected, there was a significant decrease in RMSE from general to site specific volume models.

A comparison between allometric models for total tree volume of miombo woodlands [9] and Montane/humid forests [21] and volume allometric model developed in this study with dbh only as explanatory variable is shown in Figure 3. Miombo woodlands volume model overestimated trees with dbh greater than 65 cm.

The selected general models (models (7) and (8)) were also tested to each study site (Table 4). For total tree volume, the prediction error was found to be not significantly different from zero ($p > 0.05$) and found to be more efficient (model efficiency above 0.87) than sectional models. When general sectional models were tested, except for model (8) for branches volume, mean prediction error was found to be significantly different from zero ($p < 0.05$). Site specific sectional model had low mean prediction error and is more efficient than general sectional volume models.
Table 2: Parameter estimates and performance criteria of five ht-dbh models.

| Site       | Model | Parameter estimates | Error | RMSE | $R^2$ | AIC   |
|------------|-------|---------------------|-------|------|-------|-------|
|            |       | $a$     | $b$     | $c$     |       |       |
| Dindili    | 1     | 19.5933 | 0.0415 | 0.9023 | 0.314 × $dbh^{0.6304}$ | 2.65 | 0.67 | 402.76 |
|            | 2     | 24.0599 | 18.3594 | 5.6557 | 0.317 × $dbh^{0.6271}$ | 2.64 | 0.68 | 402.32 |
|            | 3     | 17.9649 | 2.0739 | 0.0797 | 0.317 × $dbh^{0.6315}$ | 2.64 | 0.66 | 402.64 |
|            | 4     | 0.4239  | 0.8893 | 0.0398 | 0.318 × $dbh^{0.6264}$ | 2.64 | 0.68 | 402.28 |
|            | 5     | 19.8856 | 0.0554 | 0.9246 | 0.315 × $dbh^{0.6296}$ | 2.65 | 0.67 | 402.7 |
| Rondo      | 1     | 23.3447 | 0.0639 | 1.0728 | 2.239 × $dbh^{0.1469}$ | 2.90 | 0.61 | 1593.02 |
|            | 2     | 27.5692 | 11.2866 | 2.0427 | 2.374 × $dbh^{0.1306}$ | 2.92 | 0.61 | 1593.18 |
|            | 3     | 22.8525 | 1.9824 | 0.0888 | 2.145 × $dbh^{0.1591}$ | 2.89 | 0.61 | 1591.6 |
|            | 4     | 1.9292  | 0.3691 | 0.0369 | 2.399 × $dbh^{0.1273}$ | 2.92 | 0.61 | 1594.98 |
|            | 5     | 23.2808 | 0.0534 | 1.0454 | 2.233 × $dbh^{0.1477}$ | 2.904 | 0.61 | 1592.98 |
| All        | 3     | 21.2679 | 2.1776 | 0.0993 | 1.681 × $dbh^{0.2539}$ | 3.03 | 0.57 | 2099.2 |
|            | 4     | 2.3468  | 0.3489 | 0.0398 | 1.835 × $dbh^{0.2088}$ | 3.06 | 0.57 | 2101.98 |

Table 3: Parameter estimates and volume models performance for individual total tree and sectional volume.

| Section               | General/site specific | Model | Parameter estimates | Error | RMSE | $R^2$ | AIC   |
|-----------------------|-----------------------|-------|---------------------|-------|------|-------|-------|
|                       |                       | $a$   | $b$ | $c$ |       |       |       |
| Total tree volume     | General               | 6     | 0.00053 | 2.1620 | —     | 0.013 × $dbh^{0.8}$ | 0.90 | 0.95 | 92.32 |
|                       |                       | 7     | −0.0393 | 0.00102 | —     | 0.013 × $dbh^{0.8}$ | 0.85 | 0.95 | 92.06 |
|                       |                       | 8     | 0.000076 | 2.3488 | 0.3848 | 0.003 × $dbh^{0.5}$ | 0.90 | 0.95 | 91.64 |
|                       |                       | 9     | 0.00014  | 0.9039 | —     | 0.014 × $dbh^{0.5}$ | 1.10 | 0.92 | 107.42 |
|                       | Dindili forest        | 7     | 0.00014  | 0.9039 | —     | 0.014 × $dbh^{0.5}$ | 0.72 | 0.88 | 45.82 |
|                       |                       | 8     | 0.000041 | 2.5042 | 0.4329 | 0.002 × $dbh^{0.3}$ | 0.74 | 0.89 | 39.36 |
|                       | Rondo forest          | 7     | −0.0760 | 0.0010 | —     | 0.011 × $dbh^{0.5}$ | 0.87 | 0.96 | 46.92 |
|                       |                       | 8     | 0.00014  | 2.3176 | 0.1854 | 0.010 × $dbh^{0.5}$ | 0.92 | 0.96 | 45.34 |
| Tree branch volume    | General               | 6     | 0.00024 | 2.1658 | —     | 0.013 × $dbh^{0.8}$ | 0.84 | 0.78 | 88.74 |
|                       |                       | 7     | −0.0669 | 0.00031 | —     | 0.013 × $dbh^{0.8}$ | 0.82 | 0.78 | 88.58 |
|                       |                       | 8     | 0.000343 | 2.5514 | 0.1277 | 0.012 × $dbh^{0.5}$ | 0.83 | 0.79 | 89.78 |
|                       |                       | 9     | 0.00074  | 0.8901 | —     | 0.014 × $dbh^{0.3}$ | 0.90 | 0.73 | 99.72 |
|                       | Dindili forest        | 7     | −0.0120 | 0.00046 | —     | 0.013 × $dbh^{0.5}$ | 0.60 | 0.70 | 39.66 |
|                       |                       | 8     | 0.000045 | 2.9229 | 0.3903 | 0.002 × $dbh^{0.3}$ | 0.70 | 0.69 | 38.26 |
|                       | Rondo forest          | 7     | −0.015  | 0.00033 | —     | 0.011 × $dbh^{0.5}$ | 0.80 | 0.84 | 45.72 |
|                       |                       | 8     | 0.000045 | 2.5642 | 0.0659 | 0.010 × $dbh^{0.5}$ | 0.80 | 0.87 | 43.14 |
| Tree stem volume      | General               | 6     | 0.0003  | 2.1452 | —     | 0.028 × $dbh^{0.3}$ | 0.68 | 0.89 | 427.49 |
|                       |                       | 7     | 0.00017 | 0.00052 | —     | 0.009 × $dbh^{0.5}$ | 0.65 | 0.90 | 427.49 |
|                       |                       | 8     | 0.000051 | 2.1611 | 0.5517 | 0.008 × $dbh^{0.3}$ | 0.65 | 0.90 | 38.70 |
|                       |                       | 9     | 0.00007 | 0.9088 | —     | 0.008 × $dbh^{0.3}$ | 0.67 | 0.89 | 40.18 |
|                       | Dindili forest        | 7     | −0.0121 | 0.00047 | —     | 0.008 × $dbh^{0.3}$ | 0.42 | 0.79 | 33.9 |
|                       |                       | 8     | 0.000099 | 2.0392 | 1.2855 | 0.007 × $dbh^{0.3}$ | 0.36 | 0.86 | 4.3 |
|                       | Rondo forest          | 7     | −0.03965 | 0.00059 | —     | 0.009 × $dbh^{0.5}$ | 0.83 | 0.90 | 33.94 |
|                       |                       | 8     | 0.00011 | 2.1685 | 0.3038 | 0.009 × $dbh^{0.3}$ | 0.83 | 0.90 | 35.3 |

3.3. Total, Branch, and Stem Tree Biomass Models. Parameter estimates of total tree AGB for general and site specific models are presented in Table 5. Model with dbh alone had the lowest $R^2$ and highest RMSE. Site specific models had larger $R^2$ and lower RMSE compared to corresponding general models. Inclusion of ht into the model (models (8) and (9)) improved the model fit marginally. On the other hand, the lowest AIC and RMSE and highest $R^2$ for general and site specific models were apparent for models which include WD (model (10)). Models (7), (9), and (10) were selected for further evaluation. The distribution of observed trees AGB and projected AGB by applying the selected site specific and general models against dbh is presented in Figure 4. Observed tree AGB data for Dindili forest was systematically larger than that of Rondo forest for all trees sizes.
Table 4: Evaluation of the selected general and site specific models for tree total, branches, and stem volume.

| Type            | Tree section | Selected model | Prediction error% | All | Model efficiency | All |
|-----------------|--------------|----------------|-------------------|-----|------------------|-----|
|                 |              |                | Dindili | Rondo | All | Dindili | Rondo | All |
| General         | Total        | 7              | −2.09   | 12.78 | 8.84 | 0.87    | 0.96  | 0.94 |
|                 |              | 8              | −0.50   | 13.27 | 6.38 | 0.90    | 0.87  | 0.87 |
|                 | Branches     | 7              | −12.73  | 20.95 | 1.75 | 0.35    | 0.65  | 0.56 |
|                 |              | 8              | −0.26   | 56.12 | 27.93 | 0.66    | 0.68  | 0.68 |
|                 | Stem         | 7              | 13.72   | 15.61 | 14.66 | 0.88    | 0.89  | 0.88 |
|                 |              | 8              | 15.43   | 14.53 | 14.98 | 0.90    | 0.86  | 0.86 |
| Selected sites  | Total        | 7              | 4.08    | 6.97  | —    | 0.87    | 0.96  | —   |
|                 |              | 8              | 6.68    | 3.28  | —    | 0.90    | 0.96  | —   |
| Specific        | Branches     | 7              | 15.79   | 17.46 | —    | 0.58    | 0.66  | —   |
|                 |              | 8              | 14.28   | 18.90 | —    | 0.73    | 0.86  | —   |
|                 | Stem         | 7              | 11.75   | 15.50 | —    | 0.78    | 0.90  | —   |
|                 |              | 8              | 10.28   | 17.95 | —    | 0.74    | 0.87  | —   |

The best selected models are in bold and italic. *Significantly different from zero (p < 0.05).

Table 5: Parameter estimates and performance of general and site specific models for total tree aboveground biomass.

| General/sites | Model | Parameter estimates | Error | RMSE | R² | AIC |
|---------------|-------|---------------------|-------|------|----|-----|
| General       | 6     | 0.6881 1.9384       | 0.237 x dbh².028 | 1280.4 | 0.49 | 893.98 |
|               | 7     | 3.2064 0.6166       | 0.176 x dbh².105 | 1326.16 | 0.48 | 892.70 |
|               | 8     | 0.3571 1.7440 0.4713 | 0.274 x dbh¹.982 | 1214.68 | 0.52 | 893.44 |
|               | 9     | 0.1459 0.8601       | 0.323 x dbh¹.940 | 1169.65 | 0.54 | 892.56 |
|               | 10    | 0.0873 0.9458       | 0.559 x dbh¹.673 | 567.9 | 0.87 | 840.94 |
| Dindili forest| 6     | 0.5414 2.0591       | 0.429 x dbh¹.601 | 539.98 | 0.83 | 421.38 |
|               | 7     | 4.5076 0.6915       | 0.347 x dbh¹.860 | 506.59 | 0.84 | 421.40 |
|               | 8     | 0.2137 1.8004 0.6724 | 0.573 x dbh¹.486 | 470.50 | 0.87 | 416.48 |
|               | 9     | 0.1568 0.8613       | 0.585 x dbh¹.643 | 478.61 | 0.87 | 415.06 |
|               | 10    | 0.1014 0.9510       | 0.638 x dbh¹.675 | 467.52 | 0.89 | 418.34 |
| Rondo forest  | 6     | 0.3238 2.0673       | 0.040 x dbh².430 | 1360.97 | 0.50 | 450.04 |
|               | 7     | 0.2816 1.1654       | 0.006 x dbh².916 | 1514.67 | 0.51 | 442.78 |
|               | 8     | 0.0542 1.3326 1.4278 | 0.165 x dbh².010 | 967.08 | 0.66 | 439.90 |
|               | 9     | 0.0863 0.8544       | 0.040 x dbh².397 | 1172.15 | 0.58 | 440.64 |
|               | 10    | 0.0751 0.9477       | 0.214 x dbh¹.740 | 462.47 | 0.92 | 396.58 |

Parameter estimates and performance of general and site specific models for biomass tree section are presented in Table 6. Similar models performance trend as that of total tree AGB models were also found for sectional biomass models. Modelling all data sets significantly reduced and increased the $R^2$ and RMSE, respectively, compared to site specific models. Inclusion of ht and WD reduced AIC except for Dindili where addition of WD did not improve the model fit.

The selected general biomass models were evaluated on how best they predict the tree total, branches, and stem biomass to each study site (Table 7). Overall model with dbh or a combination of dbh and ht performed poorly. The models underestimated biomass in Dindili forest and overestimated the biomass in Rondo forest. However, the magnitude of overestimation was immense in Rondo forest when compared to the magnitude of underestimation at Dindili forest. Inclusion of WD stabilized the models’ prediction error and efficiency globally. AGB models developed by Chave et al. [12] produced small mean prediction error globally (about 5%) and performed poorly when tested at site level (prediction error > 12%). Model developed by Masota [34] significantly overestimated tree biomass in all sites. The selected site specific models were found to be efficient and produced lower mean prediction error compared to best performing general model (model (10)) when tested to site level.

4. Discussion

Lowland forests in Tanzania are generally found in areas close to the coast of Indian Ocean and some areas of the inland. The locality differences as defined by the distance of the forest from the coast influence the forest structure.
and conditions due to climatic and topographical differences. Therefore, in this study two sites of lowland forests were selected, that is, one near to the coast (wet lowland forest) and the second from further inland (dry lowland forest), to cater the variations associated with environmental factors. Since the tree selection for modelling was based on the tree size distribution from the information derived from the forest inventory data (Table 2), it is apparent that the modelling data in this study was representative. However, in tropical natural forests where hundreds of species exist per ha [35], it is impractical to represent every tree species for allometric model development. However, the priority was given to tree species which have high appearance frequency. Moreover, the larger trees which normally influence the trend of allometric model and also account for a very large part of the volume and AGB [4, 35] were well represented to avoid extrapolation.

4.1. Height-Diameter Relationships. Over 61% of variation on tree ht was explained by the selected site specific ht-dbh models. The coefficient of variation ($R^2$) in this study corresponds to that of Mugasha et al. [18] lowland forests of Tanzania where $R^2$ of 0.64 was reported. However, considerable amount of variation in ht remains unexplained. This may be due to large diversity of tree species with different ht-dbh allometry. This is also evident when modelling ht-dbh of combined data from the two sites where $R^2$ dropped to 0.57. In addition, tree allometry was found to be different among sites as indicated by slightly taller trees in Rondo than those from Dindili forest at a given dbh (Figure 3). Due to such difference in addition to drop of $R^2$ and increasing of RMSE for the combined data set, it is recommended that the site specific ht-dbh models are to be applied. Furthermore, ht of trees larger than 40 cm dbh were overestimated by ht-dbh model developed by Mugasha et al. [18]. This may be due to the fact that Mugasha et al. [18] did not include trees found in areas with similar climate conditions as that of Rondo or Dindili in their model. Studies have shown that ht-dbh relationship varies significantly with climate [12, 36]. Since climate variation affects ht, this in turn affects trees AGB and volume. Therefore, as noted by Chave et al. [12], it is important

| Section | General/sites | Model | Parameter estimates | Error | RMSE | $R^2$ | AIC |
|---------|---------------|-------|---------------------|-------|------|-------|-----|
| General |               | 6     | 0.1379 2.1738       | 0.027×dbh$^{2.456}$ | 846.89 | 0.39 | 823.10 |
|         |               | 7     | −1.6031 0.2524      | 0.042×dbh$^{2.345}$ | 677.87 | 0.41 | 826.66 |
|         |               | 8     | 0.1364 2.1697 0.0088 | 0.028×dbh$^{2.451}$ | 842.13 | 0.39 | 825.08 |
|         |               | 9     | 0.0434 0.8868       | 0.047×dbh$^{2.319}$ | 757.86 | 0.40 | 828.52 |
|         |               | 10    | 0.0270 0.9887       | 0.075×dbh$^{2.118}$ | 441.72 | 0.75 | 795.70 |
|         |               | 6     | 0.1173 2.2750       | 0.023×dbh$^{2.441}$ | 370.47 | 0.75 | 383.04 |
|         |               | 7     | −2.5456 0.3211      | 0.033×dbh$^{2.375}$ | 285.20 | 0.76 | 391.26 |
| Tree branches | Dindili | 8     | 0.1604 2.35962 −0.2205 | 0.022×dbh$^{2.455}$ | 368.64 | 0.76 | 384.92 |
|         |               | 9     | 0.0483 0.9083       | 0.032×dbh$^{2.380}$ | 420.12 | 0.62 | 390.90 |
|         |               | 10    | 0.04624 0.9549      | 0.020×dbh$^{2.510}$ | 296.64 | 0.72 | 388.60 |
|         |               | 6     | 0.3133 2.0777       | 0.046×dbh$^{2.277}$ | 619.55 | 0.46 | 422.62 |
|         |               | 7     | −0.1403 0.9548      | 0.041×dbh$^{2.303}$ | 620.00 | 0.46 | 421.78 |
|         | Rondo | 8     | 0.0000007 0.5631 4.9456 | 0.141×dbh$^{1.890}$ | 531.55 | 0.64 | 405.46 |
|         |               | 9     | 0.0288 0.8912       | 0.047×dbh$^{2.249}$ | 594.47 | 0.51 | 416.26 |
|         |               | 10    | 0.05347 0.8840      | 0.205×dbh$^{1.763}$ | 345.94 | 0.85 | 394.66 |
| Tree stem | Dindili | 6     | 0.3859 1.7794       | 0.135×dbh$^{1.994}$ | 570.48 | 0.49 | 811.60 |
|         |               | 7     | −1.0523 0.2482      | 0.109×dbh$^{2.053}$ | 618.81 | 0.49 | 811.76 |
|         |               | 8     | 0.07646 1.5073 1.0172 | 0.203×dbh$^{1.859}$ | 472.48 | 0.62 | 803.40 |
|         |               | 9     | 0.1683 0.7287       | 0.174×dbh$^{1.903}$ | 494.66 | 0.60 | 801.86 |
|         |               | 10    | 0.0848 0.8726       | 0.333×dbh$^{1.458}$ | 259.49 | 0.85 | 772.30 |
|         |               | 6     | 0.2451 2.0119       | 0.086×dbh$^{1.108}$ | 358.30 | 0.56 | 390.86 |
|         |               | 7     | −1.1567 0.2895      | 0.103×dbh$^{2.009}$ | 343.87 | 0.57 | 390.92 |
|         | Rondo | 8     | 0.0395 1.3879 1.4583 | 0.181×dbh$^{1.825}$ | 212.42 | 0.84 | 377.04 |
|         |               | 9     | 0.0869 0.8392       | 0.118×dbh$^{1.966}$ | 260.67 | 0.77 | 388.60 |
|         |               | 10    | 0.0853 0.8798       | 0.108×dbh$^{1.994}$ | 277.39 | 0.68 | 380.18 |
|         |               | 6     | 0.3944 1.7607       | 0.200×dbh$^{1.869}$ | 549.37 | 0.49 | 417.66 |
|         |               | 7     | −5.4258 0.2147      | 0.104×dbh$^{2.043}$ | 668.71 | 0.48 | 422.10 |
|         |               | 8     | 0.0278 1.2617 1.5116 | 0.344×dbh$^{1.494}$ | 441.80 | 0.67 | 412.20 |
|         |               | 9     | 0.0808 0.8026       | 0.213×dbh$^{1.830}$ | 493.90 | 0.59 | 412.35 |
|         |               | 10    | 0.06812 0.8888      | 0.779×dbh$^{1.395}$ | 271.52 | 0.89 | 391.32 |

Table 6: Parameter estimates and performance of general and site specific models for biomass of tree sections.
Table 7: Evaluation of the selected general and site specific models for tree total, branches, and stem biomass.

| Type               | Section | Selected model | Prediction error% | Model efficiency |
|--------------------|---------|----------------|-------------------|------------------|
|                    |         |                | Dindili | Rondo | All | Dindili | Rondo | All |
| Total tree biomass | 7       | –1.26          | 53      | 50.28 | 0.81 | –0.61   | –0.10 |
|                    | 9       | –6.59          | 60      | 53.12 | 0.83 | 0.87    | –0.25 |
|                    | 10      | –14.97         | 19.10   | 2.06  | 0.81 | 0.91    | 0.87  |
|                    |         |                | –12.59  | 23.24 | –5.33| 0.85    | 0.86  |
|                    |         | Chave et al., 2014 [12] | 25.07    | 151.30 | 88.1 | 0.84 | –1.78 | –0.84 |
|                    |         | Masota, 2015 [34] | 25.07    | 151.30 | 88.1 | 0.84 | –1.78 | –0.84 |
|                    | 6       | –13.58         | 80      | 56.66 | 0.60 | –0.47   | –0.02 |
|                    | 8       | –13.96         | 87      | 56.68 | 0.60 | –0.47   | –0.02 |
|                    | 10      | –14.87         | 47.17   | 16.16 | 0.59 | 0.84    | 0.74  |
|                    |         | 6              | 38      | –4.40 | 0.30 | 0.48    | 0.44  |
|                    | 9       | –21.95         | 29.96   | 4.32  | 0.48 | 0.59    | 0.56  |
|                    | 10      | 9.17           | 23.57   | 16.37 | 0.72 | 0.91    | 0.86  |
| Branches biomass   | 6       | 5.16           | –       | –     | 0.94 | –       | –     |
|                    | 7       | –              | 6.47    | –     | 0.72 | –       | –     |
|                    | 10      | 3.75           | 4.31    | –     | 0.88 | 0.93    | –     |
|                    | 6       | 4.82           | –       | –     | 0.87 | –       | –     |
|                    | 9       | 1.68**         | –       | –     | 0.94 | –       | –     |
|                    | 10      | 4.62           | –4.00   | –     | 0.88 | 0.76    | –     |
| Stem biomass       | 6       | 9.06           | 9.39    | –     | 0.83 | 0.72    | –     |
|                    | 9       | 7.07           | 7.17    | –     | 0.93 | 0.80    | –     |
|                    | 10      | 17.52          | 12.73   | –     | 0.71 | 0.91    | –     |

** The best selected models are in bold and italic. *Significantly different from zero (p < 0.05).

Figure 3: Comparison of lowland forest, miombo woodlands, and Montane/humid volume models. Lowland volume estimates computed by model (8). Total tree height was estimated using the developed ht-dbh models.

Figure 4: Scatter plot and biomass estimates by applying model (9). Total tree height was predicted using the developed ht-dbh models.

to include ht as an explanatory variable in AGB or volume models to accommodate variation triggered by climate and other environment factors.

4.2. Volume and Biomass Allometric Models. Over 73% of variation in tree volume was explained by dbh or by both dbh and ht. Site specific models slightly improved the model fit compared to general models. Model (7) (with only dbh) and model (8) (with both ht and dbh) were selected for all tree section. However, model (8) with ht included outperformed model (7) with only dbh. This observation also underscores the importance of including ht in volume allometric models as also suggested by Chave et al. [12].

The comparison between the developed volume models and that of miombo woodlands and Montane/humid forest shows that the volume of trees with dbh greater than 65 cm
| Forest | Tree # | Botanical name          | Local name | Family               | WD ± SD (g cm\(^{-3}\)) |
|-------|-------|-------------------------|------------|----------------------|-------------------------|
| Dindili | 1    | Manilkara sulcata       | Msezi      | Sapotaceae           | 0.70 ± 0.11             |
| Dindili | 2    | Ricinodendron heudelotii | Mkungunolo  | Euphorbiaceae        | 0.41 ± 0.06             |
| Dindili | 3    | Manilkara sulcata       | Msezi      | Sapotaceae           | 0.74 ± 0.04             |
| Dindili | 4    | Combretum schumannii    | Mkatakorongo| Combretaceae         | 0.82 ± 0.06             |
| Dindili | 5    | Albizia gummifera       | Mkenge     | Fabaceae             | 0.62 ± 0.06             |
| Dindili | 6    | Terminalia sambesiaca   | Mpululu    | Combretaceae         | 0.69 ± 0.16             |
| Dindili | 7    | Tamarindus indica       | Mkwaju     | Fabaceae             | 0.69 ± 0.04             |
| Dindili | 8    | Commiphora zimmermannii | Mtwini     | Burseraceae          | 0.40 ± 0.08             |
| Dindili | 9    | Pteleopsis myrtifolia   | Mngoji     | Combretaceae         | 0.67 ± 0.04             |
| Dindili | 10   | Pteleopsis myrtifolia   | Mngoji     | Combretaceae         | 0.70 ± 0.03             |
| Dindili | 11   | Combretum schumannii    | Mkatakorongo| Combretaceae         | 0.78 ± 0.04             |
| Dindili | 12   | Tamarindus indica       | Mkwaju     | Fabaceae             | 0.70 ± 0.01             |
| Dindili | 13   | Vepris nobilis          | Mzindizi   | Rutaceae             | 0.77 ± 0.08             |
| Dindili | 14   | Terminalia sambesiaca   | Mpululu    | Combretaceae         | 0.58 ± 0.13             |
| Dindili | 15   | Holarrhena pubescens    | Mmelemele  | Apocynaceae          | 0.44 ± 0.03             |
| Dindili | 16   | Sterculia appendiculata | Mgude      | Sterculiaceae        | 0.46 ± 0.08             |
| Dindili | 17   | Sterculia appendiculata | Mgude      | Sterculiaceae        | 0.49 ± 0.11             |
| Dindili | 18   | Lannea sp.              | Muumbu     | Anacardiaceae        | 0.52 ± 0.21             |
| Dindili | 19   | Terminalia sambesiaca   | Mpululu    | Combretaceae         | 0.70 ± 0.12             |
| Dindili | 20   | Combretum schumannii    | Mkatakorongo| Combretaceae         | 0.80 ± 0.06             |
| Dindili | 21   | Scorodophloeus fischeri | Mhande     | Fabaceae             | 0.76 ± 0.06             |
| Dindili | 22   | Terminalia sambesiaca   | Mpululu    | Combretaceae         | 0.62 ± 0.05             |
| Dindili | 23   | Scorodophloeus fischeri | Mhande     | Fabaceae             | 0.70 ± 0.07             |
| Dindili | 24   | Cussonia zimmermannii   | Mkongonolo | Araliaceae           | 0.40 ± 0.05             |
| Dindili | 25   | Terminalia sambesiaca   | Msezi      | Sapotaceae           | 0.80 ± 0.04             |
| Dindili | 26   | Scorodophloeus fischeri | Mhande     | Fabaceae             | 0.71 ± 0.06             |
| Dindili | 27   | Celtis sp.              | Mkom Chuma | Ulmaceae             | 0.79 ± 0.12             |
| Dindili | 28   | Sterculia africana      | Moza       | Sterculiaceae        | 0.81 ± 0.07             |
| Dindili | 29   | Cussonia zimmermannii   | Mkongonolo | Araliaceae           | 0.63 ± 0.16             |
| Dindili | 30   | Scorodophloeus fischeri | Mhande     | Fabaceae             | 0.60 ± 0.17             |
|       |      | **Mean value**           |            |                      | **0.65 ± 0.13**         |
| Rondo  | 1    | Xylopia sp.             | Nami       | Annonaceae           | 0.51 ± 0.01             |
| Rondo  | 2    | Blighia unijugata       | Mkalanga   | Sapindaceae          | 0.44 ± 0.06             |
| Rondo  | 3    | Tabernaemontana ventricosa | Mnongoli  | Apocynaceae          | 0.45 ± 0.02             |
| Rondo  | 4    | Cussonia zimmermannii   | Mtumbitumbi| Araliaceae           | 0.27 ± 0.02             |
| Rondo  | 5    | Parinari excelsa        | Mmula      | Rosaceae             | 0.49 ± 0.02             |
| Rondo  | 6    | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.29 ± 0.06             |
| Rondo  | 7    | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.26 ± 0.02             |
| Rondo  | 8    | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.21 ± 0.04             |
| Rondo  | 9    | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.35 ± 0.04             |
| Rondo  | 10   | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.21 ± 0.03             |
| Rondo  | 11   | Cussonia zimmermannii   | Mtumbitumbi| Araliaceae           | 0.32 ± 0.07             |
| Rondo  | 12   | Antiaris toxicaria      | Nkalale/Nkarale | Moraceae      | 0.36 ± 0.13             |
| Rondo  | 13   | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.23 ± 0.03             |
| Rondo  | 14   | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.26 ± 0.03             |
| Rondo  | 15   | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.30 ± 0.03             |
| Rondo  | 16   | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.25 ± 0.07             |
| Rondo  | 17   | Ricinodendron heudelotii| Mtene      | Euphorbiaceae        | 0.21 ± 0.04             |
| Rondo  | 18   | Porlerandia penduliflora | Nakatumbaku| Rubiaceae             | 0.54 ± 0.01             |
| Rondo  | 19   | Trilepsium madagascariense | Nulumbuki | Sapotaceae           | 0.48 ± 0.02             |
| Rondo  | 20   | Euphorbia sp.           | Milembutuka Mweusi | Euphorbiaceae | 0.57 ± 0.03             |
was overestimated by the miombo woodlands model while all trees sizes were overestimated by Montane/humid volume model. This pattern provides an insight into the actual volume difference between trees in miombo woodlands and Montane/humid forests and that of lowland forests at a given tree size. This variation may be attributable to the tree architectural differences since lowland forests are characterised by very tall trees as opposed to short and very wide crowned trees in miombo woodlands (Figure 2) [37]. While branching pattern for lowland forest is similar to Montane/humid forests, the biomass differences revealed in this study may be due to the fact that trees in Montane/humid forest are taller than those found in lowland forests [1, 18]. Due to large variation in branching patterns among tree sizes and species in lowland, the model fit to the tree branches was not as good as the model fit of the tree total and stem models. It can also be noted that even though the total volume models are affected by the branches, the model fits were still better than those of the stem models. The most plausible explanation for this is the fact that the demarcation point for merchantable stem relies on considerations not only on size (minimum diameter), but also on subjective stem quality assessments for timber which adds variability to the relationship between dbh and stem. Evaluation of general volume models to the sites indicates that models (7) and (8) can be reliably applied to lowland forests of Tanzania while for tree sectional tree volume the site specific volume models are recommended.

Although the selected general biomass model performed well globally, the selected site specific AGB models performed far better. The model fit improved with addition of ht and WD. In contrast to volume models, AGB varied significantly between sites. The variation is highly associated with WD (see Table 8). This explains why model (10) (with WD) performed relatively well for site specific AGB models as well as for general AGB model. Similar trend was found for biomass sectional models where inclusion of WD also improved the model fit and efficiency significantly (e.g., from $R^2$ values from 0.62 to 0.85 and model efficiency value from 0.80 to 0.91 from model (8) to model (10), resp., for stem general biomass model). However, the mean prediction error of general biomass model (model (10)) was large and inefficient compared to site specific models when tested at site level.

This may be due to actual differences between the two forests as a function of climate and other environmental factors which shape the forest structure and conditions [20, 38]. It is therefore recommended that, for lowland forests, the selected site specific biomass models (Table 7) be applied since their prediction error is within the acceptable range ($p > 0.05$, Table 7). For the sites which are situated inland, the AGB model developed for Dindili forest may be used and for lowland forests near the coast, the AGB model developed for Rondo forest may be used. Furthermore, for improved estimation of AGB, the model with ht and WD included is highly recommended. Model developed by Chave et al. [12] underestimated and overestimated AGB in Rondo and Dindili forest, respectively, and gave unbiased biomass estimates at global scale.

### 5. Conclusion

From the findings in this study, site specific ht-dbh model is recommended since the tree allometry was found to differ significantly between dry and wet lowland forests. The selected general tree total volume model may be applied in lowland forests of Tanzania since no significant difference in prediction error was found when tested to each study site. Due to biased biomass estimates of general aboveground biomass model, the application of selected site specific biomass models is recommended, that is, dry and wet lowland forests biomass models developed in Dindili and Rondo forest, respectively. Application of models with WD in addition to dbh and ht is highly recommended for improved estimates accuracy.

### Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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