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Allometric models for estimating biomass, carbon and nutrient stock in the Sal zone of Bangladesh

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Allometric models are commonly used to estimate biomass, nutrients and carbon stocks in trees, and contribute to an understanding of forest status and resource dynamics. The selection of appropriate and robust models, therefore, have considerable influence on the accuracy of estimates obtained. Allometric models can be developed for individual species or to represent a community or bioregion. In Bangladesh, the nation forest inventory classifies tree and forest resources into five zones (Sal, Hill, Coastal, Sundarbans and Village), based on their floristic composition and soil type. This study has developed allometric biomass models for multi-species of the Sal zone. The forest of Sal zone is dominated by *Shorea robusta* Roth. The study also investigates the concentrations of Nitrogen, Phosphorus, Potassium and Carbon in different tree components. A total of 161 individual trees from 20 different species were harvested across a range of tree size classes. Diameter at breast height (DBH), total height (H) and wood density (WD) were considered as predictor variables, while total above-ground biomass (TAGB), stem, bark, branch and leaf biomass were the output variables of the allometric models. The best fit allometric biomass model for TAGB, stem, bark, branch and leaf were: ln (TAGB) = -2.460 + 2.171 ln (DBH) + 0.367 ln (H) + 0.161 ln (WD); ln (Stem) = -3.373 + 1.934 ln (DBH) + 0.833 ln (H) + 0.452 ln (WD); ln (Bark) = -5.87 + 2.103 ln (DBH) + 0.926 ln (H) + 0.587 ln (WD); ln (Branch) = -3.154 + 2.798 ln (DBH) - 0.729 ln (H) - 0.355 ln (WD); and ln (Leaf) = -4.713 + 2.066 ln (DBH), respectively. Nutrients and carbon concentration in tree components varied according to tree species and component. A comparison to frequently used regional and pan-tropical biomass models showed a wide range of model prediction error (35.48 to 85.51%) when the observed TAGB of sampled trees were compared with the estimated TAGB of the models developed in this study. The improved accuracy of the best fit model obtained in this study can therefore be used for more accurate estimation of TAGB and carbon and nutrients in TAGB for the Sal zone of Bangladesh.

Keywords: Common Model, Forest Inventory, Phytomass, Tropical Forest

Introduction

Allometric models are commonly used for estimating forest biomass (Picard et al. 2015). The models use mathematical functions that relate tree biomass with easily measurable tree variables such as diameter at breast height (DBH), total height (H) and wood density (WD – Sileshi 2014). Allometric equations can be developed for individual species or multiple species covering local, regional or pan-tropical scale. Species specific allometric models should logically provide a greater level of accuracy at a given location (Ketterings et al. 2001) to assist the assessment of biomass dynamics, net primary productivity, nutrient cycling and budgeting for research purpose (Mahmood et al. 2008, Litton 2008). However, equations developed from small sample sizes may misrepresent the broader population and reduce the accuracy of results (Sileshi 2014). Regional and pan-tropical allometric models consider multiple species collectively defined by a climatic or geophysical association. Capturing species variability within such models has been overlooked in some notable examples (Brown 1997, Chave et al. 2005), while other models have addressed species variability with an additional variable such as wood density (Nelson et al. 1999, Chave et al. 2014). At local or sub-regional scale, the use of allometric biomass models for multiple species within a particular forest types can provide robust results while avoiding the frequently used pan-tropical or regional biomass models which are likely to be based on broader, more generalized suite of sample species (Brown et al. 1989, Brown & Lugo 1992, Brown 1997, Chave et al. 2005, 2014,

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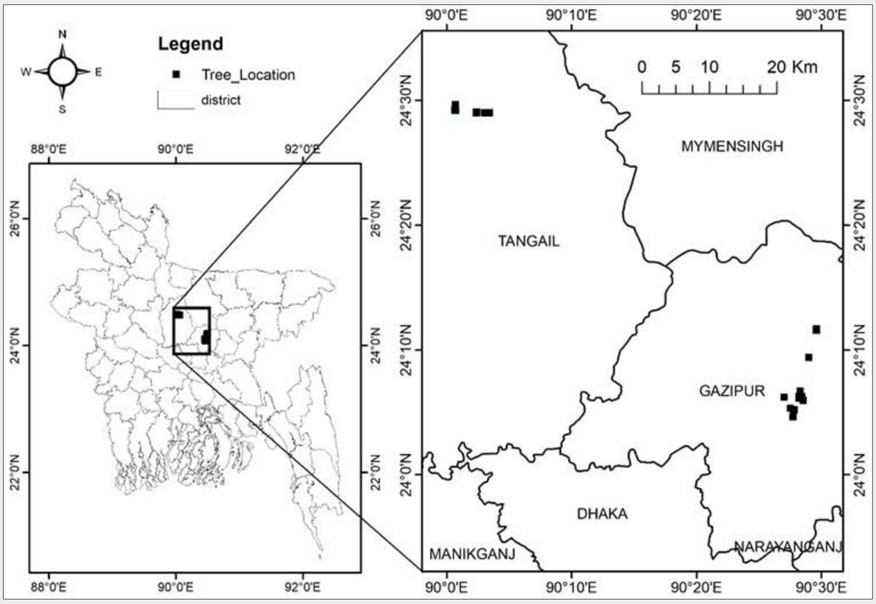

Fig. 1 - Location of study area in the Sal zone of Bangladesh.

Maulana et al. 2016, Nam et al. 2016).

Forests in Bangladesh have been actively managed for over 100 years (Iftekhar & Saenger 2008). Indeed, sixteen inventories have been carried out in different forests types at different scales since 1960. Over this period, the objectives of forest monitoring have evolved from a focus on volume for timber resources to biomass for carbon related values. The National Forest and Tree Resources Assessment (NFA) in 2007 was the first country-wide inventory to measure tree biomass (FD 2017). In this assessment, biomass was calculated according to the Brown & Lugo (1992) method using a generalized volume model, wood density and a biomass expansion factor (AGB = volume over bark × wood density × biomass expansion factor), with an average wood density of 0.57 t m^{-3} and a biomass expansion factor of 6 to represent the tropical Asia (FD 2007).

Tab. 1 - Species and families of the sampled individuals in this study.

Family	Species
Anacardiaceae	*Mangifera indica*
Combretaceae	*Terminalia arjuna*
	Terminalia bellerica
Dipterocarpaceae	*Shorea robusta*
Elaeocarpaceae	*Elaeocarpus serratus*
Fabaceae	*Acacia auriculiformis*
	Acacia mangium
	Albizia procera
Lamiaceae	*Tectona grandis*
Malvaceae	*Grewia microcosm*
Moraceae	*Artocarpus heterophyllus*
Myrtaceae	*Psidium guajava*
	Syzygium cumini
Oxalidaceae	*Averrhoa carambola*
Phyllanthaceae	*Phyllanthus emblica*
Rhamnaceae	*Ziziphus mauritiana*
Rutaceae	*Aegle marmelos*
	Citrus grandis
	Zanthoxylum rhetsa
Sapindaceae	*Litchi chinensis*

Similarly, carbon stock in the Sundarbans mangrove forest was estimated using the pan-tropical allometric biomass models of Chave et al. (2005) and Komiyama et al. (2005) during 2009 to 2010 (Rahman et al. 2015). Tree species and their DBH, height and wood density ranges of pan-tropical models are not similar to the species available in different zones of Bangladesh. These generalized models sometimes fail to capture both variations in forest type (Chave et al. 2005, Litton 2008) and diversity of the natural vegetation communities, which range from mangrove forest in south-west, to tall tropical forests in the hilly areas in the east, and Sal (*Shorea robusta* Roth) dominated areas on inland terraced soils (FD 2017). Relying on pan-tropical models across such distinct structural forest types may distort estimates of biomass and carbon in the tropical forests (Van Breugel et al. 2011, Manuri et al. 2014). For these reasons, initiatives to develop local allometirc models in Bangladesh have been undertaken (Mahmood et al. 2016).

The Bangladesh Forest Department has formalized the stratification of its forest areas into to five distinct zones: Sal, Hill, Sundarbans, Coastal and Village to represent different forest types (BFD 2016). The zones are defined by their relative climatic and geophysical properties as described by Akhter et al. (2016). This process allows the development of a localized, multiple species allometric models to represent a specific vegetation community within a narrower suite of plant functional types. The aims of this study were: (1) to derive total and component wise (leaf, branch, stem and bark) allometric biomass models for the Sal zone of Bangladesh; (2) to measure nutrients (N, P and K) and carbon concentration in leaf, branch, stem and bark of the studied tree species; and (3) to compare the model efficiency of frequently used regional and pan-tropical biomass model.

Materials and methods

Description of the study area

This study was conducted in the Sal zone of Bangladesh (Fig. 1). This zone comprises 121,000 ha of non-contiguous land scattered across the central and northern part of the country in the Districts of Gazipur, Tangail, Mymensingh, Jamalpur, Comilla, Dinajpur, Thakurgaon, Rangpur and Rajshahi. Soils of this zone are heterogeneous, well drained, acidic and have clayey to fine loamy texture (Hoque et al. 2008). *Shorea robusta*, locally known as Sal, is the dominant species within the zone in association with *Albizia* spp., *Swietenia* spp., *Terminalia* spp., *Azadirachta indica* A. Juss. and *Adina cordifolia* (Roxb.). However, most of the area is heavily degraded due to intense population pressure, resulting in agricultural, industrial developments encroaching into forest areas and a legacy of unregulated or illicit timber extraction (Islam & Sato 2012). In many areas the dominant Sal trees have been replaced with fast growing timber species (such as *Acacia auriculiformis* A.Cunn. ex Benth., *A. mangium* Willd. and *Eucalyptus camaldulensis* Dehnh.) and horticultural trees (Rahman et al. 2010).

Measurement of biomass

Sample collection

Sample trees were harvested from areas of natural Sal forest, woodlots of fast growing species, and wooded homestead areas within the Sal zone. A total of 161 sample trees from 20 species (belonging to 14 families – Tab. 1) were selected in the districts of Tangail and Gazipur during 2016 and 2017. Sample trees were selected purposively, avoiding suppressed or diseases trees or those with broken tops, hollows, or other damages. All sampled trees were within a diameter at breast height (DBH) range of 6 to 38 cm, and total height (H) range of 4 to 29 m, respectively (see Tab. S1 in Supplementary material).

Biomass measurement

DBH of the selected trees were measured before felling. The trees were felled as close to ground level as possible and total tree length was measured using a linear tape to representing total height. The felled trees were separated into leaves, small branches (diameter < 7 cm), bigger branches (diameter > 7 cm) and stem, based on the method described by Picard et al. (2015). The fresh weight of leaves and branches were weighed in the field using a portable digital hanging balance of 100 kg capacity. The stem was sectioned into suitable size for easy handling and their biomass was measured using a hanging digital balance of 400 kg capacity. Stem sections (1 m long) from different positions (base, middle and top) were debarked in the field to get fresh weight proportions of stem and bark to estimate bark and stem wood biomass of the individual sampled trees (Mahmood et al. 2004, 2015). Ten sub-samples (0.25 kg) of each part (leaf, smaller branch, bark, disk of bigger branches and stem) of individual species were taken randomly from the felled trees and transported to laboratory for further analysis. These sub-samples were oven-dried at 105 °C until a constant weight was achieved to estimate the fresh to oven-dry weight conversion factor. The respective conversion factors were used to estimate the oven-dry weight of individual trees.

Carbon and nutrients (N, P and K) in total above-ground biomass (TAGB)

The oven-dried sub-samples of each part of individual species were grounded and sieved through a 2-mm mesh (Allen 1989). The processed samples were acid digested using Kjeldhal digestion method and the sample extract was analyzed according to Beathgen & Alley (1989) to determine Nitrogen in plant samples. Tri-acid (HNO_3, H_2SO_4 and $HClO_3$ in 10:1:3 ratio) digestion was adopted to determine phosphorus and potassium in sample extracts (Allen 1989). Phosphorus concentration in sample extracts was measured according to Murphy & Riley (1962), while a flame photometer (PFP7, Jenway Ltd., UK) was used to measure potassium concentration in sample extracts. Carbon content was measured by the loss of ignition method (Allen 1989). Average and standard error of nutrients (N, P and K) and carbon concentration in leaf, branch, stem and bark of sampled tree species were also estimated.

Data analysis

Allometric equations

Descriptive statistics of predictors (DBH, H and WD) and output variables (TAGB, stem, branch and leaf biomass) were calculated. The wood density values of the sampled tree species were collected from Sattar (1981). These variables were transformed to natural logarithm (ln) to improve the linearity and homoscedasticity. The eight most frequently used pan-tropical or regional biomass allometric equations were tested for the prediction of TAGB (Tab. 2) using R statistical software. Studentized residual analysis was performed to detect the outlier data. Natural logarithm transformation introduced a systematic bias during biomass estimation. Therefore, a correction factor (CF) was calculated for each equation to minimize the systematic bias introduced during the back transformation to biomass value. This correction factor (CF) was multiplied with the exponential factor of Ln biomass value to minimize the inherent systematic bias during biomass estimation (Sprugel 1983).

Model selection

The best fit allometric model was selected based on goodness-of-fit statistics. The model having the lowest Akaike Information Criterion (AIC) and Residual Standard Error (RSE), and the highest Akaike Information Criterion weight (AICw) and coefficient of determination (R^2) values was selected as best fit model (Sileshi 2014, Picard et al. 2015). However, very small difference among the AIC values of models may lead to a false sense of confidence during model selection process. Therefore, AICw was calculated to overcome this confusion and to describe the relative performance of the models (Wagenmakers & Farrell 2004). AICw was calculated from the following equation (eqn. 1):

$$AICw=\frac{\exp\left\{-\frac{1}{2}\Delta i\left(AIC\right)\right\}}{\sum_{k-1}^{k}\exp\left\{-\frac{1}{2}\Delta k\left(AIC\right)\right\}} \tag{1}$$

where Δi(AIC) is the difference between the model having minimum AIC value and AIC of the individual model.

Test of multicollinearity is important for the models containing identical multiple predictors (Sileshi 2014). Therefore, multicollineary among the predictors of model 2, 3, 4, 6 and 7 were tested using Variance Influential Factor (VIF). Models having VIF>5 indicate the existence of multicollinearity among the predictors (Sileshi 2014). VIF was calculated using the following formula (eqn. 2):

$$VIF=\frac{SD^2\left(n-1\right)SE^2}{MSR} \tag{2}$$

where SD is the standard deviation of individual predictor, SE is the standard error of each predictor, (n-1) is the total degree of freedom for the model, and MSR is the mean square residual.

Regional and pan-tropical model evaluation

Frequently used regional and pan-tropical biomass models were compared with the measured biomass data of the sampled trees of Sal zone in terms of model prediction error (MPE), model efficiency (ME) and root mean square error (RMSE – Mayer & Butler 1993), which were calculated using the following equations (eqn. 3, eqn. 4, eqn. 5);

$$MPE(\%)=\frac{100}{n}\cdot\sum\left[\frac{\left(Yp-Yo\right)}{Yo}\right] \tag{3}$$

$$ME=1-\left[\frac{\sum\left(Yo-Yp\right)^2}{\sum\left(Yo-\bar{Y}\right)^2}\right] \tag{4}$$

$$RMSE=100\cdot\sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(Yp-Yo\right)^2} \tag{5}$$

where n is the number of trees, Yp is the predicted biomass from model, Yo is the observed biomass in field measurement and $\bar{Y}$ is the mean of the observed biomass.

Regression between Yp (in the X-axis) and Yo (in the Y-axis) was derived for the listed pan-tropical and regional models for TAGB estimation (Tab. 2) and significance of slope (b = 1) and intercept (a = 1) were also tested in accordance with Piñeiro et al. (2008). This analysis helped to understand graphically the overestimation or underestimation of the predicted biomass value using each model from 1:1 line (Sileshi 2014).

Results

Model selection

The mean DBH, H, and WD of the sample trees were 16.078 cm, 13.498 m and 0.669 g cm^{-3}, respectively. A total of 1.242% data was observed as outlier for TAGB. Model 3 [ln (B) = ln (a) + b ln (DBH) + c ln (H) + d ln (WD)] of TAGB, stem, bark and branch had lowest AIC (-177.416, -128.402, -18.043 and 247.098) and RSE (0.136, 0.158, 0.223 and 0.508); and highest adjusted R^2 (0.977, 0.973, 0.955 and 0.756) and AICw (0.918, 0.907, 0.614 and 0.550) values compared

Tab. 2 - Frequently used pan-tropical and regional allometric equations.

Model no.	Model	Source	Type
1	ln (B) = a + b ln (DBH)	Brown (1997)	Pan-tropical
2	ln (B) = a + b ln (DBH) + c ln (H)	Nelson et al. (1999)	Central Amazon
3	ln (B) = a + b ln (DBH) + c ln (H) + d ln (WD)	Nelson et al. (1999), Chave et al. (2005)	Central Amazon; Pan-tropical
4	ln (B) = a + b ln (DBH) + c (ln (DBH))^2 + d (ln (DBH))^3 + e ln (WD)	Chave et al. (2005)	Pan-tropical
5	ln (B) = a + b ln (DBH^2 × H × WD)	Brown et al. (1989), Chave et al. (2005), Chave et al. (2014)	Pan-tropical
6	ln (B) = a + b ln (DBH) + c ln (WD)	Djomo et al. (2010)	Tropical Africa
7	ln (B) = a + b ln (DBH^2 × H) + c ln (WD)	Djomo et al. (2010)	Tropical Africa
8	ln (B) = a + b ln (DBH^2 × H)	Brown et al. (1989), Djomo et al. (2010)	Pan-tropical; Tropical Africa

Tab. 3 - Parameter estimates (*a*-*e*) and comparison among the allometric models for different components of trees of Sal zone. Models labelled with an asterisk (*) are the best-fit models.

Component	No.	*a*	*b*	*c*	*d*	*e*	Adj-R^2	RSE	AIC	AICw	CF	VIF
Total above-ground biomass	1	-2.212	2.397	-	-	-	0.959	0.183	-86.341	0.000	1.017	-
	2	-2.527	2.188	0.349	-	-	0.976	0.139	-172.596	0.082	1.01	*b*=1.428, *c*=1.428
	3*	-2.46	2.171	0.367	0.161	-	0.977	0.136	-177.416	0.918	1.009	*b*=1.214, *c*=1.497, *d*=1.055
	4	3.477	-3.805	2.22	-0.261	0.03	0.959	0.181	-83.751	0.000	1.017	*b*=10560, *c*=43036, *d*=11181, *e*=1.016
	5	-2.071	0.844	-	-	-	0.932	0.236	-4.028	0.000	1.028	-
	6	-2.204	2.397	0.016	-	-	0.959	0.183	-84.38	0.000	1.017	*b*=1.006, *c*=1.006
	7	-2.381	0.859	0.38	-	-	0.941	0.22	-24.429	0.000	1.025	*b*=1.00, *c*=1.00
	8	-2.54	0.859	-	-	-	0.935	0.231	-11.576	0.000	1.027	-
Stem without bark	1	-2.856	2.449	-	-	-	0.889	0.32	93.878	0.000	1.052	-
	2	-3.562	1.98	0.783	-	-	0.966	0.177	-94.318	0.000	1.016	*b*=1.428, *c*=1.428
	3*	-3.373	1.934	0.833	0.452	-	0.973	0.158	-128.402	0.907	1.013	*b*=1.367, *c*=1.497, *d*=1.055
	4	1.749	-2.748	1.949	-0.24	0.131	0.888	0.319	98.545	0.000	1.053	*b*=10560, *c*=43036, *d*=11181, *e*=1.016
	5	-3.079	0.911	-	-	-	0.965	0.179	-93.176	0.000	1.016	-
	6	-2.793	2.445	0.122	-	-	0.889	0.319	95.118	0.000	1.053	*b*=1.006, *c*=1.006
	7	-3.359	0.925	0.492	-	-	0.972	0.162	-123.849	0.093	1.013	*b*=1.00, *c*=1.00
	8	-3.565	0.925	-	-	-	0.963	0.184	-83.41	0.000	1.017	-
Bark	1	-5.339	2.679	-	-	-	0.871	0.382	151.379	0.000	1.076	-
	2	-6.115	2.164	0.861	-	-	0.946	0.246	11.134	0.000	1.031	*b*=1.428, *c*=1.428
	3*	-5.87	2.103	0.926	0.587	-	0.955	0.223	-18.043	0.614	1.026	*b*=1.671, *c*=1.497, *d*=1.055
	4	-5.815	3.156	-0.112	0.005	0.217	0.87	0.38	155.503	0.000	1.076	*b*=10560, *c*=43036, *d*=11181, *e*=1.016
	5	-5.606	1	-	-	-	0.951	0.235	-4.806	0.001	1.028	-
	6	-5.225	2.671	0.22	-	-	0.871	0.38	151.64	0.000	1.076	*b*=1.006, *c*=1.006
	7	-5.856	1.012	0.625	-	-	0.955	0.225	-17.113	0.386	1.026	*b*=1.00, *c*=1.00
	8	-6.119	1.012	-	-	-	0.944	0.252	16.859	0.000	1.032	-
Branch	1	-3.628	2.348	-	-	-	0.704	0.563	276.164	0.000	1.172	-
	2	-3.007	2.761	-0.69	-	-	0.754	0.512	247.499	0.450	1.141	*b*=1.428, *c*=1.428
	3*	-3.154	2.798	-0.729	-0.355	-	0.756	0.508	247.098	0.550	1.14	*b*=1.478, *c*=1.497, *d*=1.055
	4	2.383	-2.992	1.431	-0.107	-0.038	0.706	0.556	277.791	0.000	1.171	*b*=10560, *c*=43036, *d*=11181, *e*=1.016
	5	-2.64	0.714	-	-	-	0.509	0.726	357.744	0.000	1.301	-
	6	-3.662	2.351	-0.066	-	-	0.702	0.563	278.092	0.000	1.173	*b*=1.006, *c*=1.006
	7	-2.921	0.727	0.292	-	-	0.511	0.722	357.913	0.000	1.3	*b*=1.00, *c*=1.00
	8	-3.044	0.728	-	-	-	0.511	0.724	356.77	0.000	1.299	-
Leaf	1*	-4.713	2.066	-	-	-	0.533	0.713	304.322	0.402	1.289	-
	2	-4.927	1.968	0.187	-	-	0.533	0.71	305.295	0.247	1.289	*b*=1.35, *c*=1.35
	3	-4.826	1.936	0.226	0.278	-	0.532	0.708	306.601	0.129	1.29	*b*=1.412, *c*=1.448, *d*=1.076
	4	-2.24	-0.072	0.583	-0.046	0.185	0.525	0.711	309.671	0.028	1.295	*b*=9797, *c*=39949, *d*=10394, *e*=1.015
	5	-4.737	0.743	-	-	-	0.509	0.731	311.299	0.012	1.306	-
	6	-4.618	2.058	0.179	-	-	0.531	0.712	306.017	0.172	1.291	*b*=1.07, *c*=1.07
	7	-4.883	0.75	0.531	-	-	0.507	0.73	312.876	0.006	1.308	*b*=1.00, *c*=1.00
	8	-5.098	0.749	-	-	-	0.502	0.736	313.419	0.004	1.312	-

Tab. 4 - Carbon concentration (%) in different parts of sampled species in the Sal zone of Bangladesh.

Species	Leaf	Smaller branch	Bigger branch	Bark	Stem
Acacia auriculiformis	46.87 ± 0.03	48.77 ± 0.18	49.73 ± 0.04	44.93 ± 0.03	49.75 ± 0.05
Aegle marmelos	50.20 ± 1.70	56.90 ± 3.01	-	51.05 ± 2.58	59.50 ± 3.99
Albizia procera	45.45 ± 0.65	49.22 ± 1.08	50.63 ± 1.50	45.52 ± 1.30	52.43 ± 1.58
Artocarpus heterophyllus	46.24 ± 2.28	46.88 ± 0.78	53.77 ± 0.81	43.93 ± 1.56	54.78 ± 1.59
Averrhoa carambola	49.26 ± 1.36	49.11 ± 1.51	-	47.48 ± 0.17	59.23 ± 1.91
Citrus grandis	43.89 ± 0.37	49.04 ± 0.25	-	43.22 ± 1.77	52.79 ± 1.80
Elaeocarpus serratus	57.34 ± 4.20	54.35 ± 1.64	54.45 ± 0.33	60.21 ± 2.64	56.66 ± 0.41
Grewia microcosm	45.04 ± 0.53	52.75 ± 0.55	54.25 ± 1.11	53.59 ± 1.69	52.86 ± 1.04
Litchi chinensis	44.33 ± 0.87	55.44 ± 0.97	53.65 ± 2.36	44.34 ± 2.34	53.50 ± 1.32
Mangifera indica	57.96 ± 2.89	51.74 ± 1.86	56.13 ± 1.78	48.88 ± 1.00	55.86 ± 0.29
Phyllanthus emblica	55.95 ± 2.23	49.66 ± 1.64	53.51 ± 0.17	66.31 ± 2.51	53.67 ± 1.54
Psidium guajava	50.59 ± 1.87	48.02 ± 1.29	-	48.88 ± 0.70	51.00 ± 0.40
Shorea robusta	49.74 ± 0.97	43.89 ± 6.68	50.94 ± 0.61	52.85 ± 2.16	56.24 ± 2.21
Spondias pinnata	-	44.71 ± 0.68	48.86 ± 0.90	50.17 ± 2.18	53.53 ± 1.48
Syzygium cumini	50.15 ± 0.39	46.86 ± 0.93	55.37 ± 1.40	50.59 ± 0.73	52.72 ± 0.08
Tectona grandis	41.80 ± 0.92	49.07 ± 0.44	-	46.82 ± 1.44	57.77 ± 1.30
Terminalia arjuna	47.88 ± 1.03	56.89 ± 3.25	56.61 ± 0.32	48.16 ± 0.98	52.41 ± 1.64
Terminalia bellirica	59.25 ± 1.67	55.26 ± 1.88	55.24 ± 3.63	44.73 ± 1.09	58.23 ± 3.38
Zanthoxylum rhetsa	-	50.22 ± 2.66	53.40 ± 1.05	55.21 ± 2.68	53.55 ± 1.05
Ziziphus mauritiana	47.50 ± 4.01	52.52 ± 0.39	52.31 ± 1.96	50.47 ± 4.03	54.73 ± 2.02

Tab. 5 - Comparison of the frequently used regional and pan-tropical biomass models.

No	Source	Equation	Type	n	R^2	MPE (%)	ME	RMSE
1	Brown 1997 (Moist)	B = exp (-2.134 + 2.5430 ln (DBH))	Pan-tropical	170	-	63.556	-0.093	10666.328
3	Nelson et al. 1999	ln (B) = -1.8985 + 2.1569 ln (DBH) + 0.3888 ln (H) + 0.7218 ln (WD)	Central amazon	132	0.991	42.958	0.636	6159.087
4	Chave et al. 2005	B = WD × exp (-1.499 + 2.148 ln (DBH) + 0.207 (ln (DBH))^2 - 0.0281 (ln (DBH))^3)	Pan-tropical	1808	-	85.508	-1.878	17312.340
5	Brown et al. 1989 (Moist)	B = exp (-2.4090 + 0.9522 ln (DBH^2 ×H × WD))	Pan-tropical	94	0.99	65.820	-0.164	11009.597
	Chave et al. 2005	B = exp (-2.977 + ln (DBH^2 × H × WD))	Pan-tropical	1505	-	35.480	0.404	7877.611
	Chave et al. 2014	B = exp (-2.6986 + 0.976 ln (DBH^2 × H × WD))	Pan-tropical	4004	-	48.892	0.184	9217.913
8	Brown et al. 1989 (Moist)	B = exp (-3.1141 + 0.9719 ln (DBH^2 × H))	Pan-tropical	168	0.97	42.676	0.376	8057.775
	Djomo et al. 2010	ln (B) = -3.2249 + 0.9885 ln (DBH^2 × H)	Tropical Africa	274	0.971	46.016	0.228	8964.925

to other models. Model 4 of TAGB, stem, bark, branch and leaf has shown VIF>5 for its predictors compared to other models, which indicated multicollinearity among the identical independent variable (Tab. 3). Therefore, model 3 has appeared as best fit for estimating TAGB, stem, bark and branch biomass for the Sal zone and indicates that inclusion of wood density as predictor has improved the model accuracy. For leaf estimates, model 1 [ln (B) = ln (a) + b ln (DBH)] is the best model considering the AIC, AICw and adjusted R^2 values (Tab. 3).

Nutrients (N, P and K) and carbon in tree components

Nutrients (N, P, and K) concentration were found to vary among the tree components and species. However, comparatively higher concentration of nitrogen (1.76 to 4.06%), phosphorus (0.02 to 0.54%) and potassium (0.28 to 3.10) were observed in leaves, while the lowest concentration was observed in woody components, especially the stem (Tab. S2 in Supplementary material). Conversely, comparatively higher concentration of carbon was observed in woody components of tree-like stems and larger branches. The ranges of carbon concentration in stems and bigger branches of the represented species was 48.86 to 56.61% and 49.75 to 59.23%, respectively. Moreover, species-specific variation in carbon concentration was also observed among individual species (Tab. 4).

TAGB model evaluation

The comparison among the eight regional and pan-tropical biomass models has demonstrated that model 3 of Chave et al. (2005) contained first lowest MPE (35.480%) and RMSE (7877.611) followed by model 8 (moist) of Brown et al. (1989 – Tab. 5). Visualization of the observed and predicted biomass has demonstrated deviation in biomass estimation from the line of significance of slope (b = 1) and intercept (a = 1), which indicates that all the regional and pan-tropical biomass models overestimated the biomass of the sampled trees of the Sal zone (Fig. 2).

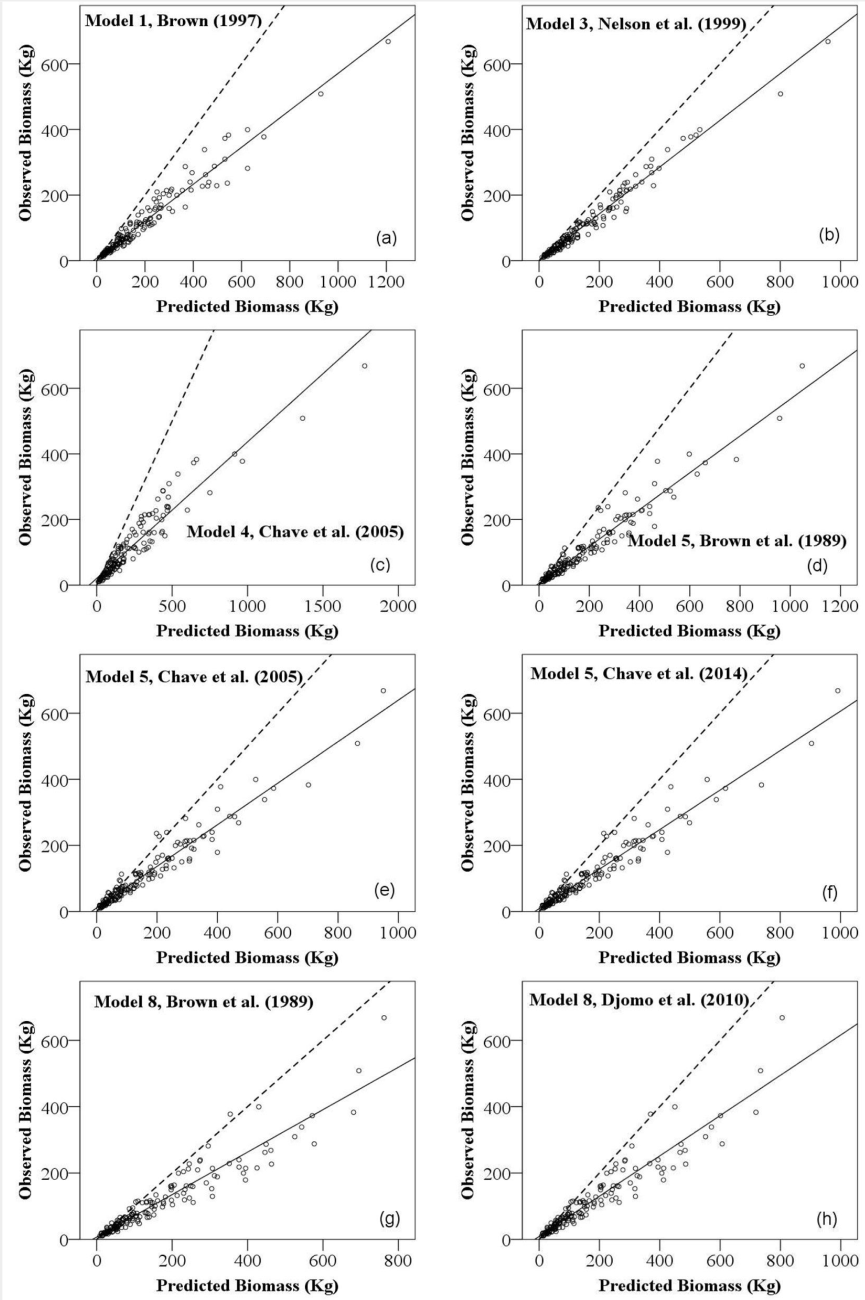

Fig. 2 - Regression between observed and predicted values of frequently used regional and pan-tropical biomass models. Solid line is the regression line and broken line is the significance of slope (b = 1) and intercept (a = 1). (a): Model 1 (Brown 1997); (b): Model 3 (Nelson et al. 1999); (c): Model 4 (Chave et al. 2005); (d): Model 5 (Brown et al. 1989); (e): Model 5 (Chave et al. 2005); (f): Model 5 (Chave et al. 2014); (g): Model 8 (Brown et al. 1989); (h): Model 8 (Djomo et al. 2010).

Discussion

The use of allometric models presents a

source of uncertainty in biomass estimation (Nam et al. 2016), which can be minimized through a process of selection and critical analysis of the parameters used (Mahmood et al. 2016). Model accuracy and the inclusion of predictor(s) are important considerations when selecting the best fit model (Sileshi 2014). In our study, we have included 20 species with wood density ranging from 0.492 to 0.854 g cm^{-3} and a model with DBH, H and WD as identical predictors appeared as the best fit compared to other models, except leaf (Tab. 3). Several other studies have also demonstrated that multi-species allometric biomass models using DBH, H and WD as identical predictors resulted in accurate biomass estimation (Nelson et al. 1999, Chave et al. 2005, 2014, Djomo et al. 2010).

Estimates of nutrient and carbon stock in trees is crucial to understand nutrient cycling and budgeting, which is important to maintain forest productivity (Binkley 1986, Mahmood 2014). This study has shown that differences are evident in nutrient and carbon concentration across tree components and species, and this is related to the characteristics of nutrients, stage of growth (sapling and tree) and availability to plants under various environmental conditions (Binkley 1986, Marschner 1995, Mahmood 2004). Nitrogen is the major component of amino acid, enzymes, nucleic acid, chlorophyll and alkaloid and consequently a higher content is observed in photosynthetic tissue. Phosphorus is most abundant in meristematic tissue (Mayer & Butler 1993). While potassium is highly mobile and found to accumulate in physiologically active tissue, carbon is found to accumulate in the structural components of plants (Marschner 1995). The above physiological function and mobility nature of N, P, K and C may lead to a higher concentration of nutrients in leaves and higher carbon concentration in branch and stem (Mahmood 2004).

The observed TAGB of sampled trees were compared with estimated TAGB from the frequently used regional and pan-tropical models. Model 4 by Chave et al. (2005) and model 5 by Brown et al. (1989) showed the higher prediction error (65.82% to 85.508) and resulted in a higher overestimation. Similarly, the pan-tropical model 5 of Chave et al. (2005) with second higher model efficiency (0.404) also showed the lowest model prediction error (35.48%) in predicting the TAGB for the studies samples. This has implications for the estimation of forest biomass across broad-scales as these models are a commonly used option, particularly in developing countries for which they are relevant, where they may be applied under programmes such as REDD+ (Gibbs et al. 2007, Koch 2010). As this process is fundamentally based on estimation, allometric models will always present some level of error. The quantum of that error will determine the extent to which our understanding of the truth is distorted and subsequently influence how we understand the impacts of deforestation and environmental degradation resulting from forest disturbance potentially driven by climate change (Kumar & Mutanga 2017). Therefore, the development of improved allometric models, their validation and comparison with the existing pantropical and regional models to assess their uncertainty and suitability at local scale is a prudent step in forest biomass estimation (Sileshi 2014, Nam et al. 2016). Indeed, there remains numerous examples where biomass estimation using pan-tropical and regional models produce a higher bias compared to those from locally developed models, for instance the biomass study of Kalimantan (Basuki et al. 2009), Sarawak (Kenzo et al. 2009), Columbia (Alvarez et al. 2012, Ngomanda et al. 2014), Indonesia (Manuri et al. 2014, Maulana et al. 2016), and Vietnam (Nam et al. 2016). The context provided by these studies and the results presented herein demonstrate that at present, our derived model will more accurately estimate the TAGB and biomass of other components (stem, bark, branch and leaf) for the Sal zone of Bangladesh.

Conclusion

Regional and pan-tropical allometric models offer methodological efficiencies for biomass estimation compared to those developed for individual species at specific locations. However, they have the potential to misrepresent local, species- or community-specific variations and anomalies, and therefore can lead to increased error. The use of pan-tropical and regional models should therefore be scrutinized with respect to the source of sampling used to develop the model against local forest variation, before they are widely applied. The results of this study demonstrate that the development of local models derived from an appropriate sample of representative species can greatly improve the estimation of TAGB, as well as Carbon, Nitrogen, Phosphorus, and Potassium in TAGB. In summary, the best fit models presented in this study can provide greater confidence when estimating biomass in the Sal zone of Bangladesh.

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Supplementary Material

Tab. S1 - Observed biomass data of sampled trees of the Sal zone of Bangladesh.

Tab. S2 - Nutrients (N, P and K) concentration in different parts of sample tree species of the Sal zone of Bangladesh.

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