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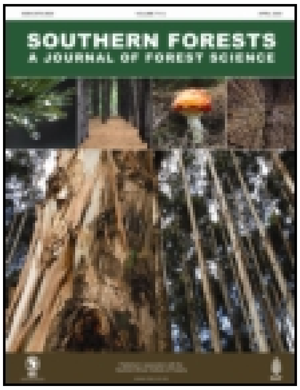

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Developing allometric equations for estimating leaf area and leaf biomass of *Artocarpus chaplasha* in Raghunandan Hill Reserve, Bangladesh

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Estimation of leaf area (LA) and leaf biomass (LB) is important to understand plant physiological and carbon assimilation processes, and tree growth models. The aim of this study was to develop and compare allometric equations for predicting LA and LB of *Artocarpus chaplasha* Roxb. taking diameter at breast height (DBH) and tree height as predictors. Data of tree parameters were collected randomly from 200 healthy and well-formed trees. Among all the models developed, models I and IX were based on only a single predictor of DBH and showed more statistical accuracy. Both models were also validated with a distinct data set having the same range of DBH and tree height of the previous data set on the basis of linear regression and *t*-test for mean difference between observed and predicted LA and LB. These models produced a range of prediction values closer to the upper and lower limits of the observed mean values and suggest their application for LA and LB estimation of *A. chaplasha* in this region.

Keywords: allometric model, *Artocarpus chaplasha*, DBH, leaf area, leaf biomass

Introduction

Estimation of leaf area (LA) and leaf biomass (LB) is important for plant physiological processes such as evapotranspiration, photosynthetic efficiency, atmospheric deposition and carbon assimilation in forest ecosystems (Hietz 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), whereas canopy LB is the product of leaf dry matter content and leaf area index (Tobin et al. 2006). Both LA and LB estimations aid evaluation of plant performance at the individual, community and even ecosystem level (Meier and Leuschner 2008). Leaf area strongly regulates plant growth and productivity through its influences on light interception and therefore it has been constantly used as a key trait in ecophysiological studies. Leaf biomass constitutes one of the most important pools of essential nutrients, which is vital for forest nutrient cycling (Waring and Schlesinger 1985), including carbon cycling. Estimation of LB has been significantly improved by addition of biometric information relating to crown structure (Tobin et al. 2006). So far, direct (destructive) or indirect (non-destructive) methods have been used to measure total LA of trees. However, indirect methods are user friendly and less expensive (Norman and Campbell 1989).

Allometric models for LA and LB studies have been used worldwide and researchers have produced a voluminous number of allometric relationships for several species and tree components (Calvo-Alvarado et al. 2008, Hietz et al. 2010). Given that site-specific allometric models are the most accurate (Levia 2008), different tree parameters such as DBH, height and basal area have been widely used to quantify the LA and LB of individual trees of specific sites (Gajardo-Caviedes et al. 2005). However, site- or species-specific allometric models for estimating LA and LB are very scarce in Bangladesh. *Artocarpus chaplasha* Roxb. is one of the dominant tree species in both the natural and plantation forests in Raghunandan Hill Reserve, Bangladesh (Choudhury et al. 2004). Thus, the aim of this research was to develop allometric models for estimating LA and LB of *A. chaplasha* using different tree parameters such as DBH and tree height. In this study, we evaluate several models and based on different statistical criteria we propose reliable and accurate models for estimating the LA and LB using non-destructive measurements.

Materials and methods

Study site

The research was conducted at Raghunandan Hill Reserve, Bangladesh (Figure 1). The reserve (4 047 ha) comprises semievergreen natural patches, plantation stands, bamboo forest and grassland (Feeroz 2003). The natural forest (242.82 ha) was declared as Satchari National Park in 2006. In the reserve, large deciduous trees are mixed with evergreen smaller trees and bamboos. The top canopy includes *A. chaplasha*, *Dipterocarpus turbinatus*, *Elaeocarpus floribundus*, *Dillenia pentagyna* and *Castanopsis tribuloides* (Choudhury et al. 2004). The reserve area is undulating, with slopes and hillocks ranging from 10 to 50 m above mean sea level (Chemonics 2002). The soil texture is sandy loam to silty clay, and more acidic than the adjoining ecological zones (Choudhury et al. 2004). The average annual rainfall is 4 162 mm and the relative humidity is about 74% during December and over 90% during July–August (BBS/UNDP 2005).

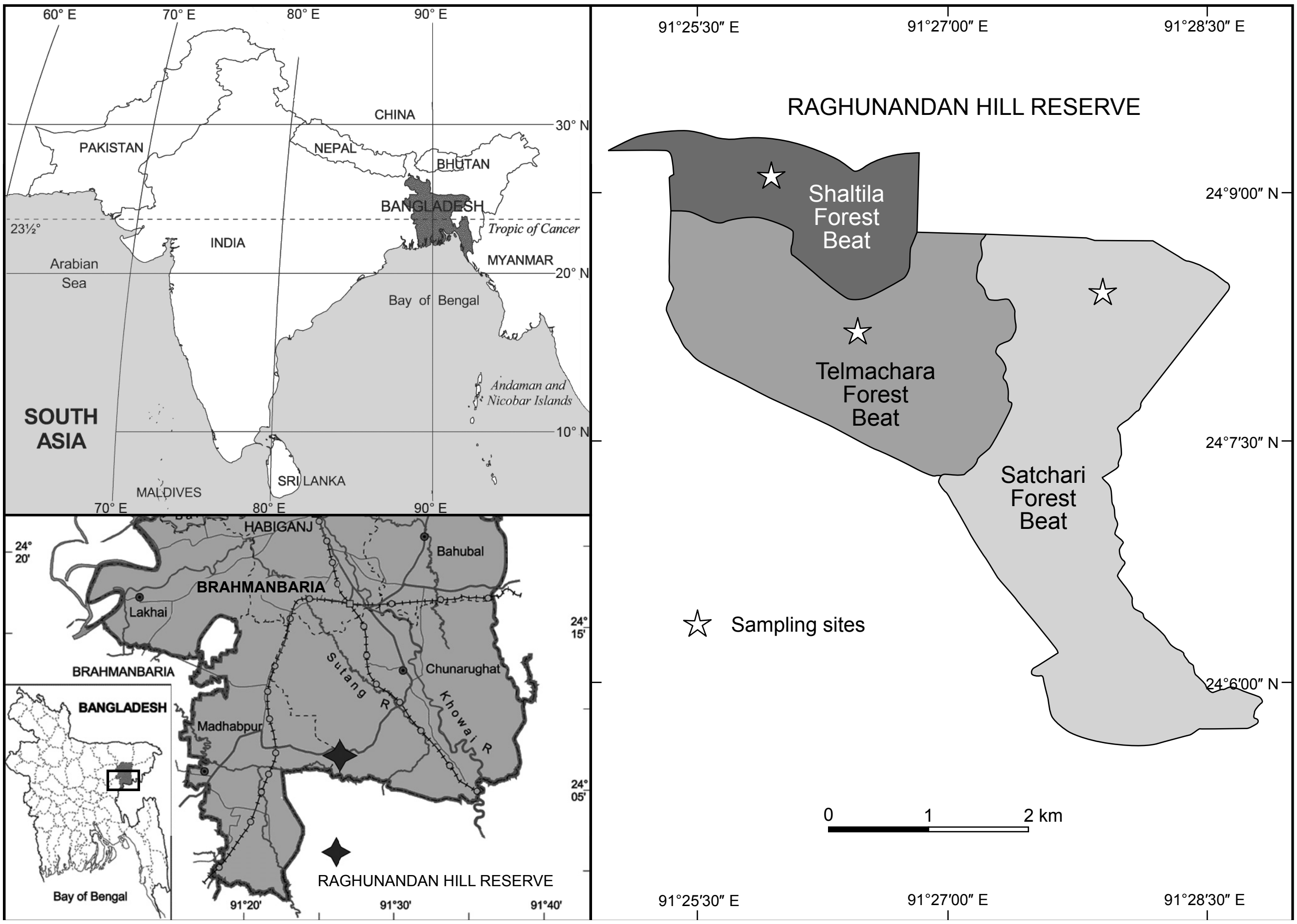

Figure 1: Study site (adapted from Choudhury et al. 2004)

Species description

Artocarpus chaplasha is a large deciduous tree with a tall straight bole, attaining a height of about 30–40 m, with milky latex, young shoots covered with long hairs, and 150 cm in diameter. The tree usually has a spreading and umbrella-shaped crown. The leaves are very large and up to 90 cm long. The species is shade tolerant while young but requires a moderate amount of light for its best development. The species naturally grows in the Sub-Himalayan tract, India (Sikkim, Assam and Andaman) and Bangladesh (Sylhet, Cox's Bazar and Chittagong Hill tracts) (Das and Alam 2001).

Sampling and field measurements

At the Raghunandan Hill Reserve 200 healthy, well-formed *A. chaplasha* trees with a full crown were selected randomly for sampling. Buttressed trees with a swollen bole were not selected for sampling (e.g. Mehedi et al. 2012). Diameter at breast height (DBH; at 1.3 m height from ground level) and tree height (H) were measured with Suunto clinometers (Suunto PM5-360, Vantaa, Finland) and tree calipers (Haglöf Graduated Aluminum Tree Caliper, Ben Meadows, Janesville, Wisconsin, USA). The trees' DBH ranged from 11.5 to 101.2 cm and the tree height ranged from 8.8 to 38.0 m, respectively (Table 1). Leaves were collected using the protocols of Cornelissen et al. (2003). For allometric model construction, maintaining data accuracy is the key issue. In this regard, data on tree parameters are usually measured and collected after harvesting for improving data accuracy (Tobin et al. 2006, Calvo-Alvarado et al. 2008, Hietz et al. 2010). However, because of an ongoing moratorium on felling in the forests (Sarker et al. 2011), we had to collect leaf data manually (by climbing the tree). To retain high data accuracy, we used stratified random sampling for calculation of the leaf number per individual tree. We performed the following steps to count the leaves of each sampled tree: (1) the diameter of all of the main branches was measured; (2) the diameter of the main branch closest to the mean diameter was selected as the model main branch (MMB); (3) subbranches of all main branches were counted; (4) three subbranches were selected randomly from the MMB; (5) twigs of each subbranch were counted and the mean twig number per subbranch was calculated; (6) three twigs were selected randomly from each selected subbranch; (7) the average number of leaves per twig was calculated; (8) the leaf number per subbranch was calculated by multiplying the mean twig number per subbranch and mean leaf number per twig; and (9) the total leaf number per tree was calculated by multiplying the total number of subbranches and estimated leaf number per subbranch.

Table 1: Descriptive statistics for the different variables of *A. chaplasha*

Variable	Mean	SD	Min.	Max.	Skewness	Kurtosis
DBH (cm)	50.6	20.8	11.5	101.2	0.272	−0.757
Height (m)	24.3	6.8	8.8	38.0	−0.195	−0.872
Individual leaf area (cm²)	287.8	42.2	203.2	426.2	1.344	2.535
Individual dry leaf biomass (gm)	2.9	0.8	1.7	4.1	0.874	1.120

Table 2: Different models used in this study

Model no.	Allometric model
I	ln (leaf area(m²)) = *a* + *b* * ln (DBH(cm))
II	ln (leaf area(m²)) = *a* + *b* * ln (H(m))
III	ln (leaf area(m²)) = *a* + *b* * ln (DBH(cm)) + *c* * ln (H(m))
IV	ln (leaf area(m²)) = *a* + *b* * DBH(cm)
V	ln (leaf area(m²)) = *a* + *b* * H(m)
VI	ln (leaf area(m²)) = *a* + *b* * DBH(cm) + *c* * H(m)
VII	ln (leaf area (m²)) = *a* + *b* * DBH(cm) + *c* * DBH²(cm)
VIII	ln (leaf area (m²)) = *a* + *b* * H(m) + *c* * H²(m)
IX	ln (leaf biomass (kg)) = *a* + *b* * ln (DBH(cm))
X	ln (leaf biomass (kg)) = *a* + *b* * ln (H(m))
XI	ln (leaf biomass (kg)) = *a* + *b* * ln (DBH(cm)) + *c* * ln (H(m))
XII	ln (leaf biomass (kg)) = *a* + *b* * DBH(cm)
XIII	ln (leaf biomass (kg)) = *a* + *b* * H(m)
XIV	ln (leaf biomass (kg)) = *a* + *b* * DBH(cm) + *c* * H(m)
XV	ln (leaf biomass (kg)) = *a* + *b* * DBH(cm) + *c* * DBH²(cm)
XVI	ln (leaf biomass (kg)) = *a* + *b* * H(m) + *c* * H²(m)

Leaves were categorised as small, medium and large, and three leaves of each category were collected randomly from subbranches. In total, nine leaf samples were collected from each tree and packed in a plastic bag. The leaf area of each sample leaf was measured with a leaf area meter (CI-202, CID, Inc., Vancouver, Washington, USA) for small and medium leaves, and Adobe Photoshop CS5 software for large leaves. The projected leaf area for each sample tree (LA; cm²) was calculated by multiplying the average LA and total leaf number. The fresh mass of each leaf was measured with a digital balance. Measured leaves were oven-dried at 65 °C for 72 h and weighed to determine the fresh mass:dry mass ratio. Total leaf volume per tree was estimated by multiplying total LA and leaf thickness. Thickness of each leaf sample was calculated using a digital caliper (Absolute Digimatic CD-6″ CS, Mitutoyo Corporation, Kanagawa, Japan). Leaf density was measured by dividing the average leaf fresh mass by leaf volume of the nine sampled leaves per tree. Total leaf biomass per tree was estimated by multiplying total leaf volume and leaf density.

Data analysis

Allometric models development and evaluation

For prediction of LA and LB, 16 allometric models were developed using DBH and/or tree height (H) as predictor/s and the expressions of the models are presented in Table 2. We used R statistical software version 2.15.2 for data analysis (R Development Core Team 2012). Before establishing the model, scatter plots were used to see whether the relationship between independent and dependent variables was linear. Given the presence of heteroscedasticity, we transformed the data for linear regression using natural logarithm. However, this transformation induced a systematic bias in the estimation that was corrected using a correction factor (CF) when back-transforming the calculation into LA and LB (Sprugel 1983, Son et al. 2001, Sah et al. 2004, Chave et al. 2005). The CF was calculated using Equation 1 (Sprugel 1983).

$$CF = e(SEF^2/2) \qquad (1)$$

where SEF = standard error of the estimate.

Equations were evaluated for goodness of fit using adjusted R^2 and residual plots were compared. Diagnostic residual plots were used to check the following statistical assumptions (Robinson and Hamann 2011): (1) the models detain a relationship, (2) errors have constant variance, (3) errors are normally distributed, and (4) the sample represents the population. The Durbin–Watson test was used to check for autocorrelation. Performance of the developed models was evaluated by examining the goodness of fit (R^2), root mean squared error (RMSE), Akaike information criterion (AIC), and average deviation (%). The average deviation was computed from the absolute difference between predicted and observed values and expressed as the percentage of observed value, and then all deviations were averaged (Nelson et al. 1999, Cairns et al. 2003, Chave et al. 2005). The equation to calculate average deviation (δB; %) is shown in Equation 2. The deviation was calculated after the prediction was back-transformed to the unit values and corrected using a CF.

$$\overset{n}{\underset{n=1}{\delta B}} = |\check{D}\acute{W} - DW|/DW*100)/n \qquad (2)$$

where ĎẂ = estimated value, DW = observed value and n = number of observations.

Model validation

For validation of the models, we followed two different approaches. Firstly, we regressed the observed LA and LB of the test data from a distinct data set (n = 50) against the predicted LA and LB using linear regression. Secondly, we compared mean difference between the observed and predicted LA and LB using a *t*-test.

Results

Model development and selection

The LA and LB of sampled trees ranged from 203.2 to 426.2 cm² and 1.7 to 4.1 gm, respectively (Table 1). The parameter estimates and the goodness-of-fit statistics of the different equations tested for estimating LA and LB from tree DBH and height or combination of both are shown in Table 3. Out of the 16 developed models (Table 2), the best ones were determined according to selection criteria described in the Materials and methods. The LA and LB were best estimated using models I and IX, respectively (Table 3). The goodness of fit adjusted for the degrees of freedom (R^2) for the selected models was highly significant and explained more than 95% variation (Table 3). For both parameters, the R^2 value of regressions was lower when using tree height as a predictor. Among the tested models, models I and IX had the lower average deviations (15.818% and 16.269%, respectively). To compare the equations, the AIC value was calculated and the results are presented in Table 3. The AIC values for models I and IX were lower than that of other tested models indicating statistical robustness of the selected models (I and IX). The RMSE values were also lower for the selected models (Table 3).

We plotted regression residuals versus fitted values for the models to check the existing relationship of the equations. In the scatter plot, we noted that the residual scatter plot showed slight heteroscedastic behaviour for the selected models (Figures 2 and 3). In addition, we used the Durbin–Watson test to detect the presence of autocorrelation among the residuals. The test statistics of the selected models were 1.986 and 2.070 for LA and LB, respectively, and were almost within the range of the acceptable limit of 2. In this context, the model coefficients cannot be used reliably unless the CF is applied to remove the heteroscedasticity. Correction factors showed a rather narrow variation for both cases (Table 3). Therefore, the final model of LA is LA = exp(−1.52096 + 1.89265 × ln(DBH)), which can be written as LA = 0.2185 × $(\mathrm{DBH})^{1.89265}$. The bias-corrected model is LA = 0.2185 × $(\mathrm{DBH})^{1.89265}$ × 1.0201, and the final form of this model is LA = 0.222894 × $(\mathrm{DBH})^{1.89265}$. The final model of LB is LB = exp(−4.44814 + 2.0483 × ln(DBH)), and can be written as LB = 0.0117 × $(\mathrm{DBH})^{2.0483}$. The bias-corrected model is LB = 0.0117 × $(\mathrm{DBH})^{2.0483}$ × 1.019, and the final form of this model is LB = 0.011923 × $(\mathrm{DBH})^{2.0483}$.

Models performance assessment

For validating such models, we re-estimated the models with distinct samples. In the model validation, the goodness of fit (R^2) showed that there was a highly reliable

Table 3: Different models tested for estimation of leaf area and leaf biomass of *A. chaplasha*. RMSE = Root mean squared error, AIC = Akaike information criterion, CF = Correction factor

Model	Estimated coefficients			RMSE	Adjusted R^2	F	AIC	Average deviation (%)	CF	Durbin–Watson
	a	*b*	*c*							
I	−1.52096***	1.89265***		0.198	0.9506	2889	−53.797	15.818	1.020	1.986
II	0.2295	1.7442***		0.714	0.3609	85.7	332.841	95.474	1.295	2.169
III	−1.16114***	1.83592***	−0.039	0.199	0.8861	584	73.389	17.357	1.047	2.121
IV	3.65426***	0.04090***		523.9	0.8922	1243	64.064	25.651	1.045	2.157
V	3.835695***	0.0774***		524.2	0.3382	77.6	338.114	99.101	1.307	2.169
VI	3.678422***	0.04125***	−0.001	523.8	0.8916	617	65.917	25.675	1.045	1.941
VII	2.558***	0.0895***	−0.001***	523.9	0.9472	1348	−42.838	16.513	1.021	1.960
VIII	2.022941**	0.24424***	−0.0035**	524.2	0.3693	44.9	331.813	93.067	1.290	2.153
IX	−4.44814***	2.0483***		0.192	0.9592	3523	−58.298	16.269	1.019	2.070
X	−2.6371	1.9134		0.767	0.3705	89.3	354.570	109.055	1.347	2.140
XI	−4.11469***	2.14563***	−0.224***	0.202	0.9419	1894	−57.747	17.500	1.028	2.090
XII	1.136855***	0.04455***		52.51	0.902	1381	73.886	26.659	1.047	2.078
XIII	1.310436***	0.08525***		52.89	0.3501	81.8	359.402	113.054	1.360	1.966
XIV	1.136***	0.04454***	0.0001	52.51	0.9013	686	75.886	26.659	1.047	1.963
XV	0.02564	0.09414***	−0.001***	52.55	0.9517	1480	−32.094	17.701	1.023	1.982
XVI	−0.503999	0.25224***	−0.003**	52.88	0.3761	46.2	354.205	106.823	1.344	2.089

* $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$

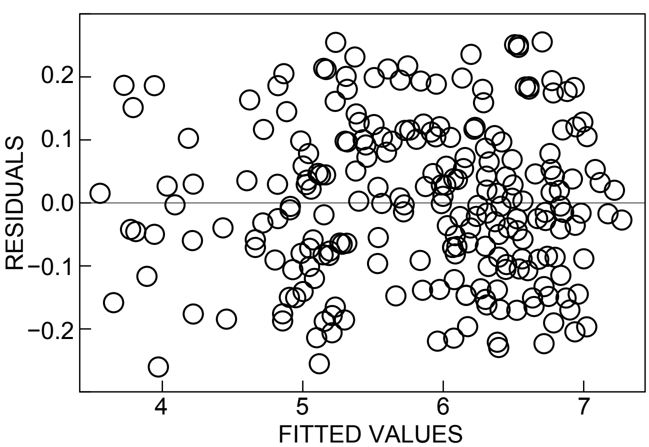

Figure 2: Diameter at breast height (DBH) residuals against predicted leaf area (model I)

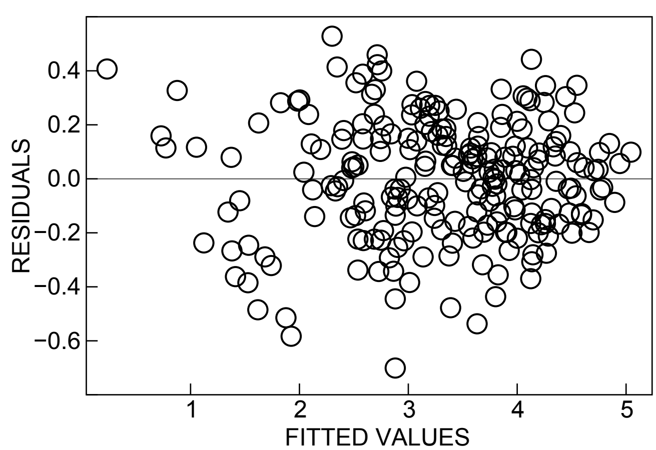

Figure 3: Diameter at breast height (DBH) residuals against predicted leaf biomass (model IX)

relationship between estimated and observed data for both cases (LA and LB). The R^2 values between them for models using LA or LB were 0.981 and 0.986, respectively (Figure 4). The predicted LA and LB using models I and IX produced the same trend as the observed data (Figure 5). At a 95% confidence interval, the mean of the observed and the proposed models predicted data were not significantly different (Table 4). For such models, there is a high probability that estimated values are closest to the observed values.

Discussion

Owing to slight heteroscedastic residual scatter, lower AIC value and average deviation, we propose logarithmic equations for estimation of LA and LB. However, such logarithmic transformation induces a systematic bias in the estimation, which was corrected using a CF in the final model (Sprugel 1983, Son et al. 2001, Sah et al. 2004, Chave et al. 2005, Deb et al. 2012). Therefore, the bias-corrected logarithmic models can predict the variation in LA and LB more accurately than other tested models. Similarly, using a paired t-test presented in Table 4 the mean of the observed data was not significantly different from the predicted mean of the proposed equations, which signify the accuracy of the proposed models.

The proposed models accounted for more than 95% of the variation based on DBH in the LA and LB models (Table 2), and provided a sound, nondestructive means to predict these canopy properties in similar semi-evergreen forests of Bangladesh. Estimation of LA and LB using randomised branch sampling may include errors in estimates that reduce the accuracy of the model (Hietz et al. 2010). Using a nondestructive sampling technique for LA estimation, Grace et al. (1998) and Vertessy et al.

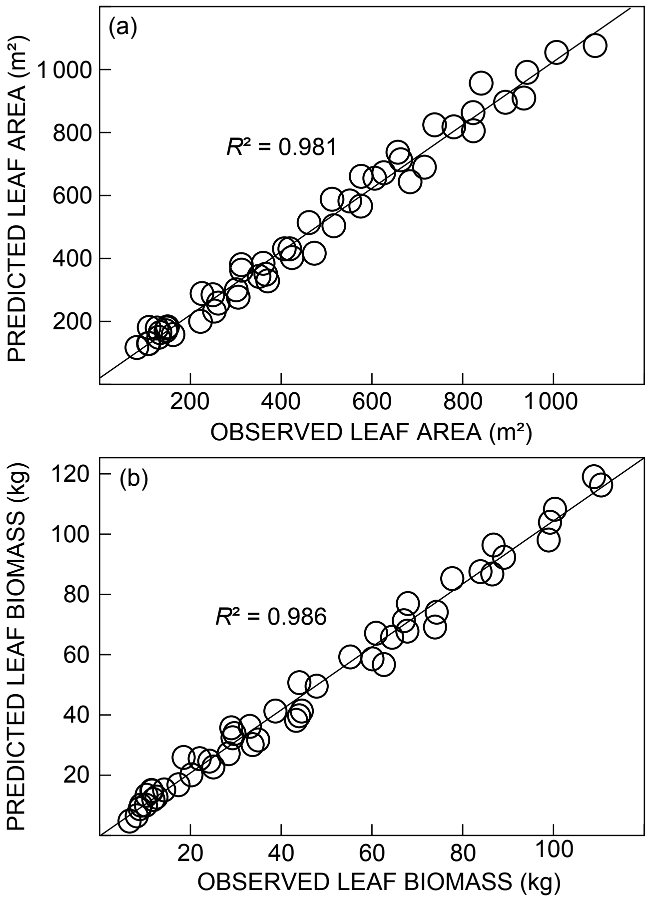

Figure 4: Linear regression between observed and predicted leaf area (a) and predicted leaf biomass (b)

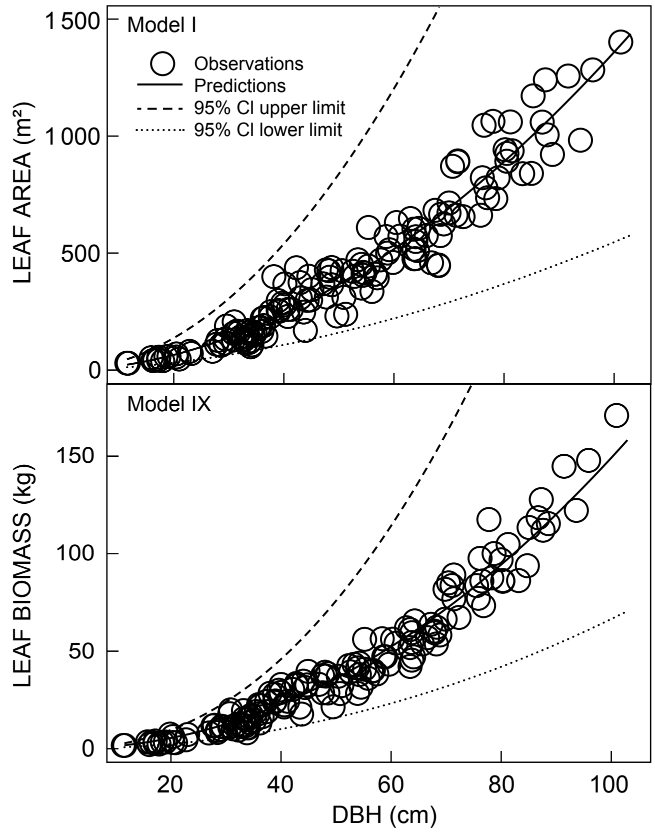

Figure 5: Predicted leaf area and leaf biomass against diameter at breast height (DBH) using model I and IX with observed data at 95% confidence intervals (CI)

Table 4: Confidence interval (CI) of the mean leaf area (m²) and leaf biomass (kg) and paired t-test for *A. chaplasha*

Parameter	Leaf area				Leaf biomass			
	Observed	Model I	t	Significance	Observed	Model IX	t	Significance
Mean	425.168	426.258	−0.167	0.566	43.345	43.425	−0.136	0.554
95% CI lower limit	374.397	376.646			37.708	38.014		
95% CI upper limit	475.94	475.869			48.983	48.837		

(1995) found that DBH could explain 91% of the variation in LA of *Acacia koa* and *Eucalyptus regnans*, respectively. Compared to DBH, tree height was found to be an improper predictor of canopy properties in the present study. This result is consistent with the findings of Calvo-Alvarado et al. (2008) and Pokorný and Tomášková (2007). Unfortunately, we could not compare our results with other similar works in similar forests because allometric equations on canopy properties are unavailable in Bangladesh or other South Asian countries. Although sapwood area (AS) or sapwood volume have proved to be good predictors of tree canopy properties in different temperate and tropical forests (Whitehead et al. 1984, Keane and Weetman 1987), a number of studies (e.g. Burton et al. 1991, Turner et al. 2000) suggest that estimates of canopy properties based on DBH provide more accurate results than AS and are also cost effective. Hence, we precluded AS from our study.

The development of LA and LB equations using nondestructive methods is a highly reliable option where whole tree removal is not possible, as is the case in Bangladeshi forest reserves (Dobbs et al. 2011). *Artocarpus chaplasha* is the dominant and largest deciduous tree species in the semi-evergreen hill forests of Bangladesh and on the basis of the results from the present study, DBH, which is easily measured in the field, rather than complex sapwood measurements or other destructive methods, can be used to estimate LA and biomass in a reliable and cost-effective manner. However, further development of these equations through destructive methods and increased sample sizes would facilitate development of regional estimates of LA and LB. Finally, the results of this study could serve as a basis for more precise quantification of tree physiological and environmental processes in the semi-evergreen hill forests of north-eastern Bangladesh mostly dominated by *A. chaplasha* and possibly in other similar forests of Bangladesh.

Conclusion

In this study, different equations were tested using DBH and tree height or combination of both as predictors to select the best-fitting model for measuring LA and LB of *A. chaplasha*. On the basis of different statistical criteria, bias-corrected logarithmic models (I and IX) showed robustness in predicting both parameters. Strong statistical dependency of LA and LB on DBH also indicates their simplicity in application and capacity to produce results with the same level of accuracy. Therefore, these models will enable foresters and researchers to make nondestructive estimation of LA and LB for *A. chaplasha* in this region.

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