

Allometric equations, wood density and partitioning of aboveground biomass in the arboretum of Ruhande, Rwanda

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ARTICLE INFO

Keywords:

Biomass carbon
Biomass estimation models
Climate mitigation
Plantation forests
Southern Rwanda

ABSTRACT

There is growing interest in plantation forests throughout Africa because of their role in environment, economy and people's livelihoods. However, the contribution of planted forests to climate mitigation is poorly understood, partly due to lack of allometric equations for biomass estimation. This study aimed to determine wood density and biomass fractions in aboveground components, and to develop biomass estimation equations for multispecies plantation forests in the arboretum of Ruhande in Rwanda. Allometric equations were developed by regressing diameter at breast height (DBH) alone or in combination with height or wood density or age of trees against the biomass of 45 trees harvested from a 200-ha site. Biomass estimates obtained from destructively sampled trees were up-scaled to estimate the amount of carbon stocked in the arboretum of Ruhande, assuming a stem density of 250 stems per ha. Wood density varied among the species but not tree size. The greatest fraction of aboveground biomass was allocated to stems (71–77%) compared to branches (19–27%) and leaves (1–8%) and varied by species. Equations developed fit the data well with DBH explaining over 90% of the observed variation in aboveground and stem biomass. Including height or wood density as supporting parameters reduced the relative error for aboveground biomass by 6.4 and 8.0% and improved model fit by 2.1 and 2.9%, respectively. Akaike information criterion (AIC) showed that wood density (AIC=63.6) and height (AIC=48.2) were the most suitable parameters to support DBH as a proxy for aboveground and stem biomass, respectively. Allometric equations developed in this study are useful tool for estimating carbon stocks of plantation forests in Rwanda and can enhance the accuracy of biomass predictions where site-specific equations rather than generalized models are recommended. Further studies focusing on development of allometric equations on belowground biomass in such systems are recommended.

1. Introduction

Estimation of biomass carbon has gained much attention and significance because of potential market-based instruments that reward afforestation and reforestation activities as climate mitigation actions. This follows scientific evidence and consensus that unabated climate change threatens sustainable development and worsens other pressures that affect people and the environment (IPCC, 2014). Consequently, calls to combat climate change and its impacts have increased, with forests emerging as important nature-based solutions for climate change mitigation (Grassi et al., 2017). The Paris Agreement injected a new impetus into calls to fight climate change, placing more emphasis on

the role of forests in maintaining and enhancing sinks and reservoirs of carbon (Grassi et al., 2017). Forests are, thus, expected to contribute to emission reductions as pledged by countries that have ratified the agreement. Apart from asking countries to take voluntary climate action, the agreement also invites countries to account for anthropogenic greenhouse gases in their nationally determined contributions. These developments have created a clear need for robust and viable methods for estimating biomass carbon in all land use systems, including plantation forests.

Estimation of biomass can be achieved by direct or indirect methods. Direct methods involve measuring actual biomass of plants in quadrats. All trees within a quadrat are harvested and the weight of

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stem, branches, leaves, stump or roots determined. Oven dried mass of these components is then determined and summed to obtain total biomass of a tree. The direct method is the most accurate approach of assessing dry mass of plants (Brown, 1997; Gibbs et al., 2007). It also allows development of biomass estimation equations, which can be used to obtain biomass from ground-based measurements (Brown, 1997). However, cutting and weighing all trees in an area is time consuming, labor intensive and not allowed in certain areas or on species that are under protection or threatened (Gibbs et al., 2007). Direct method is also restricted to a small area or small tree sample sizes as it is not feasible to conduct large-scale biomass estimation using destructive sampling (Brown, 1997; Gibbs et al., 2007). Besides, biomass estimates would be affected by the time when harvesting is done, due to variability in phenology and seasonality in growth since (Borchert et al., 2015). Indirect methods of biomass estimation (e.g. biomass estimation equations or geographic information systems or remote sensing) have therefore been developed to avoid drawbacks of direct method (Petrokofsky et al., 2012).

Allometric equations are the most widely used means for estimating tree biomass. To develop allometric equations, trees of different sizes are felled and the weights of component determined (Dietz and Kuyah, 2011). Mathematical expressions are then used to describe the regression between the dry weights of tree components and measurement of DBH or tree height or wood density or crown area. Once developed, the equations are applied to inventory data to provide a non-destructive way of estimating biomass. There are efforts to develop non-destructive alternatives for developing allometric equations, for example using functional branch analysis (FBA) (MacFarlane et al., 2014; van Noordwijk and Mulia, 2002). However, FBA is still at infancy and has only been tested for trees in agricultural landscapes (MacFarlane et al., 2014; van Noordwijk and Mulia, 2002). In addition, FBA require expert to climb trees or equipment that can measure various parts of a tree to obtain the necessary measurements for calibration (MacFarlane et al., 2014). Destructive sampling therefore remains the most feasible way of developing allometric equations, and data harvested for establishing allometric equations can serve to calibrate non-destructive approaches (Petrokofsky et al., 2012).

Allometric equations exhibit diverse relationships depending on tree species, terrains, temperature and rainfall gradients (Chave et al., 2014). Consequently, variations in allometric coefficients account for differences in biomass estimates in different contexts. The accuracy of biomass estimates can be improved by developing equations that account for the sources of variation in the allometric coefficients. For example, DBH is widely recognized as the most robust parameter for estimating tree biomass. The applicability of DBH in biomass estimation cuts across different ecosystems (e.g. forestry or agroforestry), species, or growth forms (e.g. shrubs, lianas or trees). DBH is also highly correlated with biomass and can be measured easily with high accuracy compared to other variables (Brown, 1997). However, DBH alone may not be adequate for estimation of biomass where tree geometry is variable. For example, trees planted closely tend to develop small crowns that are even while free standing trees often have regular widespread crowns (Moncrieff et al., 2014). Fast growing trees tend to have low wood density compared to trees that grow slowly (Pretzsch et al., 2018). It is therefore important to use DBH in combination with other dendrometric variables or site characteristics when estimating biomass of trees whose geometry differ because of diversity of species and site quality. Wood density is one of the variables that support DBH as a proxy for biomass estimation (Nam et al., 2016). Wood density values can be obtained from literature or determined in the field. The accuracy of biomass estimates from allometric equations that includes wood density from empirical values or literature is not known.

Estimation of biomass in Rwanda is constrained by lack of allometric equations applicable to different forest ecosystems. A study by Nduwamungu (2011) revealed that no comprehensive forest inventory has been carried out so far on plantation forests in Rwanda.

Much of the biomass estimates in the country e.g. in Nyungwe forest (Nyirambangutse et al., 2017) is derived from general-purpose equations cited in IPCC guidelines (Brown, 1997; Chave et al., 2014, 2005). The application of these equations to forest ecosystems in Africa has been questioned (Basuki et al., 2009; Kuyah et al., 2012a) and instead species-specific and/ or site-specific equations recommended (Basuki et al., 2009). There are some species-specific equations for estimating tree biomass in eastern Africa; for example, for eucalyptus trees in Kenya (Kuyah et al., 2013) and Tanzania (Kilawe et al., 2001); *Grevillea robusta* A. Cunn. ex R.Br., in Uganda (Tumwebaze et al., 2013); *Cedrela serrata* Royle., in Rwanda (cited in Henry et al., 2011); and *Cupressus lusitanica* Mill., in Ethiopia (Berhe et al., 2013). However, application of these equations in plantation forests with mixed species stands is limited by species composition and variations in site conditions. Trees in plantations are grown in even spaced stands compared to trees in natural forests which grow in closed canopies; or trees on farms that often grow in open stands and are regularly managed by pruning or pollarding. Consequently, allometric equations derived from naturally established stands are limited by lack of prescribed management in the naturally established stands as is the case of planted forests; while species-specific equations are limited in their generalized transferability. To bridge the gap, this study determined wood density and biomass fractions in aboveground components, and developed robust and reliable mixed species, site specific biomass estimation equation for forest plantations in Rwanda.

2. Materials and methods

2.1. Site description

The study was conducted in the Arboretum of Ruhande, a plantation forest located on Ruhande hill in the southern Province of Rwanda. The Arboretum is located in the transitional tropical rainforest zone in Huye district at latitude 2°36'55.2"S, longitude 29°44'53.8"E and elevation 1638–1737 m). The climate in South-Western Rwanda is sub-humid with annual mean rainfall of 1232 mm. The rainfall has a bimodal pattern with long rains occurring between March and May and short rains occurring between October to December. There are two dry seasons from January to February and from June to September, corresponding to the short and long dry seasons, respectively. The mean annual temperature in the region is 19.6 °C with a minimum of 13.7 °C and a maximum of 24.6 °C. Soil in arboretum is classified as a Ferralsols. The arboretum was established in 1934 on a 200-ha land that is subdivided into 500 plots of monospecific stands, each measuring 50 × 50 m (Nsabimana, 2009). Prior to establishment of the plantation, the whole of Ruhande was used as human settlement with croplands dominating the landscape. So far there are about 227 tree species in the arboretum. Fifty of these are native to Rwanda. The rest are exotic, including 69 *Eucalyptus* spp., and 57 conifers (Nsabimana, 2009).

2.2. Experimental design

The study included five species (*Eucalyptus saligna* Sm., *Eucalyptus tereticornis* Sm., *C. lusitanica*, *G. robusta* and *C. serrata*) ranging from 22 to 76-year. These species were selected because they dominate the plantation of arboretum of Ruhande, their abundance and importance in agricultural systems and their allometric equations were not yet developed in Rwanda. Each of the species was planted in a plot measuring 50 m × 50 m (2500 m²). Three plots were randomly selected for biomass sampling for *E. saligna* (plots 20, 375 and 259), *E. tereticornis* (plots 16, 450 and 354), *G. robusta* (plots 150, 322 and 347), *C. serrata* (plots 36, 111, 56) and *C. lusitanica* (plots 38, 108 and 320). *E. saligna* and *E. tereticornis* were planted at a spacing of 1.5 × 1.5 m giving a density of 4444 stem per ha while *G. robusta*, *C. serrata* and *C. lusitanica* were planted at 2.5 × 2.5 m, giving densities of 1600 stem per ha. The spacing varies across species due to differences in growth architecture, growth

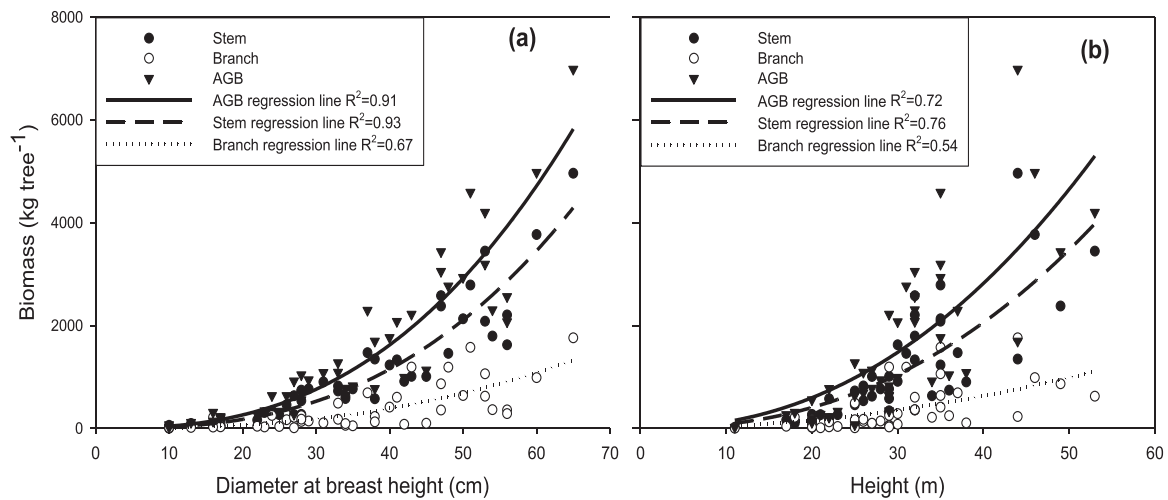


Fig. 1. Relationship between (a) diameter at breast height and aboveground biomass; and (b) height and aboveground biomass of trees sampled in the arboretum of Ruhande in South-Western Rwanda.

requirement of each species (e.g. light, nutrients) and the management plan assigned to each species in arboretum. Assuming management of the plantation for timber and poles, trees thinned at eight years give a density of 250 from 500 stem per ha. A description of the selected species and the variables measured is presented in supplementary material.

2.3. Measurement and biomass sampling

Forty-five trees were selected for destructive sampling (9 trees for each plot) to provide data for assessment of wood density, partitioning of biomass in aboveground components and development of allometric equations. DBH and height measurements were taken prior to felling selected trees. DBH was measured over bark at 1.3 m above the ground using a calliper. Measurement were taken twice (crosswise; to account for irregular stems) and averaged. The caliper was held tight and horizontal to the stem axis when taking diameter measurements. Methods outlined by Kuyah and Dietz (2011) were used to maintain consistence in obtaining diameter measurements for trees with abnormal or irregular stems. Three trees per plot were selected for determination of wood density based on their sizes: small (DBH < 25 cm), medium (DBH between 25 and 45 cm) and large (DBH > 45 cm). Samples for determination of wood density were collected from the stem by drilling around the DBH using a brace and bit. A good spot (i.e. away from branches, swellings or cracks) was selected on the stem where a core was drilled perpendicular to the trunk axis. The material (wood chips) was extracted from the hole using a spatula and their fresh weight determined on electronic balance. The ratio of dry weight of wood chips to volume of the core drilled was used to calculate wood density. The volume of the core was calculated using the formula $v = \pi * r^2 * h$, where r is the radius and h is the depth of the core.

The trees were harvested by cutting at the lowest point and their heights (the length from the base to the highest tip) determined using 50 m measuring tape. Harvested trees were separated into stem, branches and leaves. The leaves were stacked into sacks of known tare weight and their fresh weight determined. The stem and larger branches were partitioned into 2-m long segments and their fresh weight determined using weighing scale. Representative samples of the stem, branches and leaves were taken for determination of fresh weight using an electronic balance (± 0.1 kg). The samples were oven dried at 105 °C (stem and branches) and 70 °C (leaves) to a constant weight and their dry weight determined. The biomass of the stem, branches and leaves was calculated by multiplying sample dry-to-fresh weight ratio with the fresh weight of each component. Aboveground biomass of each tree was determined by summing up the biomass of stem, branches and leaves.

2.4. Data analysis

Scatter diagrams were used to evaluate the relations between dependent variables (stem, branch and aboveground biomass) and independent variables (diameter at breast height and height). Raw data is normally transformed to make the it linear and normally distributed. Transformation of data introduces error which is usually corrected by multiplying the estimate by a correction factor determined from the residual standard error of the regression model (Sprugel, 1983). For this study, the general model of generalized linear models' option of regression analysis was used with gamma distribution and logarithm as a link function to avoid the problem of back transformation. This approach was previously used to develop allometric equations for trees on farms in western Kenya (Kuyah et al., 2012b, 2012a). The power law function ($BM = a * X^b$) and its linear form ($\ln(BM) = a + b * \ln(X)$) was used to predict biomass from independent variables; where BM is the biomass, X is the predictor variable, and a and b are the allometric coefficients. Data was analyzed and graphs produced in the R programming language 3.4.2 (R Core Team, 2018). The following allometric relationships were tested for aboveground biomass and stem biomass using DBH as the main predictor variable, and height (H), wood density (ρ) and age of the trees as additional predictor variables to DBH.

$$\ln(BM) = a + b * \ln(DBH) \tag{1}$$

$$\ln(BM) = a + b * \ln(DBH) + c * \ln(H) \tag{2}$$

$$\ln(BM) = a + b * \ln(DBH) + c(\rho) \tag{3}$$

$$\ln(BM) = a + b * \ln(DBH) + c(age) \tag{4}$$

The natural logarithm of DBH, height, wood density and age were fitted separately so that each can be attributed their own scaling parameter. Kuyah et al. (2012a,b) showed that fitting additional explanatory variables with compound derivatives of DBH, height and wood density produces an identical scaling that inhibits detailed assessment of supporting variables. Allometric equations were built from 45 trees; 40 trees served as a training set while five trees were used for validation. One tree was randomly selected from each diameter class for the validation set, and the remainder used to develop the model. Because five trees are few as a validation set, the process was repeated with different random selections of holdout sets such that each tree in the sample was used once as validation data. Parameters from the different holdouts were averaged to form the equations.

Coefficient of determination (R^2), adjusted coefficient of determination and Akaike information criterion (AIC) were used to assess the equations developed. R^2 was used to assess model fit for equations with a single explanatory variable while adjusted coefficient of determination was preferred for models with two or more explanatory variables. AIC, determined as $AIC = -2\ln(L)+2k$ (L is the maximum likelihood of the fitted equation and k is the total number of parameters estimated from the data) was used to select the most suitable equation i.e. the one with the lowest AIC value (Akaike, 1981). AIC works by balancing changes in the goodness-of-fit versus differences in the number of parameters (Akaike, 1981). The accuracy of the equations (expressed as relative error) was determined by calculating the bias between the predicted and the true biomass measured for each tree as shown in Eq. (5).

$$RE(\%) = \frac{\text{predicted biomass} - \text{measured biomass}}{\text{measured biomass}} \times 100 \quad (5)$$

Separation of the relative error for different diameter class was determined to highlight the bias associated with the equation for trees of different sizes. Biomass estimates obtained from destructively sampled trees were up-scaled to estimate the amount of carbon stocked in the arboretum of Ruhande, assuming a stem density of 250 stems per ha.

3. Results

3.1. Dendrometric relationships

Trees harvested from arboretum of Ruhande in South-Western Rwanda for development of allometric equation varied in size and ranged between 10 and 65 cm in DBH and 11 to 53 m in height (Table 1). DBH had a strong positive correlation with biomass (Fig. 1a), both for aboveground (stem, branches and leaves) biomass ($R^2 = 0.91$) and the stem biomass ($R^2 > 0.93$). However, the correlation between DBH and branch biomass was moderate ($R^2 = 0.67$). The relationship between height and biomass was moderate for all the biomass compartments; aboveground ($R^2 = 0.72$), stem ($R^2 = 0.76$) and branch ($R^2 = 0.54$) (Fig. 1b). The relationship between DBH and height was also moderate and near linear ($R^2 = 0.52$), although a power function model showed a better relationship ($R^2 = 0.57$). The distribution of DBH and height values was slightly negatively skewed though the variance was not high. More than 73% of the heights were between 20 and 40 m, 47% of the DBH were 20–40 cm; while 35% of the DBH were greater than 40 cm and only 11% of the heights were above 40 m.

The stem held most of the aboveground biomass, between 71.9 and 77.4% of the total biomass while the branch and foliage held between 19.4 and 27.4% and 0.7 and 8.1% respectively. The proportion of stem and branch biomass increased slightly with increase in diameter, although differences in individual biomass in each diameter class were large. Leaf biomass declined from 8% in lower DBH class (DBH 20–30 cm) to 4% in trees with DBH > 40 cm; although trees with DBH < 20 cm has lower leaf biomass, 4%. Eucalyptus species had the highest allocation of biomass in stems: 77.4 and 75.4% for *E. saligna*, and *E. tereticornis*, respectively. *C. serrata* allocated less than one percent of the total biomass in leaves while all other species allocated between 5 and 8% of aboveground biomass in leaves. Biomass for the harvested trees amounted to 60.7 Mg, with stem, branches and leaves contributing 50.1, 16.3 and 3.3 Mg, respectively. Using the default carbon fraction 47% recommended by IPCC for tropical trees (IPCC, 2006), and assuming a planting density of 250 stems per hectare, the amount of carbon held in aboveground biomass in the arboretum of Ruhande vary from an average of 111.9 Mg C ha⁻¹ for *C. lusitanica* to 278.0 Mg C ha⁻¹ for *E. saligna* (Table 1).

3.2. Wood density

Wood density for all the tree species ranged between 0.44 and 0.93 g cm⁻³ with a mean of 0.59±0.02 g cm⁻³ and tended to aggregate between 0.5 and 0.6 g cm⁻³. When all species were combined, there was

Table 1 Summary statistics of variables measured for trees sampled in the arboretum of Ruhande. The values represent means and standard deviations for diameter at breast height (DBH), basal area (BA), height and wood density (WD), aboveground biomass (AGB) and carbon (AGB-C). Aboveground biomass carbon per ha (*AGB-C) was obtained by multiplying the mean estimate of the species per plot by the average number of trees in a plot, assumed to be 250 trees per ha.

Species	Family	Age (year)	DBH (cm)	BA (m ² ha ⁻¹)	Height (m)	WD (g cm ⁻³)	Aboveground biomass (Mg tree ⁻¹)			AGB-C Mg tree ⁻¹	*AGB-C Mg ha ⁻¹
							Stem	Branch	Leaf		
<i>Cedrela serrata</i>	Meliaceae	55.0	35.1 ± 15.5	0.11 ± 0.08	26.0 ± 7.7	0.50 ± 0.05	0.34 ± 0.46	0.01 ± 0.02	1.23 ± 1.14	0.58 ± 0.54	144.2
<i>Cupressus lusitanica</i>	Proteaceae	58.7	36.1 ± 13.1	0.11 ± 0.08	25.2 ± 5.0	0.48 ± 0.03	0.14 ± 0.12	0.08 ± 0.05	0.95 ± 0.76	0.45 ± 0.36	111.9
<i>Eucalyptus saligna</i>	Myrtaceae	53.7	40.3 ± 13.8	0.14 ± 0.08	39.6 ± 9.8	0.59 ± 0.04	0.46 ± 0.34	0.12 ± 0.07	2.37 ± 1.61	1.11 ± 0.76	278.0
<i>Eucalyptus tereticornis</i>	Myrtaceae	53.7	35.4 ± 16.6	0.12 ± 0.10	30.9 ± 7.6	0.76 ± 0.08	0.55 ± 0.67	0.11 ± 0.09	2.25 ± 2.29	1.06 ± 1.08	264.2
<i>Grevillea robusta</i>	Proteaceae	38.3	27.1 ± 12.1	0.07 ± 0.06	26.1 ± 4.0	0.62 ± 0.07	0.33 ± 0.38	0.05 ± 0.05	0.95 ± 0.92	0.45 ± 0.43	112.0

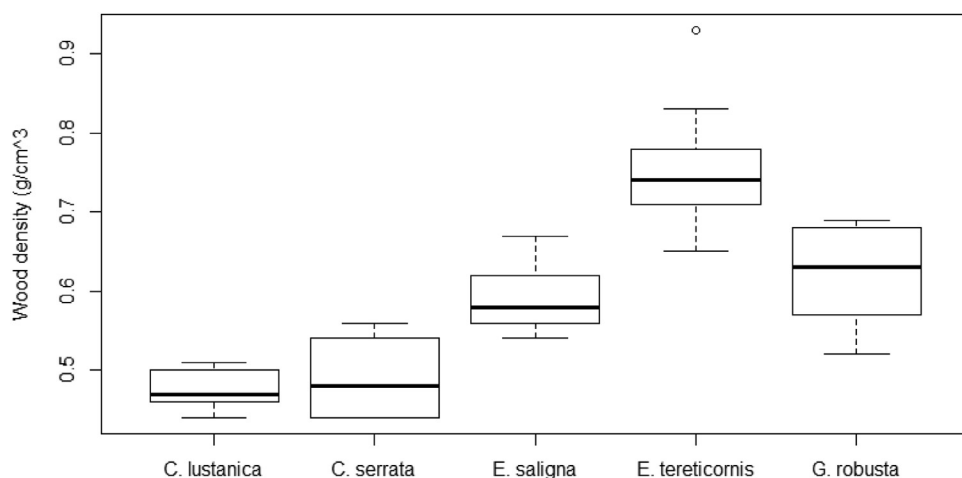


Fig. 2. Wood density of tree species (*Cupressus lusitanica*, *Cedrela serrata*, *Eucalyptus saligna*, *Eucalyptus tereticornis* and *Grevillea robusta*) sampled in the arboretum of Ruhande in South-Western Rwanda.

Table 2.

Allometric equations for estimating aboveground biomass using diameter at breast height (DBH) only (Eq. (6)) or DBH supported by: height (Eq. (7)), wood density (Eq. (8)) and age (Eq. (9)). The letters a, b and c represent the allometric coefficients, R² is the coefficient of determination (R² for Eqs. (6), (8) and (9) represent adjusted coefficient of determination), AIC is the Akaike information criterion while RE represent the relative error of the equation.

Equation	a	b	c	P-value	R ²	AIC	RE (%)
Eq. (6)	0.202(0.403)	2.447(0.116)		<0.001	0.905		14.8
Eq. (7)	0.028(0.492)	1.893(0.142)	1.153(0.221)	<0.001	0.926	70.4	8.4
Eq. (8)	0.403(0.326)	2.451(0.088)	1.334(0.220)	<0.001	0.934	63.6	6.8
Eq. (9)	0.223(0.466)	2.490(0.152)	-0.065(0.146)	0.627	0.882	108	14.3

no clear trend in variability of wood density scatter across trees of different sizes. Mean wood density for different size classes were rather constant, ranging between 0.58–0.61 g cm⁻³; and the differences were not significant. Higher mean wood density values were observed in *E. tereticornis* (0.76 g cm⁻³) than other species (Fig. 2). Mean wood density values for *G. robusta* (0.62 g cm⁻³) and *E. saligna* (0.59 g cm⁻³) were comparable while mean wood densities for *C. serrata* (0.50 g cm⁻³) and *C. lusitanica* (0.48 g cm⁻³) were about the same, but lower than the other species. Differences in wood density among the species were significant (P<0.001). Differences among trees of various ages were also significant (P<0.05).

3.3. Biomass estimation equations

Diameter at breast height alone predicted aboveground biomass with 90.5% accuracy. Including height and wood density as an additional predictor variable to DBH reduced the relative error by 6.4 and 8%, respectively while age did not improve the model accuracy (Table 2). Height and wood density improved model fit marginally, although the improvement by wood density was larger (2.9%) than the improvement by height (2.1%); age sank the model fit by 2.3%. AIC shows that compared to height (AIC = 70.4) and age (AIC = 108), wood density (AIC = 63.6) was the most suitable additional predictor variable to DBH for estimating aboveground biomass of tree in the arboretum of Ruhande.

Table 3 presents biomass prediction equations for stem biomass and the effect of including height, wood density and age as additional predictor variables. Tree diameter alone predicted stem biomass with about 93% accuracy. Height and wood density reduced the relative error by 8.8 and 7.2%, respectively while age did not improve the model accuracy i.e., reduced the relative error by 0.1%. Height data slightly improved model fit by 4.2%, while wood density lowered the model fit by 2%. Age improved model fit by 4%. AIC shows that height (AIC = 48.2) and age (AIC = 47.4) are the most suitable additional predictor variable

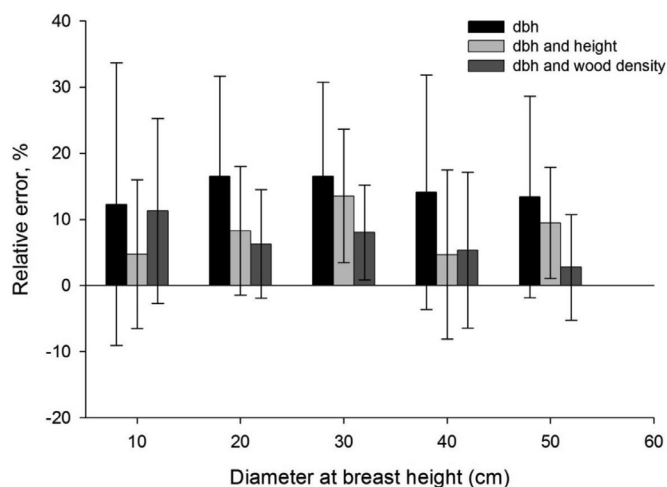


Fig. 3. Separation of the relative error for trees of different sizes for allometric equations developed using diameter at breast height (DBH) alone, DBH and height, and DBH and wood density.

than wood density (AIC = 122.9) for stem biomass. Disaggregation of bias across tree size showed a tendency to overestimate by all equations (Fig. 3). The equations with DBH alone had about the same relative error across tree size, varying between 12.3 and 16.5%. The equation with height as an additional predictor variable improved accuracy for trees with DBH below 30 cm and above 40 cm. The equation with wood density as an additional predictor variable showed increase in accuracy with increase in tree size from 11.3% for smaller trees (DBH <20 cm) to 2.8% for trees with DBH >50 cm.

Table 3.

Allometric equations for estimating biomass of stem using diameter at breast height (DBH) only (Eq. (10)) or DBH supported by: height (Eq. (11)), wood density (Eq. (12)) and age (Eq. (13)). a, b and c represent the allometric coefficients, R^2 is the coefficient of determination (R^2 for Eqs. (11)–(13) represent adjusted coefficient of determination), AIC is the Akaike information criterion while RE represent the relative error of the equation.

Equation	a	b	c	P-value	R^2	AIC	RE (%)
Eq. (10)	0.137(0.354)	2.461(0.102)		<0.001	0.928		10.6
Eq. (11)	0.013(0.310)	1.824(0.089)	1.354(0.139)	<0.001	0.970	48.2	1.9
Eq. (12)	0.268(0.227)	2.480(0.061)	1.395(0.153)	<0.001	0.909	122.9	3.4
Eq. (13)	0.148(0.409)	2.498(0.133)	-0.054(0.128)	0.515	0.968	47.4	10.6

4. Discussion

Diameter at breast height had a strong positive relationship with aboveground biomass and stem biomass, evidenced by a strong correlation between DBH and biomass. This was expected since good fits of R^2 above 85% have been reported for relationships between DBH and aboveground biomass or stem biomass in *E. globulus* plantations of central Ethiopia (Zewdie et al., 2009), *E. saligna* plantation in Tanzania (Kilawe et al., 2001) and farmed eucalyptus species in western Kenya (Kuyah et al., 2013). The relationships between DBH and branch biomass, height and stem or aboveground biomass, and DBH and height were, however, moderate. Moderate to weak trends of height or branch biomass as a function of DBH can be attributed to differences in species attributes and the fact that these structures are short-lived and affected more by changes that alter the scaling relationships between an attribute of the tree and size.

The contribution of different parts of the tree to aboveground biomass varied greatly. The stem had the greatest share of aboveground biomass in all species, followed by branches; leaves had the least quota. Differences in biomass fractions among parts of trees is normally detected when comparing trees of different species or age or trees from different locations. Studies evaluating biomass allocation in eucalyptus plantations in Ethiopia (Zewdie et al., 2009), farmed eucalyptus in western Kenya (Kuyah et al., 2013, 2012a) revealed that the stem component account for the largest portion of total biomass. In contrast, Dimobe et al. (2018) found that the branch biomass had the greatest portion of aboveground biomass for *Combretum glutinosum* Perr. ex DC., and *Terminalia laxiflora* Engl. & Diels., sampled in Burkina Faso. This contrast is probably due to differences in resource allocation, with trees in plantation forest investing more resources for height growth in order to compete favorably for light while trees studied by Dimobe et al. (2018) invested more biomass in branches in order to out-compete neighbors by expanding their canopy. Even though trees accrue biomass as they grow, apportioning among components changes with age, evidenced in this study by the slight increase in the mass fraction of stem and branches with increase in diameter. The results suggest that tree allocate more biomass in woody components compared to leaves as they increase in size.

The results suggest greater carbon storage in eucalyptus spp. as compared to the other species. On average, *E. saligna* had more aboveground biomass carbon, corresponding to large tall trees (mean±SD for DBH = 40.3 ± 13.8; height: 39.6 ± 9.8). In Tanzania, Kilawe et al. (2001) found that *E. saligna* stores more carbon than *Pinus patula* Schiede ex Schltdl. & Cham., at the same diameter because of higher wood density, higher stockings and good stem form compared to *P. patula*. Although *C. lusitanica* and *C. serrata* had the oldest individuals, they did not have larger dendrometric variables or biomass compared to eucalyptus spp.

The amount of aboveground biomass up-scaled for the species (Table 1) using a density of 250 trees per ha is higher than estimates obtained for Gishwati forest reserve, but lower than estimates reported for Nyungwe National Park in Rwanda. Trees in Gishwati forest reserve were found to contain 84.9 Mg ha⁻¹ of aboveground biomass, corre-

sponding to 39.9 Mg C ha⁻¹ (Courard-Hauri et al., 2016). On the other hand, Nyungwe National Park was found to stock low biomass carbon (76 Mg C ha⁻¹) in late successional stages and high (185 Mg C ha⁻¹) in early successional stages (Nyirambangutse et al., 2017). Another study estimated aboveground biomass carbon in different stratum in Nyungwe National Park to range from (mean±SD) 89.49±9.60 to 178.80±26.74 Mg C ha⁻¹ (Van der Heyden, 2016). Biomass carbon up-scaled for the species under this study is also higher than the mean carbon in forest biomass, estimated to be 71.6 Mg ha⁻¹ at global level and 82.8 Mg ha⁻¹ in Africa (FAO, 2010). Because commercial wood exploitation is prohibited in the arboretum, there is a likelihood of increased biomass carbon storage compared to regular plantation forests, where continuous commercial extraction of wood is likely to reduce carbon stocks.

Allometric equations were developed for estimating aboveground biomass of mixed plantation forests in Rwanda. Even though DBH alone provided a fitting proxy for estimation of aboveground and stem biomass, its performance was enhanced by including height and wood density data. This findings agree with previous reports that height and wood density improve the accuracy of biomass predictions (Chave et al., 2014, 2005, 2001; Feldpausch et al., 2012). DBH explained over 90% of the total variation in aboveground biomass and stem biomass and had a relative error of 14.8 and 10.6%, respectively. DBH has been shown to be a strong indicator aboveground biomass in different tropical ecosystems, including natural forests (Basuki et al., 2009; Brown, 1997), plantation forests (Kilawe et al., 2001; Zewdie et al., 2009), agroforestry systems (Kuyah et al., 2012a) and miombo woodlands (Kuyah et al., 2014). Height as a secondary predictor variable reduced the relative error for aboveground biomass by 6% and improved model fit by 2.1%. Height data also reduced the relative error of biomass estimates for stem by 8.7% and improved the goodness of fit by 4.2%. Similar effects of height have been reported for species-specific equations for *E. globulus* coppice plantations (Zewdie et al., 2009) and also in generalized equations (Bastien-Henri et al., 2010; Chave et al., 2001), where inclusion of tree total height data increased R^2 . However, the results vary from those reported for farmed eucalyptus in western Kenya (Kuyah et al., 2013) and other generalized equations (Basuki et al., 2009) where height data neither improved the relationship between DBH and any of the component (aboveground, stem, branch or leaf) biomass nor significantly reduced the relative error. A tropics-wise analysis of height-diameter measurements from 327 plots across four continents revealed that allometric equations that include height reduce errors in estimates of carbon stocks by about 13% (Feldpausch et al., 2012).

Wood density varied across species but not tree size. This observation concurs with reports that wood density varies among and within species (Kuyah et al., 2012a), and that wood density does not necessarily increase with increase in DBH (Baker et al., 2004; Basuki et al., 2009). Wood density values obtained for this study varied considerably when compared to estimates reported in literature (Zanne et al., 2009). Mean wood density for *G. robusta* (0.62±0.07 g cm⁻³), *C. serrata* (0.50±0.05 g cm⁻³) and *C. lusitanica* (0.48±0.03 g cm⁻³) were higher than 0.510–0.517 g cm⁻³ reported for *G. robusta* and 0.390 g cm⁻³ reported for *C. serrata* and *C. lusitanica* (Zanne et al., 2009). Only values for *E. tereticornis* (0.76±0.08) and *E. saligna* (0.59±0.04) were within

the range (0.679–0.972 and 0.56–0.97 g cm⁻³, respectively) reported in literature (Zanne et al., 2009). Even though these means are well within the range of 0.3–0.9 g cm⁻³ reported for tropical African forests (Brown, 1997), differences between estimates obtained in this study and database values suggest that wood density from databases can introduce error in biomass estimates. Except for *G. robusta* and *C. lusitanica* whose estimates are sampled or derived from data collected in Africa, wood density values for *E. saligna* and *E. tereticornis* are from trees sampled in Australia while that for *C. serrata* are from South-East Asia. Wood density from field measurements can therefore greatly improve precision of allometric equations compared to using estimates from literature.

Wood density is a supporting parameter for biomass prediction, and is recommended when developing allometric equations for mixed species or trees of the same species from different locations (Dietz and Kuyah, 2011). Our results agree with reports on pantropical biomass estimation equations (Chave et al., 2014, 2005) and regional mixed-species equations (Basuki et al., 2009; Kuyah et al., 2012a) that wood density data improves biomass prediction when compared to equations that use DBH as the only predictor variable. AIC showed that wood density is the most suitable supporting predictor variable to DBH for aboveground biomass estimation (Table 1) while height is the best proxy for estimation of stem biomass (Table 2) for trees in the arboretum of Ruhande.

5. Conclusion

Establishment of plantation forests with fast growing species appears to be a good strategy to increase biomass carbon storage in the study region as evidenced by biomass carbon in eucalyptus species. We develop highly significant species-specific allometric models for estimation of aboveground biomass of five species (*C. serrata*, *C. lusitanica*, *E. saligna*, *E. tereticornis* and *G. robusta*) that are common in Rwanda. Accurate estimation of aboveground biomass of these trees is crucial for various reasons, including commercial use of wood and timber, sustainable management of forests and estimation their contribution to climate protection through carbon sequestration. Allometric equation combining DBH with height or wood density provided reliable predictions of aboveground and stem biomass with over 91% accuracy. Even though these equations are specific to mixed planted forests in Ruhande, Rwanda; the results maintain the proposition that wood density or height data does improve biomass predictions. Yet, collection of height or wood density data presents several tradeoffs between accuracy, cost and feasibility of measurements. Unlike DBH, height and wood density are not easy to measure in field survey, increase the cost of measurements and can introduce errors in biomass estimates. The most efficient way to optimize accuracy-to-cost trade-offs is to build allometric equations based on destructive measurements of trees that cover the range of species and tree sizes found in the landscape. Future work should focus on valuation of climate related ecosystem services of plantation forests in order to establish possible trade-offs and/or co-benefits.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Competing Interest

None.

Acknowledgment

We thank the management of the Arboretum of Ruhande for logistical support during fieldwork.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2020.100050.

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