
Volume models for single trees in tropical rainforests in Tanzania

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Abstract: The present study was the first to develop total tree, stem and branches volume models for rainforests in south-eastern Africa based on destructive sampling. The number of sample trees was 60 and diameter at breast height (*dbh*) and total tree height (*h*) ranged from 6 to 117 cm and from 6.4 m to 50 m, respectively. Large parts of the total volume and stem volume variations were explained by the models (Pseudo-R² ranged from 0.85 to 0.93) and they performed relatively well over different size classes. When considering the challenges in height measurements in rainforests, we in general recommend applying model 3 with *dbh* only as independent variable. For large trees we recommend model 2 (*dbh* and *h* as independent variables) because of the moderating effect *h* has on volume predictions. If accurate stem volumes are needed for forestry licensing or for calculating compensation of timber loss, we also recommend model 2. As long as the allometry of the trees obviously is not different from that of our study site, the developed models may also be applied for rainforests elsewhere in Tanzania, but further testing of the models is also recommended.

Keywords: Total, Branches and Stem Volume, Form Factor, Destructive Sampling

1. Introduction

In Tanzania rainforests are estimated to cover about 2 million ha, occurring mainly in mosaics (URT, 2009). These forests are rich in terms of flora and fauna diversity and have high catchment values (Frontier Tanzania, 2001; [Munishi and Shear, 2004](#); URT, 2009), thus, most of them are protected for soil, water and biodiversity conservation. However, because of growing human needs for forest products and services, tropical rainforests are under threat due to high annual deforestation rates ([Mayaux et al., 2013](#)), and measures towards sustainable forest management are important (Castañeda, 2011).

Sustainable forest management requires among others knowledge on the total volume of the growing forest stock. Usually volume is estimated as total volume per unit area, whereby models predicting total tree volume of individual trees are used. According to the substantial review of volume models made by [Henry et al. \(2011\)](#) on rainforests in sub-

Saharan Africa, almost all efforts have been put into developing species-specific models predicting stem (merchantable) volume. Many of these models have been developed in west-African countries for commercial timber species ([Akindede and LeMay, 2006](#)). The only general (multiple species) model predicting total tree volume referred to in the review was developed by [Alder \(1982\)](#) in Ghana. In addition, we know that [Munishi and Shear \(2004\)](#) and [Adekunle \(2007\)](#) have developed general models predicting total tree volume based on inventory data from rainforests in Tanzania and Nigeria, respectively.

The only general total tree volume model for tropical rainforest that we know from east-Africa was developed by [Munishi and Shear \(2004\)](#) based on data from Eastern Arc Mountains in Tanzania. In this study they regressed individual total tree volume against diameter at breast height. However, the observed individual tree volume (*v*) used in this

model was not based on destructive sampling, but computed as a product of basal area (g) and total tree height (h) adjusted for taper by the cone formula ($v = g \times h/3$). It is quite obvious that uncertainty in volume estimation is larger for models based on such computations compared to if destructive sampling is applied, and volume is determined by summarizing accurately measured sections of trees.

In the lack of better alternative total volume models, the general volume equation ($v = g \times h \times f$) that relates the product of g and h to a form factor (f), has frequently been used to estimate v . A form factor is the ratio of measured volume for a tree to a cylinder volume based on diameter at breast height (dbh) and h of the tree. Although f vary between trees, $f = 0.5$ has routinely been applied in Tanzania across many different forest types (Kashaigili *et al.*, 2013; Zahabu, 2008), including rainforests (Mpanda *et al.*, 2011). This value appears to be correct for plantation species characterized by straight stems and small crowns (Malimbwi *et al.*, 1998) but it has never been checked or verified for natural forest types in Tanzania. It is quite obvious that the uncertainty of volume estimation also related to such practices is large. Variations in the relationship between dbh and h , and consequently in f , are related to numerous environmental factors such as soil nutrients, climate, disturbance regime, successional status and topographic position, but also to tree species and several genetic factors (Feldpausch *et al.*, 2011; Mugasha *et al.*, 2013).

Tree volume models are generally scant in Tanzania, although a few exist for plantation forest (Malimbwi and Philip, 1989) and for miombo woodland (Malimbwi *et al.*, 1994; Chamshama *et al.*, 2004). Tanzania has recently carried out her first national forest inventory through a systematic sample plot design (National Forest Resources Monitoring and Assessment (NAFORMA) (URT, 2010; Tomppo *et al.*, 2014). This will require reliable total tree volume models specific for different forest types, including rainforests. The country also needs total tree and stem volume models that can be applied for forest management planning in general, in the forestry licensing systems (Abbot *et al.*, 1997; MNRT, 2007), for allocation of forest areas to harvest and for calculation of compensation of timber loss due to damages during for example, road construction. Models quantifying volume of branches that potentially can be used for firewood may also provide important information for the management of the forest resources (Dadzie, 2013).

The main objective of the present study was therefore to develop models for prediction of tree volume in tropical rainforests in Tanzania based on destructive sampling. Models for total volume, stem volume and branch volume were developed. Since the general volume equation using $f = 0.5$ is frequently applied in Tanzania, we also assessed the appropriateness of such practices. In addition, we compared the performance of the developed models with previously developed volume models for tropical rainforests in sub-Saharan Africa and elsewhere.

2. Materials and Methods

2.1. Study Area and Selection of Sample Trees

Data collection for this study was carried out between October 2011 and September 2012, in Amani Nature Reserve (ANR), which is situated at 5°05'–5°14'S and 38°40'–38°32'E in Usambara Mountains. These mountains are parts of the Eastern Arc Mountains. ANR covers 8,380 ha of tropical rainforests with elevation ranges between 190 and 1130 m above sea level (Frontier Tanzania, 2001). The mean annual rainfall ranges from 1800 to 2200 mm and the mean annual temperature is about 20°C, with mean daily minimum and maximum temperatures of about 16 and 24°C, respectively. The forest is dominated by trees of genera *Afrosorsalisia*, *Allanblackia*, *Celtis*, *Drypetes*, *Ficus*, *Isobertinia*, *Leptonychia*, *Macaranga*, *Myrianthus*, *Newtonia*, *Parinari*, *Sorindeia*, *Strombosia*, *Syzygium*, and *Tabernaemontana* (Newmark, 2001). Historically, ANR has been under commercial logging activities for more than 100 years and they continued until the mid-1980's (Frontier Tanzania, 2001). Also, ANR is a biodiversity hotspot, with high water catchment values and environmental conservation. In spite of its importance, Mpanda *et al.* (2011) reported that ANR was subjected to illegal activities including excessive collection of medicinal plants, pit sawing, encroachment, mining and collection of building poles.

Selection of trees for destructive sampling was guided by the species distribution and dbh range observed on 142 systematically distributed permanent sample plots (PSPs) established in 1999 (Frontier Tanzania 2001) and remeasured in 2008 and 2009 (Mpanda *et al.*, 2011; Mgumia, 2014). Almost 6,000 trees comprising 240 different species, with dbh range between 10 and 270 cm, were recorded on these plots. Based on this information we determined which tree species were most frequent so that we could focus our sampling on those. A total of 60 trees from 34 different tree species were selected to uniformly cover as much as possible of the observed dbh distribution of the 142 PSPs. Sample trees were measured both for dbh and h while standing. A calliper or diameter tape was used to measure dbh , while h was measured by using a Vertex hypsometer. For leaning trees on slope the breast height point was determined from the upper side of the tree (Dietz and Kuyah, 2011; URT, 2010). For trees with buttresses extending beyond breast height, dbh was measured at 30 cm above the buttresses. The sample trees were the same as those used by Masota *et al.* (2014) for development of biomass models. The details of sample trees (tree species, dbh and h) are shown in Appendix I. Summary statistics of the trees are shown in Table 1.

Table 1. Summary statistics of dbh and h of sample trees

Variable	n	Mean	Min.	Max.	St. dev.
dbh (cm)	60	50.8	6.0	117.0	25.6
h (m)	60	27.3	6.4	50.0	10.4

2.2. Destructive Sampling and Data Processing

The selected sample trees were cut at heights of 30 cm from the ground level. Felled trees were crosscut into two main components, namely stem (from the stump to the point where the first large branch protrudes the stem) and branches. Diameter cut-off between branches and twigs was 2.5 cm, and no volume from twigs was included. Stems and branches were crosscut into sections with lengths generally ranging between 1-2 m, but down to 0.5 m for the stems of the largest trees. Thereafter all stem and branch sections were measured separately for mid-diameter (cm) and length.

Data processing and analysis was carried out with SAS 9.2 software (SAS[®] Institute Inc., 2004). Volume (v) of individual stem and branch sections were calculated by Huber's formula (Philip, 1994; Abbot et al., 1997) and summed to obtain tree volume. Statistics of tree components volume are presented in Table 2. On average, the proportion of stem volume to total volume was 63% with a range between 11% and 92%. The average branch volume was 37% with a range from 7% to 89%. Plots of branches, stem and total tree volume (m^3) versus tree dbh (cm) are shown in Figure 1.

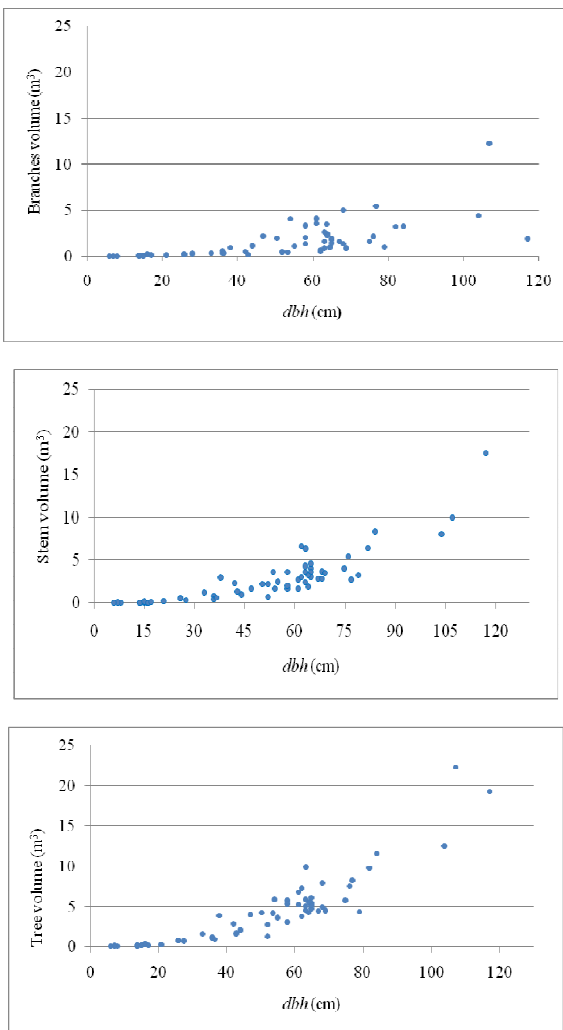


Figure 1. Plots of branches, stem and total volume (m^3) versus tree dbh (cm)

Table 2. Statistics of tree components volume (m^3)

Component	n	Mean	Min.	Max.	St. dev.
Stem	60	2.769	0.006	17.502	2.994
Branches	60	1.599	0.004	12.285	1.984
Total tree	60	4.367	0.017	22.372	4.358

2.3. Modelling of Volume

2.3.1. The Form Factor Approach

The shape of a tree can be approximated by a solid of revolution, or by a combination of several solids of revolution (neiloids, cones and paraboloids). Thus, if the basal area and the height are known, the volume of a tree can be estimated using a form factor ($g \times h \times f$). As mentioned earlier, it has been common to use a fixed f of 0.5, even though f varies with many factors, for example tree size. To assess the accuracy of this practice, we therefore used $f=0.5$ in prediction of total volume for the trees observed in our data, and then differences ($diff$) from the observed values were calculated (observed minus predicted). Furthermore, we also calculated the mean f for each of the volume components; total volume (f_{tm}), stem volume (f_{sm}), and branch volume (f_{brm}). These mean factors were also used in prediction of volume of their respective components, and $diff$ -values were calculated. This approach is similar to using the fixed f , but it is calibrated for each component. However, since f is dependent on tree size, volume predictions using a mean f will be biased, at least for specific ranges of tree size. Thus, we also developed component specific models of f dependent on dbh (Model 1). As for the approach using a mean f , volumes were also in this approach predicted, but using predicted f dependent on dbh . Similar to the other approaches, $diff$ -values were calculated.

$$f_x = a + b \times \ln(dbh) \quad (\text{Model 1})$$

where f = form factor, subscript x is either t (total volume), s (stem volume) or br (branch volume), a and b are parameters to be estimated. To represent v directly, model 1 can be incorporated in the general volume equation as in model 2.

$$v = g \times h \times (a + b \times \ln(dbh)) \quad (\text{Model 2})$$

2.3.2. Single Tree Volume Models

Although the general volume model relying on basal area, height and form factor, has some intuitive and nice properties, it is very common to fit empirical models dependent on h and/or dbh . Depending on allometry, different model forms may be appropriate. In the current study we initially considered a number of different model forms found in the literature. The alternative model forms were evaluated according to the root mean square error (RMSE). In addition, statistical significance and signs of the model parameter estimates were considered. We chose to present results for two (Models 3 and 4) nonlinear models adopted from Segura and Kanninen (2005) and Malimbwi et al. (1994). The models were fitted using the PROC NLIN procedure of SAS. A broad range of initial values for the model parameters were tested to ensure global convergence solutions.

$$v = \exp(a + b \times \ln(dbh)) \tag{Model 3}$$

$$v = \exp(a + b \times \ln(dbh) + c \times \ln(h)) \tag{Model 4}$$

where *a*, *b* and *c* are model parameters to be estimated. The model parameters are presented in Table 4.

2.3.3. Model Testing

The relative mean prediction error (MPE%) were computed from the calculated differences (*diff*) between the predicted and the observed volumes, both for the approaches based on the general volume equation and the empirical models. The MPE% was calculated both for all observations and for different size classes according to both *dbh* and *h*. Student *t*-tests were applied to test if the differences were significantly different from zero (Triola, 2012).

$$MPE\% = (\sum (diff/n)/MOV) \times 100 \tag{5}$$

where MOV is the mean observed volume (m³).

The results from application of the general volume equation are displayed in Table 3, and the results from application of the empirical models can be found in Tables 5-7. For comparison, results from the use of the general volume equation with *f* dependent on *dbh* (Model 2) are shown in these tables as well.

2.3.4. Test of Previously Developed Volume Models

Similarly, we also applied a number of previously developed total tree volume models (Munishi and Shear, 2004; Adekunle, 2007; Adekunle et al., 2013) and then compared predicted volumes with observed volumes by means of MPE values that were tested for statistical significance by means of student *t*-tests. The results are shown in Table 8.

From Munishi and Shear (2004) we applied the following model:

$$v = 194.8803 \times dbh^{2.3982}$$

The model was based on rainforest data from Usambara and Uluguru mountains in Tanzania. A total of 120 trees from 30 different tree species ranging from 13.5 cm to 195.0 cm in

dbh were included in their modelling data. The volume determination of the trees were not based on destructive sampling, but computed as a product of *g* and *h* adjusted for taper by the cone formula ($v = g \times h/3$). In their study, *h* was defined as the height from ground to 90% of the crown length.

From Adekunle (2007) we applied the following volume model:

$$v = 43.36(1 - e^{-0.067 \times g})^3,$$

where *e* is the base of the natural logarithm. The model was based on data from a rainforest in southwest Nigeria. A total of 421 trees from 61 different tree species ranging from 20 cm to 200 cm in *dbh* were included in their modelling data. The volume determination of the trees was not based on destructive sampling, but computed from Newton's formula (Husch et al., 2003) based on basal area of the trees at the base, at middle of the bole height and at the top of the bole height, and *h*. In their study *h* was defined as the height from ground to the top of the crown and bole height was defined as from ground to where the first large branch protrudes the stem.

From Adekunle et al. (2013) we applied the following model:

$$\ln(v) = 2.76 + 1.33 \times \ln(g),$$

The model was based on data from tropical moist forest in the state of Uttar Pradesh in northern India. A total of 535 trees from 25 different tree species, with *dbh* range from 10.2 to 63.5 cm were included in the modelling data. The volume determination and definitions of *h* and bole height was exactly the same as described above for Adekunle (2007).

3. Results

The *f_{tm}* was 0.59 and ranged between 0.15 and 1.15, *f_{sm}* was 0.36 and ranged between 0.06 and 1.0 and *f_{brm}* was 0.23 and ranged between 0.03 and 0.70 (Figure 2). The model fits were relatively poor (low Pseudo-R² values), but all form factors were significantly decreasing degressively with tree *dbh*.

Table 3. Performance of the general volume equation over dbh and h classes by using different form factors

Class	n	Total volume (m ³)			Stem volume (m ³)			Branches volume (m ³)			
		Observed	<i>f</i> =0.5	<i>f_t</i>	<i>f_{tm}</i>	Observed	<i>f_s</i>	<i>f_{sm}</i>	Observed	<i>f_{br}</i>	<i>f_{brm}</i>
			MPE%	MPE%	MPE%		MPE%	MPE%		MPE%	
dbh≤28	14	0.231	-31.2*	-3.9	-18.6*	0.136	-3.6	-16.5	0.094	-4.3	-21.3
dbh≤28	15	2.533	-14.2	-0.4	1.5	1.577	-2.7	-1.1	0.956	3.4	6.3
28<dbh≤55	15	5.435	-11.3	-4.2	5.0	3.375	-5.1	2.6	2.059	-2.7	9.5
55<dbh≤64.5	16	8.705	8.2	6.4	28.1*	5.620	2.9	20.3**	3.085	12.7	42.8
h≤20.4	14	0.282	-32.9*	-9.3	-20.6*	0.166	-7.9	-17.9	0.116	-11.2	-24.2
20.4<h≤27.6	16	3.215	-9.2	-0.8	7.5	1.943	0.7	7.8	1.271	-3.2	7.3
27.6<h≤34	15	5.239	-6.4	-0.6	10.8	3.176	1.2	10.9	2.064	-3.2	11.1
h>34	15	8.537	5.4	5.0	24.7*	5.672	-1.5	13.8	2.864	17.9	46.9
All	60	4.367	-1.6	-0.9	16.5	2.769	-1.5	3.7	1.598	6.1	25.7

* = *p*<0.05, ** = *p*<0.01, *** = *p*<0.001

Table 3 shows the MPE-values when applying the general volume equation ($v = g \times h \times f$) using *f*=0.5 and predicted *f_t*, *f_s*

and *f_{br}*, in addition to the observed *f_{tm}*, *f_{sm}* and *f_{brm}*. The results are distributed over different tree size classes (*dbh* and *h*) and

for all trees, irrespective of size. For the $f=0.5$, total volume of small tree size classes was significantly underpredicted and magnitudes of underprediction decreased with increase of tree size classes. For the f_t , f_s and f_b , the overall MPE values increased from total to branches volume, but were not significantly different from zero. The table shows that application of the f_{tm} significantly underpredicted and

overpredicted total volume in small tree size and larger tree classes, respectively. For f_{sm} it significantly overpredicted stem volume in larger tree size classes. For the f_{bm} , there was no significant over- or underpredictions; however, the magnitudes of underprediction and overprediction were higher in larger tree size classes both in terms of dbh and h .

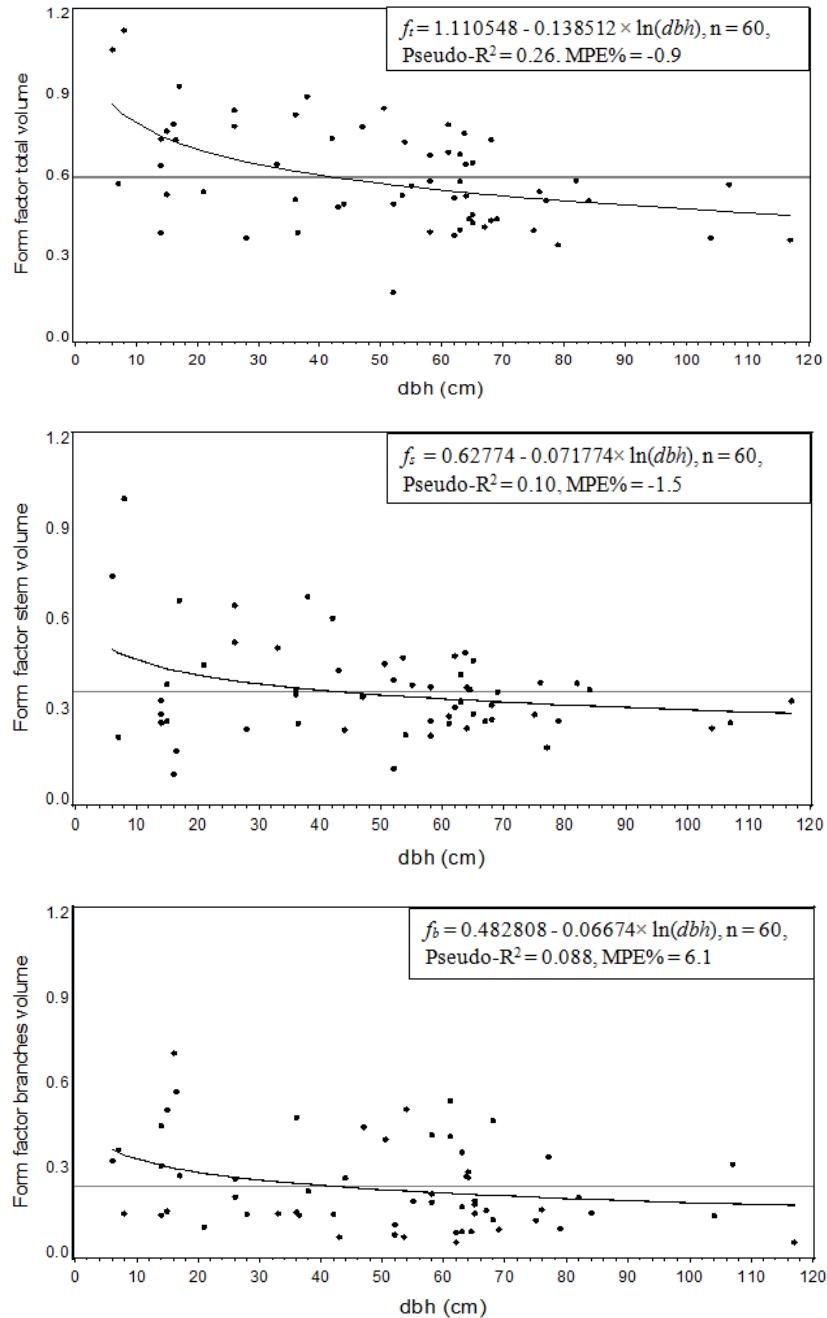


Figure 2. Plots of form factor for total, stem and branches volume over tree dbh (cm)

The fit of all alternative models are presented in Table 4. Based on RMSE, Pseudo- R^2 , and the significance of parameter estimates, models 2, 3 and 4 were judged to be the best for total and stem volume, while models 2 and 3 were the best for branches volume. For branches volume, model 4 with both dbh and h as predictor variables, had insignificant

parameter estimate ($p < 0.05$) for h . Generally when considering the tree components, the Pseudo- R^2 values decreased from total tree to branches.

The performances of best models for total, stem and branches volume are presented in Tables 5 to 7. The overall MPE values for the total volume models ranged between -

0.9% and 0.0%. In tree size classes, models 3 and 4 significantly overpredicted volume of small tree size classes ($dbh \leq 28$ cm and $h \leq 34$) (Table 5). For the stem volume, the overall MPE values for the models ranged between -2.0% to -0.9%. No significant under- or overpredictions were

observed over tree size classes (Table 6). For branches volume, the overall MPE values were 6.1 % and 1.8% for models 2 and 3, respectively. However, model 3 significantly overpredicted volume of branches in small tree size classes (Table 7).

Table 4. Parameter estimates for the different models for prediction of total (vt), stem (vs) and branches volume (vbr)

Dependent variable	Model		RMSE (m ³)	Pseudo-R ²	MPE%
vt	2	$g \times h \times (1.414741 - 0.21174 \times \ln(dbh))$	1.343	0.91	-0.9
vt	3	$\exp(-7.41201 + 2.1901527 \times \ln(dbh))$	1.537	0.88	-0.3
vt	4	$\exp(-8.12477 + 1.653497 \times \ln(dbh) + 0.852048 \times \ln(h))$	1.355	0.91	0.0
vs	2	$g \times h \times (0.6251 - 0.07064 \times \ln(dbh))$	0.881	0.91	-1.5
vs	3	$\exp(-8.89962 + 2.428768 \times \ln(dbh))$	1.176	0.85	-2.0
vs	4	$\exp(-10.4281 + 1.434108 \times \ln(dbh) + 1.63197 \times \ln(h))$	0.823	0.93	-0.9
vbr	2	$g \times h \times (0.789641 - 0.14111 \times \ln(dbh))$	1.508	0.43	6.1
vbr	3	$\exp(-6.88089 + 1.831149 \times \ln(dbh))$	1.469	0.46	1.8
vbr	4	$\exp(-6.80703 + 1.894992 \times \ln(dbh) - 0.09859NS \times \ln(h))$	1.481	0.46	1.7

NS: Insignificant parameter estimate

Table 5. Performance of best models (models 2, 3 and 4) for total volume over dbh and h classes

Class	n	Observed volume (m ³)	Models		
			2	3	4
			MPE%	MPE%	MPE%
$dbh \leq 28$	14	0.231	-3.9	24.1**	24.6**
$28 < dbh \leq 55$	15	2.533	-0.4	-5.7	4.4
$55 < dbh \leq 64.5$	15	5.435	-4.2	-8.3	-4.4
$dbh > 64.5$	16	8.705	6.4	5.3	1.9
$h \leq 20.4$	14	0.282	-9.3	33.9*	16.3*
$20.4 < h \leq 27.6$	16	3.215	-0.8	19.4	3.7
$27.6 < h \leq 34$	15	5.239	-0.6	1.1	-0.4
$h > 34$	15	8.537	5.0	-10.1	-0.5
All	60	4.367	-0.9	-0.3	0.0

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Table 6. Performance of best models (models 2, 3 and 4) for stem volume over dbh and h classes

Class	n	Observed volume (m ³)	Models		
			2	3	4
			MPE%	MPE%	MPE%
$dbh \leq 28$	14	0.136	-3.6	-4.1	-7.2
$28 < dbh \leq 55$	15	1.577	-2.7	-14.8	2.0
$55 < dbh \leq 64.5$	15	3.375	-5.1	-10.8	-3.5
$dbh > 64.5$	16	5.620	2.9	6.5	-0.1
$h \leq 20.4$	14	0.166	-7.9	9.5	-19.5
$20.4 < h \leq 27.6$	16	1.943	0.7	18.4	-12.0
$27.6 < h \leq 34$	15	3.175	1.2	2.4	-2.9
$h > 34$	15	5.672	-1.5	-12.2	4.8
All	60	2.769	-1.5	-2.0	-0.9

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Table 7. Performance of best models (models 2 and 3) for branches volume over dbh and h classes

Class	n	Observed volume (m ³)	Models	
			2	3
			MPE%	MPE%
$dbh \leq 28$	14	0.094	-4.3	80.6**
$28 < dbh \leq 55$	15	0.956	3.4	8.2
$55 < dbh \leq 64.5$	15	2.059	-2.7	-6.2
$dbh > 64.5$	16	3.085	12.7	2.9
$h \leq 20.4$	14	0.117	-11.2	80.3**
$20.4 < h \leq 27.6$	16	1.272	-3.2	18.9
$27.6 < h \leq 34$	15	2.064	-3.2	-2.6
$h > 34$	15	2.864	17.9	-6.0
All	60	1.599	6.1	1.8

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

The results of applying the previously developed volume models (Munishi and Shear, 2004; Adekunle, 2007; Adekunle et al., 2013) to our modelling dataset are presented in Table 8. Generally all models significantly underpredicted

total tree volume. The display of the models developed in the present study (models 3 and 4) and the model developed by Munishi and Shear (2004) over extrapolated *dbh* are shown in Figure 3.

Table 8. Performance of total volume models developed by Munishi and Shear (2004), Adekunle (2007), and Adekunle et al. (2013) over *dbh* and *h* classes

Class	n	Observed volume (m ³)	Munishi& Shear 2004	Adekunle (2007)	Adekunle et al. (2013)
			MPE%	MPE%	MPE%
<i>dbh</i> ≤28	14	0.231	-26.0*	-19.8	-45.7**
28< <i>dbh</i> ≤55	15	2.533	-32.6*	-49.1**	-38.1**
55< <i>dbh</i> ≤ 64.5	15	5.435	-30.3**	-53.9***	-30.9**
<i>dbh</i> >64.5	16	8.705	-14.3	-51.6***	-7.3
<i>h</i> ≤20.4	14	0.282	-16.7	-16.6	-35.4**
20.4< <i>h</i> ≤27.6	16	3.215	-9.8	-39.5***	-11.1***
27.6< <i>h</i> ≤34	15	5.239	-22.0**	-15.7***	-21.2***
<i>h</i> >34	15	8.537	-27.2**	-58.5***	-21.5***
All	60	4.367	-22.1***	-51.6***	-19.5***

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

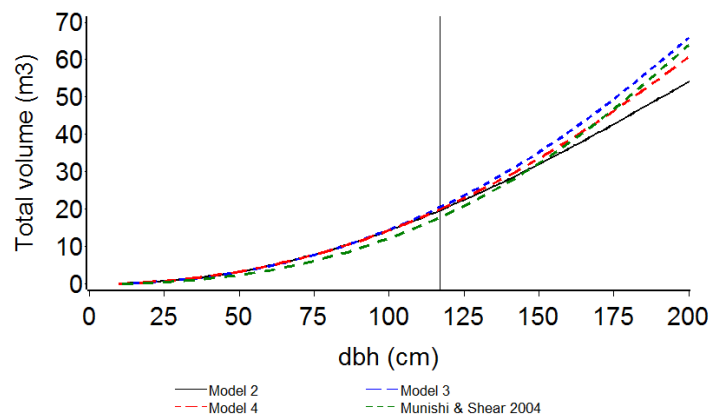


Figure 3. Display of the total tree volume models developed in this study (Models 2, 3 and 4) and the model developed by Munishi and Shear (2004) over *dbh*. When applying models 2 and 4, *h* was predicted by means of diameter-height relationship models developed by Mugasha et al. (2013). Vertical line shows *dbh* range of the modelling data

4. Discussion

The number of sample trees used for modelling in the present study (60) was relatively high compared to many studies on rainforests in sub-Saharan Africa (Henry et al., 2011). Some of the previously developed volume models were based on more sample trees than used in the present study, however the volume determination was in many cases not based on destructive sampling, but computed from different tree parameters (Munishi and Shear, 2004; Adekunle, 2007). The selection of sample trees in this study was based on a previous systematic sample plot inventory to secure species distribution to be representative and that the *dbh* range was covered. Although 34 different tree species is a relatively low number in relation to the over 200 species that are present in the study area (Frontier Tanzania, 2001), we were able to include the most frequently occurring species in addition to some of the rare species (see Appendix).

To our knowledge, no general model for total tree volume has previously been developed based on destructive sampling

for rainforests in Africa. When considering the high diversity of tree forms in rainforests (Feldpausch et al., 2011; Mugasha et al., 2013), it is quite obvious that the accuracy of observed volume will be more accurate with destructive sampling as compared to if volume is computed analytically from tree parameters measured on standing trees like Munishi and Shear (2004) and Adekunle (2007) did. In the data collection we also emphasized the accuracy in the measurements of the independent variables (*dbh* and *h*) by for example considering prevailing rules regarding leaning trees and buttresses (Dietz and Kuyah, 2011). Measuring tree height in closed-canopy forests is of course generally challenging (Larjavaara and Muller-Landau, 2013; Hunter et al., 2013), but at least we used a Vertex hypsometer in the measurements. This instrument is more flexible and probably provides more accurate height measurement than most other instruments.

As previously mentioned, the general volume equation with $f = 0.5$ routinely has been applied in Tanzania across many forest types (Zahabu, 2008; Mpanda et al., 2011; Kashaigili et

al., 2013). Since the form factor depends on the diameter-height relationship of trees, it will not only vary between forest types but also between sites within the same forest type. The mean form factor based on total volume for our site was 0.59. Thus, by applying a form factor of 0.5 for the trees we would immediately produce a bias in total volume. However, also when applying the mean tree component specific form factor, biases were produced (Table 3). In addition to a general overprediction of total, stem and branches volume (MPE%=16.5%, 3.7 % and 25.7%), we also got a ~20% underprediction of volume for the smallest trees and a ~25% and 28% overprediction for the largest trees. Also for stem volume overprediction of 20.3% was found in *dbh* class of $55 < dbh \leq 64.5$ while for branches volume MPE values in tree size classes ranged between ~-24% to ~47%. Generally there will always be biases between the dependent (form factor) and the independent (*dbh*) variables if the relationship is non-linear (Gertner, 1991). By applying values predicted from the form factor model (Figure 2), the MPE values for total, stem and branches volume was reduced to -0.9%, 1.5% and 6.1%, respectively (Table 3). Continued practices of applying a form factor of 0.5 or a mean form factor derived from a particular sample of trees should therefore be avoided. However, if the form factor models developed in the present study are applied, the volume determination may be reasonably accurate as long as tree allometry of rainforests is not very different from that of our data.

Large parts of the variation in total volume were explained by models 2, 3 and 4 (Table 4). The overall MPE values for the models were less than 1% when tested on the modelling data, but significant differences between observed and predicted values (overprediction and underprediction) were seen for the smallest and largest trees for models 3 and 4 (Table 5). For model 2, no significant MPE% values were seen in any of the size classes. When comparing models 2 and 4, that both require *h* as input in addition to *dbh*, model 2 is therefore recommended. We initially tested several alternative model forms, in addition to model 3, to see if we could reduce MPE% for the smallest trees, but the model presented had the best performance. Since the overprediction of total volume for the smallest trees in absolute terms is small when applying model 3 (and also model 4), and since large trees usually account for a very large part of the total volume in rainforests, volume per unit area will probably in most cases be appropriate. In rainforests under early succession stages with many small trees there might be a slight overprediction of total volume when applying these models.

According to the review of volume models made for sub-Saharan Africa by Henry *et al.* (2011), both models with *dbh* only and models with *dbh* and *h* are commonly used. However, difficulties related to tree height measurements (e.g. Abbot *et al.*, 1997; Segura and Kanninen, 2005; Larjavaara and Muller-Landau, 2013; Hunter *et al.*, 2013) have made models with *dbh* only as independent variable the most commonly used. For the total volume models developed in the present study little was gained in terms of model fit when

including *h* as independent variable in addition to *dbh* (Table 4). Therefore, when considering the challenges in height measurements in rainforests, we in general recommend applying the model with *dbh* only as independent variable (model 3). However, for trees with very large *dbh*, it will probably be safer to apply the model 2 because *h* in such a model has a moderating effect of *dbh* on volume (see Figure 3). For such cases, recently developed general height-diameter models for different forest types in Tanzania including rainforests (Mugasha *et al.*, 2013) could be applied if *h* is not available from the inventory.

For the stem volume models, the gain in model fit when including *h* (models 2 and 4) was larger than for the total volume models (Table 4). Since model 2 generally gave lower MPE% values over size classes than model 4, especially for the smallest size classes, we recommend this model. Although the use of the height-diameter models developed by Mugasha *et al.* (2013) will accumulate errors, inclusion of *h* when predicting stem volume will probably improve accuracy as compared to applying the model with *dbh* only (model 3). In the rare cases where all trees are measured for height, for example if accurate stem volumes are needed for forestry licensing systems or for calculating compensation of timber loss due to for example road construction, we clearly recommend to apply model 2.

The model fit of the branches volume models were generally poor. Pseudo- R^2 was much lower than compared to total and stem volume models (Table 4). In addition, for model 4 the parameter estimate of *h* was not significantly different from zero. The high variation in branches volume (see Table 2, Figure 1) is mainly due to a generally high diversity in branching patterns in tropical rainforest as a result of high species diversity, and large differences in light availability, succession stages and tree density (Sterck and Bongers, 2001). The high variation, however, is also affected by criterion used for separating stem and branches volume; stem comprised of volume from the stump to the point where the first large branch protruded the stem, while branches comprised the volume of remaining of the tree up to a branch diameter of 2.5 cm. The point where the first large branch protrudes the stem of course varies a lot between trees, and is thus affecting the variation in branches volume. Similar large variations in branches volume have also been observed by Dadzie (2013) in Ghana's tropical rainforests. Although the variation in branches volume was large in our modelling data, the overall MPE% of model 3 was near zero (Table 7), although it significantly overpredicted branches volumes for smaller trees. This model 3 may therefore still provide useful information on branches volume quantities in rainforests.

The application of the previously developed total tree volume models on our modelling data revealed significant underpredictions of volume (Table 8). We cannot rule out different site conditions and tree allometry as reasons for the underprediction when applying the model developed by Munishi and Shear (2004), but since their model was partly based on data from Usambara Mountains in Tanzania, where also our data were collected, this explanation is probably not

the most important. The method applied to determine observed volume is a more likely explanation for the underprediction, especially since the cone formula, indicating a form factor of 0.33, which is much lower than the one observed for our data, was applied. It is therefore reason to believe that our models predict a more realistic volume than the previously developed model for Tanzania. The two other models (Adekunle, 2007; Adekunle et al., 2013) tested for their potential application in Tanzanian rainforests clearly also demonstrated their inappropriateness, irrespective of whether this was due to different site conditions or allometry, or to the analytical (non-destructive) method used to determine observed volume.

The developed volume models in this study are based on data from one rainforest site, and we know little about how well these data are representing rainforests elsewhere in Tanzania. However, most of the rainforests in the country, including Amani Nature Reserve where our data were collected, are parts of the Eastern Arc Mountains, and similarities regarding growth conditions and allometry are likely present. As long as the allometry of the trees obviously is not different from that of Amani Nature Reserve, we therefore believe that our volume models may be applied for rainforests outside this site. However, further testing of the developed models, if data from other rainforest sites in Tanzania becomes available, is recommended.

5. Conclusions

The present study was the first to develop total tree, stem

and branches volume models for rainforests in south-eastern Africa based on destructive sampling. The results showed that large parts of volume variation were explained by the models and that they performed relatively well when tested over different tree size classes. When considering the challenges in height measurements in rainforests, we in general recommend applying model 3 with *dbh* only as independent variable. For large trees we recommend model 2 because of the moderating effect *h* has on volume predictions. If accurate stem volumes are needed for forestry licensing or for calculating compensation of timber loss, we clearly recommend model 2. As long as the allometry of the trees obviously is not different from that of our study site, the developed models may also be applied for rainforests elsewhere in Tanzania, but further testing of the models is also recommended. Continued practices of applying the general volume equation with a form factor of 0.5 should be avoided.

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Appendix

List of trees used for development of volume models

Species	<i>dbh</i> (cm)	<i>h</i> (m)
<i>Maesopsis eminii</i> Engl.	63.6	41
<i>Allanblackia stuhlmannii</i> (Engl.) Engl.	21	15.6
<i>Maesopsis eminii</i> (Engl.)	33	30
<i>Allanblackia stuhlmannii</i> (Engl.) Engl.	36	24
<i>Synsepalumcerasiferum</i> (Welw.) T.D.Penn.	65	32
<i>Cephalosphaerausambarensis</i> (Warb.) Warb.	65	43.2
<i>Myrianthusholstii</i> Engl.	36	12.4
<i>Synsepalumcerasiferum</i> (Welw.) T.D.Penn.	28	27.5
<i>Myrianthusholstii</i> Engl.	26	18.5
<i>Anisophylleaobtusifolia</i> Engl. &Brehmer	36.5	24.8
<i>Zanhagolungensis</i> Hiern	55	26.4
<i>Isobertia scheffleri</i> (Harms)	67	31
<i>Allanblackia stuhlmannii</i> (Engl.) Engl.	42	27.9
<i>Englerodendronusambarensis</i> (Harms)	26	16.3
<i>Funtumiaafricana</i> (Benth.) Stapf	14	11.1
<i>Annickia kummeriae</i> (Engl. & Diels) Setten & Maas	8	6.4
<i>Maesopsis eminii</i> Engl.	16	20.4
<i>Blighiaunijugata</i> Baker	14	10
<i>Annickia kummeriae</i> (Engl. & Diels) Setten & Maas	15	12.3
<i>Isobertia scheffleri</i> (Harms)	64.5	38.6
<i>Quasia undulate</i> (Guill. &Perr.) F.Dietr.	44	26.9
<i>Alchorneahirtella</i> (Benth.)	7	7.9

Species	dbh (cm)	h (m)
<i>Macaranga capensis</i> (Baill.) Benth. ex Sim.	6	8.4
<i>Greenwayodendron suaveolens</i> (Engl. & Diels) Verdc.	14	15.8
<i>Isobertia scheffleri</i> (Harms)	15	17
<i>Parinari excelsa</i> Sabine	53.5	35
<i>Sorindeia madagascariensis</i> (Thou.) ex DC.	16.5	13.5
<i>Cephalosphaera sambarensis</i> (Warb.) Warb.	62	46.7
<i>Leptonychia sambarensis</i> K. Schum.	17	8
<i>Lannea welwitschii</i> (Hiern) Engl.	65	24
<i>Croton sylvaticus</i> Hochst.	52	34.7
<i>Newtonia buchanani</i> (Baker f.)	107	44
<i>Cephalosphaera sambarensis</i> (Warb.) Warb.	117	50
<i>Sapium ellipticum</i> (Hochst.) Pax	104	40
<i>Anthocleista grandiflora</i> (Gilg.)	63	36.8
<i>Annickia kummeriae</i> (Engl. & Diels) Setten & Maas	52	26.5
<i>Parinari excelsa</i> Sabine	54	35.5
<i>Newtonia buchanani</i> (Baker f.)	84	41.5
<i>Funtumia africana</i> (Benth.) Stapf	76	31
<i>Croton sylvaticus</i> Hochst.	64	25.6
<i>Strombosia scheffleri</i> Engl.	47	29
<i>Chrysophyllum perpulchrum</i> Mildbr.	75	33
<i>Harungana madagascariensis</i> Lam. ex Poir.	61	23
<i>Polyscias fulva</i> Hiern	50.5	25
<i>Xylopii aethiopia</i> (Dun.) A. Rich.	61	34
<i>Quasia undulate</i> (Guill. & Perr.) F. Diétr.	82	32
<i>Annickia kummeriae</i> (Engl. & Diels) Setten & Maas	62	33
<i>Syzygium guineense</i> (Willd.) DC.	64	27
<i>Isobertia scheffleri</i> (Harms)	63	33
<i>Anisophyllea obtusifolia</i> Engl. & Brehmer	68	32
<i>Allanblackia stuhlmannii</i> (Engl.) Engl.	43	23
<i>Morinda asterolocera</i> K. Schum.	79	26
<i>Xylopii aethiopia</i> (Dun.) A. Rich.	58	38
<i>Macaranga capensis</i> (Baill.) Benth. ex Sim.	58	30
<i>Zanahogolungensis</i> Hiern	77	35
<i>Antiaristoxicaria</i> (Pers.) Lesch.	69	27
<i>Parinari excelsa</i> Sabine	58	30
<i>Erythrophleum suaveolens</i> (Guill. & Perr.) Brenan	68	30
<i>Maesopsis eminii</i> Engl.	38	38
<i>Synsepalum solo</i> (Engl.) Engl.	63	24

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