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Allometric Modeling for Leaf Area and Leaf Biomass Estimation of *Swietenia mahagoni* in the North-eastern Region of Bangladesh

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Abstract

Leaf area (A_0) and leaf biomass (M_0) estimation are significant prerequisites to studying tree physiological processes and modeling in the forest ecosystem. The objective of this study was to develop allometric models for estimating A_0 and M_0 of *Swietenia mahagoni* L. from different tree parameters such as DBH and tree height of mahogany plantations in the northeastern region of Bangladesh. A total of 850 healthy and well formed trees were selected randomly for sampling in the five study sites. Then, twenty two models were developed based on different statistical criteria that propose reliable and accurate models for estimating the A_0 and M_0 using non-destructive measurements. The results exposed that model iv and xv were selected on a single predictor of DBH and showed more statistically accuracy than other models. The selected models were also validated with an additional test data set on the basis of linear regression and t-test for mean difference between observed and predicted values. After that, a comparison between the best logarithmic and non-linear allometric model shows that the non-linear model produces systematic biases and underestimates A_0 and M_0 for larger trees. As a result, it showed that the bias-corrected logarithmic model iv and xv can be used to help quantify forest structure and functions, particularly valuable in future research for estimating A_0 and M_0 of *S. mahagoni* in this region.

Key Words: leaf area, leaf biomass, DBH, *Swietenia mahagoni*

Introduction

The leaf area (A_0) of individual trees and of forests is biological factor that determines the light interception and the efficiency of the photosynthetic and transpiration rate (Pereira et al. 1997) and also valuable for gap models and individual tree growth models (Peter et al. 2010). Leaf area is defined as the surface area available for the interception of radiant energy, the absorption of carbon dioxide, and the circulation of water between the foliage and the atmosphere (Margolis et al. 1995) and the plant leaf area is crucial for the evaluation and understanding of the vegetative growth and water loss from the plant. Canopy leaf biomass is the product of the leaf dry matter content and leaf area index (Tobin et al. 2006) and it constitutes one of the most important pools of essential nutrients, which is vital for forest nutrient cycling including carbon cycling. Leaf biomass (M_0) estimates were significantly improved when additional biometric information relating to crown structure was added (Tobin et al. 2006).

Both A_0 and M_0 estimations aid evaluation of plant performance at the individual, community and even ecosystem

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level (Meier and Leuschner 2008). Moreover, a number of studies ranging from insect-forest interactions (Paine et al. 1990), light competition (Waring 1983), and direct manipulative studies focused on A_0 response to thinning and fertilization (Vose and Allen 1988; Velazquez-Martinez et al. 1992) have used A_0 estimates. Inter-specific variation in A_0 is connected with climatic variation, geology, altitude or latitude whereas this variation can also be linked to allometric factors (plant size, twig size, anatomy and architecture) and ecological strategy (Cornelissen et al. 2003). A_0 measurements have become major tools for forest ecosystem and silvicultural studies over the last few decades.

Total A_0 and M_0 of trees have been measured by either destructive (direct) (Calvo-Alvarado et al. 2008; Peter et al. 2010) or nondestructive (indirect) (Norman and Campbell 1989; Sarker et al. 2013; Das 2014) methods. Measurement of the destructive method is very time consuming, labour intensive, eco-unfriendly and depends on very small samples. But, nondestructive methods were found user friendly, less expensive, and can give accurate A_1 and B_1 estimates (Waring 1983; Norman and Campbell 1989; Paine et al. 1990; Sarker et al. 2013; Das 2014). For the estimation of allometric models are particularly in statistical shape analysis for its theoretical developments (Zianis 2005) and it is unquestionable that researchers have produced a voluminous amount of allometric relationships for several species and tree components (Calvo-Alvarado et al. 2008; Peter et al. 2010). To quantify the A_0 and M_0 of individual trees with DBH (diameter at breast height) of allometric relationship have been widely used (Gajardo-Caviedes et al. 2005). Generally, allometric models are developed by fitting a linear relationship between log-transformed diameter and leaf data.

Tree species of *Swietenia mahagoni* L. is largely planted on barren forest lands and roadsides in connection with the agroforestry and social forestry programs in Bangladesh (Das and Alam 2001). A substantial portion of the total afforested area (11%) is located in the north-eastern region of Bangladesh. Though there is no scientific record yet, my experience is that *S. mahagoni* covers a considerable portion of the forest cover of this region. It has great potential for reforestation and afforestation, particularly for improving soil and environmental conditions. In this study, I evaluate several models based on different statistical criteria that propose reliable and accurate models for estimating the A_0 and M_0 using non-destructive measurements. Thus, the objective of this study was to develop allometric models for estimating A_0 and M_0 of *S. mahagoni* from different tree parameters such as DBH and tree height of mahogany plantations in the north-eastern region of Bangladesh.

Materials and Methods

Site description

The research was conducted on the five sites of Sylhet Forest division, named Kamalganj, Rajkandi, Kulaura, Juri and Barlekha, which are in the Moulovibazar District of north-eastern Bangladesh (Fig. 1). The area lies between 24.11 and 24.42° N and between 91.45 and 92.15° E. This district is located in the semi-evergreen hill forest zone and the characteristic vegetation comprises deciduous to semi-evergreen species in natural forest patches with a closed canopy. The average annual rainfall is 4150 mm and the relative humidity is about 72 percent during December and over 92 percent during July-August. Forests in this area occupy gentle to very steep slopes. Soils have developed over consolidated or unconsolidated bedrocks, and are imperfect to excessively drain. Generally, the subsoil is yellow to strong brown, friable, porous, sandy loam to sandy or silty clay loam, and strongly to extremely acidic (Banglapedia 2003).

Species description

Swietenia mahagoni (L.) is a tall tree, up to 30 m high, with a short, buttressing base, up to 1 m in diameter and a large, spherical crown, many heavy branches and dense shade. The tree is deciduous in areas where it is subject to drought. Its leaves even, pinnate, 10-18 cm long, and bearing 4-10 pairs of leaflets that are shiny, dark green, lance-shaped, 2.5-5 cm long by 0.7-2 cm broad (Das and Alam 2001). *S. mahagoni* is suitable for large-scale timber production plantations because of its excellent timber quality. The wood can be used for construction materials, plywood (veneer), high-grade furniture and cabinet making. It grows naturally in tropical America and it has been extensively planted mainly in Southern Asia and the Pacific including India, Bangladesh, Indonesia, Philippines and Sri Lanka (Soerianegara and Lemmens 1993).

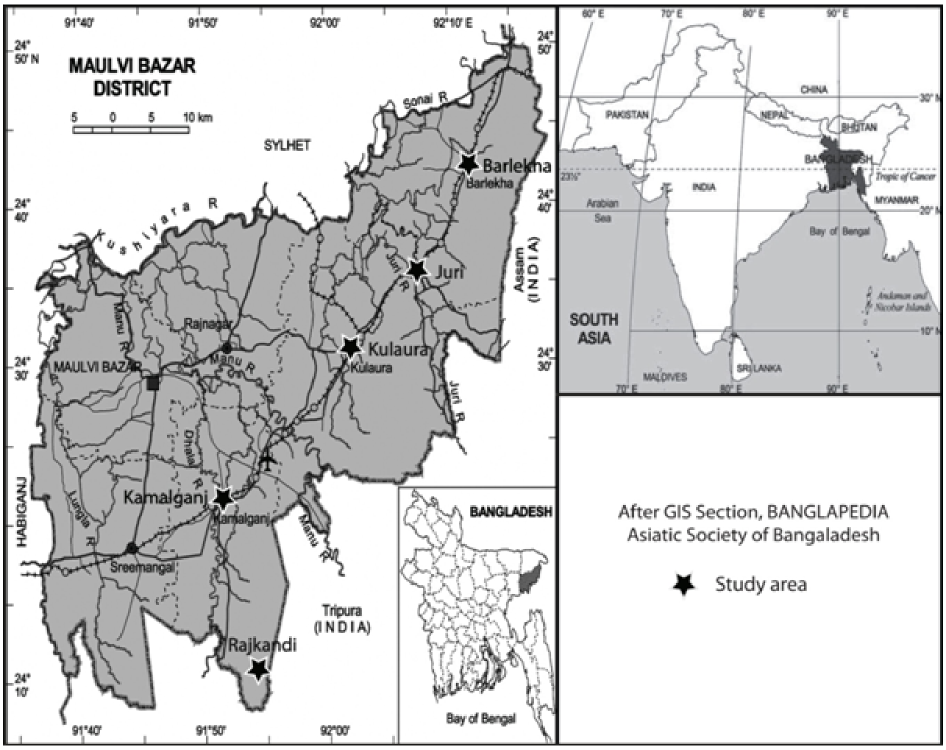

Fig. 1. Map of the Study site.

Table 1. Descriptive statistics for the different variables of *S. mahagoni*

Variables	Mean	Maximum	Minimum	SD	Skewness	Kurtosis
DBH (cm)	26.625	53.10	10.09	10.070	0.181	-0.733
Height (m)	10.190	18.86	4.97	3.069	0.742	-0.433
Validation DBH (cm)	23.731	51.40	11.24	13.173	0.185	-0.750
Validation Height (m)	9.890	17.25	5.02	2.192	0.683	-0.427
Individual leaf area (cm^2)	25.517	34.37	10.36	3.614	0.238	0.217
Individual dry leaf biomass (g)	0.492	0.782	0.21	0.282	0.116	0.105

Field measurements

A total of 850 healthy and well formed *S. mahagoni* trees were selected randomly for sampling. Data on tree height and DBH (Table 1) were measured by Sunnto Clinometers and Tree Calipers. The leaves were collected by using the protocols of Cornelissen et al. (2003). But, because of moratorium on felling in the forests (Sarker et al. 2011), the leaf data was collected manually (climbing on tree). To retain high data accuracy, I used stratified random sampling in calculating leaf number of individual trees. The method is equally suitable to estimate A_0 where randomly sub-sampled branches are used to calculate whole-tree A_0 based on the relative importance of the branches (Peter et al. 2010; Das 2014). I maintained the following steps to count the leaves of each sampled trees: (I) diameter of all the main branches were measured, (II) main branch's diameter near to mean diameter was selected as model main branch (MMB), (III) sub-branches of all the main branches were counted, (IV) three sub-branches were selected randomly from the MMB, (V) twigs of each sub-branch were counted and mean twigs number/sub-branch was calculated, (VI) thee twigs were selected randomly from each selected sub-branch, (VII) average leaves/twig was calculated,

(VIII) leaf number/sub-branch was calculated by multiplying mean twigs number/sub-branch and mean leaf numbers/twig and (IX) total leaf number of a tree was calculated by multiplying total sub-branches and estimated leaf number/sub-branch (Sarker et al. 2013; Das 2014). The leaves were categorized into small, medium and large size and five leaves of each category were collected randomly from sub-branches. In total, fifteen leaf samples were collected from each tree and packed in a plastic bag. After that, data of DBH, tree height, leaf samples and total leaf number per tree from an additional 200 trees were collected and used as a test data set for validating the models. Leaf area of each sample leaf (Table 1) was measured by leaf area meter (CI-202, CID, Inc., Vancouver, Washington, USA) and the fresh mass of each leaf was measured with a digital balance meter. Thickness of each sample leaf was estimated with digital caliper (Absolute Digimatic CD-6″ CS, Mitutoyo Corporation, Kanagawa, Japan). Measured leaves were oven dried at 65°C for 72 hours and weighted to determine fresh mass: dry mass ratios. The projected leaf area for each sample tree (A_0, m^2) was calculated by multiplying average A_0 and total leaf number. Total leaf volume/tree was estimated by multiplying total A_0 and leaf thickness. Leaf density was measured by dividing the average leaf fresh mass by leaf volume of the fifteen sampled leaves per tree. Total leaf biomass per tree was estimated by multiplying the total leaf volume and leaf density (Sarker et al. 2013; Das 2014).

Model development and validation

From Fig. 2, it was clear that both DBH and tree height of the model data set were not normally distributed (for DBH: Shapiro-Wilk p=5.536e-06; for tree height p=3.491e-05 at α=0.05). For estimation of A_0 and M_0 of *S. mahagoni*, I tested of four regression models (linear, power, exponential and quadratic). Total twenty two models were developed using DBH and height for the best allometric relationship between the response and predictors (Table 2). Diagnostic residual plots were used to check five statistical assumptions (Robinson and Hamann 2011), such as I) the models detain a relationship, II) errors have constant variance, III) errors are normally distributed, IV) sample represents the population and V) error terms are independent. The developed models were evaluated by examining root mean squared error (RMSE), goodness of fit (R^2), Akaike information criterion (AIC), Bayesian information criterion (BIC) and average deviation (%). The Durbin-Watson test for autocorrelation was used to check the autocorrelation. Due to the presence of heteroscedasticity, I transformed the data for linear regression using natural logarithm and this transformation induced a systematic bias in the estimation which was corrected using a correction factor (CF) when back transforming the calculation into A_0 and M_0 (Son et al. 2001; Sah et al. 2004; Chave et al. 2005). Thus, the correction factor (CF) is calculated according to the usual formula (Sprugel 1983):

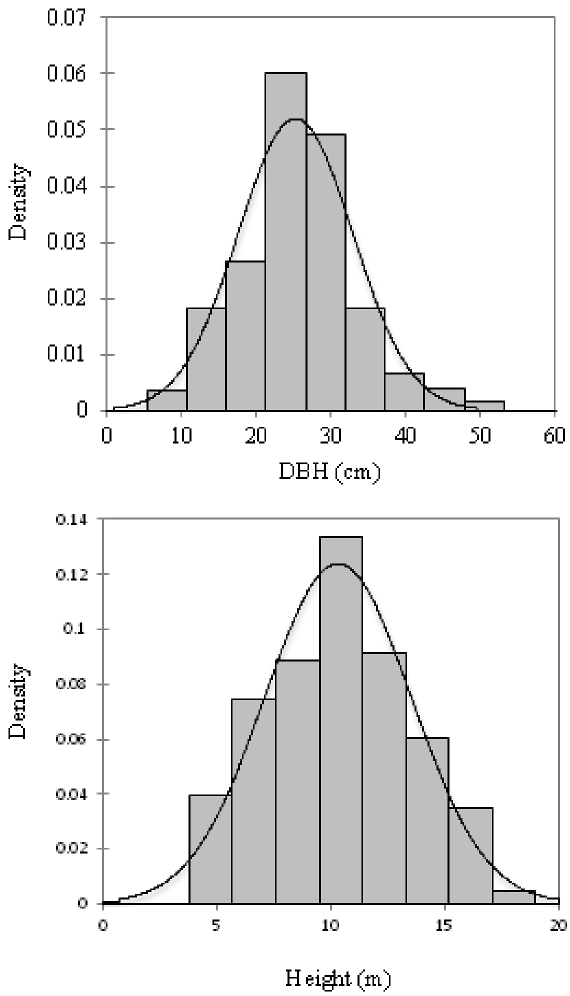

Fig. 2. Diameter at breast height (DBH; cm) and tree height (m) distributions of the model fitting data set.

Table 2. Different models used in this study

Model no.	Allometric models
i	LA=a+b*DBH
ii	LA=a+b*H
iii	LA=a+b*DBH+c*H
iv	lnLA=a+b*lnDBH
v	lnLA=a+b*lnH
vi	lnLA=a+b*lnDBH+c*lnH
vii	lnLA=a+b*DBH
viii	lnLA=a+b*H
ix	lnLA=a+b*DBH+c*H
x	lnLA=a+b*DBH+c*DBH^2
xi	lnLA=a+b*H+c*H^2
xii	FB=a+b*DBH
xiii	FB=a+b*H
xiv	FB=a+b*DBH+c*H
xv	lnFB=a+b*lnDBH
xvi	lnFB=a+b*lnH
xvii	lnFB=a+b*lnDBH+c*lnH
xviii	lnFB=a+b*DBH
xix	lnFB=a+b*H
xx	lnFB=a+b*DBH+c*H
xxi	lnFB=a+b*DBH+c*DBH^2
xxii	lnFB=a+b*H+c*H^2

$$\mathrm{CF} = \exp^{((SEE*2.303)^2/2)}$$

where SEE=standard error of the estimate. The average deviation was computed from the absolute difference between predicted and observed values and expressed as the percentage of observed values, and then all deviations were averaged (Cairns et al. 2003; Chave et al. 2005). The average deviation (δB) is calculated as follows:

$$\delta\mathrm{B}\ (\%) = \sum_{n=1}^{n} |\check{\mathrm{D}}\mathrm{W} - \mathrm{DW}\,|/\mathrm{DW}*(100/\mathrm{n})$$

where ĎW=estimated, DW=observed and n=number of observations. It was calculated after the prediction was back-transformed to the unit values and corrected using a CF. This model was then compared with the relevant logarithmic model with bias correction.

I used R statistical software version 3 (R Development Core Team 2013) for data analysis. I regressed the observed A_0 and M_0 of the test data from an additional test data set (n = 200) against the predicted A_0 and M_0 uses linear regression for validating the models. Then, I compared the mean difference between the observed and predicted A_0 and M_0 using a t-test. In addition, I developed best fit non-linear regression model for estimating A_0 and M_0 and these models were then compared to the bias corrected logarithmic models.

Results

Model development and evaluation

From the development of twenty two models, the best ones were determined according to the selection criteria described in materials and methods and the A_0 and M_0 were best estimated using models iv and xv, respectively (Table 3). For both parameters, the goodness of fit adjusted (R^2) of regressions was highly significant while using the DBH as a predictor and explained more than 93% variation. To compare the models, the AIC and BIC values for models iv and xv were lower than that of other tested models indicating the statistical robustness of the selected models (iv and xv) and the RMSE values were also lower for the selected models (Table 3). Among the tested models, model iv and xv had the lowest average deviations (17.304 and 20.447%, respectively).

To check these statistical assumptions, for first assumption, I plotted regression residuals versus fitted values for the models in order to check whether the linear model captures the relationship. In this scatter plot, I noted that the residual scatter plot had the slight heteroscedastic behavior of the selected models (Figs. 3A, 4A). After that, I also plotted the normal Q-Q plot of the standardized residuals against the normal distribution line and the errors showing slight departure from the line (Figs. 3B, 4B) that have constant variance (assumption II) and were normally distributed (assumption III). In addition, to check assumption II, I plotted the square root of the absolute residuals against the fitted values (Figs. 3C, 4C), and the figures show no deviations from the horizontal line. However, such kind of deviations from the horizontal line is often acceptable as described in large sample theory (Robinson and Hamann 2011). The leverage of the observations against the standardized residuals showed that the Cook's distance was less than 1 in both cases (Figs. 3D, 4D). This indicates that the adequacy of the sample as a representative of the population

Table 3. Estimated parameters of the different models tested for predicting A_0 and M_0 of *S. mahagoni*

Model	Estimated Coefficients			RMSE	F	R^2	Adjusted R^2	AIC	BIC	CF	AD	Durbin Watson
	a	b	c									
i	-83.3269***	7.10880***		20.112	5,924	0.8953	0.8951	6,144.42	6,161.74	-	40.246	1.036
ii	-105.352**	24.978**		45.311	611	0.4687	0.4679	7,269.56	7,290.38	-	135.15	1.494
iii	-80.5471***	7.2174***	-0.7196	20.117	2,963	0.8955	0.8951	6,145.83	6,167.09	-	42.368	1.073
iv	-2.96749***	2.28677***		0.2096	12,140	0.9460	0.9459	-192.58	-182.06	1.0222	17.304	1.957
v	-2.12996**	3.12390***		0.5790	988	0.5878	0.5872	1,211.27	1,230.29	1.1824	64.803	2.113
vi	-3.07579***	2.20725***	0.17899**	0.2099	6,154	0.9428	0.9426	-190.63	-180.71	1.0229	18.990	1.904
vii	1.681304***	0.102639***		0.3041	5,400	0.8863	0.8861	317.79	335.44	1.0473	19.682	0.960
viii	1.17847***	0.38620***		0.6169	788	0.5321	0.5314	1,297.46	1,318.47	1.2095	56.238	1.867
ix	1.507932***	0.095863***	0.0448***	0.2999	2,788	0.8896	0.8893	298.94	321.38	1.0459	18.027	0.969
x	0.4893***	0.2127***	-0.002***	0.2246	5,243	0.9381	0.9379	-95.25	-80.68	1.0255	30.912	1.726
xi	-3.75163***	1.681444***	-0.081***	0.5522	578	0.6256	0.6245	1,145.10	1,170.02	1.1646	84.165	2.250
xii	-7.20572***	0.636409***		2.0460	4,588	0.8688	0.8686	2,968.41	2,985.02	-	35.682	1.465
xiii	-9.29298**	2.25213**		4.1451	593	0.4613	0.4606	3,947.66	3,966.41	-	122.29	1.585
xiv	-7.09026***	0.64092***	-0.02989	2.0471	2,291	0.8688	0.8684	2,966.38	2,991.36	-	38.431	1.478
xv	-5.22514***	2.25004***		0.2430	8,740	0.9365	0.9364	9.42	23.61	1.0299	20.447	2.014
xvi	-4.42117***	3.08403***		0.5813	955	0.5796	0.5790	1,214.47	1,235.95	1.1840	64.988	2.105
xvii	-5.34700***	2.16057***	0.20141**	0.2455	4,429	0.9275	0.9273	10.49	25.56	1.0305	20.982	1.965
xviii	-0.64179***	0.100578***		0.3343	4,291	0.8610	0.8608	451.24	466.98	1.0574	21.994	1.103
xix	-1.14913**	0.38047**		0.6196	758	0.5224	0.5217	1,305.73	1,324.61	1.2116	45.681	1.858
xx	-0.82855***	0.093279***	0.0483***	0.3298	2,214	0.8649	0.8645	431.82	453.74	1.0558	23.627	1.112
xxi	-1.90365***	0.217069***	-0.002***	0.2542	3,964	0.9197	0.9195	72.55	91.84	1.0328	37.416	1.850
xxii	-6.22750***	1.714661***	-0.082***	0.5511	571	0.6228	0.6217	1,141.89	1,167.11	1.1639	98.243	2.268

*p<0.01, **p<0.001, ***p<0.0001.
AD=Average deviation (%), CF= Correction factor.

(assumption IV). The basic diagnostic plot cannot check assumption V because it doesn't have the option to check the independence of the error terms. To check this assumption, the Durbin-Watson test for autocorrelation among the residuals showed that the selected models were 1.957 and 2.014 for A_0 and M_0, respectively and nearly lies within the range of the acceptable limit of 2. In this context, the model coefficients cannot be reliably used unless the correction factor is applied to remove the heteroscedasticity. Correction factors showed a rather narrow variation for both cases (Table 3).

Therefore, the final model of A_0 is, A_0=exp (-2.96749+ 2.28677xln (DBH)), which can be written as A_0= 0.051432x(DBH)$^{2.28677}$. The bias corrected model is, A_0 =0.051432x(DBH)$^{2.28677}$x1.0222, and the final form of this model is A_0=0.052574x(DBH)$^{2.28677}$.

The final model of leaf biomass is, M_0=exp (-5.22514 +2.25004xln (DBH)), and can be written as M_0= 0.00538x(DBH)$^{2.25004}$. The bias corrected model is, M_0 =0.00538x(DBH)$^{2.25004}$x1.0299, which finally formed as M_0=0.00554x(DBH)$^{2.25004}$.

Model performance estimation

In the model validation, the goodness of fit (R^2) showed that there was a highly reliable relationship between estimated and observed data for both cases (A_0 and M_0). The R^2 between them for models using A_0 and M_0 was 0.982 and 0.965, respectively (Fig. 5). At 95% CI, the mean of the observed and the proposed models predicted data were not significantly different (p=0.998 for A_0 and p=0.993 for M_0) and there is a high probability that estimated values are closest to the observed values (Table 4). The predicted A_0 and M_0 using model iv and xv produced the same trend as the observed data (Fig. 6). In addition, I compared the best fitted nonlinear and the bias corrected logarithmic models (Table 5). The adjusted R^2, AIC and BIC values of the non-linear allometric model were 0.944, 5531.527 and 5558.043 for A_0, 0.924, 2693.836 and 2715.838 for M_0, respectively. On the other hand, for the logarithmic model those were 0.9459, -192.58 and -182.06 for A_0, 0.9364,

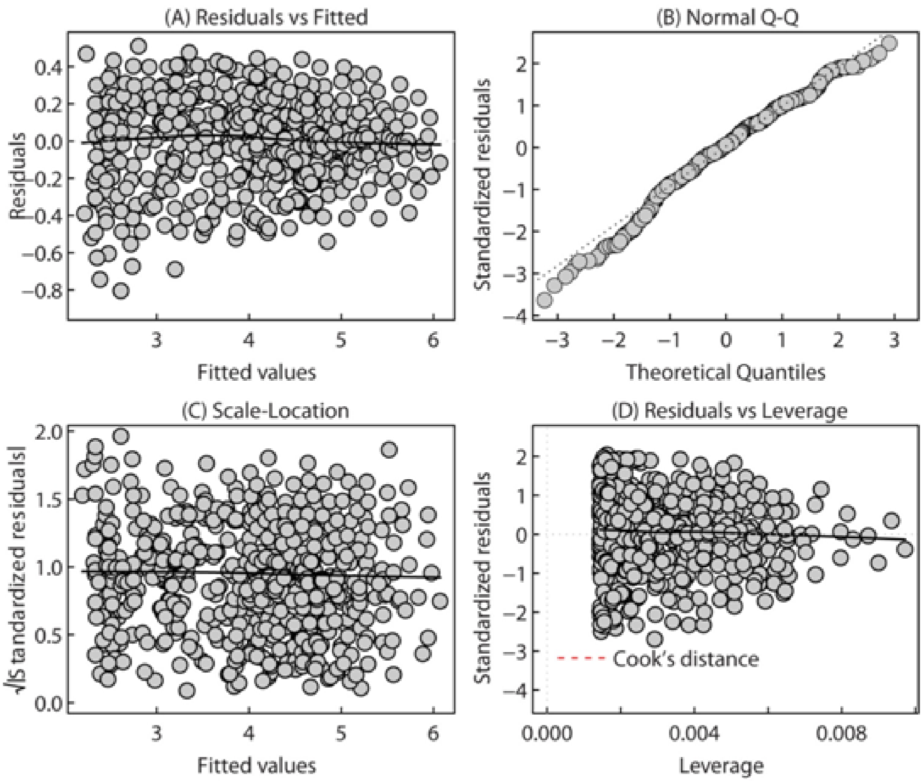

Fig. 3. Diagnostic plots for model iv.

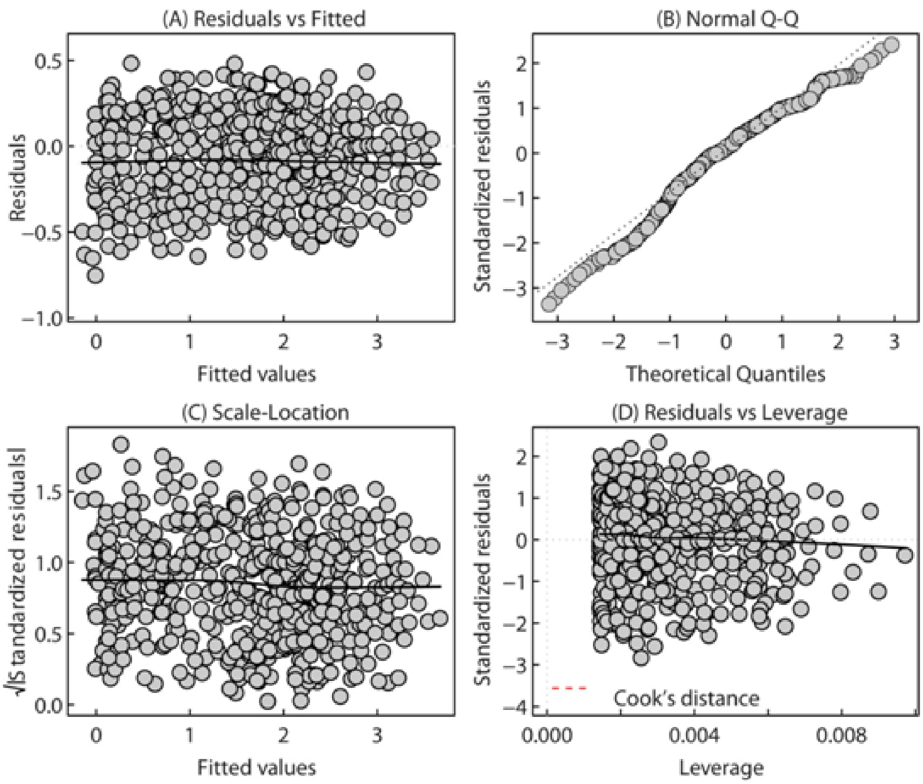

Fig. 4. Diagnostic plots for model xv.

Table 4. The confidence interval (CI) of the mean A_0 (m^2) and M_0 (kg) for observed and best fit model data, and paired *t*-test for this species

	Parameters	Observed	Model	SEE	*t*-test	Significance
A_0	Mean	75.285	76.797	0.526	-2.872	0.998
	95% CI Lower limit	70.660	71.940			
	95% CI Upper limit	79.910	81.654			
M_0	Mean	6.993	7.164	0.068	-2.480	0.993
	95% CI Lower limit	6.573	6.719			
	95% CI Upper limit	7.414	7.609			

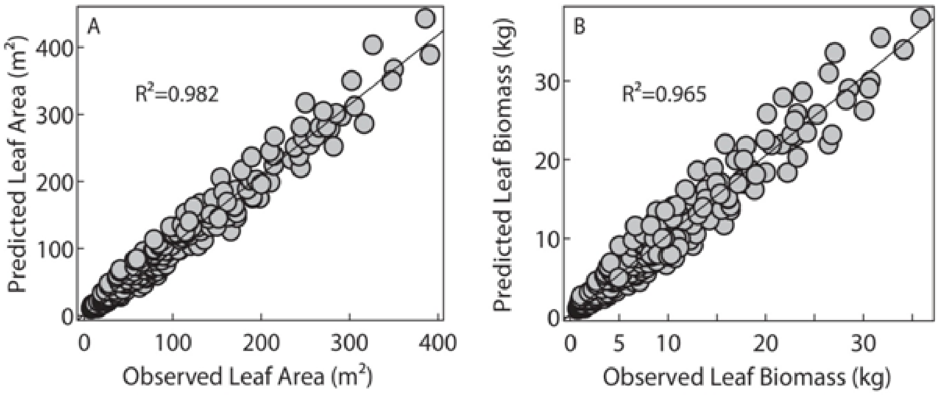

Fig. 5. Linear regression between observed and predicted leaf area (A); between observed and predicted leaf biomass (B).

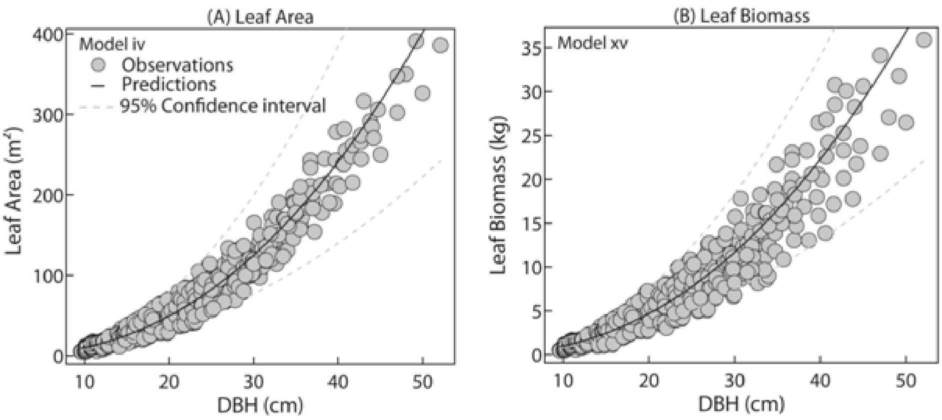

Fig. 6. Predicted leaf area (A) and leaf biomass (B) against diameter at breast height (DBH) using model iv and xv with observed data at 95% confidence intervals (CI).

9.42 and 23.61 for M_0. Despite of similar R^2 values, the AIC and BIC values were lower for logarithmic models in both cases. Moreover, nonlinear allometric models showed a propensity of underestimation of A_0 and M_0 with an increase of DBH (Fig. 7).

Discussion

The selected logarithmic models (iv and xv) were proposed according to slight heteroscedastic residual scatter, lower RMSE, AIC, BIC value and average deviation for estimation of A_0 and M_0. Though, logarithmic transformation induces a systematic bias in the estimation, which was corrected using a CF in the final model (Son et al. 2001; Sah et al. 2004; Chave et al. 2005). Consequently, the bias-corrected final allometric models produced a range of prediction values closer to the upper and lower limits of the observed mean values. These models accounted for more

Table 5. Estimated parameters for the best fit nonlinear model iv of A_0 and model xv of M_0

Parameters		Estimate	Std. Error	*t*-value	p-value
A_0	Intercept	0.074941	0.00494	15.14	<2e-16***
	Power	2.174058	0.01881	115.55	<2e-16***
M_0	Intercept	0.010102	0.00092	10.90	<2e-16***
	Power	2.062322	0.02625	78.54	<2e-16***

***Significant at α=0.00.

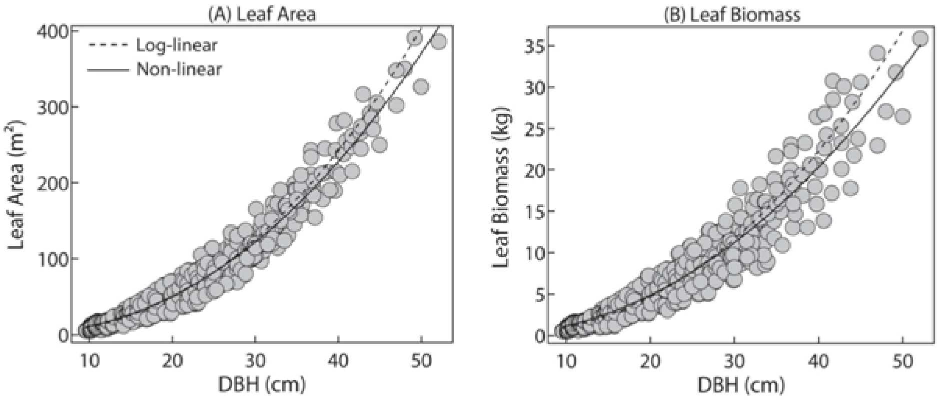

Fig. 7. Best fit logarithmic and nonlinear allometric models for leaf area (A) and leaf biomass (B).

than 93% variation based on DBH in A_0 and M_0 estimation (Table 3), providing a sound and reliable means to predict these canopy properties in the north-eastern region of Bangladesh. Burton et al. (1991) found that DBH is the best predictor for estimating A_0 and M_0 (R^2>0.90). After that, the development of A_0 and M_0 models using non-destructive methods is a highly steady option where whole tree removal is not possible, as is the case in Bangladeshi forest reserves (Dobbs et al. 2011). Thus, modified randomized branch sampling used in this study will in most cases remain the only feasible method and this study showed a strong statistical dependence between A_0 and M_0 with DBH. Using a non-destructive sampling technique for A_0 estimation, Grace and Fownes (1998) found that DBH could explain 91% variation in A_0 of *Acacia Koa*. Leaf area and biomass are positively related to DBH (Tobin et al. 2006; Calvo-Alvarado et al. 2008) and Vertessy et al. (1995) showed that DBH could explain more than 91% of true A_0 of *Eucalyptus regnans*. Das (2014) found that the developed models are explained for more than 96% of the variation based on DBH and height with A_0 and M_0 of *Lagerstroemia speciosa*. Sarker et al. (2013) also showed that DBH could explain 95% variation in A_0 and M_0 of *Artocarpus chaplasha*. Other studies found higher (Waring et al. 1982; Long and Smith 1988; Fownes and Harrington 1991; Zianis and Mencuccini 2003; Tobin et al. 2006; Peter et al. 2010) correlations with DBH. As a result, the selected allometric models are significant to tree growth models of this species and ecological purposes. It will tend to estimate A_0 and M_0 for trees exhibiting leaf loss due to such factors as pruning, insect defoliation etc. After that, I expect these relationships to prove valuable quantification of tree physiological and environmental processes. Therefore, the results obtained support that the regression models can be used on stands of different vigour and it is probably valid in Bangladesh and other tropical countries.

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