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Original article

## Potential species for high biomass production and allometric modelling of even-aged native tropical lowland trees of Indonesia

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### ABSTRACT

The use of native trees is necessary for land restoration and the sequestration of carbon that is stored in forest biomass production in Indonesia. Meanwhile, the biomass prediction model used for native tropical lowland trees of Indonesia is limited to only specific locations and focuses on aboveground biomass (AGB). This study aimed to select and evaluate potential native tree species for high biomass and to develop the best allometric model for estimating tree biomass production (AGB, belowground/BGB, and total/TB) in lowland ecosystems in Indonesia. Trees were selected using the following five criteria: nativeness, ecosystem type, morphological appearance, multipropagation ability, and economic value. Biomass content was quantified for 102 sample trees (56 trees aged 4 years and 46 trees aged 8 years), using the destructive method. Effective growth biomass and species ecological data indicated five species as potential trees for land restoration in tropical lowlands of Indonesia: *Litsea garciae*, *Terminalia bellirica*, *Pterospermum javanicum*, *Anisoptera marginata*, and *Cananga odorata*. The best allometric model of this study is highly recommended for implementation with native trees of tropical lowlands in Indonesia, especially those in early stages (less than 8 years).

**Keywords:** aboveground biomass, belowground biomass, total biomass, species selection, restoration, tropical lowland

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## Introduction

Indonesia was the world's largest emitter of greenhouse gases in 2019, contributing 54% of world carbon dioxide (CO<sub>2</sub>) emissions, mainly due to the conversion of lands and forests (Land-Use Change and Forestry/LUCF) (Climate Watch 2022). CO<sub>2</sub> emissions due to LUCF accounted for about 58% of the annual total in Indonesia, followed by the energy sector through the use of fossil fuels at about 40%, and the industrial sector at 2.2%. From 2010 to 2020, Indonesia had the world's third highest average annual forest loss at about 0.75 million hectares (ha), after Brazil with 1.5 million ha and the Democratic Republic of the Congo with 1.1 million ha (FAO 2020). This problem has persisted because recovery capability through forest and land rehabilitation was only 32% of annual forest loss (MoEF 2020).

Since the 'One Man One Tree' campaign initiated in 2008 (Peraturan Presiden 2008), the Indonesia Government has integrated the forest and land rehabilitation program with national action to reduce greenhouse gas emissions. The government provided one million seedlings of *Samanea saman* (Jacq.) Merr. to each province following Forestry Minister regulation (letter number S.86/Menhut-V/2009). In addition, a number of tree species were recommended for growing, including *Falcataria falcata* (L.) Greuter & R.Rankin, *Tectona grandis* L.f., *Swietenia mahagoni* (L.) Jacq., *Gmelina arborea* Roxb. ex Sm., *Neolamarckia cadamba* (Roxb.) Bosser, *Santalum album* L., *Melaleuca arcana* S.T.Blake, *Aleurites moluccanus* (L.) Willd., *Magnolia champaca* (L.) Baill. ex Pierre, *Pinus merkusii* Jungh. & de Vriese, and *Aquilaria malaccensis* Lam. (Peraturan Menteri Lingkungan Hidup dan Kehutanan 2018).

Restoration could be one of the most important ways of improving ecosystem quality and enhancing carbon sequestration capacity (Locatelli *et al.* 2015; Vásquez-Grandón *et al.* 2018; Indrajaya *et al.* 2022). Previous studies in tropical regions found the use of native trees to have slightly higher productivity compared to exotic species (Davis *et al.* 2012; Lu *et al.* 2017). One prerequisite of restoration on a large scale is the use of native trees (Tang *et al.* 2007; Ong 2012). In fact, Indonesia has a high level of plant biodiversity with about 30,000–40,000 species, representing 15.5% of all plant species worldwide, including ferns and Gymnospermae, which makes choosing trees for restoration easier (Widjaja *et al.* 2014; Britannica 2022).

Analysis and planning for land restoration and carbon sequestration in the tropics, and especially in Indonesia, involves many uncertainties. Some researchers have recommended native trees for land rehabilitation based on species abundance at a certain location, such as in degraded secondary forests (Kartawinata 1994), lowland dry forests (Rochmayanto *et al.* 2021), riparian forests and

peatlands (Partomihardjo 2020). Meanwhile, biomass and carbon estimates in Indonesia have been highly variable, with only a few studies controlling for age (even-aged plantation) and growth characters of native trees. Biomass allometric models have been available for almost every forest ecosystem in Indonesia, but not for all locations, and most only focused on aboveground biomass (AGB) (Krisnawati *et al.* 2012). Some AGB allometric models for mixed forests have become references, such as for secondary forests (Ketterings *et al.* 2001), dipterocarp forests (Basuki *et al.* 2009), and pioneer trees of secondary forests (Hashimoto *et al.* 2004).

To simultaneously halt forest degradation and enhance carbon sequestration capacity, restoration with native trees of each ecosystem is required. In addition, more comprehensive studies are needed to address the lack of AGB, belowground biomass (BGB) and total biomass (TB) estimation models for native trees of lowland forest ecosystems in Indonesia. Therefore, this study aimed to select and evaluate potential native tree species for high biomass and to select the best allometric model for estimating biomass production in these ecosystems. The selected tree species serve as a basis for selecting native trees for land restoration and carbon sequestration in the region. Furthermore, the selected allometric models and detailed information about biomass proportion (AGB, BGB and TB) will be useful for scientific purposes (such as carbon sequestration studies) in Indonesia.

## Materials and methods

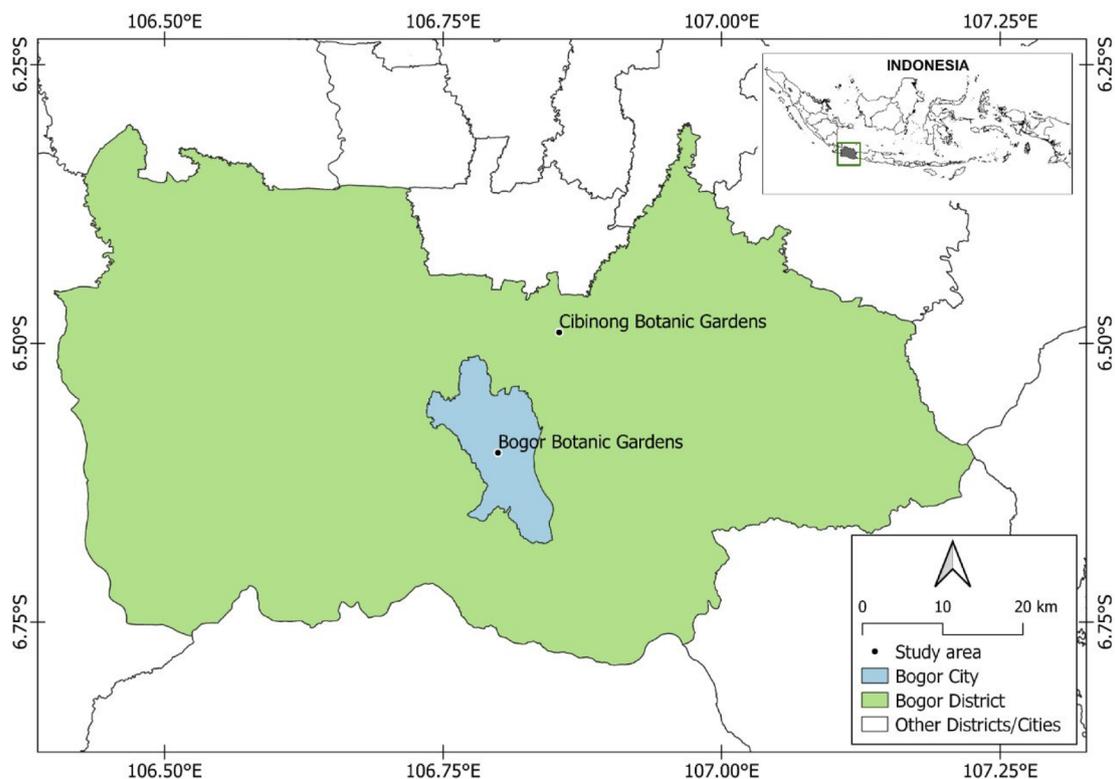
### Study sites

The study was conducted at the Bogor Botanic Gardens (BBG) and the Cibinong Botanic Gardens (CBG) (Fig. 1). Seedlings were produced in the BBG nursery, and after one year they were planted in demonstration plots (demplots) of CBG.

The climate type of the two study locations is very wet (Type A according to Schmidt-Ferguson). During 2015–2019, the average annual rainfall was 3606.74 mm, the average temperature was 26.04 °C, the average humidity was 81.28%, and the average irradiation time was 57.2% (BMKG 2022). The soils of BBG and CBG have relatively similar chemical and physical properties (Purnomo *et al.* 2023). BBG soil had a pH of 5.27, C-organic content of 1.59%, P-available of 4.15 ppm, cation exchange capacity (CEC) of 19.83 cmol/kg, base saturation of 65%, and sand, dust and clay fractions of 12.25%, 38% and 49.75%, respectively. CBG soil had a pH of 5.10, C-organic content of 1.89%, P-available of 5.05 ppm, CEC of 16.44 cmol/kg, base saturation of 61.25%, sand, dust and clay fractions of 12.5%, 39.75% and 47.75%, respectively (Available at Table S1).



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**Figure 1.** Study sites

### Data collection

This research uses the living plant collection of BBG, which is a rigorously documented and reliable source of research material (Jackson & Sutherland 2017). The reliable plant collection data of BBG facilitates the selection of potential high biomass native tree species. Tree species of the BBG living collection were filtered by five criteria: 1. nativeness (distribution range in Malesia region); 2. wet lowland habitat with an altitude of 0 – 1000 m above sea level (m asl); 3. large size (adult stage capable of reaching diameter at breast height (dbh) >20 cm, height >20 m, and age >20 years); 4. seed availability (annual seed production); and 5. supporting factors to attract public interest (such as wood, medicine, food, and ornamental potential) (Purnomo *et al.* 2023). Large trees with greater longevity store more biomass and play an important role in forest ecosystems (Slik *et al.* 2013; Mildrexler *et al.* 2020). Seed availability, i.e., abundantly available throughout the year, is a prerequisite for restoration programs (McCormick *et al.* 2021). Supporting factors that attract public interest are needed for wide planting of the selected tree species involving the community and not only the government (Meli *et al.* 2014).

Thus, 16 native tree species and three exotic species (reported as invasive in some countries) were selected for multi-propagation and growing treatment (App. 1). All seeds (a total of 1900 seeds comprising 19 species i.e., 100 seeds

for each species) were germinated under the same treatment until they reached the height of 1 – 1.5 m (age ± one year) and were ready to be planted in demplots. Seedlings were planted (10 seedlings for each species) with respect to the amount of light. During the first two years, surrounding trees were pruned and weeds removed. The seedlings were subsequently allowed to grow until they were ready to be harvested for biomass measurements (*destructive method*) at ages of 4 and 8 years.

Three individuals, between 4 and 8 years of age, per species were randomly selected for harvest. Biomass was divided into four components: stem (including bark), branch (secondary stem that grows from a primary stem, including twig), leaf (leaflet and petiole) and root (stumps and coarse root diameter > 2 mm). Dry weight was measured using three samples of each biomass component, which were placed in an oven at a temperature of 105 °C (for stem, branch and root samples) or 70 °C (for twig and leaf samples) until they reached an equilibrium dry mass. Biomass was calculated as:  $BM = (DW_s \times FW) / FW_s$ . Where  $BM$ =biomass (kg),  $DW_s$ = sample dry weight (gr),  $FW$ = total component fresh weight (kg), and  $FW_s$ = sample fresh weight (gr).

Wood density (*wood density*/ $\rho$ =gr/cm<sup>3</sup>) is another important factor that affects biomass and was measured by taking three samples of wet wood for each species. Furthermore, wet sample volume was measured using the water-displacement method (Pérez-Harguindeguy *et al.* 2013).

## Data analysis

### Biomass among species and components

The Duncan test was used to compare the means of various variables, including those related to tree growth (height, diameter and biomass), between species and biomass proportion between diameter classes. The means of goodness of fit criteria (Adj.R<sup>2</sup>, RMSE, MAE, AIC and BIC) between models in a 10-fold cross validation were also compared by the Duncan test. The proportion of each biomass component was calculated after mixing all samples (regardless of species) grouped by diameter class.

### Model development

Correlations between biomass variables (AGB, BGB, and TB) and measured variables (diameter, height, and wood density) were analyzed. All variables were log transformed to normalize residuals and heteroscedasticity of variances (Chave *et al.* 2014; Djomo & Chimi 2017; Nath *et al.* 2019). The following four allometric models were chosen according to the type of tropical lowland forest and because they have often been used to generate correlations between biomass and predictors:

Model 1: $\text{Ln}(\text{BM}) = \text{Ln}(a) + b\text{Ln}(D)$	(Brown 1997)
Model 2: $\text{Ln}(\text{BM}) = \text{Ln}(a) + b\text{Ln}(D^2H)$	(Brown <i>et al.</i> 1989)
Model 3: $\text{Ln}(\text{BM}) = \text{Ln}(a) + b\text{Ln}(\rho D^2H)$	(Chave <i>et al.</i> 2014)
Model 4: $\text{Ln}(\text{BM}) = \text{Ln}(a) + b\text{Ln}(D) + c\text{Ln}(H) + d\text{Ln}(\rho)$	(Nath <i>et al.</i> 2019)

where BM = biomass (kg), D = dbh (cm), H = tree height (m),  $\rho$  = wood density ( $\text{gr}/\text{cm}^3$ ), a = intercept, and b, c and d are coefficients.

There were 102 samples in total, consisting of 90 from native tree species and 12 from exotic tree species. All 90 native samples were used for model training and validation. An allometric model was developed for three categories: aboveground biomass (ABG), belowground biomass (BGB), and total biomass (TB). Log-linear regression analysis was used to show the relationship between total biomass and the three categories (formulated into four models), using PAST 4.03 software (Hammer *et al.* 2001).

### Model validation

Cross validation is a highly recommended method for estimating the accuracy of model performance (Yuen *et al.* 2016; Nath *et al.* 2019; Annighöfer *et al.* 2022). Five-fold or 10-fold validations are commonly used to obtain a balance between bias and variance (Nath *et al.* 2019). A 10-fold cross validation was implemented here for the 90 samples of tropical lowland native trees. The goodness of fit criteria calculated in the training model and the 10-fold cross validation consisted of five units: 1) Adjusted Coefficient of Determination (Adj.R<sup>2</sup>), an adjustment of the Coefficient of Determination that takes into account the number

of variables in the data set; 2) Root Mean Square Error (RMSE), the standard deviation of the residuals (prediction errors); 3) Mean Absolute Error (MAE), measure of the average magnitude of errors in a set of predictions, without considering their direction; 4) Akaike Information Criterion (AIC), a mathematical method for evaluating how well a model fits the data and model parsimony, and 5) Bayesian Information Criterion (BIC), a criterion for model selection among a finite set of models (Chave *et al.* 2005; Nath *et al.* 2019). Adj.R<sup>2</sup>, AIC and BIC were calculated using IBM SPSS Statistics 25, while RMSE and MAE were calculated using the following mathematical formulas, respectively:

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (M_o - M_p)^2}; \quad MAE = \frac{1}{n} \sum_{i=1}^n |M_o - M_p|$$

where  $M_o$  = observed biomass from sampled trees,  $M_p$  = predicted biomass from model, and n = number of trees. The best model was determined from the average of the goodness of fit values for the 10-fold cross validation. The Duncan test was implemented to ensure average value discrimination.

### Best model vs. generic model

To understand model performance, the best model resulting from this study was compared to a selected generic allometric model. The selected generic model was chosen based on habitat type suitability and biomass component classification (AGB, BGB, and TB) (App. 2).

The best R<sup>2</sup>, RMSE, MAE, AIC, and BIC values of the resulting model were compared to those of a generic model. Model performance was evaluated by comparing model predictions for the 102 samples, visualized on a quadratic function graph consisting of the relationship among diameter, observed biomass, and predicted biomass for each model.

## Results

### Growth and biomass for each tree species

*Pterospermum javanicum* (6.19 kg), *Terminalia bellirica* (5.59 kg), and *Litsea garciae* (4.84 kg) were the top three species in biomass at the 4<sup>th</sup> year (Fig. 2, App. 3), while *L. garciae* (123.89 kg) *T. bellirica* (117.38 kg), and *Anisoptera marginata* (73.60 kg) were the top three after the 8<sup>th</sup> year (Fig. 2, App. 4). *Terminalia bellirica* and *L. garciae* exhibited consistent growth with the highest biomass gain, far exceeding that of *Castilla elastica* (an exotic species). However, *C. elastica* had the greatest diameter growth at 4 years (6.70 cm), but its vertical growth (5.63 m) was not the highest. *Cananga odorata* and *A. marginata* had greater



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biomass growth at 8 years than did *C. elastica*. All individuals of *Bombax anceps*, *Cassia grandis*, and *Samanea saman* died after the 8<sup>th</sup> year of growth (no individuals remaining), due to their inability to compete with other trees. Like *C. elastica*, *C. grandis* and *S. saman* are introduced species that were used as exotic tree species in this study.

Diameter and height growth commonly affected the biomass of each tree species. In addition, wood density at 8 years was relatively greater than at 4 years (App. 3, App. 4). In some cases, such as for *A. marginata*, wood density had a strong influence on increasing biomass. Height and stem diameter growth of *A. marginata* were lower than those for *C. odorata* and *C. elastica*, but *A. marginata* had high wood density so its biomass was relatively higher. Wood density did not differ significantly between 4 and 8 years for *Pongamia pinnata* (0.89 vs. 0.89, respectively), *Canarium vulgare* (0.75 vs. 0.76), and *Litsea garciae* (0.71 vs. 0.72).

### Proportion of biomass allocation per diameter class

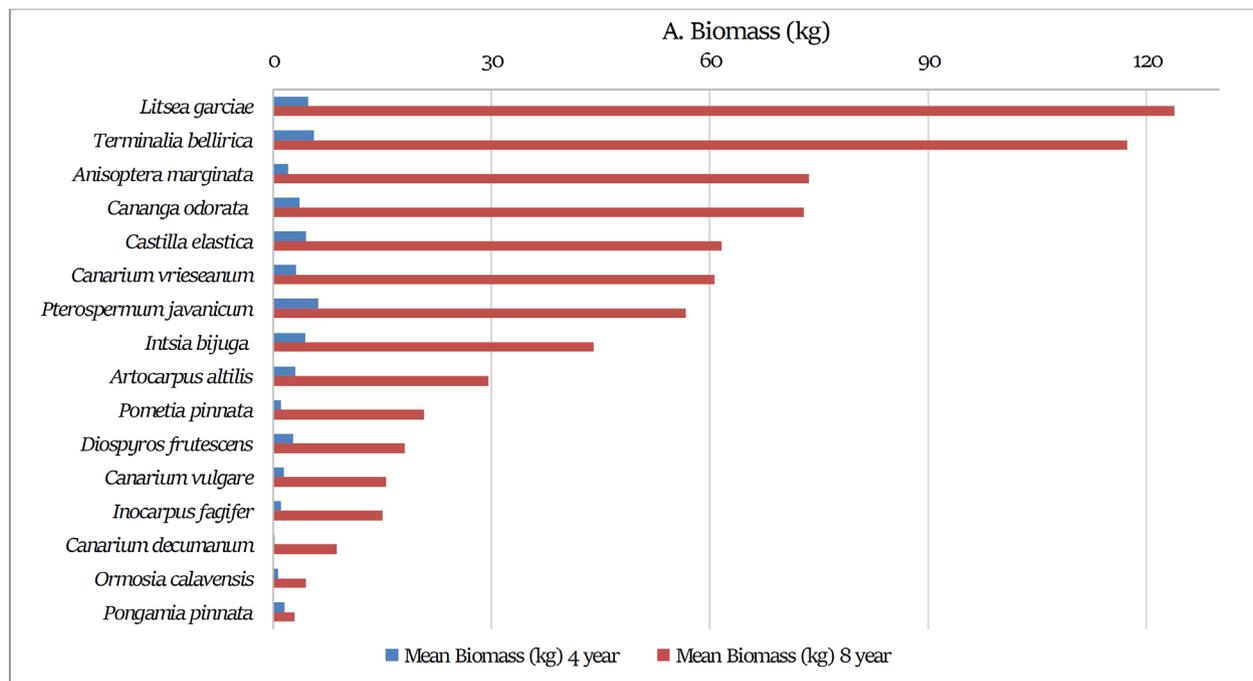
The proportion of BGB across all diameter classes was 14.48% (3.33±6.67 kg) of total individual tree biomass (22.9±44.01 kg). The largest AGB allocation was for stems (57.46%), followed by branches (19.92%) and leaves (8.18%) (Fig. 3). Changes in biomass proportions among components occurred after 8 years of growth, with stems and branches increasing and leaves and roots decreasing. Biomass of the >15 cm diameter class was significantly higher ( $P < 0.05$ ) than that of the other diameter classes

(Table S2). Increasing stem diameter consistently affected the proportion of leaf biomass, but not the proportions of the other components.

### Allometric model development

All allometric models were considered good models due to having adjusted  $R^2$  (Adj. $R^2$ ) values ranging 0.815 – 0.906 in model training (Table 1). Model 4 had the highest Adj. $R^2$  value for all biomass components and the lowest values for RMSE, MAE, AIC and BIC. However, this did not correctly predict biomass because the wood density variable ( $\rho$ ) was not significant at  $P < 0.05$ .

There was a log-linear relationship between total biomass (TB) and four predictor variables, namely: diameter (D), diameter-height ( $D^2H$ ), wood density-diameter-height ( $\rho D^2H$ ) (Fig. 4) and an unstandardized predicted value from a triple variable ( $D+H+\rho$ ). All variables in this study met the assumption of linearity (e.g., scatter plot of TB model prediction, Fig. 4), with the value of each predicted variable not deviating far from the principal axis. On the other hand, the scatter plot of residuals showed a randomly dispersed pattern, indicating no heteroscedasticity for the TB model prediction. Similar results were also found for AGB and BGB, with the predictor variable meeting the assumption of linearity. The Adj. $R^2$  value reached 0.882 when the correlation of biomass with diameter and height, formulated by ( $D^2H$ ), was included, which was higher than the Adj. $R^2$  of 0.844 when only diameter was used.



**Figure 2.** Trends for: a. biomass, b. diameter, and c. height. Species are listed from highest biomass above to lowest biomass below.



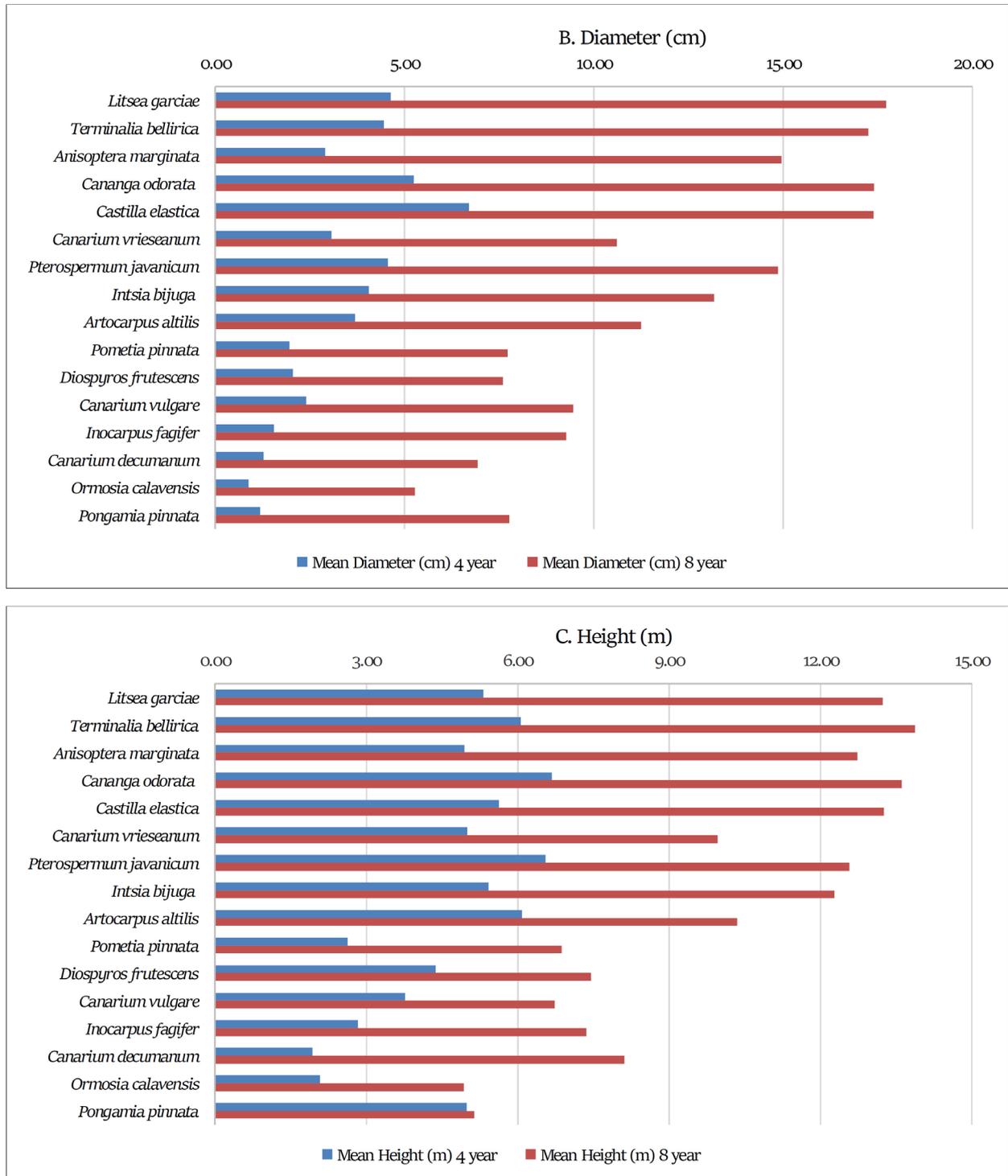
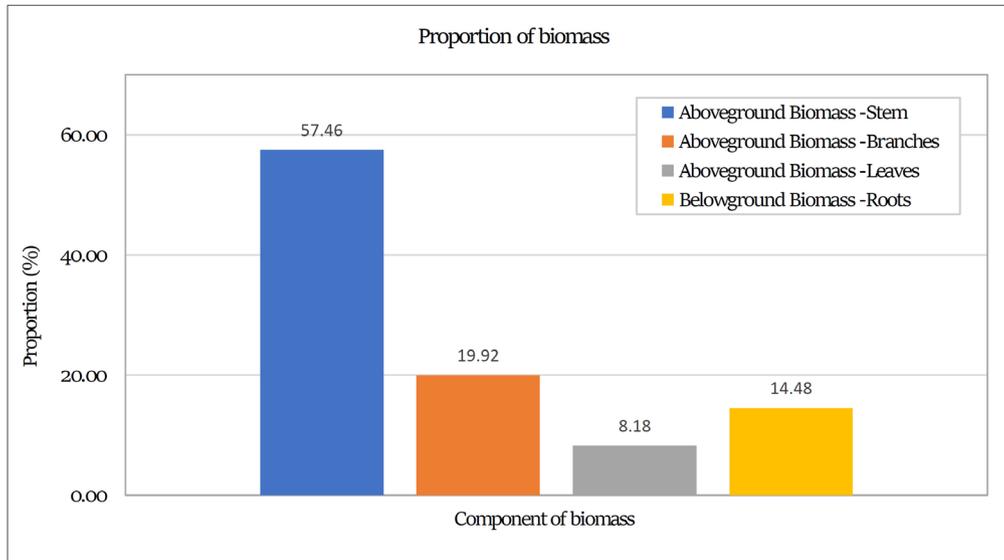


Figure 2. Cont.



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**Figure 3.** Proportion of biomass per component of native tropical lowland tree species in Indonesia

**Table 1.** Allometric model of aboveground biomass, belowground biomass, and total biomass

Model	a	b	c	d	Adj.R <sup>2</sup>	RMSE	MAE	AIC	BIC
Aboveground Biomass (ABG)									
1	-1.3799	1.8205			0.845	0.690	0.536	194.675	202.174
2	-2.0695	0.7198			0.881	0.604	0.477	170.573	178.073
3	-1.7133	0.7320			0.878	0.612	0.454	173.085	180.584
4	-2.926	0.7467	1.9294	0.3811*	0.906	0.531	0.412	147.633	155.132
Belowground Biomass (BGB)									
1	-2.5936	1.5952			0.798	0.710	0.538	201.458	208.991
2	-3.1991	0.6310			0.833	0.645	0.503	184.291	191.824
3	-2.8615	0.6360			0.815	0.679	0.530	193.108	193.384
4	-4.0788	0.6459	1.6671	0.0069*	0.852	0.600	0.474	171.317	171.593
Total Biomass (TB)									
1	-1.1117	1.7798			0.844	0.676	0.520	192.567	200.100
2	-1.7857	0.7037			0.881	0.591	0.467	168.662	176.194
3	-1.4326	0.7145			0.875	0.606	0.449	172.548	180.080
4	-2.6423	0.7324	1.8744	0.3084*	0.904	0.525	0.409	147.286	154.818

Note: Model 1:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(D)$ ; Model 2:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(D^2H)$ ; Model 3:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(\rho D^2H)$ ; and Model 4:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(D) + c\text{Ln}(H) + d\text{Ln}(\rho)$ . D: dbh (cm), H: height (m),  $\rho$ : wood density ( $\text{gr}/\text{cm}^3$ ), a: intercepts, b, c, d: coefficients. All models were significant ( $P < 0.001$ ). \*not significant at  $P < 0.05$ . Adj.R<sup>2</sup> = Adjusted Coefficient of Determination; RMSE = Root Mean Square Error; MAE = Mean Absolute Error; AIC = Akaike Information Criterion; BIC = Bayesian Information Criterion.

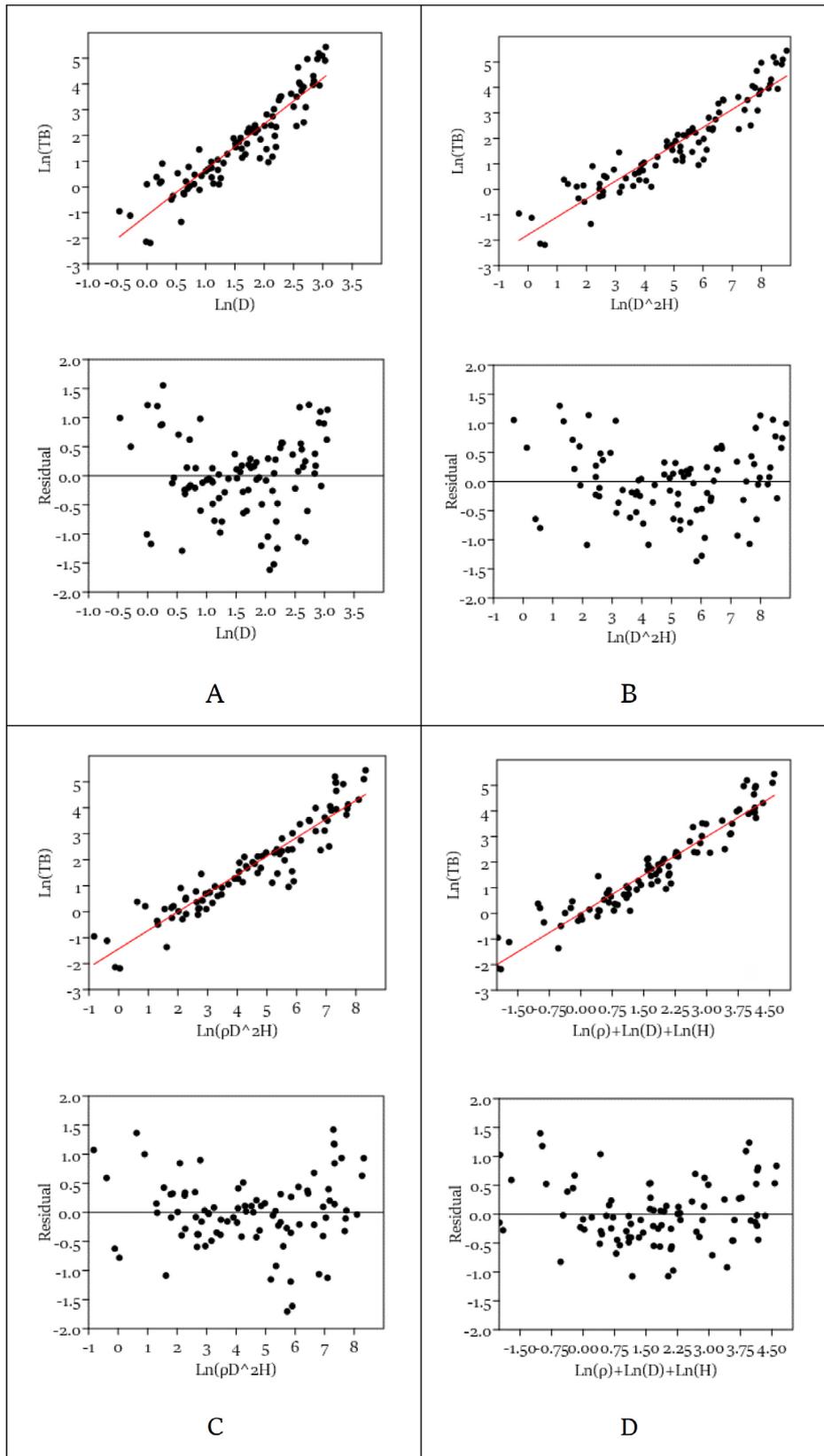
### Model validation

Cross validation showed that training and testing had slightly different RMSE and MAE values, indicating adequate model biomass prediction (Table 2). In general, Model 4 had the highest Adj.R<sup>2</sup> value and the lowest error value. However, Model 2 was preferable for selection because it had a high Adj.R<sup>2</sup> value and a significant variable affecting biomass. Model 3 had slightly lower MAE error values for AGB and TB than did Model 2, but means did not differ significantly at  $P < 0.05$ .

### Best model vs. generic model

AGB predictions by the models of Chave *et al.* (2014) and Nath *et al.* (2019) have better trustworthiness compared to the models of the present study (Table 3). The present study tended to have small error considering RMSE and MAE. Even though they overestimate biomass prediction at small diameters ( $D < 10\text{cm}$ ), the AGB models of Chave *et al.* (2014) and Nath *et al.* (2019) consistently approached the observed value at larger diameters ( $D > 10\text{cm}$ ) (Fig. 5). The model prediction of BGB in the present study seemed to





**Figure 4.** Relationship between total biomass ( $\ln(TB)$ ) and variables a.  $\ln(D)$  ( $Adj.R^2 = 0.844$ ); b.  $\ln(D^2H)$  (0.881); c.  $\ln(\rho D^2H)$  (0.875); d.  $\ln(D) + \ln(H) + \ln(\rho)$  (0.904). D: dbh (cm), H: height (m),  $\rho$ : wood density ( $gr/cm^3$ ), TB: total biomass (kg),  $Adj.R^2$ : Adjusted Coefficient of Determination



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**Table 2.** The result of 10-fold cross validation of four models of aboveground biomass, belowground biomass, and total biomass

Model	Adj.R <sup>2</sup>	RMSE	MAE	AIC	BIC
Aboveground Biomass (AGB)					
1	0.845 ± 0.008 <sup>c</sup>	0.711 ± 0.064 <sup>a</sup>	0.553 ± 0.080 <sup>a</sup>	21.400 ± 3.796 <sup>a</sup>	21.991 ± 3.796 <sup>a</sup>
<b>2</b>	<b>0.881 ± 0.007<sup>b</sup></b>	<b>0.622 ± 0.064<sup>a</sup></b>	<b>0.490 ± 0.065<sup>ab</sup></b>	<b>19.172 ± 3.049<sup>ab</sup></b>	<b>19.764 ± 3.049<sup>ab</sup></b>
3	0.878 ± 0.008 <sup>b</sup>	0.622 ± 0.092 <sup>a</sup>	0.464 ± 0.080 <sup>b</sup>	19.537 ± 4.086 <sup>ab</sup>	20.128 ± 4.086 <sup>ab</sup>
4	0.906 ± 0.006 <sup>a</sup>	0.568 ± 0.100 <sup>b</sup>	0.443 ± 0.095 <sup>b</sup>	16.454 ± 4.113 <sup>ab</sup>	17.046 ± 4.113 <sup>b</sup>
Belowground Biomass (BGB)					
1	0.798 ± 0.013 <sup>d</sup>	0.724 ± 0.137 <sup>a</sup>	0.555 ± 0.103 <sup>a</sup>	21.763 ± 3.934 <sup>a</sup>	21.354 ± 4.617 <sup>a</sup>
<b>2</b>	<b>0.833 ± 0.011<sup>b</sup></b>	<b>0.660 ± 0.116<sup>a</sup></b>	<b>0.519 ± 0.094<sup>a</sup></b>	<b>20.104 ± 4.196<sup>a</sup></b>	<b>20.695 ± 4.196<sup>a</sup></b>
3	0.815 ± 0.012 <sup>c</sup>	0.664 ± 0.100 <sup>a</sup>	0.528 ± 0.078 <sup>a</sup>	21.666 ± 3.821 <sup>a</sup>	22.258 ± 3.821 <sup>a</sup>
4	0.852 ± 0.010 <sup>a</sup>	0.723 ± 0.220 <sup>a</sup>	0.599 ± 0.219 <sup>a</sup>	18.821 ± 4.624 <sup>a</sup>	19.413 ± 4.624 <sup>a</sup>
Total Biomass (TB)					
1	0.844 ± 0.009 <sup>c</sup>	0.696 ± 0.076 <sup>a</sup>	0.537 ± 0.086 <sup>a</sup>	20.892 ± 3.771 <sup>a</sup>	20.484 ± 3.763 <sup>a</sup>
<b>2</b>	<b>0.881 ± 0.007<sup>b</sup></b>	<b>0.610 ± 0.069<sup>b</sup></b>	<b>0.482 ± 0.063<sup>ab</sup></b>	<b>18.684 ± 3.011<sup>ab</sup></b>	<b>19.276 ± 3.011<sup>ab</sup></b>
3	0.875 ± 0.008 <sup>b</sup>	0.616 ± 0.099 <sup>b</sup>	0.463 ± 0.079 <sup>b</sup>	19.394 ± 3.920 <sup>ab</sup>	19.966 ± 3.917 <sup>ab</sup>
4	0.904 ± 0.006 <sup>a</sup>	0.545 ± 0.072 <sup>b</sup>	0.424 ± 0.066 <sup>b</sup>	16.081 ± 4.274 <sup>b</sup>	16.673 ± 4.274 <sup>b</sup>

Note: Model 1:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(D)$ ; Model 2:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(D^2H)$ ; Model 3:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(\rho D^2H)$ ; and Model 4:  $\text{Ln}(\text{TB}) = \text{Ln}(a) + b\text{Ln}(D) + c\text{Ln}(H) + d\text{Ln}(\rho)$ . D: dbh (cm), H: height (m),  $\rho$ : wood density ( $\text{gr}/\text{cm}^3$ ). Adj.R<sup>2</sup> = Adjusted Coefficient of Determination; RMSE = Root Mean Square Error; MAE = Mean Absolute Error; AIC = Akaike Information Criterion; BIC = Bayesian Information Criterion. Values are means and standard deviation (mean ± sd). Values in the same column followed by different superscript letters differ significantly at  $P < 0.05$ .

**Table 3.** Comparisons between the best model of the present study and other generic models

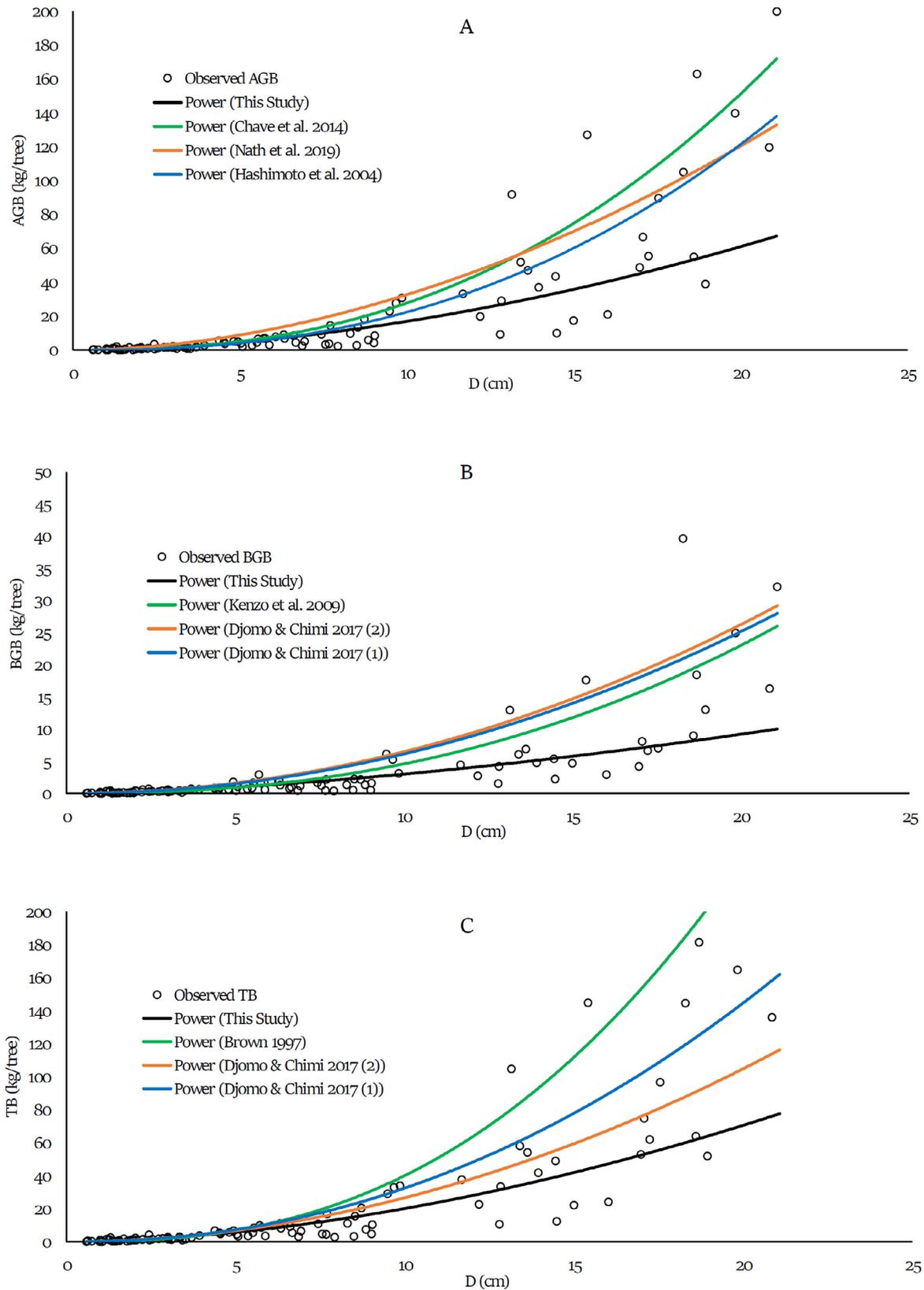
Model	Forest Type	Range of D	Observed (kg)	Predicted (kg)	R <sup>2</sup>	RMSE	MAE	AIC
Aboveground Biomass (AGB)								
Present study	moist	0.9–17.7	1947.77	1396.96	0.897	0.613	0.494	193.72
Hashimoto <i>et al.</i> (2004)	moist	3.2–20.3	1947.77	2156.71	0.867	0.870	0.627	220.13
Chave <i>et al.</i> (2014)	pan tropical	10–158	1947.77	2846.71	0.899	0.803	0.593	191.94
Nath <i>et al.</i> (2019)	pan tropical	10–90	1947.77	2730.24	0.899	0.922	0.786	191.94
Belowground Biomass (BGB)								
Present study	moist	0.9–17.7	321.81	231.94	0.857	0.643	0.504	204.15
Kenzo <i>et al.</i> 2014	moist	0.1–20.4	321.81	423.62	0.831	0.943	0.727	221.29
Djomo & Chimi 1 (2017)	moist	4–121	321.81	514.64	0.831	0.913	0.736	221.29
Djomo & Chimi 2 (2017)	moist	4–121	321.81	550.99	0.810	0.993	0.761	233.51
Total Biomass (TB)								
Present study	moist	0.9–17.7	2269.57	1642.28	0.897	0.600	0.483	189.41
Brown (1997)	moist	5–148	2269.57	3999.27	0.867	0.956	0.706	215.20
Djomo & Chimi 1 (2017)	moist	4–121	2269.57	2835.04	0.867	0.788	0.592	215.20
Djomo & Chimi 2 (2017)	moist	4–121	2269.57	2290.49	0.897	0.642	0.512	189.41

Note: Fit of models for 102 samples, according to the relationship between observed and predicted biomass: D: dbh (cm); R<sup>2</sup> = Coefficient of Determination; RMSE = Root Mean Square Error; MAE = Mean Absolute Error; AIC = Akaike Information Criterion.

be superior to another generic model, especially regarding error value (RMSE and MAE) and compliance level of AIC and BIC. The BGB model of Djomo and Chimi (2017), using only diameter (D), was actually better than the addition of wood density ( $\rho$ ). The predictive value of the BGB model of Kenzo *et al.* (2009) was closer to that of the BGB model of the present study than to the two models (1 and 2) of

Djomo and Chimi (2017). The model of the present study and model 2 of (Djomo & Chimi (2017) revealed similar goodness of fit values for TB, which were also better than those of other generic models. These models have the highest R<sup>2</sup> values and the lowest AIC and BIC values. In addition, the model of the present study had the lowest RMSE and MAE values.





**Figure 5.** Comparison of the best biomass prediction model of the present study with a generic model based on diameter: a. Aboveground biomass (AGB) model, b. Belowground biomass (BGB) model, and c. Total biomass (TB) model



## Discussion

### *Native trees with high biomass accumulation*

Overall, of the selected and sampled tree species, *Litsea garciae*, *Terminalia bellirica*, *Pterospermum javanicum*, *Anisoptera marginata*, and *Cananga odorata* produced high biomass accumulation. Both *L. garciae* and *T. bellirica* are able to adapt to various type of habitats, which allowed these species to have superior growth (Lim 2011; Kumari *et al.* 2017). These two species achieved greater biomass than *Castilla elastica* because they had proportionately greater diameter and height growth. *Litsea garciae* is commonly found in sandy soil of disturbed mixed dipterocarp forest along river margins to sloping hills of 200 m asl (Lim 2011).

*Terminalia bellirica* is another potential biomass producing tree that consistently grows higher than *C. elastica*. It is able to adapt to a wide variety of habitat types, such as seasonal forest, deciduous-mixed forest and deciduous dried-leaf dipterocarp forest at 2000 m asl (Kumari *et al.* 2017). *Terminalia bellirica* has been reported to have high carbon sequestration in India (Aggarwal & Chauhan 2014; Dhyani *et al.* 2021). It also has above-average carbon sequestration capacities among naturally growth vegetation in a mining recovery project in Indonesia (Purnomo *et al.* 2022).

*Cananga odorata* was able to reach a height of 40 m in its natural habitat (App. 1). This tropical tree species possesses several characteristics, such as the following: moderate to high growth, occurrence as a pioneer, ability to grow in various soil textures and types, and ability to compete when growing in densely mixed forest (Parrotta 2009). *Cananga odorata* is the dominant tree species in the Tangkoko Natural Reserve, Indonesia, where it responsible for a high biomass contribution (Langi 2023). The species has the highest carbon sequestration capacity among naturally growing vegetation in a mining recovery project in Indonesia (Purnomo *et al.* 2022). Surprisingly, *A. marginata* has better growth than *C. elastica*, even though its diameter and height are less. Belonging to the family Dipterocarpaceae, *A. marginata* is tolerant of various environmental conditions, yet it grows better under sufficient shade and is adapted to savanna ecosystems (Otsamo 1998).

The biomass potential of *P. javanicum* is only slightly below that of *C. elastica* and *Canarium vrieseanum*. However, based on secondary data records and the stature of the sample of the BBG collection (App. 1), the species is highly recommended as a potential high biomass tree. It is recorded as having the highest carbon storage in agroforestry (Ariyanti *et al.* 2018). Even though in the case of the tropical abandoned land, the species exhibits instability in biomass growth (Karyati *et al.* 2019).

All ten individuals of *Bombax anceps*, *Cassia grandis*, and *Samanea saman* in the present study died after 8 years of growth. Further study is needed into why these young

individual trees died when competing with other individual trees. Specific studies on the growth of *B. anceps*, either in plantations or in natural conditions (forest), are very limited. It has been reported that seedlings of *C. grandis* require regular pruning for optimal growth during the early stage (Orwa *et al.* 2009). Although *S. saman* is very dominant in the adult phase, it requires more sunlight (light demanding) in the juvenile phase (Staples & Elevation 2006).

Based on the results of the present study, five tree species are recommended for potential use in restoration in tropical lowlands of Indonesia: *Litsea garciae*, *Terminalia bellirica*, *Pterospermum javanicum*, *Anisoptera marginata*, and *Cananga odorata*. Better biomass growth, and the availability of information about their ecology, make these species reasonable selections. There are five criteria that species need to meet to be considered for restoration purposes: dominance, natural regeneration ability, habitat area, social value and simple cultivation (Meli *et al.* 2014). These criteria are in accordance with Indonesian Government policy about how to rehabilitate forests and lands (Peraturan Menteri Lingkungan Hidup dan Kehutanan 2020). Thus, the plant species used for intensive reforestation of conservation and protected forests should be long-lived local species that are beneficial to the local community.

### *Proportion of biomass per component for every diameter class*

The biomass proportion of each tree component is an important finding of the present study, as information related to under ground biomass is very limited (Krisnawati *et al.* 2012; Yuen *et al.* 2016; Annighöfer *et al.* 2022). The division into stem (including branches), leaf, and root components was able to better describe the dynamics of tree growth compared to shoot:root ratio (Poorter & Nagel 2000). The dynamic proportions of the biomass components of several age and diameter classes indicated that the trees were continuously growing and competing at carbon dioxide and nutrient absorption, which was subsequently converted to biomass (Kuyah *et al.* 2013; Li *et al.* 2018).

Biomass allocation was greatest for stem (57%), followed by branch (20%), root/BGB (15%), and leaf (8%). These values were similar those found for a tropical Amazon Forest: stem (62%), branch (22%), root (11%), and leaf (4%) (Woortmann *et al.* 2018). The native tropical lowland trees of Indonesia had a 15% higher BGB proportion than did the trees from tropical Amazon (Woortmann *et al.* 2018), but lower than total tree in tropical agricultural landscapes (21%) (Kuyah *et al.* 2013).

Biomass proportions change after 4 years of growth, with that of stem and branch increasing and that of leaf and root decreasing. At 8 years of age, canopy growth caused a decrease in incoming light intensity. Furthermore, plants respond to a lack of nutrients in the soil surface by allocating growth to shoots (Poorter & Nagel 2000; Poorter *et al.* 2011). Branch development then became faster than stem mass increase, similar to what Poorter *et al.* (2011) reported with



the stem mass fraction increasing at a lesser extent than specific stem length.

The >15 cm diameter class had significantly greater biomass ( $P < 0.05$ ) than did the other size classes for all categories of biomass components. This indicates optimum growth in all components of the tree. Meanwhile, the proportion of leaf biomass gradually decreased as that of stem diameter increased. This occurred because the tree adapted to strengthen stem, branch and root components for supporting (biomechanical) growth (Kuyah *et al.* 2013). The leaf is a beneficial organ for photosynthesis and respiration and is faster to dry and fall to become litter. The process of losing biomass from part of a tree is considered a mechanism of adaptation to the availability of resources in the environment (Chapin *et al.* 2002).

#### *The best allometric model*

An allometric model of tropical lowland trees developed in Indonesia (Ketterings *et al.* 2001; Hashimoto *et al.* 2004; Basuki *et al.* 2009), was based on a sample from a natural forest that has uncertainty in its biophysical environment. Tree biomass in a forest is affected by biotic (vegetation density) and abiotic (temperature, precipitation, light, water and nutrient) factors in its surrounding (Poorter & Nagel 2000; Chen *et al.* 2021). The present study used samples of even-aged trees obtained by controlled planting (with germination, acclimatization, and growth in demplots) under uniformly controlled environmental conditions. However, a drawback of the present model was that it was based on a limited period of growth (only 8 years, with a resulting diameter range of 5.28 – 17.73 cm). Further studies are needed to complete optimum growth for samples of trees > 15 cm in diameter.

The selection of predictors for the allometric model followed several previous studies, confirming that, in addition to tree diameter, height and wood density should also be considered (Chave *et al.* 2014; Djomo & Chimi 2017; Nath *et al.* 2019). Consideration must also be given to the selected mathematical formulas to obtain simple variables for ease of model implementation and validation (Sileshi 2014). In addition to the selection of relevant predictors, the method for validating the model also needs to be considered. A 10-fold cross validation was used here to avoid bias in biomass prediction and reduce the problem of over-fitting (Sileshi 2014). The use of k-fold cross validation has been reliably used in the building of several allometric models (Yuen *et al.* 2016; Nath *et al.* 2019; Annighöfer *et al.* 2022). The 10-fold cross validation used here resulted in an average value (from 10 calculations) for each of the five goodness of fit criteria used, thereby facilitating decision making for choosing the best model.

The allometric model that resulted from this study is ideal because it had an Adj. $R^2$  value greater than 70% (Djomo & Chimi 2017). The use of the single variable of

diameter (D) alone produced less prediction accuracy than the combination of tree diameter and height ( $D^2H$ ). This situation was a consistent result of cross validation, with the use of a combination variable ( $D^2H$ ) giving a model with greater prediction accuracy and lower error. However, when the wood density variable was added ( $\rho D^2H$ ), accuracy decreased. The use of the wood density variable with the triple variable ( $D+H+\rho$ ), gave a model with higher prediction accuracy and lower error. However, this model was not chosen because wood density was not significantly affecting biomass prediction. These findings differed from that of another study that integrated some variables (diameter, height, and wood density) and obtained the best model for predicting biomass (Chave *et al.* 2014; Nath *et al.* 2019). Other studies also found an inconsistent relationship between forest biomass and wood density (Basuki *et al.* 2009; Stegen *et al.* 2009; Kachamba *et al.* 2016). These studies used several species and trees of different ages, resulting in inconsistency in the simultaneous effects of wood type density to diameter and height. Good wood type density data are required, either by measuring more samples across species and ages (>3 samples for each individual at the same age) or using reliable literature data.

#### *Comparison of generic models*

All models of the present study tended to have low error values because they were fitted to sample characters used (Nath *et al.* 2019; Djomo & Chimi 2017). Although their error values were not as good as those of the best model of the present study, the models of Chave *et al.* (2014) and Nath *et al.* (2019) for predicting AGB had a higher  $R^2$  and lower AIC values than the best model developed here. The models of Chave *et al.* (2014) and Nath *et al.* (2019) were developed for all tropical ecosystem types (pan-tropical), which required more samples.

Although the two AGB models of Chave *et al.* (2014) and Nath *et al.* (2019) were comparable, the model from Chave *et al.* 2014 was more favorable (lower RSME and MAE values) and could be implemented in this study. The model of Hashimoto *et al.* (2004) was not adequate for use with the sample of this study even though it was built based on the same ecosystem type (moist tropical ecosystem) of Indonesia. This was because the Hashimoto *et al.* (2004) model was built using standing pioneer samples that tend to grow quickly in the early growth phase.

A BGB model from Djomo and Chimi (2017) (model 1) that only used diameter was actually better than adding the wood density variable. This contrast was likely due two factors: wood density had no effect on the BGB component and the effect of the uncertainty value of wood density. A BGB model from Djomo and Chimi (2017) (model 1) is more properly implemented with large native trees ( $D > 20$ cm) from tropical lowlands, compared to the model of Kenzo *et al.* (2009) ( $D = 0.1 - 20.4$ cm).



A TB model from Djomo and Chimi (2017) (model 2), integrating diameter variable and height, as done in the present study ( $D^2H$ ), provided much better biomass prediction, and so can be implemented for native trees of tropical lowlands of Indonesia. Tree height has a high correlation with adding total tree biomass (Chave *et al.* 2014; Djomo & Chimi 2017; Nath *et al.* 2019). Although there were many alternative recommendations for selecting an allometric model with a single variable, the use of two variables (D and H) was not burdensome and still acceptable (Sileshi 2014).

## Conclusion

The native tree species of *Litsea garciae*, *Terminalia bellirica*, *Pterospermum javanicum*, *Anisoptera marginata*, and *Cananga odorata* have effective biomass growth and so are recommended for land restoration in tropical lowlands of Indonesia. Biomass allocation was highest for stem (57%), followed by branch (20%), root/BGB (15%), and leaf (8%), whereas stem and branch (as opposed to root and leaf) increased after 4 years of growth. The best allometric model of the present study is highly recommended for implementation with native trees of tropical lowlands, especially for early stages (less than 8 years). For large trees ( $D > 20\text{cm}$ ), we recommended three models for tropical lowland forests in Indonesia, namely the AGB model of Chave *et al.* (2014), the BGB model (model 1) of Djomo and Chimi (2017) (with D variable), and the TB model (model 2) of Djomo and Chimi (2017) (with  $D^2H$  variable).

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## Supplementary material

The following online material is available for this article:

**Table S1.** Climatic and soil conditions in two study sites.

**Table S2.** Proportion of biomass per component of native trees in tropical lowland of Indonesia.

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**Appendix 1.** Native tree species selected for land restoration and carbon sequestration enhancement in tropical lowlands of Indonesia.

Species name/Local name/Family	Reference Data (PROSEA 2019; POWO 2022)										Samples of BBG's Collection		
	Native distribution	A up to (m asl)	Tree size up to		GR (%)	Major economic values					N	Ar (yr)	Dr (cm)
			H (m)	D (cm)		Tc	Ed	Md	Or	Of			
<i>Anisoptera marginata</i> Korth./ Mersawa/Dipterocarpaceae	BR, ML, SM	1200	45	135	80 – 90	v					4	3 – 107	5.6 – 195.5
<i>Artocarpus altilis</i> (Parkinson) Fosberg/Sukun/Moraceae	CI, LSI, MK, MRN, NG, PH, SOL, SL	600	30	180	90 – 95		v				5	19 – 29	27.4 – 168.0
<i>Bombax anceps</i> Pierre/Randu hutan/Malvaceae	CAM, JW, LO, LSI, ML, MY, SM, TH, VIE	750	45	400	90	v					6	81 – 91	37.3 – 174.5
<i>Cananga odorata</i> (Lam.) Hook. f. & Thomson/ Kenanga/ Annonaceae	BR, JW, LSI, ML, NG, PH, QS, SO. SL, SM, TH, VIE	1200	40	75	n/a			v	v	v	7	39 – 80	47.5 – 85.2
<i>Canarium decumanum</i> Gaertn./Kenari/Burseraceae	BIS, BR, MK, NG, SL	450	60	200	25 – 100		v			v	3	28 – 90	23.0 – 149.6
<i>Canarium vrieseanum</i> Engl./Kenari/Burseraceae	PH, SL	500	31	45	25 – 100	v	v			v	2	40	53.0 – 65.0
<i>Canarium vulgare</i> Leenh./Kenari/Burseraceae	LSI, JW, LSI, MK, NG, SOL, SL	1200	45	70	25 – 100	v	v			v	2	12 – 12	16.3 – 28.3
<i>Diospyros frutescens</i> Blume/ Ki gentel/Ebenaceae	BR, JW, ML, SL, SM, TH	700	25	40	45 – 95	v					4	39 – 87	13.7 – 44.9
<i>Inocarpus fagifer</i> (Parkinson ex F.A.Zorn) Fosberg/ Gayam/Fabaceae	BIS, CHR, FJ, JW, LSI, ML, NG, PH, ST, SI, SOL, SL, SM, TG, TB, VAN, WAL	500	30	65	n/a		v	v	v	v	7	8 – 85	18.0 – 144.1
<i>Intsia bijuga</i> (Colebr.) Kuntze/Merbau/Fabaceae	TZ, MD, SIB, ME, NAU, PN	600	50	250	n/a		v	v			6	94 – 118	53.5 – 119.7
<i>Litsea garciae</i> Vidal Count Kalangkala Lauraceae	PH, TW, INA, MAL	n/a	20	50	n/a	v	v	v			8	14 – 36	28.6 – 61.5
<i>Pometia pinnata</i> J.R. Forst. & G. Forst./Matoa/ Sapindaceae	SL, AI, SEA, TW, FJ, SM	1700	47	140	85 – 95	v	v	v			6	19 – 118	22.9 – 115.6
<i>Pongamia pinnata</i> (L.) Pierre/Malapari/Fabaceae	PK, IND, SL, SEA, NAS, FJ, JP	1200	25	80	n/a	v		v	v	v	6	18 – 59	16.3 – 46.3
<i>Pterospermum javanicum</i> Jungh. Count/Bayur/ Sterculiaceae	JW, LSI, SM, SR, SB, CEK	600	59	54	45 – 100	v					7	5 – 41	7.7 – 70.2
<i>Terminalia bellirica</i> (Gaertn.) Roxb. Count/ Jaha/ Combretaceae	ASS, BLD, BR, CAM, CSC, EH, IND, JW, LO, LSI, ML, MK, MY, NP, PK, SL, SL, SM, TH, VIE	600	50	300	85 – 100		v	v		v	2	93	59.4 – 90.3
<i>Ormosia calavensis</i> Azaola ex Blanco/Kacang mata kuda/ Fabaceae	BR, CI, JW, MK, NG, PH, SL	1800	30	100	50	v		v		v	4	46 – 52	20.9 – 92.2
<i>Samanea saman</i> (Jacq.) Merr.*/Trembesi/Fabaceae	BL, COL, CR, EC, EL, HO, NI, PN, VE	1000	40	200	90					v	2	58 – 94	144.3 – 145.6
<i>Cassia grandis</i> L.f.*/Johar/Fabaceae	CMX, TA	n/a	25	60	70	v		v	v		2	n/a	47.9 – 59.8
<i>Castilla elastica</i> subsp. <i>costaricana</i> (Liebm.) C.C.Berg*/ Karet Panama/Moraceae	CUS, COL	850	30	90	n/a					v	2	28 – 81	33.5 – 95.2

Note: Reference Data according PROSEA (2019) and POWO (2022): Native distribution: BR: Borneo (Kalimantan, Brunei, Sabah, Sarawak), ML: Malaya, SM: Sumatra, CI: Caroline Is, LSI: Lesser Sunda Is, MK: Maluku, MRN: Marianas, NG: New Guinea, PH: Philippines, SOL: Solomon Is, SL: Sulawesi, CAM: Cambodia, JW: Jawa, LO: Laos, TH: Thailand, VIE: Vietnam, QS: Queensland, BIS: Bismarck Archipelago, CHR: Christmas Is, FJ: Fiji Is, ST: Santa Cruz Is, SI: Society Is, TG: Tonga, TB: Tubuai Is, VAN: Vanuatu, WAL: Wallis-Futuna Is, TZ: Tanzania, MD: Madagascar, SIB: Southern India and Burma, MLS: Malesia, NAS: Northern Australia, PL: Polynesia, TW: Taiwan, INA: Indonesia, MAL: Malaysia, SL: Sri Lanka, AI: Andaman Is, SEA: Southeast Asia, SM: Samoa, PK: Pakistan, IND: India, JP: Japan, SR: Sarawak, SB: Sabah, CEB: Central and East Borneo, ASS: Assam, BLD: Bangladesh, CSC: China South-Central, EH: East Himalaya, NP: Nepal, BL: Belize, COL: Colombia, CR: Costa Rica, EC: Ecuador, EL: El Salvador, HO: Honduras, NI: Nicaragua, PN: Panamá, VE: Venezuela, CMX: Central Mexico, TA: Tropical America, CUS: Central America. A: altitude, H: height, D: diameter, GR: germination rate, and economic. Several GR was determined by the same genus. Major economic values: Tc: timber construction/furniture; Ed: edible fruit, seed or other; Or: ornamental or shading tree; Of: other materials function as oil, resin, dye, rubber, handicraft, firewood, or cattle feeding. \*Introduced species as a control: *Samanea saman* invasive in Fiji, Hawaii, Brazil, Madagascar, Cuba; *Cassia grandis* invasive in Australia, India and Ecuador; *Castilla elastica* invasive in Pacific. Samples of BBG's Collections (observed in 2012): N: sample number of BBG's collection, Ar: age range, Dr: diameter range. n/a: not available in this reference/collection data.



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**Appendix 2.** The generic model (aboveground biomass, belowground biomass, and total biomass) selected for comparison with the best model of the present study.

Model	Equation	Reference
<b>Aboveground Biomass (AGB)</b>		
Model AGB 1:	$\text{Ln}(\text{AGB}) = -2.510 + 2.44\text{Ln}(D)$	(Hashimoto <i>et al.</i> 2004)
Model AGB 2:	$\text{Ln}(\text{AGB}) = -2.699 + 0.976\text{Ln}(\rho D^2 H)$	(Chave <i>et al.</i> 2014)
Model AGB 3:	$\text{Ln}(\text{AGB}) = -1.139 + 0.750\text{Ln}(\rho D^2 H)$	(Nath <i>et al.</i> 2019)
<b>Belowground Biomass (BGB)</b>		
Model BGB 1:	$\text{Ln}(\text{BGB}) = -3.844 + 2.33\text{Ln}(D)$	(Kenzo <i>et al.</i> 2009)
Model BGB 2:	$\text{Ln}(\text{BGB}) = -2.883 + 2.039\text{Ln}(D)$	(Djomo & Chimi 2017 (1))
Model BGB 3:	$\text{Ln}(\text{BGB}) = -2.267 + 1.042\text{Ln}(\rho D^2)$	(Djomo & Chimi 2017 (2))
<b>Total Biomass (TB)</b>		
Model TB 1:	$\text{Ln}(\text{TB}) = -2.134 + 2.530\text{Ln}(D)$	(Brown 1997)
Model TB 2:	$\text{Ln}(\text{TB}) = -1.475 + 2.153\text{Ln}(D)$	(Djomo & Chimi 2017 (1))
Model TB 3:	$\text{Ln}(\text{TB}) = -1.942 + 0.768\text{Ln}(D^2 H)$	(Djomo & Chimi 2017 (2))

Note: D: dbh (cm), H: height (m),  $\rho$ : wood density ( $\text{gr}/\text{cm}^3$ )

**Appendix 3.** Tree species, height, diameter, wood density, and biomass component at 4 years of age for native tropical lowland trees in Indonesia.

Species	N	H (m)	D (cm)	WD ( $\text{gr}/\text{cm}^3$ )	AGB (kg)				BGB/Roots (kg)	TB (kg)
					Stem	Branches	Leafs	Total		
<i>Pterospermum javanicum</i> Jungh. Count	3	6.55 ± 0.97 <sup>ab</sup>	4.55 ± 1.39 <sup>bc</sup>	0.53 ± 0.10 <sup>e</sup>	3.26 ± 1.17 <sup>a</sup>	0.78 ± 0.31 <sup>ab</sup>	0.37 ± 0.12 <sup>abc</sup>	4.41 ± 2.68 <sup>ab</sup>	1.78 ± 1.18 <sup>a</sup>	6.19 ± 3.85 <sup>a</sup>
<i>Terminalia bellirica</i> (Gaertn.) Roxb. Count	3	6.07 ± 0.64 <sup>abc</sup>	4.45 ± 1.31 <sup>bc</sup>	0.53 ± 0.00 <sup>e</sup>	3.34 ± 1.07 <sup>a</sup>	0.94 ± 0.20 <sup>a</sup>	0.40 ± 0.10 <sup>abc</sup>	4.69 ± 2.27 <sup>a</sup>	0.91 ± 0.67 <sup>bc</sup>	5.59 ± 2.88 <sup>ab</sup>
<i>Litsea garciae</i> Vidal Count	2	5.30 ± 0.45 <sup>abcde</sup>	4.67 ± 2.35 <sup>bc</sup>	0.31 ± 0.00 <sup>b</sup>	2.31 ± 1.48 <sup>abc</sup>	0.95 ± 0.80 <sup>a</sup>	0.83 ± 0.56 <sup>ab</sup>	4.10 ± 4.03 <sup>abc</sup>	0.75 ± 0.78 <sup>bc</sup>	4.84 ± 4.80 <sup>abc</sup>
<i>Castilla elastica</i> subsp. <i>costaricana</i> (Liebm.) C.C.Berg	3	5.63 ± 0.57 <sup>abcd</sup>	6.70 ± 0.84 <sup>a</sup>	0.42 ± 0.00 <sup>g</sup>	2.90 ± 0.31 <sup>ab</sup>	0.40 ± 0.07 <sup>ab</sup>	0.26 ± 0.05 <sup>abc</sup>	3.56 ± 0.74 <sup>abcd</sup>	0.97 ± 0.32 <sup>b</sup>	4.53 ± 0.91 <sup>abcd</sup>
<i>Intsia bijuga</i> (Colebr.) Kuntze	3	5.42 ± 1.59 <sup>abcd</sup>	4.05 ± 1.78 <sup>bcd</sup>	0.72 ± 0.00 <sup>b</sup>	2.19 ± 1.20 <sup>abcd</sup>	0.94 ± 0.61 <sup>a</sup>	0.43 ± 0.27 <sup>abc</sup>	3.56 ± 3.60 <sup>abcd</sup>	0.89 ± 0.86 <sup>bc</sup>	4.46 ± 4.46 <sup>abcde</sup>
<i>Cananga odorata</i> (Lam.) Hook. f. & Thomson	3	6.68 ± 0.74 <sup>a</sup>	5.24 ± 1.76 <sup>ab</sup>	0.28 ± 0.00 <sup>h</sup>	2.29 ± 0.89 <sup>abc</sup>	0.40 ± 0.22 <sup>ab</sup>	0.29 ± 0.10 <sup>abc</sup>	2.98 ± 2.09 <sup>abcde</sup>	0.68 ± 0.53 <sup>bc</sup>	3.67 ± 2.61 <sup>abcdef</sup>
<i>Canarium vrieseanum</i> Engl.	3	5.00 ± 1.21 <sup>bcde</sup>	3.08 ± 1.26 <sup>edef</sup>	0.48 ± 0.02 <sup>f</sup>	1.44 ± 0.70 <sup>abcd</sup>	0.35 ± 0.25 <sup>ab</sup>	0.90 ± 0.63 <sup>a</sup>	2.69 ± 2.72 <sup>abcde</sup>	0.48 ± 0.35 <sup>bc</sup>	3.17 ± 3.06 <sup>abcdef</sup>
<i>Artocarpus altilis</i> (Parkinson) Fosberg	3	6.08 ± 0.64 <sup>abc</sup>	3.70 ± 0.86 <sup>bcde</sup>	0.41 ± 0.00 <sup>g</sup>	1.97 ± 0.48 <sup>abcd</sup>	0.22 ± 0.15 <sup>ab</sup>	0.18 ± 0.06 <sup>bc</sup>	2.37 ± 1.18 <sup>abcde</sup>	0.70 ± 0.27 <sup>bc</sup>	3.07 ± 1.41 <sup>abcdef</sup>
<i>Diospyros frutescens</i> Blume	3	4.37 ± 0.49 <sup>de</sup>	2.06 ± 0.38 <sup>efg</sup>	0.71 ± 0.00 <sup>b</sup>	1.05 ± 0.20 <sup>bcd</sup>	0.70 ± 0.28 <sup>ab</sup>	0.52 ± 0.20 <sup>abc</sup>	2.28 ± 1.13 <sup>abcde</sup>	0.44 ± 0.28 <sup>bc</sup>	2.72 ± 1.38 <sup>abcdef</sup>
<i>Anisoptera marginata</i> Korth.	3	4.95 ± 0.50 <sup>bcde</sup>	2.90 ± 0.91 <sup>cdef</sup>	0.59 ± 0.00 <sup>d</sup>	0.96 ± 0.36 <sup>bcd</sup>	0.35 ± 0.11 <sup>ab</sup>	0.36 ± 0.15 <sup>abc</sup>	1.67 ± 1.07 <sup>abcde</sup>	0.41 ± 0.24 <sup>bc</sup>	2.08 ± 1.32 <sup>bcdef</sup>
<i>Bombax anceps</i> Pierre	3	4.87 ± 1.20 <sup>cde</sup>	3.90 ± 1.04 <sup>bcde</sup>	0.41 ± 0.00 <sup>g</sup>	1.07 ± 0.40 <sup>bcd</sup>	0.14 ± 0.01 <sup>b</sup>	0.05 ± 0.00 <sup>c</sup>	1.25 ± 0.69 <sup>bcde</sup>	0.64 ± 0.38 <sup>bc</sup>	1.89 ± 1.07 <sup>bcdef</sup>
<i>Pongamia pinnata</i> (L.) Pierre	3	4.99 ± 0.62 <sup>bcde</sup>	1.18 ± 0.16 <sup>fg</sup>	0.89 ± 0.00 <sup>a</sup>	1.04 ± 0.30 <sup>bcd</sup>	0.15 ± 0.06 <sup>b</sup>	0.09 ± 0.03 <sup>c</sup>	1.28 ± 0.65 <sup>bcde</sup>	0.31 ± 0.12 <sup>bc</sup>	1.58 ± 0.78 <sup>bcdef</sup>
<i>Canarium vulgare</i> Leenh.	3	3.77 ± 0.88 <sup>ef</sup>	2.41 ± 0.81 <sup>defg</sup>	0.75 ± 0.01 <sup>b</sup>	0.68 ± 0.26 <sup>cd</sup>	0.25 ± 0.17 <sup>ab</sup>	0.36 ± 0.15 <sup>abc</sup>	1.29 ± 1.00 <sup>bcde</sup>	0.23 ± 0.18 <sup>bc</sup>	1.51 ± 1.18 <sup>bcdef</sup>
<i>Pometia pinnata</i> J.R. Forst. & G. Forst.	3	2.63 ± 0.29 <sup>fg</sup>	1.96 ± 0.36 <sup>efg</sup>	0.65 ± 0.00 <sup>c</sup>	0.54 ± 0.07 <sup>cd</sup>	0.07 ± 0.03 <sup>b</sup>	0.17 ± 0.06 <sup>bc</sup>	0.73 ± 0.25 <sup>de</sup>	0.38 ± 0.21 <sup>bc</sup>	1.11 ± 0.46 <sup>cdef</sup>
<i>Inocarpus fagifer</i> (Parkinson ex F.A.Zorn) Fosberg	3	2.84 ± 0.33 <sup>fg</sup>	1.55 ± 0.38 <sup>fg</sup>	0.55 ± 0.00 <sup>e</sup>	0.42 ± 0.06 <sup>cd</sup>	0.11 ± 0.05 <sup>b</sup>	0.36 ± 0.09 <sup>abc</sup>	0.89 ± 0.34 <sup>cde</sup>	0.21 ± 0.11 <sup>bc</sup>	1.10 ± 0.44 <sup>cdef</sup>
<i>Ormosia calavensis</i> Azaola ex Blanco	3	2.08 ± 0.27 <sup>g</sup>	0.89 ± 0.35 <sup>g</sup>	0.61 ± 0.02 <sup>d</sup>	0.27 ± 0.13 <sup>abcd</sup>	0.12 ± 0.05 <sup>b</sup>	0.10 ± 0.05 <sup>c</sup>	0.49 ± 0.40 <sup>de</sup>	0.16 ± 0.10 <sup>bc</sup>	0.65 ± 0.51 <sup>def</sup>
<i>Samanea saman</i> (Jacq.) Merr.	3	4.65 ± 1.40 <sup>cde</sup>	1.33 ± 0.26 <sup>fg</sup>	0.42 ± 0.00 <sup>g</sup>	0.23 ± 0.09 <sup>cd</sup>	0.04 ± 0.03 <sup>b</sup>	0.01 ± 0.00 <sup>c</sup>	0.27 ± 0.20 <sup>de</sup>	0.06 ± 0.03 <sup>bc</sup>	0.33 ± 0.23 <sup>ef</sup>
<i>Cassia grandis</i> L.f.	3	1.75 ± 0.39 <sup>g</sup>	1.16 ± 0.49 <sup>fg</sup>	0.67 ± 0.00 <sup>c</sup>	0.14 ± 0.06 <sup>d</sup>	0.01 ± 0.00 <sup>b</sup>	0.00 ± 0.00 <sup>c</sup>	0.16 ± 0.10 <sup>e</sup>	0.06 ± 0.04 <sup>bc</sup>	0.22 ± 0.15 <sup>f</sup>
<i>Canarium decumanum</i> Gaertn.	3	1.93 ± 0.64 <sup>g</sup>	1.28 ± 0.45 <sup>fg</sup>	0.59 ± 0.00 <sup>d</sup>	0.08 ± 0.01 <sup>d</sup>	0.00 ± 0.00 <sup>b</sup>	0.02 ± 0.01 <sup>c</sup>	0.12 ± 0.05 <sup>e</sup>	0.04 ± 0.04 <sup>c</sup>	0.16 ± 0.08 <sup>f</sup>

Note: N = number of samples; H = tree height; D = diameter (dbh); WD = wood density, AGB = aboveground biomass; BGB = belowground biomass; TB = total biomass. Values are mean and standard deviation (Mean ± SD). Values in the same column followed by different superscript letters differ significantly at  $P < 0.05$ .



**Appendix 4.** Tree species, height, diameter, wood density, and biomass components at 8 years of age for native tropical lowland trees in Indonesia.

Species	N	H (m)	D (cm)	WD (gr/cm <sup>3</sup> )	AGB (kg)				BGB/Roots (kg)	TB (kg)
					Stem	Branches	Leaves	Total		
<i>Litsea garciae</i> Vidal Count	3	13.24 ± 0.47 <sup>a</sup>	17.73 ± 3.71 <sup>a</sup>	0.32 ± 0.00 <sup>j</sup>	65.97 ± 15.59 <sup>a</sup>	35.61 ± 16.89 <sup>a</sup>	8.42 ± 2.88 <sup>ab</sup>	110.00 ± 58.52 <sup>a</sup>	13.9 ± 6.15 <sup>ab</sup>	123.89 ± 64.56 <sup>a</sup>
<i>Terminalia bellirica</i> (Gaertn.) Roxb. Count	3	13.87 ± 1.88 <sup>a</sup>	17.25 ± 3.84 <sup>a</sup>	0.57 ± 0.01 <sup>g</sup>	60.98 ± 24.94 <sup>ab</sup>	29.61 ± 19.54 <sup>ab</sup>	11.82 ± 4.31 <sup>a</sup>	102.40 ± 84.47 <sup>ab</sup>	14.98 ± 14.87 <sup>ab</sup>	117.38 ± 99.34 <sup>ab</sup>
<i>Anisoptera marginata</i> Korth.	3	12.73 ± 2.61 <sup>a</sup>	14.96 ± 4.24 <sup>ab</sup>	0.62 ± 0.01 <sup>e</sup>	47.40 ± 30.44 <sup>abc</sup>	10.98 ± 5.81 <sup>abc</sup>	4.57 ± 2.28 <sup>bc</sup>	62.96 ± 66.69 <sup>abc</sup>	10.64 ± 12.43 <sup>ab</sup>	73.6 ± 79.11 <sup>abc</sup>
<i>Cananga odorata</i> (Lam.) Hook. f. & Thomson	3	13.62 ± 1.75 <sup>a</sup>	17.41 ± 2.12 <sup>a</sup>	0.3 ± 0.01 <sup>k</sup>	33.39 ± 15.48 <sup>abc</sup>	15.08 ± 8.66 <sup>abc</sup>	5.31 ± 2.22 <sup>abc</sup>	53.79 ± 45.61 <sup>abc</sup>	19.12 ± 18.26 <sup>a</sup>	72.91 ± 63.86 <sup>abc</sup>
<i>Castilla elastica</i> subsp. <i>costaricana</i> (Liebm.) C.C.Berg	3	13.26 ± 1.37 <sup>a</sup>	17.39 ± 1.30 <sup>a</sup>	0.44 ± 0.01 <sup>i</sup>	48.67 ± 17.65 <sup>abc</sup>	3.50 ± 1.15 <sup>bc</sup>	3.11 ± 1.17 <sup>bc</sup>	55.28 ± 34.28 <sup>abc</sup>	6.33 ± 3.10 <sup>ab</sup>	61.61 ± 36.41 <sup>abc</sup>
<i>Canarium vrieseanum</i> Engl.	3	9.97 ± 2.22 <sup>ab</sup>	10.61 ± 4.18 <sup>bcde</sup>	0.50 ± 0.00 <sup>h</sup>	34.58 ± 24.65 <sup>abc</sup>	12.67 ± 8.55 <sup>abc</sup>	6.09 ± 3.70 <sup>abc</sup>	53.34 ± 63.91 <sup>abc</sup>	7.32 ± 8.92 <sup>ab</sup>	60.65 ± 72.83 <sup>abc</sup>
<i>Pterospermum javanicum</i> Jungh. Count	3	12.57 ± 2.50 <sup>a</sup>	14.87 ± 1.94 <sup>ab</sup>	0.59 ± 0.01 <sup>fg</sup>	43.43 ± 21.55 <sup>abc</sup>	6.41 ± 2.69 <sup>bc</sup>	0.37 ± 0.19 <sup>c</sup>	50.21 ± 40.90 <sup>abc</sup>	6.45 ± 5.71 <sup>ab</sup>	56.67 ± 46.36 <sup>abc</sup>
<i>Intsia bijuga</i> (Colebr.) Kuntze	3	12.28 ± 3.29 <sup>a</sup>	13.18 ± 4.32 <sup>abc</sup>	0.78 ± 0.02 <sup>bc</sup>	29.98 ± 11.69 <sup>abc</sup>	6.82 ± 2.98 <sup>bc</sup>	2.25 ± 0.81 <sup>bc</sup>	39.05 ± 26.74 <sup>abc</sup>	5.03 ± 2.96 <sup>ab</sup>	44.08 ± 29.7 <sup>abc</sup>
<i>Artocarpus altilis</i> (Parkinson) Fosberg	2	10.35 ± 5.02 <sup>ab</sup>	11.75 ± 3.83 <sup>abcd</sup>	0.44 ± 0.00 <sup>i</sup>	23.19 ± 15.32 <sup>abc</sup>	1.53 ± 1.18 <sup>c</sup>	1.38 ± 0.94 <sup>bc</sup>	26.1 ± 24.67 <sup>bc</sup>	3.51 ± 2.66 <sup>b</sup>	29.61 ± 27.32 <sup>abc</sup>
<i>Pometia pinnata</i> J.R. Forst. & G. Forst.	2	6.88 ± 2.51 <sup>bc</sup>	7.72 ± 2.77 <sup>cde</sup>	0.76 ± 0.01 <sup>bc</sup>	10.98 ± 5.82 <sup>bc</sup>	3.97 ± 3.06 <sup>bc</sup>	2.35 ± 1.52 <sup>bc</sup>	17.30 ± 14.70 <sup>c</sup>	3.44 ± 2.57 <sup>b</sup>	20.74 ± 17.27 <sup>bc</sup>
<i>Diospyros frutescens</i> Blume	3	7.45 ± 0.65 <sup>ab</sup>	7.60 ± 1.97 <sup>cde</sup>	0.75 ± 0.02 <sup>c</sup>	8.14 ± 2.97 <sup>bc</sup>	4.39 ± 2.87 <sup>bc</sup>	3.60 ± 1.51 <sup>bc</sup>	16.13 ± 12.73 <sup>c</sup>	1.95 ± 1.18 <sup>b</sup>	18.08 ± 13.80 <sup>c</sup>
<i>Canarium vulgare</i> Leenh.	3	6.73 ± 2.75 <sup>bc</sup>	9.46 ± 2.04 <sup>bcde</sup>	0.76 ± 0.01 <sup>bc</sup>	7.51 ± 5.43 <sup>bc</sup>	2.95 ± 1.93 <sup>c</sup>	3.28 ± 2.35 <sup>bc</sup>	13.73 ± 16.82 <sup>c</sup>	1.82 ± 2.26 <sup>b</sup>	15.55 ± 19.07 <sup>c</sup>
<i>Inocarpus fagifer</i> (Parkinson ex F.A.Zorn) Fosberg	3	7.36 ± 1.14 <sup>bc</sup>	9.27 ± 3.65 <sup>bcde</sup>	0.66 ± 0.01 <sup>d</sup>	8.72 ± 4.19 <sup>bc</sup>	1.98 ± 0.72 <sup>c</sup>	1.52 ± 0.65 <sup>bc</sup>	12.22 ± 9.62 <sup>c</sup>	2.84 ± 2.87 <sup>b</sup>	15.06 ± 12.47 <sup>c</sup>
<i>Canarium decumanum</i> Gaertn.	3	8.11 ± 0.82 <sup>bc</sup>	6.93 ± 1.70 <sup>de</sup>	0.61 ± 0.01 <sup>ef</sup>	6.57 ± 1.58 <sup>bc</sup>	0.31 ± 0.11 <sup>c</sup>	0.70 ± 0.13 <sup>c</sup>	7.58 ± 3.15 <sup>c</sup>	1.17 ± 0.62 <sup>b</sup>	8.75 ± 3.74 <sup>c</sup>
<i>Ormosia calavensis</i> Azaola ex Blanco	3	4.93 ± 0.96 <sup>c</sup>	5.28 ± 3.27 <sup>e</sup>	0.65 ± 0.02 <sup>d</sup>	2.63 ± 1.03 <sup>c</sup>	0.49 ± 0.28 <sup>c</sup>	0.62 ± 0.32 <sup>c</sup>	3.74 ± 2.78 <sup>c</sup>	0.77 ± 0.54 <sup>b</sup>	4.51 ± 3.27 <sup>c</sup>
<i>Pongamia pinnata</i> (L.) Pierre	3	5.13 ± 0.80 <sup>c</sup>	7.76 ± 0.83 <sup>cde</sup>	0.89 ± 0.00 <sup>a</sup>	2.02 ± 0.08 <sup>c</sup>	0.34 ± 0.05 <sup>c</sup>	0.12 ± 0.02 <sup>c</sup>	2.48 ± 0.24 <sup>c</sup>	0.48 ± 0.08 <sup>b</sup>	2.96 ± 0.32 <sup>c</sup>

Note: N = number of samples; H = tree height; D = diameter (dbh); WD = wood density, AGB = aboveground biomass; BGB = belowground biomass; TB = total biomass. Values are mean and standard deviation (Mean ± SD). Values in the same column followed by different superscript letters differ significantly at P < 0.05.

