Forest Ecology and Management 307 (2013) 219–225

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Generic allometric models including height best estimate forest biomass and carbon stocks in Indonesia

Ervan Rutishauser [a,*], Fatmi Noor'an [b], Yves Laumonier [a,c], James Halperin [d], Rufi'ie [b], Kristel Hergoualc'h [a], Louis Verchot [a]

[a] Center for International Forestry Research, Jl. CIFOR, Situ Gede, Bogor Barat 16115, Indonesia
[b] Dipterocarp Research Center, Forestry Research and Development Agency, Ministry of Forestry, Jl. A. Wahab Syahranie No. 68, Sempaja, Samarinda, Indonesia
[c] International Center for Research on Agronomy and Development, UPR BSEF, F-34078 Montpellier, France
[d] United States Forest Service, International Programs, Washington, DC, USA

ARTICLE INFO

Article history:
Received 15 April 2013
Received in revised form 4 July 2013
Accepted 8 July 2013
Available online 5 August 2013

Keywords:
Tropical forests
Above-ground biomass
Tree height
Allometric models
REDD+
Indonesia

ABSTRACT

The choice of an appropriate allometric model is a critical step in reducing uncertainties in forest biomass stock estimates. With large greenhouse gases emissions due to deforestation, a systematic assessment and comparison of the models available in Indonesia is crucial for accurate assessments of forest carbon stocks and implementing REDD+ projects. In the present study, we compared the ability of two regional and two generic (pantropical) allometric models to estimate biomass at both tree and plot levels. We showed that regional models had lower performance in estimating tree biomass, with greater bias (−31–8%) and higher AIC (177–204), compared to generic models (bias: −2–2%; AIC: 57–67). At the plot level, the regional models underestimated biomass stocks by 0–40% compared to the best generic model. The error in plot biomass stocks associated to models relying solely upon DBH ranged between −5 and +15%. The integration of tree height estimated regionally resulted in an overestimate of 5–10% in unmanaged forests. Despite the difficulty to accurately assess tree heights in tropical forests, integrating all or part of them in biomass assessment can reduce uncertainties.

1. Introduction

Indonesian tropical forests have been extensively logged from 2000 and 2010 (Miettinen et al., 2011), contributing to *c.* 80% of yearly emissions of greenhouse gases of the country (PEACE, 2007). The ability to accurately estimate forest carbon stocks is essential in Reducing Emissions from Deforestation and Forest Degradation (REDD+) mechanisms in order to establish reliable National Reference Emission Levels (NREL) and to estimate carbon stock changes. However, forest biomass stocks are still poorly estimated in most tropical regions and remain a major uncertainty in our understanding of the potential of tropical forests in mitigating climate change (Houghton, 2005). Several research efforts are under way to fill this gap, relying upon a combination of large-scale remotely-sensed imagery and ground-based measurements (Houghton et al., 2009; FAO, 2010). However, despite strong commitment of the Indonesian Government, its capacity to report carbon stocks from forest inventories remains low (Romijn et al., 2012). More generally, the main source of uncertainty in biomass estimates lies in the choice of a particular allometric model (Molto et al., 2013). To date, only two studies have developed biomass models in unmanaged Dipterocarp forests of Borneo (Yamakura et al., 1986; Basuki et al., 2009). However, the range of application of these models have hardly been tested and compared with more generic ones (but see Laumonier et al., 2010). Harvesting trees and weighing their components is time-consuming and most local allometric models encompassed only a small number of trees, likely not to reflect the full tree size distribution (Chave et al., 2005). To avoid this bias and to fill the lack of site-specific allometric equations, two major studies developed generic models and overcame these caveats in accounting for large pan-tropical datasets and large trees (DBH > 50 cm) (Brown, 1997; Chave et al., 2005). However the use of generic models may introduce errors in biomass stock estimates (Chave et al., 2004; Melson et al., 2011) and in Indonesia, site-specific models showed less bias in biomass estimates than generic ones (Basuki et al., 2009; Kenzo et al., 2009b). Depending on the model used, individual tree aboveground biomass (AGB) can vary by as much as a factor two (Basuki et al., 2009), introducing considerable uncertainties in forest biomass stocks computation (Nogueira et al., 2008; Laumonier et al., 2010). Although the use of generic models relies upon the

* Corresponding author.
E-mail address: er.rutishauser@gmail.com (E. Rutishauser).

0378-1127 © 2013 The Authors. Published by Elsevier B.V. Open access under CC BY-NC-SA license.
http://dx.doi.org/10.1016/j.foreco.2013.07.013

assumption that tree-level errors average out at plot level, bias is rarely assessed for forest stands across landscapes (van Breugel et al., 2011). Height and diameter relationship (H–DBH) greatly varies among forest types and regions (Feldpausch et al., 2011). Hence, at sites where no data were used to calibrate the generic models and with different H–DBH relationship, only generic models accounting for both H and DBH are expected to give reliable results (Henry et al., 2010; Vieilledent et al., 2011). Globally, accounting for tree height resulted in more accurate estimate of biomass at both tree and plot levels (Chave et al., 2005; Feldpausch et al., 2012).

Despite the vivid interest for carbon accounting in the region, no study has yet compared how the choice of allometric models affects biomass estimates in Dipterocarp forests. This study is divided into two parts. First, we compared the general accuracy of available peer-reviewed allometric models on an original destructive sample of 108 trees. Second, we investigated how these models affected carbon stock estimates across 12 forest plots representing a total area of 12 ha, focusing on the impact of tree height inclusion in these models.

Our aim was to provide guidance on estimating forest carbon stocks, in order to develop realistic scenarios of GHG emissions from land use change in Indonesia. We are notably addressing: (1) whether site-specific models better predict biomass at both tree and plot levels than generic models; (2) whether the inclusion of tree height improves biomass stock estimates at our sites and (3) how does the inclusion of tree height affect biomass estimates in forests with different H:DBH relationship.

2. Material and methods

2.1. Destructive sampling

We compiled data from destructive measurements made between 2007 and 2012 across East Kalimantan province in Indonesia, mainly from unmanaged lowland Dipterocarp forests (Noor'an, unpublished and Samalca, 2007). These trees did not come from one particular forest site and were hence not suitable to develop a local allometric model. However, we used them to test for the goodness of fit of published models. The DBH distribution ranged from 6 to 129.3 cm, not different from the average DBH distribution of primary forest plots used in this study ($X^2 = 89.9167$, $df = 80$, $P = 0.21$). The main families were Dipterocarpaceae (65%), Malvaceae (3%) and Fabaceae (3%).

2.2. Study sites and forest inventories

We used plots established in unmanaged lowland Dipterocarp forests in Sumatra and East Kalimantan, Borneo (Table 1). The climate at the Kalimantan sites is equatorial with a mean annual rainfall at Tanjung Redeb (Berau District, East Kalimantan) of 2105 mm from 1987 to 2007. All sites were classified as Ultisols (i.e. Xanthic Hapludox, Arenic Kanhapludults). Two sites were established in Community Protected Areas, where local communities historically harvested a few large trees for their own needs (1–5 trees ha^{-1}). Those plots were classified as old logged over forests. In each plot, all trees were tagged, diameter was measured at breast height (130 cm, DBH) or above buttresses and identified by a professional botanist in the field or at Bogor Herbarium. Dry wood specific gravity (WSG) was determined using the lowest level of botanical identification possible (Chave et al., 2006) and taking the appropriate value reported in the Global Wood Density Database (Zanne et al., 2009). When no botanical identification was available, we used plot-averaged WSG.

Total tree height, referred henceforth to as 'height', in the plots located in Kalimantan was systematically measured using a laser rangefinder, with a possible error of a few meters (Nikon, Forestry 550). In the plots of Sumatra, heights were estimated with a Blume Leiss hypsometer and cross-checked with measurements done by climbing trees (accuracy ± 0.5 m for small and medium trees, ±3 m for large emergent and canopy trees, Y.Laumonier pers.com). In all the other sites, a single operator did all the measurements to avoid inter-operator variability (Larjavaara and Muller-Landau, 2013).

2.3. Comparison of allometric models at tree level

Despite the importance of Dipterocarp forests in terms of area and carbon stocks, only a few suitable allometric models were found in the literature (Table 2). Two studies (Yamakura et al., 1986; Basuki et al., 2009) proposed site-specific allometric models. Two others (Ketterings et al., 2001; Kenzo et al., 2009a) developed allometric models in secondary logged-over forests. Ketterings et al. (2001) worked in a forest regrowing after slash and burn, in which cultivated species (i.e. *Artocarpus* or *Hevea*) were still present. The second study took place in an industrial logged-over forest concession, where the abundance of pioneer species such as *Macaranga spp*. or *Gluta spp*. indicated a much higher intensity of disturbance (2nd or 3rd rotation). As our study considers 'old-growth secondary forest' i.e. forest stands that have been selectively logged for at least 30 years and have not been clearcut, these last two models were judged irrelevant and were discarded. We also used the generic pan-tropical allometric models developed by Brown (1997), updated by Pearson et al. (2005), and by Chave et al. (2005). These models have been widely used, notably in the context of REDD+, and were recommended by the IPCC guidelines (IPCC 2003, 2006) for estimating carbon stocks in tropical forests.

Using the destructive sample, we compared the performance of prediction of the six models using four *ad hoc* indices, as reported in Vieilledent et al. (2011). We computed the residual standard error RSE, defined as the standard deviation of the residual errors ε_i (with $\varepsilon_i = \log(AGB_i) - \log(AGB_{iest})$, where AGB_i and AGB_{iest} represent the actual and estimated biomass of a tree *i*). Large RSE values indicate poor regression models. Second, we computed the coefficient of determination of each model, defined as:

$$R^2 = 1 - \frac{\Sigma_i \varepsilon_i^2}{\Sigma_i[\log(AGB_i) - \log(AGB)_{mean}]} \quad (1)$$

with $\log(AGB)_{mean}$ being the mean of log-transformed observed values. Models with a high number of parameters generally result in a

Table 1
Plots location, surface, average elevation, average number of stems per hectare and basal area (BA).

Plot_ID	Forest type	Location	Long	Lat.	Surface (ha)	Elevation (m)	Stems (ha^{-1})	BA (m^2/ha)
BM_PF	Unmanaged	Batu Majang, East Kalimatan	115.222	0.565	2	286	577	33.8
BM_SF	Old secondary	Batu Majang, East Kalimatan	115.220	0.559	2	213	534	24.7
BT_PF	Unmanaged	Barong Tongkok, East Kalimatan	115.415	−0.024	1	289	496	36.5
BT_SF	Old secondary	Barong Tongkok, East Kalimatan	115.548	−0.185	1	180	700	39.8
PMY_PF	Unmanaged	Pasir Mayang, Sumatra	102.093	1.083	6	100	669	30.1

Table 2
Published allometric models for mixed-species forests, sample size, DBH range of applicability and coefficient of determination (R). DBH = diameter at breast height, WSG = wood specific gravity or wood density, H = tree height.

Authors	Year	Region	Reference	Model	Sample size	Range (cm)	R^2
Yamakura & Haguiara	1986	East Kalimantan	Yamakura	Weight stem = 0.02909*(DBH^2*H)$^{0.9813}$	76	4.5–150	0.99
				Weight branch = 0.1192*(weight stem)$^{1.059}$	191		0.9
				Weight leaves = 0.09146*(weight stem + weight branch)$^{0.7266}$	191		0.92
				ln(AGB)$_{est}$ = ln(weights stem + branch + leaves)			
Basuki et al.	2009	East Kalimantan	Basuki.DBH	ln(AGB)$_{est}$ = 1.201 + 2.196*ln(DBH)	122	6.5–200	0.96
			Basuki.WSG	ln(AGB)$_{est}$ = (−0.744) + 2.188*log(DBH) + 0.832*log(WSG)	122		0.97
Chave et al.	2005	Pan-tropical	Chave.DBH	ln(AGB)$_{est}$ = (−1.499) + 2.148*ln(DBH) + 0.207*ln(DBH)^2 − 0.0281*ln(DBH)^3 + ln(WSG)	2410	5–156	1
			Chave. H	ln(AGB)$_{est}$ = (−2.977) + ln(WSG*DBH^2*H)	2410	5–156	0.99
Pearson et al.	2005	Pan-tropical	Pearson	ln(AGB)$_{est}$ = (−2.289) + 2.649*ln(DBH) − 0.021*ln(DBH)^2	226	5–148	0.98

better fit to the data and R^2 should be interpreted considering the degrees of freedom of the model $df = n_{obs} - n_{par}$, with n_{obs} the number of observations and n_{par} the number of parameters. Third, we computed the Akaike Information Criterion for each model, AIC = $-2\log(L) + 2n_{par}$, L being the model likelihood. The best model minimizes the value of AIC. Finally, we computed the overall model bias by summing each individual error (ε_i) expressed as a percentage of tree biomass and taking the median value.

$$\text{Bias} = \text{median}\left(100 * \left(\frac{1}{\exp(\varepsilon_i) - 1}\right)\right) \quad (2)$$

2.4. Inclusion of tree height in allometric models

We investigated the importance of height (H) integration in biomass computation by comparing Chave's equations (Table 2, Eqs. (4), (5)) with and without height. In addition to height measurements (N = 7389), we developed regional H:DBH relations (the two regions here are Sumatra and East Kalimantan) in order to test the minimal sample size to accurately estimate tree height. We used here a Weibull function of the form:

$$H_{regional} = a \times (1 - \exp(-b \times \text{DBH}^c)) + \varepsilon, \text{ with } \varepsilon \sim N(0, 1) \quad (3)$$

Feldpausch et al. (2012) showed that the Weibull-H function lowered the relative error in the small diameter classes (DBH < 50 cm) compared to other usual functions, and was therefore more adapted to skewed diameter distributions. In their study, the authors developed a continental model for South East Asia and Borneo (Table 3A).

We examined how the inclusion of tree height in biomass allometric models affected plot-level biomass estimates. We compared Chave's equation (Table 2, Eq. (5)) including height (1) measured in the field, (2) estimated regionally, (3) estimated continentally and (4) Chave's equation without height (Table 2, Eq. (4)). In addition, we investigated the minimal sample size required to accurately infer H from DBH for each forest type. We developed a Weibull-H function for different sample sizes (1%, 5%, 10%, 20% and 50% of initial population) and tested its ability to predict height of a given pool of trees (20% of initial population). To ensure convergence of the model, the DBH distribution of the sample was similar to the original one. We computed the average error of prediction ($100*(H_{predicted} - H_{measured})/H_{measured}$) using 500 simulations per sample size.

2.5. Plot biomass computation and confidence intervals

For each tree, we computed 1000 biomass estimates for each allometric model using two error terms for both WSG and H following the methodology developed by Feldpausch et al. (2012), assuming no error for the DBH measurements. The error terms were estimated as

$$\widehat{\text{WSG}}_i = \text{WSG}_i + \varepsilon_i, \text{ with } \varepsilon \sim N(0, \sigma_{\text{WSG}}) \text{ and } \widehat{\text{WSG}}_i \in [0.1, 1.1] \quad (4)$$

$$\widehat{H}_i = H_i + \varepsilon_i, \text{ with } \varepsilon \sim N(0, \sigma_H) \text{ and } \widehat{H}_i \in [5, 70] \quad (5)$$

where the "hat" symbol indicates estimates that include an error term randomly chosen in a Normal distribution of mean = 0 and of standard deviation (σ) of WSG or H computed per plot. Biomass stocks were computed at plot level by summing a randomly chosen estimate (for a given allometric model) among 1000 realisations for each tree present in the plot. The 95% confidence interval was calculated as the 2.5th and 97.5th percentiles of the 1000 realisations of each estimate.

All computation and analyses were carried out using R statistical software (R Development Core Team, 2013) and the code is freely available on www.runmycode.org.

3. Results

3.1. Comparison of allometric models

All models accurately predicted the biomass of our sample of felled trees (Table 4), explaining between 90 and 96% of the variation observed. But overall, regional models had lower performance, with greater bias (−31–8%) and higher AIC (177–204), compared to generic models (bias: −2–2% and AIC: 57–67).

The generic allometric model developed by Chave et al. (2005) including height was the best model with the highest coefficient of determination (0.964) and the lowest residual standard error (0.309) and AIC (56.6). On the contrary, the model developed locally in the same region by Basuki et al. (2009) greatly underesti-

Table 3
Continental (A) and regional (B, C) tree height models of the form: $H_{predicted}$ = a*(1 − exp(−b*DBH^c)).

	Source	Region	Scale	a	b	c	RSE	N
A	Feldpausch et al. (2012)	South East Asia	Continental	57.122	0.0332	0.8468	5.69	2948
B	This study	East Kalimantan	Regional	1989.144	0.0018	0.5306	5.29	3192
C	This study	Sumatra	Regional	56.703	0.0547	0.739	3.417	4013

Table 4
Comparison of regional (Yamakura, Basuki.DBH and Basuki.WSG) with generic (Chave.DBH, Chave.H and Pearson) models. R^2 is the coefficient of determination, *df* is the degree of freedom, *N* par the number of parameters, RSE the residual standard error, AIC is the Akaike Information Criterion, Bias (%) is the median model relative error.

Equation	R^2	*df*	*N* par	RSE	AIC	Bias
Yamakura	0.959	–	–	0.325	–	7.8
Basuki.DBH	0.912	106	2	0.37	177.2	−29.8
Basuki.WSG	0.903	105	3	0.359	204.6	−31.3
Chave.DBH	0.963	104	4	0.319	66.9	−1.7
Chave.H	0.964	107	1	0.309	56.6	2.0
Pearson	0.962	105	3	0.322	66.6	−0.8

mated individual tree biomass, resulting in very low aggregated biomass estimates at the plot level (average = −30%, Table 5).

3.2. Including tree height in biomass estimates

Chave.H returned slightly better fit than the one relying solely upon DBH (Chave.DBH, Table 4). Based on this comparison, we considered Chave.H as the most accurate model and served as reference.

The minimum sample size to accurately estimate tree height was low and did not vary significantly among sites (Fig. 1). Measuring only 1% (40–90 trees) reflecting the actual DBH distribution in a plot enabled to accurately estimate tree height at each site. For instance at Barong Tongkok (BT-PF), measuring 1% of the population resulted in an average error of prediction of tree height of 5.6% and 2.75% of the biomass stock versus 4.8% and 2.3% respectively for a sample size of 50%.

Additionally, we developed two regional models (Table 3B and C) to estimate tree heights, and used the continental height estimates developed by Feldpausch et al. (2012). Both regional and continental H-models were compared to the actual heights. Overall, regional models showed smaller bias in height estimates (Fig. 2A) compared to continental models (Fig. 2B). In unmanaged forest, the former showed a bias roughly constant across diameter classes with height overestimated by 10–20%. Overestimation was exacerbated in secondary forest plots, where height estimates of trees 70 < DBH < 120 cm nearly doubled.

In most plots, the overestimation of tree height by regional or continental H-models resulted in a general biomass overestimation among almost all diameter classes (Fig. 3). The only marked difference was found in Sumatra (PMY-PF) were the continental H-model slightly underestimated tree heights (Fig. 2B) and subsequent biomass estimates (Fig. 3).

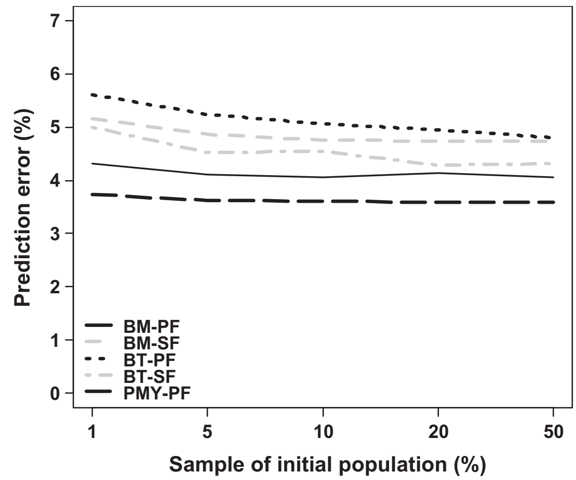

Fig. 1. Error of prediction of tree height ($H_{predicted}-H_{measured}/H_{measured}$) using a given fraction (in %) of the initial population to develop a H:DBH model. BM_PF (unmanaged forest in Batu Majang), BM_SF (old secondary forest in Batu Majang), BT_PF (unmanaged forest in Barong Tongkok), BT_SF (old secondary forest in Barong Tongkok), PMY_PF (unmanaged forest in Pasir Mayang).

3.3. Plot biomass stocks

Plotting all models and confidence intervals reviewed in this study revealed a large range in biomass stock estimates (Fig. 4), with differences greater than 100 Mg ha^{-1} depending on the models and site compared.

When compared with Chave.H model, the regional models developed by Basuki et al. (2009) and Yamakura et al. (1986) underestimated biomass stocks by 25–40% and 0–10% respectively (Table 4). Contrastingly, all generic models relying upon BDH only overestimated in average biomass stocks when compared to the best predictive model (Chave.H). For instance, using Chave.DBH resulted in an AGB overestimation of 15% in the Eastern Kalimantan unmanaged forest plots (Chave.DBH, Table 5), and in an underestimation of 5% in the Sumatran plot. The second generic model (Pearson, Table 5) showed only small differences with Chave.H model, except in the Sumatran plot. The integration of regional height estimates into Chave.H model resulted in a slight overestimate of 5–10% in unmanaged forest, and almost no departure in secondary forest (−3–0%).

Table 5
Mean, 95% confidence interval (CI) and relative difference in percent (diff.) with the equation of Chave et al. (2005) integrating height (Chave.H) by forest types. BM_PF: Unmanaged forest in Batu Majang, BM_SF: old secondary forest in Batu Majang, BT_PF: unmanaged forest in Barong Tongkok, BT_SF: old secondary forest in Barong Tongkok, PMY_PF: unmanaged forest in Pasir Mayang.

	Yamakura			Basuki.DBH			Basuki.WSG			Chave.DBH		
	Mean	CI	Diff.	Mean	CI	Diff.	Mean	CI	Diff.	Mean	CI	Siff.
BM-PF	347	(307–392)	−2	256	–	−28	256	(240–290)	−28	407	(352–453)	15
BM-SF	226	(221–259)	−4	175	–	−26	178	(174–199)	−25	262	(239–284)	11
BT-PF	388	(318–450)	−9	283	–	−34	295	(266–348)	−31	491	(407–572)	15
BT-SF	397	(346–452)	0	292	–	−26	293	(277–337)	−26	445	(387–504)	12
PMY-PF	325	(319–349)	−9	215	–	−40	227	(224–242)	−36	340	(315–349)	-5
	Chave.H			Chave.Hregio			Chave.Hcont			Pearson		
	Mean	CI	Diff.	Mean	CI	Diff.	Mean	CI	Diff.	Mean	CI	Diff.
BM-PF	354	(293–427)	0	370	(307–441)	5	406	(328–477)	15	397	–	12
BM-SF	236	(219–285)	0	228	(217–283)	−3	255	(234–306)	8	242	–	2
BT-PF	426	(314–548)	0	449	(350–567)	5	492	(371–601)	16	450	–	6
BT-SF	397	(339–501)	0	396	(341–511)	0	438	(368–539)	10	429	–	8
PMY-PF	357	(334–386)	0	393	(359–417)	10	333	(314–365)	-7	302	–	−15

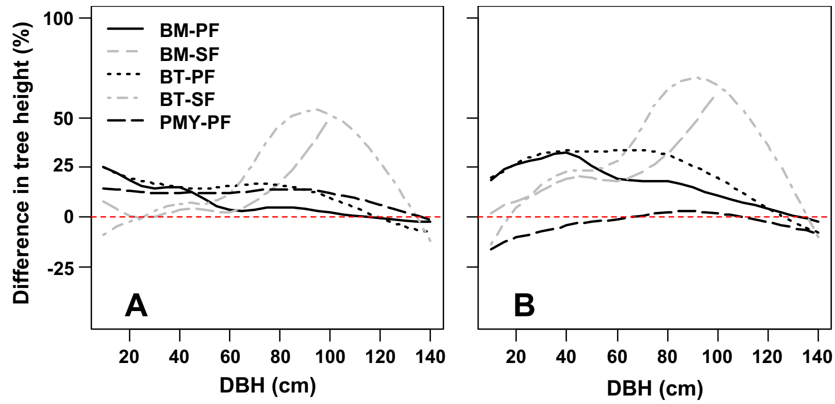

Fig. 2. Difference between measured tree height and (A) regionally estimated height, (B) continentally estimated height plotted as a function of tree DBH by forest types. The curves were smoothed by a lowess method. At BM-SF, the upper DBH limit was 100 cm. BM_PF: unmanaged forest in Batu Majang, BM_SF: old secondary forest in Batu Majang, BT_PF: unmanaged forest in Barong Tongkok, BT_SF: old secondary forest in Barong Tongkok, PMY_PF: unmanaged forest in Pasir Mayang.

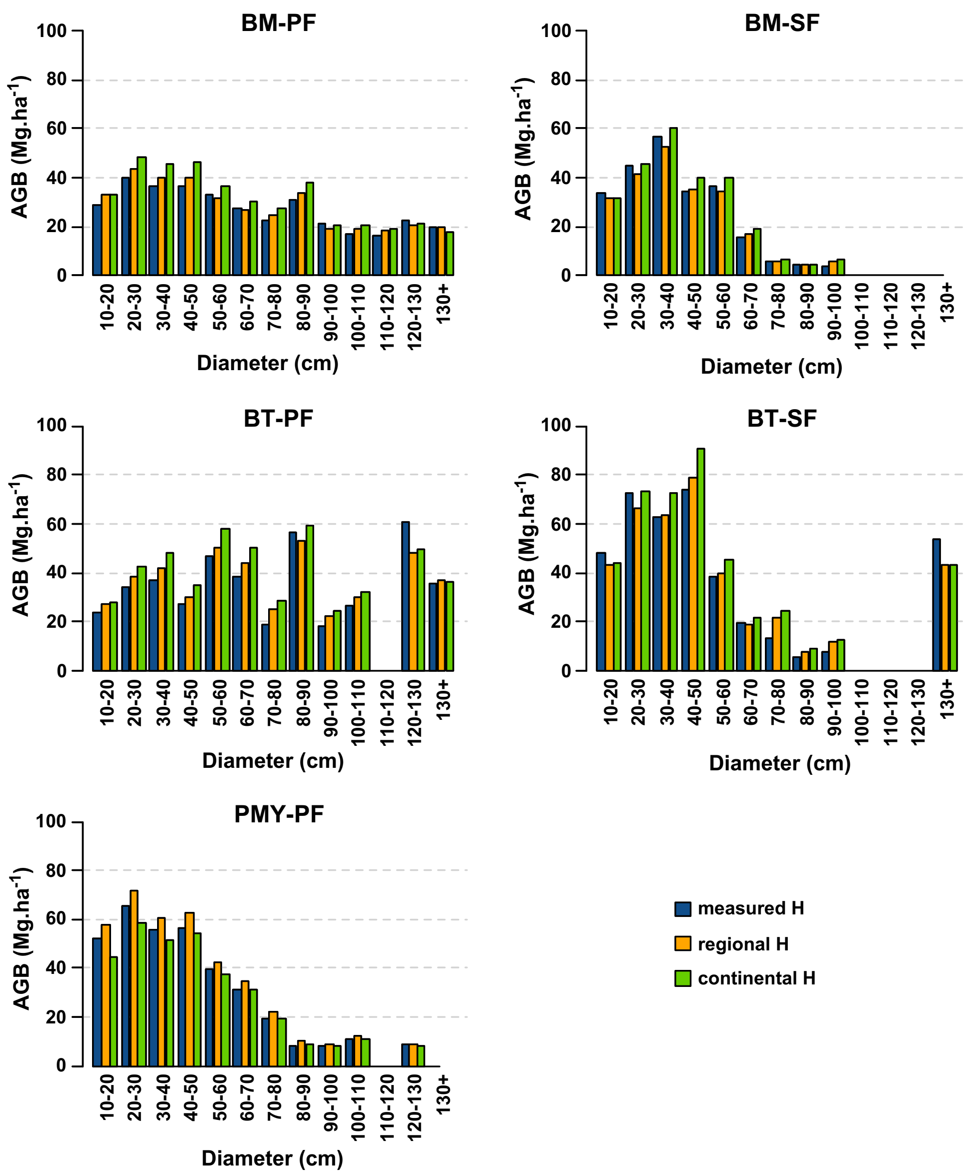

Fig. 3. Comparison of biomass stocks computed using Chave's equation (Chave.H) by diameter class per site, using measured height (blue), regional height estimates (orange) and continental height estimates (green). BM_PF: unmanaged forest in Batu Majang, BM_SF: old secondary forest in Batu Majang, BT_PF: unmanaged forest in Barong Tongkok, BT_SF: old secondary forest in Barong Tongkok, PMY_PF: unmanaged forest in Pasir Mayang. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

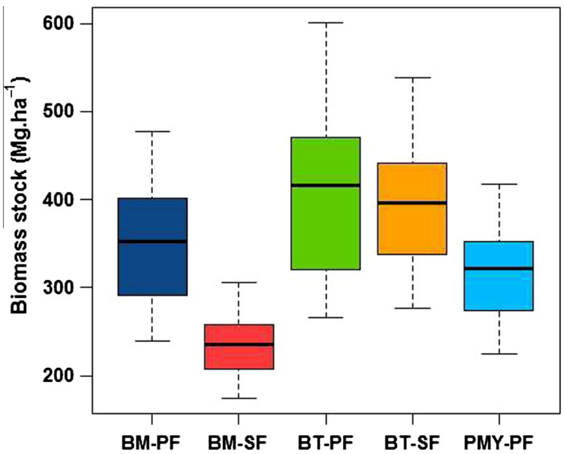

Fig. 4. Biomass stocks range combining six allometric models (Table 3) and their bootstrapped confidence intervals per forest type. Boxes represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, line represents median. BM_PF: unmanaged forest in Batu Majang, BM_SF: old secondary forest in Batu Majang, BT_PF: unmanaged forest in Barong Tongkok, BT_SF: old secondary forest in Barong Tongkok, PMY_PF: unmanaged forest in Pasir Mayang.

4. Discussion

4.1. Recommendations on the use of allometric models

The generic pantropical model developed by Chave et al. (2005) including tree height provided the best biomass estimates when applied to our destructive samples (Table 3). This result was expected as the Indonesian sites used in their study were both located in East Kalimantan, about 200 km from where trees used in this study where collected. Additionally, Chave et al. (2005) showed that H-models had smaller departure from observed values compared to DBH-models in most tropical forests, but with a notable exception in East Kalimantan. Our results are consistent with this finding, showing that generic models relying solely upon DBH and WSG (Chave.DBH or Pearson) were also very good at predicting biomass at our sites. However, these last models can result in an error of ±15% of the actual biomass stock in certain forests.

Despite the fact that Dipterocarp forests represent the dominant vegetation in Borneo, it is most likely that accounting for other forest types with different structures (i.e. kerangas forests, peat swamp forests, forests on limestone) would have given different results. For instance, in African forests where H:DBH relationship is very different and from which no data were used to calibrate those generic models, Chave.DBH model largely overestimated biomass while Chave.H gave very good fit (Henry et al., 2010; Vieilledent et al., 2011; Fayolle et al., 2013).

As tree height is generally not recorded in forest inventories, models relying solely upon DBH are likely to remain widely used by foresters. We showed here that the generic model developed by Brown (1997), updated by Pearson et al. (2005), showed similar performance to the model integrating WSG and DBH (Chave.DBH), but with slightly smaller bias. Both models outperformed the regional models developed in East Kalimantan. In conclusion, generic models relying solely upon DBH and WSG remain appropriate, but should be used with caution as they generally overestimate biomass.

4.2. Measuring tree height in tropical forests

With advances in laser instruments, it has become easier to accurately and rapidly assess tree height in the field. In a tropical forest, direct vertical measurements of the last branch was found to underestimate of actual tree height by 20% (Larjavaara and Muller-Landau, 2013). It is likely that the error remains proportional to tree height, affecting primarily emergent trees. Rapid advances in LiDAR-derived mean canopy height might help to overcome this caveat and seems to be a promising way of integrating average forest stand height into plot carbon stocks measurements (Asner et al., 2011).

Despite similar continental H:DBH relationships found across Asia, Africa and the Guyana Shield (Feldpausch et al., 2011), we found that continental H:DBH models only poorly explained the variance observed at our sites, notably in old-growth secondary forests (Fig. 2). We highlight here that the continental model proposed by Feldpausch et al. (2012) was originally developed for unmanaged forests and should be used with caution in secondary forests. For instance, trees growing in logged forests in the Amazon were found to be shorter with larger crowns (Nogueira et al., 2008). This phenomenon might explain our results in secondary forests, where large trees had much smaller heights than expected. We showed that H:DBH model can be fitted with only a small fraction of the forest stand (Fig. 1), as long as the sample is equally distributed along the actual DBH distribution. In a first attempt, trees were randomly chosen, embedding the model to converge in most cases. This result is encouraging and shows that integrating tree height into carbon stock assessment would not require a lot of additional field work.

4.3. Above-ground biomass stock in trees of Dipterocarp forests

Using the best predictive model (Chave.H), we found an average value of 378 Mg ha^{-1} in unmanaged and 316 Mg ha^{-1} in secondary forests. These values are lower than those previously reported for Dipterocarp forests (Paoli et al., 2008; Slik et al., 2010). Both studies used Chave's equation based on DBH and WSG, with AGB stocks ranging from 457 to 606 Mg ha^{-1}. Our study shows that these figures are likely to be overestimated by at least 10%. Lower AGB stock in secondary forests was mainly explained by the absence of very large trees (DBH > 100 cm) that usually encompass a large fraction of AGB in tropical forests (Paoli et al., 2008; Rutishauser et al., 2010). However, these figures remained relatively high compared to forests recovering from conventional logging that range between 150 and 300 Mg ha^{-1} (Berry et al., 2010; Saner et al., 2012). This strengthens our initial postulate of considering these plots as mature secondary forests and constitutes one of the reasons we decided not to use allometric models developed in logged-over forests of Sumatra (Ketterings et al., 2001) or Borneo (Kenzo et al., 2009a). At one site (BT_SF), no logging activity was carried out over the last 40 years, while none was carried at the second site (BM_SF).

Such systematic assessment should be performed in other forest types and ecoregions across Indonesia in order to determine the validity and the choice of the appropriate allometric model.

4.4. On the choice of a suitable allometric model

The choice of a particular allometric model will remain mainly driven by data availability. Due to time and costs constraints, most forest inventories are restricted to DBH measurements and DBH-models will remain widely used. However, accounting for tree heights can reduce uncertainties surrounding biomass estimates in Dipterocarp forests. Overall, the average absolute difference in biomass stocks between H-models and DBH-models was 10–15%, in the same magnitude of what was found in Malaysian Borneo and Brunei (Feldpausch et al., 2012). Despite the fact that local H:DBH allometry can be obtained from a small sample (45–90 individuals) of the stand, regional H-models can provide a fair alternative (Fig. 2A). In the field, measuring tree heights do not represent a heavy extra-cost and required on average 3–5 min at our sites. Most models overestimate the biomass of large trees, what could be considerably reduced in measuring systematically their height. In addition to a representative sample of the DBH distribution, focusing on large trees might help improving biomass estimate and represent a good compromise between time constraints and accuracy.

Acknowledgements

This research is part of the project entitled Impacts of Reducing Emissions from Deforestation and Forest Degradation and Enhancing Carbon Stocks (I-REDD+). I-REDD+ is funded by the European Community's Seventh Framework Research Programme. Additional support was provided to CIFOR by the governments of Australia (Grant Agreement # 46167) and Norway (Grant Agreement #QZA-10/0468). This work was carried out as part of the Consultative Group on International Agricultural Research programs on Forests, Trees and Agroforestry (CRP6). Part of the data were collected by WWF Indonesia under the REDD for people and nature (RPAN) project funded by NORAD. The authors thank Ghislain Vieilledent and an anonymous reviewer for their valuable contribution that helped improving our manuscript.

References

Asner, G.P., Mascaro, J., Muller-Landau, H.C., Vieilledent, G., Vaudry, R., Rasamoelina, M., Hall, J.S., van Breugel, M., 2011. A universal airborne LiDAR approach for tropical forest carbon mapping. Oecologia, 1–14.

Basuki, T.M., Van Laake, P.E., Skidmore, A.K., Hussin, Y.A., 2009. Allometric equations for estimating the above-ground biomass in tropical lowland Dipterocarp forests. Forest Ecology and Management 257, 1684–1694.

Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., Ahmad, N., Magintan, D., Khen, C.V., Maryati, M., 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodiversity and Conservation 19, 985–997.

Brown, S., 1997. Estimating Biomass and Biomass Change of Tropical Forests: A Primer, FAO Forestry Paper edition. UN FAO, Rome, Italy.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., Perez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. Philosophical Transactions of the Royal Society B: Biological Sciences 359, 409–420.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Ter Steege, H., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecological Applications 16, 2356–2367.

FAO, 2010. Global Forest Resources Assessment 2010. Food and Agriculture Organization, Rome.

Fayolle, A., Doucet, J.-L., Gillet, J.-F., Bourland, N., Lejeune, P., 2013. Tree allometry in central Africa: testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. Forest Ecology and Management 305, 29–37.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E., Berry, N.J., Bird, M., 2011. Height–diameter allometry of tropical forest trees. Biogeosciences 8, 1081–1106.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard, G.A., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J., Comiskey, J.A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djagbletey, G., Domingues, T.F., Erwin, T.L., Fearnside, P.M., França, M.B., Freitas, M.A., Higuchi, N., Iida, E.H.C.Y., Jiménez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe, D.J., Mitchard, E.T.A., Neill, D.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., Peh, K.S.H., Pena Cruz, A., Peñuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G.M.F., Vásquez, R., Vilanova, E., Vos, V.A., White, L., Willcock, S., Woell, H., Phillips, O.L., 2012. Tree height integrated into pantropical forest biomass estimates. Biogeosciences 9, 3381–3403.

Henry, M., Besnard, A., Asante, W., Eshun, J., Adu-Bredu, S., Valentini, R., Bernoux, M., Saint-André, L., 2010. Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. Forest Ecology and Management 260, 1375–1388.

Houghton, R.A., 2005. Aboveground forest biomass and the global carbon balance. Global Change Biology 11, 945–958.

Houghton, R.A., Hall, F., Goetz, S.J., 2009. Importance of biomass in the global carbon cycle. Journal of Geophysical Research 114, G00E03.

IPCC, 2003. Good practice guidance for land use, land-use change and forestry (GPG-LULUCF). PCC-IGES, Kanagawa.

IPCC, 2006. Guidelines for National Greenhouse Gas Inventories, vol. 4. In S. Eggelstons, L. Buendia, K. Miwa, N. Todd & K. Tanabe (Eds.). Hayama, Japan: Institute for Global Environmental Strategies (IGES).

Kenzo, T., Furutani, R., Hattori, D., Kendawang, J.J., Tanaka, S., Sakurai, K., Ninomiya, I., 2009a. Allometric equations for accurate estimation of above-ground biomass in logged-over tropical rainforests in Sarawak, Malaysia. Journal of Forest Research 14, 365–372.

Kenzo, T., Ichie, T., Hattori, D., Itioka, T., Handa, C., Ohkubo, T., Kendawang, J.J., Nakamura, M., Sakaguchi, M., Takahashi, N., 2009b. Development of allometric relationships for accurate estimation of above and below-ground biomass in tropical secondary forests in Sarawak, Malaysia. Journal of Tropical Ecology 25, 371–386.

Ketterings, Q.M., Coe, R., van Noordwijk, M., Ambagau, Y., Palm, C.A., 2001. Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. Forest Ecology and Management 146, 199–209.

Larjavaara, M., Muller-Landau, H.C., 2013. Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. Methods in Ecology and Evolution (published online).

Laumonier, Y., Edin, A., Kanninen, M., Munandar, A.W., 2010. Landscape-scale variation in the structure and biomass of the hill dipterocarp forest of Sumatra: implications for carbon stock assessments. Forest Ecology and Management 259, 505–513.

Melson, S.L., Harmon, M.E., Fried, J.S., Domingo, J.B., 2011. Estimates of live-tree carbon stores in the Pacific Northwest are sensitive to model selection. Carbon Balance and Management 6, 2.

Miettinen, J., Shi, C., Liew, S.C., 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17, 2261–2270.

Molto, Q., Rossi, V., Blanc, L., 2013. Error propagation in biomass estimation in tropical forests. Methods in Ecology and Evolution 4, 175–183.

Nogueira, E.M., Fearnside, P.M., Nelson, B.W., Barbosa, R.I., Keizer, E.W.H., 2008. Estimates of forest biomass in the Brazilian Amazon: new allometric equations and adjustments to biomass from wood-volume inventories. Forest Ecology and Management 256, 1853–1867.

Paoli, G., Curran, L., Slik, J., 2008. Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. Oecologia 155, 287–299.

PEACE, 2007. Indonesia and Climate Change. World Bank & Department for International Development.

Pearson, T., Walker, S., Brown, S., 2005. Sourcebook for land use, land-use change and forestry projects. BioCarbon Fund & Winrock International.

R Development Core Team, 2013. R: a language and environment for statistical computinging. R Foundation for Statistical Computing, Vienna, Austria.

Romijn, E., Herold, M., Kooistra, L., Murdiyarso, D., Verchot, L., 2012. Assessing capacities of non-Annex I countries for national forest monitoring in the context of REDD+. Environmental Science and Policy 19–20, 33–48.

Rutishauser, E., Wagner, F., Herault, B., Nicolini, E.A., Blanc, L., 2010. Contrasting above-ground biomass balance in a Neotropical rain forest. Journal of Vegetation Science 21, 672–682.

Samalca, I.K., 2007. Estimates of forest biomass and its error: a case study in Kalimantan Indonesia. International Institute for Geo-Information Science and Earth Observation. Enschede, The Netherland.

Saner, P., Loh, Y.Y., Ong, R.C., Hector, A., 2012. Carbon stocks and fluxes in tropical lowland dipterocarp rainforests in sabah, Malaysian Borneo. PLoS ONE 7, e29642.

Slik, J.W.F., Aiba, S.-I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E., van Valkenburg, J.L.C.H., 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. Global Ecology and Biogeography 19, 50–60.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F., Hall, J.S., 2011. Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. Forest Ecology and Management 262, 1648–1657.

Vieilledent, G., Vaudry, R., Andriamanohisoa, S.F.D., Rakotonarivo, S.O., Randrianasolo, Z.H., Razafindrabe, H.N., Bidaud Rakotoarivony, C., Ebeling, J., Rasamoelina, M., 2011. A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. Ecological Applications 22, 572–583.

Yamakura, T., Hagihara, A., Sukardjo, S., Ogawa, H., 1986. Aboveground biomass of tropical rain forest stands in Indonesian Borneo. Vegetatio, 71–82.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S. L., Miller, R.E., Swnson, N.G., Wiemann, M.C., Chave, J., 2009. Global wood density database. Dryad identifier: <http://hdl.handle.net/10255/dryad.235>.