



Estimating the aboveground biomass in an old secondary forest on limestone in the Moluccas, Indonesia: Comparing locally developed versus existing allometric models



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ABSTRACT

Deforestation and forest degradation are widespread in Indonesia and pose serious threats to biodiversity and other ecosystem services. The Indonesian government is implementing several Reduction of Emissions from Deforestation and Forest Degradation (REDD+) initiatives to help support the conservation of tropical forests, but the eastern part of Indonesia has yet to be included in this effort. Tropical forests growing on limestone are a prominent feature of that region, but little is known about their ecology and management, and only limited research has been conducted on biomass and the associated carbon storage capacity of these secondary forests. Here, we estimate the aboveground tree biomass (AGB) in an old secondary forest on limestone in Seram, the Moluccas, East Indonesia. We destructively sampled all aboveground vegetation in 0.04 ha forest and developed a local allometric model ($n = 25$; diameter-range of 10.4–41.7 cm). We tested and compared the performance of our locally developed model with existing local models and a recent pantropical model (Chave et al., 2014) at our site. Total AGB in the 1-ha forest plot was estimated at 177 Mg ha⁻¹, of which 141 Mg ha⁻¹ (80%) was allocated in trees ≥ 10 cm diameter at breast height (dbh), 33 Mg ha⁻¹ (19%) in trees <10 cm dbh and 2 Mg ha⁻¹ (1%) in lianas and non-woody vegetation. Both our locally developed and the pantropical model estimated the biomass of harvested trees accurately (local model: bias = 0.1%, CV = 15.5%; pantropical model: bias = -7.7%, CV = 17.7%), while other local models had much lower performance (bias = -57.1 to -7.3%, CV = 59.2 to 75.8%). At plot-level, the AGB estimate of the pantropical model approached the estimate of our local model, while other local models considerably underestimated actual AGB. Together, our findings confirm that trees <10 cm dbh can store a large fraction of total AGB in secondary forests, and highlight the robustness of generic models. These results provide further guidance for accurate assessments of forest carbon stocks in Indonesia and more generally for REDD+ initiatives.

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1. Introduction

Deforestation and forest degradation rates in continental and insular Southeast Asia are alarming (FAO, 2010; Miettinen et al.,

2011). In Indonesia, in particular, over 6 Mha of primary forests were lost from 2000 to 2012 (Margono et al., 2014), with tremendous consequences for biodiversity and other ecosystem services (Sodhi et al., 2004; de Bruyn et al., 2014).

One approach to conservation and mitigation of environmental degradation is to develop payments and markets for environmental services. The Reduction of Emissions from Deforestation and Forest Degradation (REDD+) was proposed as a mechanism to provide financial incentives to developing countries to reduce emissions from forest loss and promote forest conservation, sustainable forest management and the enhancement of forest

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carbon stocks (Angelsen et al., 2009). A major technical challenge for REDD+ is the estimation of these carbon emissions at regional or national levels.

Aware of this situation, the Indonesian government has been among the first to implement a national forest carbon initiative (Indonesian REDD+ Task Force, 2012), but the eastern part of the country has yet to get involved. At the request of the local government of the Moluccas in eastern Indonesia, a feasibility research and development program on land zoning, land-use planning and ecosystem services assessment was carried out on one of the largest islands of the region, Seram. It included research on biomass stocks, biodiversity management and maintenance of ecosystem services through community participation in and around a large conservation area: the Manusela National Park (MNP) in the Central Moluccas regency (Kabupaten Maluku Tengah).

One unique feature of the MNP is the large limestone massif, spanning from sea level up to 3000 m.a.s.l. Limestone karsts cover an area of around 400,000 km² in Southeast Asia, mostly concentrated in Indonesia (145,000 km²; Clements et al., 2006). Forests on limestone tend to be water-stressed because they grow on seasonally water-depleted soil (Crowther, 1983; Whitmore, 1984). They are also known for their high levels of endemism and species diversity (Clements et al., 2006). Their ecology and management, however, are poorly known, consisting of a few studies in Peninsular Malaysia (Crowther, 1987, 1982) and Sarawak (Proctor et al., 1983) in Malaysia; and Sumatra (Laumonier, 1997), Western New Guinea (Takeuchi, 2003; Johns et al., 2007) and the Moluccas (Edwards et al., 1990; Ranlund, 2011; Stas, 2014) in Indonesia, with limited research on secondary forests and biomass stocks. Like elsewhere in Indonesia, lowland limestone forests in the Moluccas are under high pressure of agrarian changes, and proper understanding of secondary succession is crucial for future landscape management and restoration.

Biomass and associated carbon estimates are highly sensitive to the choice of a particular allometric equation (Chave et al., 2004; Van Breugel et al., 2011). Many biomass equations have been developed locally for Indonesian forests, with most studies focusing on Kalimantan and Sumatra (see Anitha et al., 2015); the eastern Indonesian region, including Sulawesi, the Moluccas, Nusa Tenggara and Western New Guinea, is seriously understudied (Anitha et al., 2015). While local allometric models perform generally well for a given site or forest type, they are laborious to develop and potentially give significant errors in biomass estimations when applied elsewhere (Chave et al., 2005). Generic models were shown to outperform local models in Indonesia (Rutishauser et al., 2013), but have not been thoroughly tested in secondary forests. Here, we destructively sampled all aboveground vegetation in 0.04 ha forest and developed a local allometric model to estimate the aboveground biomass (AGB) of trees in an old secondary forest on limestone in Seram, the Moluccas. We compared the performance of our locally developed model with a selection of existing local models (Kenzo et al., 2009; Ketterings et al., 2001) and the most recent pantropical model (Chave et al., 2014) at our site. The implications of these results for carbon accounting initiatives are discussed.

2. Material and methods

2.1. Site description

Seram island in the Moluccas, East Indonesia, covers an area of about 18,000 km². Seram's lowlands have a perhumid tropical climate and mean annual temperatures at sea level vary between 25° and 30 °C. In the northern coastal lowlands around Wahai, annual precipitation is between 2000 and 2500 mm, with a weak or no dry

season (Fontanel and Chantefort, 1978). The “drier” season is from May to October, when monthly rainfall seldom exceeds 100 mm (Edwards, 1993). The central part is characterized by large outcrops of massive limestone (circa 5% of Seram's land area), ranging from the coast up to the mountains. The vegetation on these karsts is largely protected in the Manusela National Park (MNP), the largest conservation area in the Moluccas, which represents approximately 10% of Seram (1860 km²).

Data were collected in a lowland forest (circa 70 m.a.s.l.) on soils developed on limestone, situated in the northern part of Seram near the village of Masihulan and outside the MNP, in 2011 (Fig. 1). Structure and floristics of this forest are described in Stas (2014). Information from local people was used to retrieve the disturbance history and forest usage at the study site. The forest experienced a natural fire in 1982, but its magnitude and duration and the exact locations of burned sites remain unclear; apparently, some large standing trees survived the fire. Local people, and possibly also a logging company, extracted some timber in the area in the 1990s, but probably not from the study plot. The natural fire is considered as the main disturbance and this forest can be best classified as “post-fire secondary forest”, or more broadly as “post-catastrophic secondary forest”, following the definition of Chokkalingam and de Jong (2001): “Forests regenerating largely through natural processes after significant reduction in the original forest vegetation due to a catastrophic natural disturbance or succession of such disturbances, and displaying a major difference in forest structure and/or canopy species composition with respect to nearby primary forests on similar sites”.

2.2. Data collection

2.2.1. Non-destructive measurements

All living stems ≥ 10 cm diameter at breast height (dbh; i.e. diameter at 130 cm from ground level or 30 cm above buttresses) were tagged and their dbh measured in a 1-ha plot (100 × 100 m in horizontal projection). The plot was divided into subplots of 10 × 10 m to facilitate measurement. Tree heights were measured with a Haga altimeter. Botanical samples were collected and local names recorded. Species identification was further conducted in the herbarium of Bogor, Java, Indonesia, in 2011. The taxonomy was recently updated using The Plant List (2013). Palms were not sampled.

2.2.2. Destructive sampling

After completing the non-destructive measurements, four subplots of 10 × 10 m each (in total 0.04 ha) were selected within the 1-ha plot for destructive sampling, aiming at representing the mosaics of different successional stages of the vegetation in the secondary forest plot. A total of 25 trees ≥ 10 cm dbh were cut down, in the range of 10.4–41.7 cm dbh, 10.3–23.6 m height and 0.320–0.730 g cm⁻³ wood density (see Appendix A for a tree-by-tree description). Four of the five most abundant species in the 1-ha plot (for trees ≥ 10 cm dbh), i.e. *Decaspermum bracteatum* (Myrtaceae; 24%), *Hancea penangensis* (Euphorbiaceae; 20%), *Meliosma pinnata* (Sabiaceae; 7%) and *Elaeocarpus serratus* (Elaeocarpaceae; 6%) were present in the destructive sampling.

In the selected subplots, all aboveground vegetation was cut down, as close to the ground as possible. Heights of harvested trees ≥ 10 cm dbh were measured with a measuring tape after felling. Vegetation was separated into trees ≥ 10 cm dbh, trees <10 cm dbh, lianas, epiphytes, mosses and herbs. As water content varies among compartments, trees (comprised of trees, treelets and shrubs) were further divided into leaves, twigs, branches and stems, and lianas into leaves and stems (hereafter referred to as “compartments”). The non-woody vegetation, i.e. epiphytes, mosses and herbs, was not further divided.

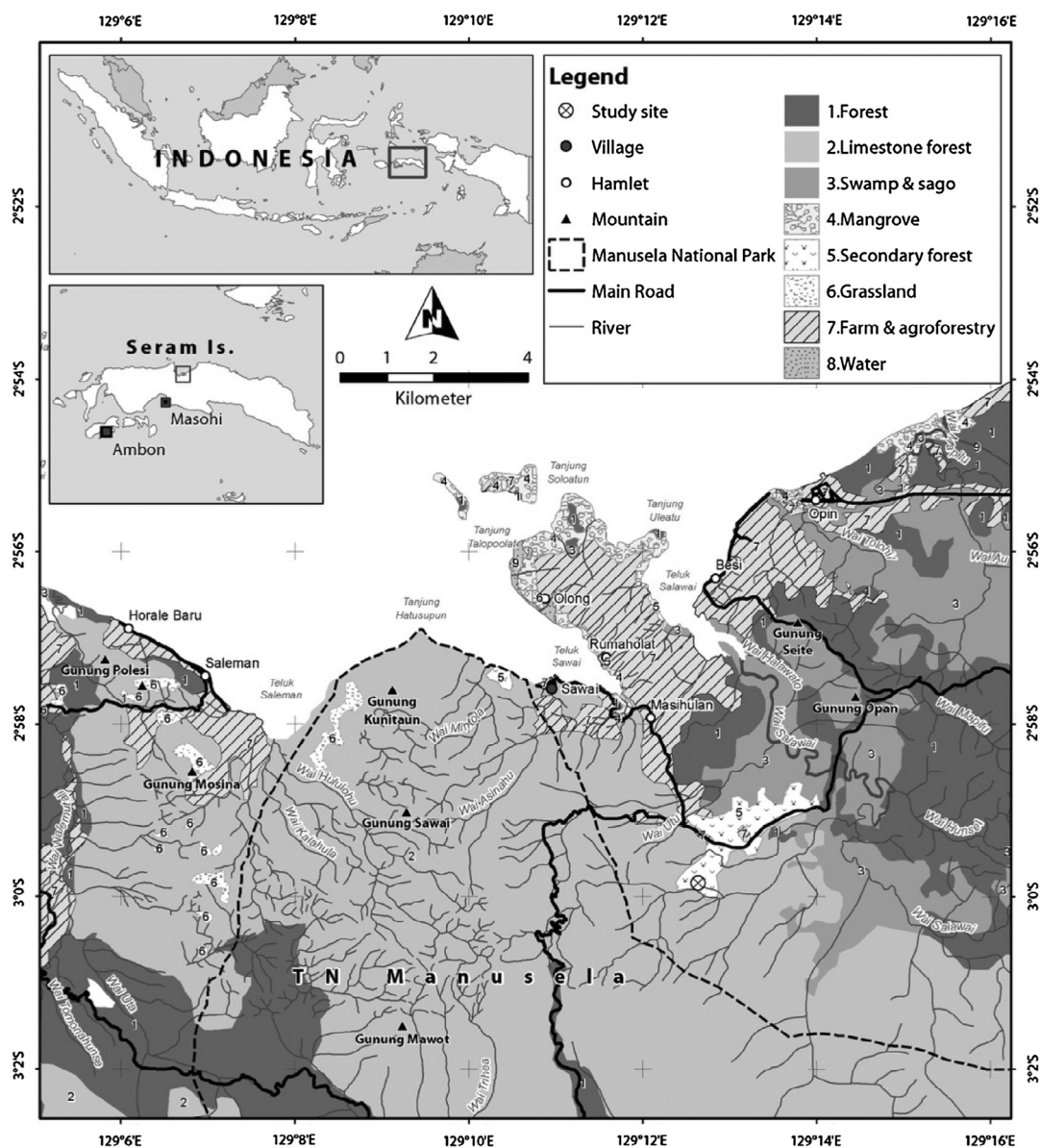


Fig. 1. Location of the forest plot (S 02° 59' 51.03"; E 129° 12' 43.51") near the village Masihulan, Central Seram, the Moluccas, Indonesia. Primary forests on non-limestone soils have been included in the category "Forest", primary forests on limestone in the category "Limestone forest" and secondary forests on limestone and non-limestone soils in the category "Secondary forest".

Total fresh weight of each compartment was weighed in the field using a hanging scale. The compartments of trees ≥ 10 cm dbh were measured for each tree separately, while for trees < 10 cm dbh, lianas, epiphytes, mosses and herbs, compartments or plants were combined and weighted per subplot. A subsample from each compartment (or the whole sample if the sample was not too big) was weighed fresh and further dried in a field oven [see Stas (2014) for more details about the subsamples]. Once constant weight was reached, oven-dry weight was measured to determine the dry/fresh weight ratio. Total fresh weights were then converted into total dry weights using the dry/fresh weight ratio of each compartment.

Following methodological recommendations from Overman et al. (1994), Henry et al. (2010) and Picard et al. (2012), the dry weight of stems ≥ 10 cm dbh and large branches was estimated as follow: diameters were measured every meter to derive the volume as a conical frustum of each 1-m length log section. To obtain oven dry weights, wood volumes were multiplied by the wood density

of the species (i.e. the oven dry mass per unit of fresh volume), derived from the DRYAD Global Wood Density (GWD) database (Chave et al., 2009; Zanne et al., 2009). Further details about the wood density values used in this study are provided in Section 2.3.1. For odd-shaped stems and large buttresses, for which it was difficult to calculate volumes accurately, fresh weights were measured in the field and wood samples were oven-dried to determine dry/fresh weight ratios in order to calculate dry weights. Finally, the above-ground dry weight of each tree ≥ 10 cm dbh was obtained by summing the dry mass of the leaves, twigs, branches and stem.

As one of the four destructively harvested subplots contained significantly more trees < 10 cm dbh, dominated by the secondary species *Lunasia amara* (Rutaceae), the harvested subplots were classified as "dense vegetation < 10 cm dbh" ($n = 1$) and "less dense vegetation < 10 cm dbh" ($n = 3$). Almost half of the subplots within the 1-ha plot contained "dense vegetation < 10 cm dbh" ($n = 44$), while the others contained "less dense vegetation < 10 cm dbh" ($n = 56$).

2.3. Data analysis

2.3.1. Wood density

Wood density data from the GWD database were used to calculate the dry weight of big stems and large branches after destructive sampling and as parameters in the allometric models. For species occurring in the database (61% of the species in the 1-ha plot), we assigned the average wood density value for tropical Southeast Asia or, when the value for this region was not available, we took the mean value from the other regions where the species occurs. Following usual methods (Baker et al., 2004; Chave et al., 2006; Slik, 2006), we estimated wood densities of species not present in the GWD database by averaging, in subsequent order, the wood densities of all species across the world within the same genus (33% of the species) or family (4% of the species). For families not present in the GWD database (2% of the species), the mean wood density for tropical Southeast Asia was taken (0.574 g cm⁻³; Chave et al., 2009).

2.3.2. Development of site-specific allometric models and model comparison

We developed four mixed-species equations for our site. Models 1 and 2 were selected from Chave et al. (2005) and Models 3 and 4 from Chave et al. (2014), based on their mathematical simplicity and low number of parameters to avoid overfitting. These models are of the following form:

$$AGB = \exp(a + b \ln(dbh) + c \ln(H) + d \ln(\rho)) + \varepsilon \quad (M.1)$$

$$AGB = \exp(a + b \ln(dbh) + \ln(\rho)) + \varepsilon \quad (M.2)$$

$$AGB = \exp(a + b \ln(dbh^2 * H * \rho)) + \varepsilon \quad (M.3)$$

$$AGB = \exp(a + bE + c \ln(\rho) + d \ln(dbh) + e \ln(dbh)^2) + \varepsilon \quad (M.4)$$

where AGB is the aboveground biomass (in kg); *dbh* the diameter at breast height (in cm); *H* the total tree height (in m); ρ the wood density (in g cm⁻³); *a*, *b*, *c*, *d* and *e* the model parameters; *E* a bioclimatic stress variable, which compiles information on temperature variability, precipitation variability and drought intensity; and ε the model residual error approximated with a normal distribution $N(0, \sigma^2)$. Intercepts (*a*) account for the back-transformation correction from $\ln(AGB)$ to AGB values, by applying the correction factor (CF) (Baskerville, 1972). These equations were used to estimate individual tree biomass.

We assessed which of these equations (Models 1–4) best fit our dataset of harvested trees, using the models' residual standard error (RSE), adjusted R², significance value (*p*) and bias (error). The bias measures the deviation between predicted (modelled) and measured (weighed) AGB of the felled trees, expressed as a percentage of measured AGB. All analyses were conducted using the R environment (R Core Team, 2015).

2.3.3. Plot-level AGB estimation

After model selection, the best local model was used to estimate the biomass of all trees ≥ 10 cm dbh in the 1-ha plot. Oven-dried mass of trees <10 cm dbh in the destructively harvested subplots were averaged by class ("dense vegetation <10 cm dbh" and "less dense vegetation <10 cm dbh") and calculated for the 1-ha plot by using the frequency of occurrence of these classes within the plot. Biomass values of lianas, epiphytes, mosses and herbs were averaged among the four subplots and expressed on 1-ha basis. Plot-level total AGB (Mg ha⁻¹) was calculated by adding dry weights of trees ≥ 10 cm dbh, trees <10 cm dbh, lianas and the non-woody vegetation.

2.3.4. Test and compare the performance of allometric models

The performance of our best local model was tested and compared with existing local ones (Ketterings et al., 2001; Kenzo et al., 2009) and with the most recent pantropical model (Chave et al., 2014) at (i) tree-level, using the models' bias (systematic error, as defined above) and the coefficient of variation in AGB [CV; total error, including random error, see Chave et al. (2014)] on felled trees and (ii) at plot-level, by calculating AGB of all trees ≥ 10 cm dbh in the 1-ha forest plot and the bias in estimated AGB compared to our best local model. As the trees felled for this study were included in the pantropical model (Chave et al., 2014), we used a modified equation in which all harvested trees from the global database were included, except those from our study site. Site information and regression equations of the local and pantropical models are shown in Table 1.

3. Results

3.1. Development and selection of local allometric models

All allometric models fitted the data well, with slight overestimates of the actual AGB value in Models 1, 3 and 4 and slight underestimates in Model 2 (Table 2). Model 1 had the lowest RSE value, highest adjusted R², a highly significant regression

(*p*-value) and the smallest error between predicted and measured AGB value, indicating the best biomass prediction. Therefore, Model 1, based on dbh, height and wood density, was used in the analyses hereafter to calculate the AGB for trees ≥ 10 cm dbh in our forest plot.

3.2. Estimation of plot-level AGB

Trees ≥ 10 cm dbh (*n* = 537) formed the main carbon pool, with 80% (141 Mg ha⁻¹) of total AGB in the plot (177 Mg ha⁻¹). Another 19% (33 Mg ha⁻¹) was allocated in trees <10 cm dbh, 1% (2 Mg ha⁻¹) in lianas, and a negligible fraction (0.6 Mg ha⁻¹) in epiphytes, mosses and herbs.

Table 1
Existing local and pantropical allometric models. The regression equations give the aboveground biomass (AGB) in kg; diameter at breast height (dbh) in cm; height (H) in m; wood density (ρ) in g cm⁻³. In the formula of Ketterings et al. (2001), we evaluated the relationship between height and diameter at our site to determine the last parameter (2.442).

Site	Forest type	Regression	Reference
Sarawak, Malaysia	Logged-over forests	$AGB = 0.1525 * dbh^{2.34}$	Kenzo et al. (2009) (1)
Sarawak, Malaysia	Logged-over forests	$AGB = 0.1083 * (dbh^2 * h)^{0.80}$	Kenzo et al. (2009) (2)
Sumatra, Indonesia	Mixed secondary forests	$AGB = 0.11 * \rho * dbh^{2.442}$	Ketterings et al. (2001)
Pantropical	Old-growth and secondary forests	$AGB = \exp(-2.699 + 0.976 * \ln[\rho * dbh^2 * h])$	Modified Chave et al. (2014)

Table 2

The four local allometric models constructed for our site and parameters for the model comparison. The aboveground biomass (AGB; kg) can be predicted by diameter at breast height (dbh; cm), height (H; m) and wood density (ρ ; g cm⁻³, expressed in oven dry mass per fresh volume).

Model	RSE	Adj. R ²	p	Bias (%)
M.1: $AGB = \exp(-1.927 + 1.837 * \ln(dbh) + 0.905 * \ln(H) + 1.164 * \ln(\rho))$	0.148	0.961	<10 ⁻⁴	0.1
M.2: $AGB = \exp(-0.245 + 2.082 * \ln(dbh) + \ln(\rho))$	0.201	0.924	<10 ⁻⁴	-1.2
M.3: $AGB = \exp(-1.982 + 0.901 * \ln(dbh^2 * H * \rho))$	0.162	0.952	<10 ⁻⁴	0.6
M.4: $AGB = \exp(0.940 + 1.140 * \ln(\rho) + 1.281 * \ln(dbh) + 0.144 * \ln(dbh)^2)$	0.206	0.923	<10 ⁻⁴	0.2

Table 3

Parameters to assess the performance of our locally developed model and existing allometric models for the 25 harvested trees at our site (tree-level), and the estimated AGB of trees ≥ 10 cm dbh and the bias with our best local model in the 1-ha plot (plot-level).

Model	Tree-level		Plot-level	
	Bias (%)	CV (%)	AGB (Mg ha ⁻¹)	Bias (%)
Local model	0.1	15.5	141	0.0
Kenzo et al. (2009) (1)	-7.3	59.3	108	-23.4
Kenzo et al. (2009) (2)	-38.8	59.2	71	-49.6
Ketterings et al. (2001)	-57.1	75.8	59	-58.2
Modified Chave et al. (2014)	-7.7	17.7	131	-7.1

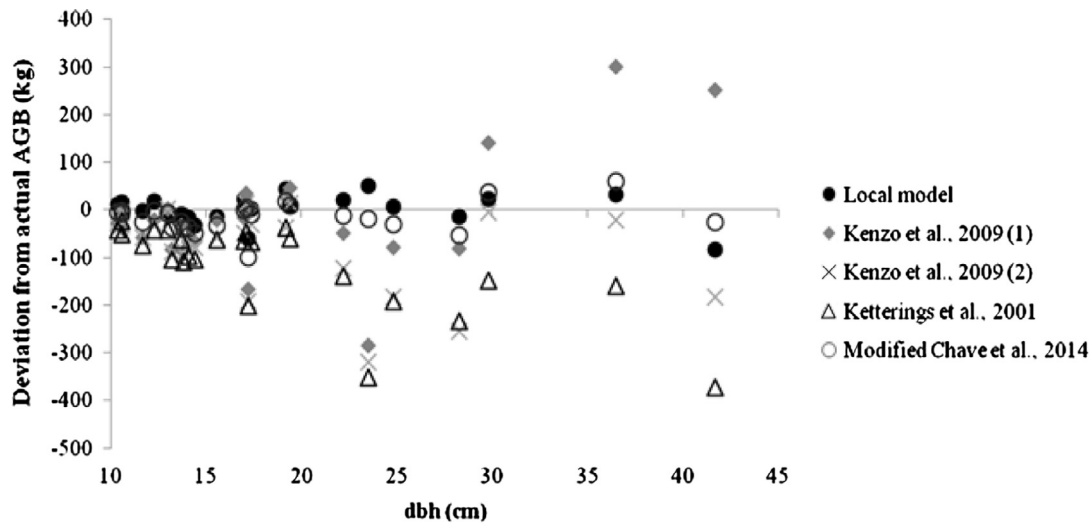


Fig. 2. Deviation from actual AGB for individual trees when using the various allometric models. The horizontal zero-line corresponds with the weighed AGB for each individual tree. A positive deviation from this line indicates an overestimation in AGB by the allometric model, while a negative value indicates an underestimation.

3.3. Performance of existing allometric models at our site

Summed AGB of the 25 harvested trees was equal to 5069 kg. Our best local model (Model 1) estimated tree biomass most accurately (bias = 0.1%, CV = 15.5%), followed by the modified pantropical model (bias = -7.7%, CV = 17.7%), indicated by low bias and CV values (Table 3). Along the whole diameter range, our local model and the pantropical model estimated the AGB of individual trees accurately (Fig. 2). Existing local models had a much lower performance in estimating biomass values of the harvested trees, indicated by high bias and CV values and large deviations from weighed AGB values for individual trees. When applying Kenzo et al. (2009:1), the bias was relatively low, while the CV was high. This is because for small trees (i.e. small dbh), Kenzo et al. (2009:1)'s model underestimated actual AGB values, while for large trees, AGB was overestimated, resulting in a high CV, in spite of a relatively low overall bias.

At plot-level, all existing models underestimated the AGB of trees ≥ 10 cm dbh, compared to the estimate with our local model.

The AGB estimate with the pantropical model was most similar to the estimate with our local model (Table 3).

4. Discussion

4.1. Requirements of local allometric equations

Here, we tested the performance of several allometric equations for the estimation of tree-level aboveground biomass. The best model included dbh, height and wood density, which are well-known to vary greatly among trees and spatial scales (Chave et al., 2005; Feldpausch et al., 2011). Accounting for these three variables captures most of the variability in AGB. For this reason, pantropical models including height were shown to better estimate tree AGB in both primary and logged-over forests in East Kalimantan, Indonesia, compared to simpler models based on dbh only (Rutishauser et al., 2013). Most studies carried out in Indonesia developed allometric models based on dbh only (Anitha et al.,

2015) and inclusion of tree height measurements in future REDD+ projects should be promoted.

While more efforts should be focused on better understanding the forest ecology in remote and isolated areas of Indonesia, such as our study site, our results confirm the wide range of application of pantropical models for various forest types and regions, including secondary limestone forests.

4.2. Performance of local versus pantropical models

Our local model and the most recent pantropical model provided good AGB estimates at our site, while the AGB values with existing local models showed significant deviations from the actual plot-level AGB. A vast literature has addressed the causes underpinning differences in biomass allometric model estimates. It has been previously shown that most of the variation across existing models is due to too small sample sizes of destructively harvested trees rather than to intrinsic differences in the physiognomy of vegetation types (Chave et al., 2014; Paul et al., 2016). Most harvested trees used to develop the modified pantropical model of Chave et al. (2014) come from undisturbed forests (94%) and probably none are on limestone substrate. Our study thus provides solid evidence of the robustness and wide range of applicability of this pantropical model.

At global scale, Chave et al. (2014) tested whether models developed locally predicted biomass better than their pantropical model, and found no major bias. In comparison with local models, AGB prediction errors (CV) at tree-level were only slightly higher in the pantropical model, while the spread of systematic error (bias) across sites was more than three times higher, which is corroborated by our results.

4.3. Importance of accounting for small trees in tropical forests

Our study revealed that as much as 19% of total AGB was allocated in small trees in a secondary forest, i.e. all stems <10 cm dbh. The contribution of small trees to total AGB is generally small in primary forests; for instance, Laumonier (1997) and Nascimento and Laurance (2002) found that around 5–6% of total AGB was allocated in trees <10 cm dbh. For this reason, stems <10 cm dbh are general disregarded from most long-term forest plot networks. A notable exception is the Center for Tropical Forest Science plot network (<http://www.forestgeo.si.edu/>) in which all stems ≥ 1 cm dbh have been mapped and repeatedly measured. From this network, the contribution of stems <10 cm dbh to aboveground carbon stocks ranged from 2 to 4% in mature tropical forests and raised up to 10% in some disturbed forests (Chave et al., 2008). Disturbances, either natural or human-induced, generate canopy openings that create favourable conditions for seedling establishment and growth (Brokaw, 1985). Over time, competition for light and nutrients will lead to thinning of suppressed saplings and results in an absolute increase in basal area and biomass stocks per unit area (Coomes et al., 2003; Farrior et al., 2016). In natural forest stands, the relative contribution of small stems to aboveground biomass stocks likely depends on type, frequency and intensity of the disturbance (Lin et al., 2015). For instance, for secondary forest successions, Lugo (1992) found that the AGB of woody understorey plants (dbh <4 cm) was 30% of total AGB in an old field succession and 17% in a young secondary forest, both in Puerto Rico. Lawrence (2005) showed that on average 24% of the AGB >5 cm dbh was allocated in stems 5–10 cm dbh in secondary forests 9–12 years after shifting cultivation in West-Kalimantan, Indonesia. Similar

contributions of small stems were found in plantations, where the relative contribution of stems 2.5–10 cm dbh was on average 15% of the AGB at stands <20 years old (Preece et al., 2012). While trees <10 cm dbh can store a large fraction of total AGB in secondary and disturbed forests, it is not yet common practise to sample small stems in biomass inventories (e.g. see the recent study of Pfeifer et al., 2016). Apart from their contribution to carbon stocks, small trees may also significantly contribute to tree diversity (Memiaghe et al., 2016) and shape forest structure of forests facing seasonal droughts (Uriarte et al., 2016).

5. Conclusions

While better carbon stock assessments and validation of generic models are needed for eastern regions of Indonesia such as the Moluccas, Sulawesi and Western New Guinea, our study provides a first evidence of the wide applicability of generic models, notably in secondary forests growing on limestone substrate. Locally developed models often perform well on the sites for which they are developed, but they remain site- and forest-type specific, potentially with important bias when applied elsewhere. To avoid time-consuming development of site-specific allometric models in future REDD+ projects or National Reference Emissions Levels, we recommend instead using generic models. Further, our results confirm the importance of accounting for biomass in trees <10 cm dbh in secondary forests, in order to reduce uncertainty in forest carbon accounting.

6. Author contributions

Y.L. proposed this specific study as part of the CoLUPSIA project; S.M.S, Y.L. and N.P.R.A. conceived and designed the research; S.M.S collected the data; S.M.S, E.R. and J.C. analyzed the data; S.M.S., Y.L. and E.R. wrote the manuscript, with contributions from the other authors.

7. Conflict of interests

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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Appendix A

Detailed information of the 25 trees ≥ 10 cm dbh that were harvested during the destructive sampling in 0.04 ha secondary forest. Tree height was measured with a measuring tape after felling, dbh = diameter at breast height; H = height; ρ = wood density, expressed in oven dry weight per fresh volume, taken from the GWD database (Chave et al., 2009; Zanne et al., 2009); DW = biomass, expressed in oven dry weight.

Species	Family	Local name	dbh (cm)	H (m)	ρ (g cm ⁻³)	DW stem (kg)	DW branches (kg)	DW twigs (kg)	DW leaves (kg)	Total DW (kg)
<i>Decaspermum bracteatum</i>	Myrtaceae	Kayu merah daun halus	10.4	13.3	0.722	38.1	22.4	1.1	3.4	65.0
<i>Decaspermum bracteatum</i>	Myrtaceae	Kayu merah daun halus	10.6	15.9	0.722	64.1	8.0	1.2	3.1	76.4
<i>Aglaia sapindina</i>	Meliaceae	Wapane	10.6	11.1	0.420	21.1	12.4	1.1	2.7	37.3
<i>Decaspermum bracteatum</i>	Myrtaceae	Kayu merah daun halus	11.7	14.6	0.722	77.8	23.7	1.3	3.6	106.4
<i>Gonocaryum litorale</i>	Cardiopteridaceae	Kopi hutan	12.3	13.2	0.662	53.6	14.2	1.5	6.8	76.1
<i>Elaeocarpus serratus</i>	Elaeocarpaceae	Mataharihale	13.0	16.8	0.327	49.6	6.2	1.0	3.1	60.0
<i>Decaspermum bracteatum</i>	Myrtaceae	Kayu merah daun halus	13.2	15.6	0.722	68.4	73.2	2.2	4.3	148.2
<i>Hancea penangensis</i>	Euphorbiaceae	Wasu wate	13.7	12.3	0.590	57.8	34.7	4.4	5.2	102.1
<i>Decaspermum bracteatum</i>	Myrtaceae	Kayu merah daun halus	13.8	15.4	0.722	108.1	41.5	2.2	6.1	157.9
<i>Casearia glabra</i>	Salicaceae	-	14.1	15.0	0.627	68.4	62.9	3.1	7.9	142.3
<i>Glochidion zeylanicum</i>	Phyllanthaceae	Tombe tombe hutan	14.4	14.8	0.550	78.5	53.7	6.5	5.9	144.5
<i>Hancea penangensis</i>	Euphorbiaceae	Wasu wate	15.6	10.3	0.590	78.9	32.7	1.7	1.8	115.1
<i>Hancea penangensis</i>	Euphorbiaceae	Wasu wate	17.0	13.8	0.590	70.6	52.0	4.1	4.5	131.2
<i>Meliosma pinnata</i>	Sabiaceae	Wasa heli	17.1	16.7	0.320	71.8	9.9	0.6	1.2	83.5
<i>Decaspermum bracteatum</i>	Myrtaceae	Kayu merah daun halus	17.2	15.7	0.722	178.5	94.6	3.0	8.3	284.4
<i>Melanolepis multiglandulosa</i>	Euphorbiaceae	Kapor	17.4	14.5	0.442	99.5	17.5	0.5	0.8	118.3
<i>Hancea penangensis</i>	Euphorbiaceae	Wasu wate	19.2	12.0	0.590	104.9	17.0	1.9	2.2	126.0
<i>Meliosma pinnata</i>	Sabiaceae	Wasa heli	19.4	17.6	0.320	94.6	12.8	0.6	2.3	110.4
<i>Hancea penangensis</i>	Euphorbiaceae	Wasu wate	22.2	15.8	0.590	164.4	85.9	5.4	8.1	263.8
<i>Homalium foetidum</i>	Salicaceae	Samar	23.5	23.6	0.730	378.1	136.5	4.2	11.8	530.6
<i>Hancea penangensis</i>	Euphorbiaceae	Wasu wate	24.8	16.6	0.590	242.4	95.5	8.0	12.2	358.1
<i>Hancea penangensis</i>	Euphorbiaceae	Wasu wate	28.3	15.9	0.590	295.3	139.4	11.3	15.7	461.8
<i>Meliosma pinnata</i>	Sabiaceae	Wasa heli	29.8	21.1	0.320	254.9	30.1	0.9	3.2	289.1
<i>Meliosma pinnata</i>	Sabiaceae	Wasa heli	36.5	19.5	0.320	270.0	112.6	1.5	5.6	389.7
<i>Meliosma pinnata</i>	Sabiaceae	Wasa heli	41.7	22.3	0.320	443.9	217.4	5.1	24.9	691.3

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