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ORIGINAL ARTICLE

# Allometric equations considering the influence of hollow trees: A case study for tropical peat swamp forest in Sarawak

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**ABSTRACT** Biomass estimations in tropical peat swamp forests are quite complex when hollow trees are frequently found due to the unavailability of data on hollow size and the limited data on accurate measures of biomass. Destructive samplings were done for both above- (AGB) and belowground biomass (BGB) and hollow sizes of remained trees at a logged-over peat swamp forest in Sarawak, Malaysia. Subsequently, allometric equations taking hollows into account for both the above- and belowground biomass of tropical peat swamp forests were also being developed. It was observed that these were hollows in *Shorea albida* and *Combretocarpus rotundatus* trees with diameters at breast height (DBH) exceeding 40 cm; *S. albida* is a dominant or co-dominant species, and *C. rotundatus* grows in peat swamp forests throughout Sarawak. The hollow volumes ranged from 0.23 to 1.08 $m^3$, and occupied 42.3% of stem volume on average. The larger biomass produced by previous allometric models were partially due to the presence of hollows. Thus, new models for estimating both AGB and BGB were developed that included one (only DBH), two (DBH and height [H] or wood density [WD]), or three (DBH, H, and WD) predictor variables, and $[\ln(\mathrm{DBH})]^2$ was added as predictor variable indicating the biomass loss by cavity formation. AGB model with three predictor variables and BGB model with one predictor variable performed the best where; they had the highest adjusted coefficients of determination and lowest Furnival index and Akaike information criterion (AIC).

**Key words:** cavity biomass loss, aboveground biomass, belowground biomass, Malaysia, REDD+

## INTRODUCTION

Tropical peat swamp forests are now being developed for agricultural development for both economic and social needs. The anthropogenic effects on these forests are of concern because of its endemic flora and fauna (Phillips 1998, Verhoeven & Setter 2010, Jason 2011). Accurate estimation of forest carbon stock is required to assess these impacts. Attempts have been made to quantify the effects of agricultural conversion on peat swamp forests by using extrapolations from other forest types (Fargione et al. 2008). However, allometric equations that are specific to peat swamp forests are required for accurate biomass estimation to conduct new initiatives, for example the program for REDD+, reducing emissions from deforestation and forest degradation and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries (https://unfccc.int/methods/redd/methodological_guidance/items/4123.php).

*Shorea albida* is dominant or co-dominant in the peat swamp forests of Sarawak and Brunei (Anderson 1961, Whitmore 1975). Most large *S. albida* specimens have hollows in their stems (Anderson. 1972) that contain no biomass. Biomass is overestimated when the hollows are not taken into account, but this topic has not been examined to date in *S. albida* or other species. Several sets of allometric equations have been developed to estimate above- (AGB) and belowground (BGB) biomass in tropical rain forests (*e.g.* AGB: Yamakura et al. 1986, Basuki et al. 2009; BGB: Niiyama et al. 2010). Allometric relations in peat swamp forest trees have rarely been studied (Nishimura & Suzuki 2001 [seedlings up to 98 cm tall], Suwarna et al. 2012). In these previous studies, hollow trees have not been considered in model development. If hollow trees are relatively common in peat swamp forests, they should be included in biomass assessments.

In Sarawak, the structure of forest vegetation shifts from the edge to the center of each peat swamp basin. Anderson (1961) divided this sequence of structure into six forest types (a form of phasic community), which are quite well defined in terms of structure, physiognomy, and species composition. The three main forest types having many large trees than other forest types: "mixed peat swamp forest", "Alan Batu forest", and "Alan Bunga forest" referred to hereafter as PC (phasic community) 1, PC2, and PC3, respectively. We focused on these forest vegetation types.

The objectives of this study were: to assess the appropriateness of applicating allometric models developed for tropical rainforests and tropical peat swamp forest to the peat swamp forest in Sarawak, by comparing them with our empirical biomass database obtained by destructive sampling; to quantify the effects of hollows on tree biomass; and to develop new AGB and BGB allometric equations for peat swamp forests.

## MATERIALS AND METHODS

### Study site

Our study was performed in a logged-over peat swamp forest located in an oil palm concession area in Betong division, Sarawak (01°24.218'N, 111°18.411'E), which is adjacent to Maludam National Park. This area has a humid tropical climate. Annual precipitation was 2325 mm and temperature ranged from 27 to 32℃ in 2002 at Beladin, Maludam National Park (Melling and Hatano 2004). The peat swamp basin is low-lying and generally like an inverted saucer with the highest surface topography *i.e.* the peat dome of not more than 12 m above msl (Melling and Hatano 2004). PC1 has the most decomposed and least woody peat. PC2 and PC3 are more woody peat (Melling et al. 2007). The mean bulk density of peat was about 0.1 g $cm^{-3}$, soil pH ($H_2O$) was 3.7 at a depth of 0−25 cm and 3.6 at a depth of 25−50 cm, and the average pH of the peat water was 4.39 (Melling and Hatano 2004).

Anderson (1961) described the forest types as follows. PC1 appears at the margins of the swamp and covers large areas of relatively undeveloped coastal wetland. The forest crown is not uniform with the tallest layer reaches a height of 40−45 m, and all layers are exceptionally well developed. The principal dominants are *Gonystylus bancanus*, *Dactylocladus stenostachys*, *Shorea platycarpa*, *Shorea scabrida*, and *Shorea uliginosa*. PC2 is transitional between PC1 and PC3. The crown of PC2 is not uniform and is dominated by very large *S. albida* trees. The species compositions of the middle and lower stories are closely similar to those of PC1; the physiognomies are also similar. PC3 covers extensive areas of the second and fourth divisions of Sarawak and the Badas area of Brunei. The upper story is a pure, even canopy of *S. albida* 50−60 m high. The oil palm concession areas have been selectively logged.

*Shorea albida* trees have been classified by wood density (WD). Trees with high WD are referred to as "Alan Batu" and those with low WD are called "Alan Bunga." Here, we refer to these two types of trees as *S. albida* (Batu) and *S. albida* (Bunga), respectively. In general, *S.albida* used as timber is *S.albida* (Bunga) (Tropical Agriculture Research Center 1977).

### Destructive sampling

Destructive samplings were performed in December 2009, March and August 2010, March 2011, February 2012, and August 2013. In total, 44 trees were sampled from 14 dominant species in the peat swamp forest (specimens were taken from PC1, PC2, and PC3) (Tables 1 and 2). Diameter at breast height (DBH) was measured before destructive sampling. Tree height (H) was measured after sample trees had been felled. AGB is defined as the biomass measured in plant parts above the ground, while BGB was measured for parts below the ground regardless of the presence of buttress roots.

### Biomass measurement

Sample trees were felled and aboveground parts were separated into stems, branches, and leaves. For the quantification of the stem volume by the Smalian method, the stems of sample trees were sawed into logs of 0.5 or 1.0 m long. Biomass loss to sawdust was ignored. All log diameters were measured with a measuring tape, and fresh weights were determined. Where possible, all branches and leaves were weighed. For very large canopies, measurements were made on one half or one quarter of the branches and leaves and extrapolated to the whole canopy. Belowground parts (stumps and roots) were manually excavated in a procedure that included most coarse roots (>2 mm). A mechanical excavator was used in some cases; belowground parts of the target trees were separated from the excavated roots and peat manually. To examine BGB sampling loss during the excavation, two trees with middle DBH class were selected from sampling trees (DBH 25.7 cm and 43.8 cm). All of the belowground parts of the target trees were carefully collected from a part of the excavated peats by manually. Dry weight of these belowground parts were determined after oven-drying, and extrapolated to the whole excavated peats. To standardize these two trees and other sampling trees consistency in our

Table 1. Destructive sampling data.

| Species | DBH (cm) | H (m) | Biomass: Stem + Branch (kg) | Biomass: Leaf (kg) | Biomass: Belowground organs (kg) | Wood density ($Mg\,m^{-3}$) | Forest type | |
|---|---|---|---|---|---|---|---|---|
| *Baccaurea lanceolata* | 5.2 | 7.1 | 6.4 | 0.7 | 1.4 | 0.579 | PC1 | 3) |
| *Blumeodendron tokbrai* | 18.0 | 20.9 | 189.2 | 17.3 | – | 0.519 | PC2 | 3) |
| *Combretocarpus rotundatus* | 45.0 | 27.7 | – | 53.7 | 313.4 | 0.553 | PC2 | 3) |
| *Combretocarpus rotundatus* | 6.8 | 11.7 | 17.0 | 1.7 | 1.4 | 0.553 | PC1 | 3) |
| *Combretocarpus rotundatus* | 43.8 | 26.6 | 1125.2 | 29.5 | 884.2 | 0.553 | PC1 | 1), 3) |
| *Copaifera palustris* | 12.5 | 14.5 | 76.3 | 9.5 | – | 0.504 | PC2 | 2) |
| *Copaifera palustris* | 13.0 | 17.8 | 69.7 | 5.1 | – | 0.504 | PC1 | 2) |
| *Diospryos pseudomalbarica* | 25.7 | 23.2 | 399.4 | 8.7 | 206.9 | 0.687 | PC1 | 1), 2) |
| *Elaeocarpus marginatus* | 6.5 | 12.8 | 14.9 | 1.5 | 2.8 | 0.423 | PC1 | 2) |
| *Eugenia leucoxylon* | 19.9 | 16.7 | 203.6 | 21.6 | 31.4 | 0.585 | PC2 | 2) |
| *Eugenia leucoxylon* | 24.2 | 19.9 | 378.4 | 28.8 | – | 0.585 | PC2 | 2) |
| *Eugenia leucoxylon* | 5.5 | 8.2 | 10.1 | 3.7 | 1.5 | 0.585 | PC2 | 2) |
| *Garcinia apetala* | 15.0 | 17.1 | 142.4 | 35.9 | 13.0 | 0.640 | PC2 | 2) |
| *Gonystylus bancanus* | 9.4 | 13.8 | 37.3 | 4.2 | 3.0 | 0.477 | PC2 | 2) |
| *Gonystylus bancanus* | 7.6 | 12.7 | 18.0 | 2.7 | 4.6 | 0.477 | PC2 | 2) |
| *Gonystylus bancanus* | 14.5 | 18.0 | 128.6 | 7.3 | – | 0.477 | PC2 | 2) |
| *Gonystylus bancanus* | 14.3 | 14.2 | 113.7 | 2.3 | 31.7 | 0.477 | PC2 | 2) |
| *Gonystylus bancanus* | 9.6 | 12.6 | 34.5 | 3.1 | – | 0.477 | PC1 | 2) |
| *Gonystylus forbesii* | 7.4 | 11.6 | 18.9 | 2.2 | – | 0.477 | PC2 | 2) |
| *Litsea gracilipes* | 9.0 | 9.1 | 15.0 | 2.5 | 2.0 | 0.477 | PC1 | 2) |
| *Palaquium ridleyi* | 32.2 | 30.2 | 1034.7 | 34.6 | 117.7 | 0.484 | PC2 | 2) |
| *Shorea albida* (*Alan Batu*) | 110.8 | 49.4 | – | 210.8 | 1343.4 | 0.619 | PC2 | 2) |
| *Shorea albida* (*Alan Batu*) | 12.9 | 17.1 | 38.3 | 5.0 | 13.3 | 0.619 | PC2 | 2) |
| *Shorea albida* (*Alan Batu*) | 18.0 | 17.7 | 112.0 | 4.4 | 25.2 | 0.619 | PC2 | 2) |
| *Shorea albida* (*Alan Batu*) | 24.5 | 21.2 | 288.0 | 24.1 | 70.9 | 0.619 | PC2 | 2) |
| *Shorea albida* (*Alan Batu*) | 97.0 | 36.2 | 4121.5 | 26.5 | – | 0.619 | PC1 | 2) |
| *Shorea albida* (*Alan Bunga*) | 9.5 | 13.5 | 16.9 | 3.5 | 4.8 | 0.443 | PC2 | 2) |
| *Shorea albida* (*Alan Bunga*) | 60.0 | 34.4 | – | 43.2 | – | 0.443 | PC2 | 2) |
| *Shorea albida* (*Alan Bunga*) | 15.3 | 16.4 | 70.5 | 14.1 | – | 0.443 | PC1 | 2) |
| *Shorea albida* (*Alan Bunga*) | 17.0 | 17.2 | 87.9 | 15.3 | – | 0.443 | PC3 | 2) |
| *Shorea albida* (*Alan Bunga*) | 6.7 | 13.5 | 10.6 | 0.9 | 1.4 | 0.443 | PC3 | 2) |
| *Shorea albida* (*Alan Bunga*) | 8.0 | 15.6 | 16.4 | 1.4 | 4.5 | 0.443 | PC3 | 2) |
| *Shorea albida* (*Alan Bunga*) | 5.7 | 9.8 | 6.8 | 1.4 | 1.0 | 0.443 | PC3 | 2) |
| *Shorea albida* (*Alan Bunga*) | 9.1 | 16.1 | 22.6 | 2.4 | 4.8 | 0.443 | PC3 | 2) |
| *Xylopia fusca* | 7.5 | 10.3 | 11.3 | 2.1 | 1.9 | 0.473 | PC2 | 3) |
| *Xylopia fusca* | 6.3 | 7.7 | 8.5 | 1.1 | 1.9 | 0.473 | PC1 | 3) |
| *Xylopia fusca* | 36.3 | 24.5 | 601.3 | 22.5 | – | 0.473 | PC1 | 3) |

DBH, stem diameter at breast height; H, tree height; –, not measured. Forest type, PC 1; mixed peat swamp forest, PC 2; Alan Batu forest, PC 3; Alan Bunga forest. 1) Excavator used to obtain belowground biomass, 2) WD based on data in Tropical Agriculture Research Center (1977), 3) WD based on data in PROSEA (1998).

analysis, BGB sampling losses were not considered in biomass comparisons and model development.

Subsamples were taken from each component to determine dry to fresh weight ratios. The subsamples of stem were cut into at least three discs (5–10 cm in thickness) taken from the top, middle, and lower portions of each trunk. Subsamples (1–2 kg $tree^{-1}$) of branches, leaves, and belowground parts were collected from each individual. The subsamples were transported to the laboratory and oven-dried at 75℃ for 72 h or more to constant weight.

During destructive sampling conducted in August 2013 (*i.e.*, destructive sampling combined with measurement of hollows; described in the next paragraph), woody debris in the cavities of hollow trees were found (Fig. 1a). The presence or absence of hollows was checked only during the sampling conducted in August 2013 and the fresh weight had excluded the weight of woody debris.

### Hollow and brittle heart size measurements

The presence or absence of hollows were checked prior to measurements of hollows and brittle hearts-like parts (hereafter as brittle hearts) during the destructive sampling conducted in August 2013 (Table 2). In this study, brittle heart was defined as a fuzzy end grain at cross section when a log was cut by chainsaw. The stem, hollow, and brittle heart diameters in the cross-sections of all logs were measured using a tape measure. The presence of brittle heart was visually determined. Fresh volumes for each of these parts from their lengths and diameters were calculated using the Smalian method. Neither the lengths nor the diameters of stump hollows were measured.

The WD was estimated using three discs from the top, middle, and lower portions of each individual stem. After oven-drying, the discs were exported to the Forestry and Forest Products Research Institute (FFPRI, Tsukuba, Ibaraki, Japan). Rectangular subsamples 3 cm in width

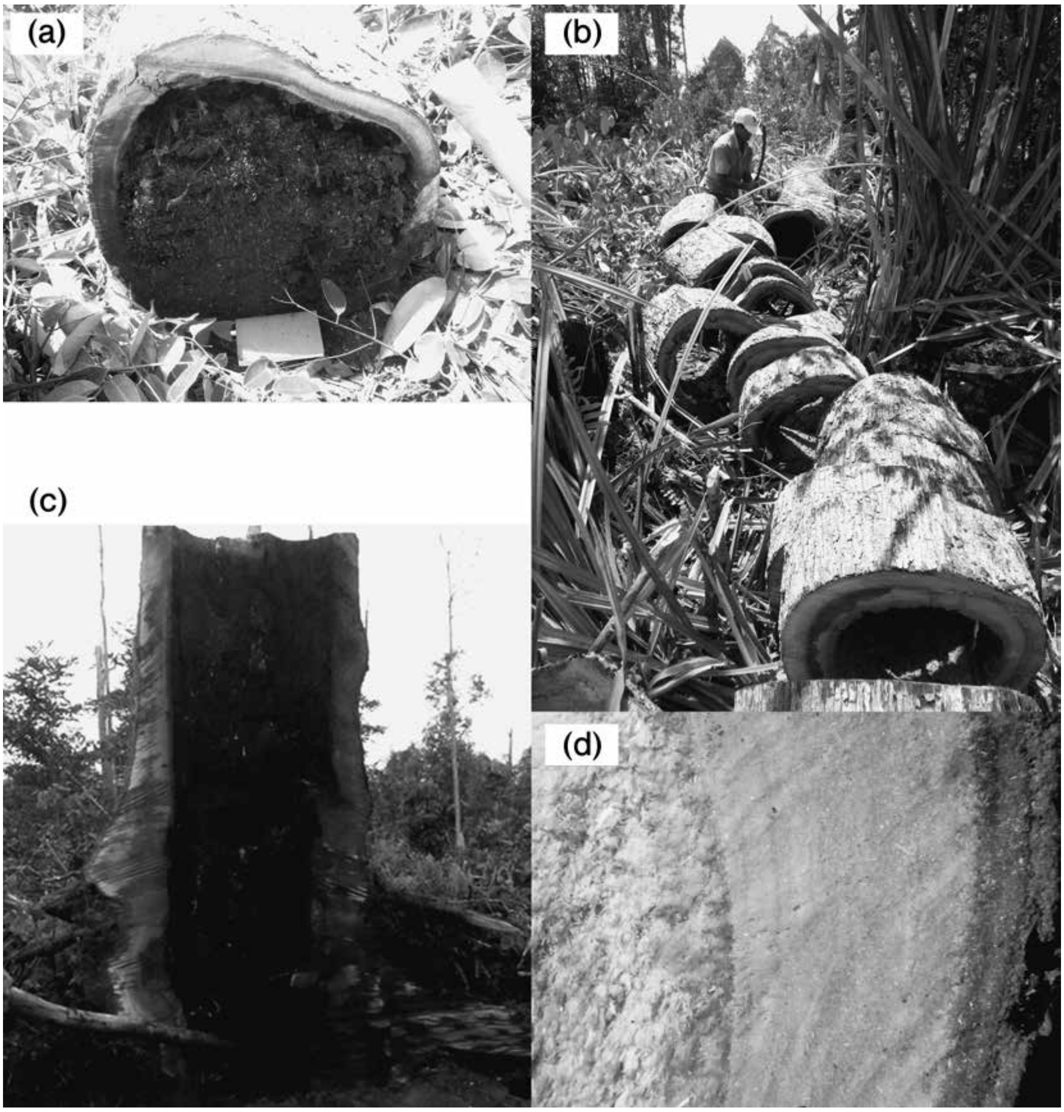


Fig. 1. Hollow stems and stumps. (a) Woody debris in a hollow *Shorea albida* [Alan Batu] tree with a diameter at breast height [DBH] of 62.9 cm, (b) Hollow cavity in the stem of a *Shorea albida* [Alan Batu] tree with a DBH of 70.2 cm, (c) Hollow cavity in the stump of a *Combretocarpus rotundatus* tree with a DBH of 40.7 cm, (d) Brittle heart in a *Shorea albida* [Alan Batu] tree with a DBH of 19.1 cm.

Table 2. Destructive sampling and hollow data in Alan Batu forest (PC2).

| Species | DBH (cm) | H (m) | Volume: Stem ($m^3$) | Volume: Hollow ($m^3$) | Volume: Brittle heart ($m^3$) | Biomass: Stem + Branch (kg) | Biomass: Leaf (kg) | Biomass: Belowground organs (kg) | |
|---|---|---|---|---|---|---|---|---|---|
| *Combretocarpus rotundatus* | 40.7 | 22.1 | 0.98 | 0.23 | – | 552.4 | 53.65 | 307.2 | 1) |
| *Litsea gracilipes* | 21.0 | 21.3 | 0.41 | – | – | 226.8 | 23.2 | 29.1 | |
| *Shorea albida* (*Alan Batu*) | 19.1 | 21.5 | 0.34 | – | 0.16 | 205.0 | 12.3 | 77.9 | |
| *Shorea albida* (*Alan Batu*) | 70.2 | 27.6 | 3.77 | 1.80 | – | 1802.4 | 205.3 | 567.3 | 1) |
| *Shorea albida* (*Alan Batu*) | 62.9 | 27.8 | 2.94 | 1.53 | – | 1177.9 | 109.43 | 558.6 | 1) |
| *Shorea albida* (*Alan Batu*) | 47.7 | 28.8 | 2.35 | 1.08 | – | 927.5 | 85.3 | 501.3 | 1) |
| *Shorea albida* (*Alan Bunga*) | 22.5 | 20.0 | 0.34 | – | 0.34 | 209.7 | 33.6 | 29.9 | |

DBH, stem diameter at breast height; H, tree height; –, not measured. 1) Excavator used to obtain belowground biomass.

without bark were extracted from each disc and cut into segments of (1) sapwood and heartwood and (2) brittle heart. Composition of each segment was visually confirmed. Fresh volume of each subsample was determined by the water immersion method (Method B) and the water replacement method (Method B2) following the American Society for Testing and Materials D2395-07a (ASTM International 2007). Subsamples were subsequently oven-dried at 70℃ to constant weight using an electronic balance. WD was then calculated as dry weight divided by saturated volume.

## Development of allometric equations

The allometric model for AGB and BGB were developed based on tree size, biomass, and WD. WD was calculated for this development procedure using a method described in the next paragraph. Four types of models with different predictor variables were selected. The model including (1) DBH, H, and WD; (2) DBH and H; (3) DBH and WD; and (4) only DBH. When the hollow cavity is a column- or conical shape, the cavity formation can be approximated by square of the hollow diameter which is considered to be related to the DBH. Therefore, $[\ln(\mathrm{DBH})]^2$ was added to models as a predictor variable. To confirm critical predictor variables from DBH, H, and WD, stepwise regression method was applied for model 1. For AGB estimation, DBH, H, and WD were selected as predictor variables. For BGB estimation, DBH was selected as predictor variable. Thus, 6 models were constructed in total, 1-6 for AGB and 1, 5-6 for BGB.

Model 1:

$$\ln(\mathrm{DW}) = a + b\ln(\mathrm{DBH}) + c\ln(\mathrm{H}) + d\ln(\mathrm{WD}) \quad (1)$$

Model 2:

$$\ln(\mathrm{DW}) = a + b\ln(\mathrm{DBH}) + c\ln(\mathrm{H}) + d\ln(\mathrm{WD}) - e[\ln(\mathrm{DBH})]^2 \quad (2)$$

Model 3:

$$\ln(\mathrm{DW}) = a + b\ln(\mathrm{DBH}) + c\ln(\mathrm{H}) - e[\ln(\mathrm{DBH})]^2 \quad (3)$$

Model 4:

$$\ln(\mathrm{DW}) = a + b\ln(\mathrm{DBH}) + d\ln(\mathrm{WD}) - e[\ln(\mathrm{DBH})]^2 \quad (4)$$

Model 5: $\ln(\mathrm{DW}) = a + b\ln(\mathrm{DBH})$ (5)

Model 6: $\ln(\mathrm{DW}) = a + b\ln(\mathrm{DBH}) - e[\ln(\mathrm{DBH})]^2$ (6)

where DW is the dry mass (kg); DBH is the diameter at breast height (cm), H is tree height (m), WD is the wood density ($\mathrm{Mg\,m^{-3}}$), and parameters *a*–*e* are regression coefficients for each model. Then each liner model was back-transformed to a power function form. Because log-transformed data causes a bias in biomass estimation (Baskerville, 1972), the back-transformed results are multiplied by the correction factor (CF) (Sprugel, 1983). CF is expressed as follows:

$$\mathrm{CF} = \exp\left(\frac{\mathrm{RSE}^2}{2}\right)$$

where RSE is the residual standard error obtained from model regression. To identify best-fit models, highest adjusted coefficients of determination ($R_{adj}^2$) and the lowest Akaike information criterion (AIC) and Furnival Index (FI) were used to evaluate the degrees of fit between measured and estimated biomass. Furnival's index (Furnival, 1961) which is able to compare models of different dependent variables was used. The index is calculated as follows:

$$\mathrm{FI} = \sqrt{\mathrm{MSE}}\left(\frac{1}{\text{Geometric mean }(y^{-1})}\right)$$

where MSE is the mean square error of the fitted model, y is the measured AGB and BGB.

WD for the biomass estimation were calculated using specific gravity in air dry (15% water content) and Suzuki's (1999) equation, which converts specific gravity in air dry to WD. Specific gravities in air dry were preferentially

Table 3. Biomass regression (kg tree$^{-1}$) models developed by Yamakura et al. (1986), Basuki et al.(2009), Suwarna et al.(2012), and Niiyama et al. (2010) for tropical rain forests and peat swamp forests.

| Reference | Biomass (kg tree$^{-1}$) | Model | Site | Forest type | n | DBH range (cm) |
|---|---|---|---|---|---|---|
| Yamakura et al. (1986) | Stem | $2.903\times10^{-2}\times(\mathrm{DBH}^2\mathrm{H})^{0.9813}$ | East Kalimantan, Indonesia | Lowland dipterocarp forest | 76 | 4.5–130 |
| | Branches | $0.1192\times(\text{Stem biomass(kg)})^{1.059}$ | | | | |
| | Leaves | $9.146\times10^{-2}\times(\text{Stem+Branches biomass(kg)})^{0.7266}$ | | | | |
| Basuki et al.(2009) | AGB | $\exp(-0.744+2.188\times\ln(\mathrm{DBH})+0.832\times\ln(\mathrm{WD}))$ | East Kalimantan, Indonesia | Lowland dipterocarp forest | 122 | 5–70 |
| Suwarna et al. (2012) | Stem | $0.088\times\mathrm{DBH}^{2.485}$ | Riau, Indonesia | Peat swamp forest | 52 | 5–63 |
| | Beanches | $0.007\times\mathrm{DBH}^{2.710}$ | | | | |
| | Twigs | $0.211\times\mathrm{DBH}^{1.470}$ | | | | |
| | Leaves | $0.143\times\mathrm{DBH}^{1.190}$ | | | | |
| | BGB | $0.064\times\mathrm{DBH}^{2.252}$ | | | | |
| Niiyama et al.(2010) | BGB | $0.023\times\mathrm{DBH}^{2.59}$ | Pasoh, Malaysia | Lowland dipterocarp forest | 54 | 2.5–116 |

obtained from data provided by the Tropical Agriculture Research Center (1977). When data were not available by this source (*loc. cit.*), data in PROSEA (1998) was used. Suzuki's equation was developed using data from the lowland dipterocarp forest of West Kalimantan, Indonesia.

All regressions were calculated with R software Windows ver. 3.0.2 (available at http://cran.r-project.org/bin/windows/base/old/3.0.2/).

**Biomass model comparisons and fitting**

The measured biomass values were compared with predictions of three previously published tropical rainforest models (Yamakura et al. 1986, Basuki et al. 2009, and Niiyama et al. 2010) and one peat swamp forest model (Suwarna et al. 2012) (Table 3), referred to hereafter as the Yamakura, Basuki, Niiyama, and Suwarna models, respectively. The Yamakura and Basuki models are allometric equations for AGB which are based on the tropical lowland dipterocarp forests of East Kalimantan, Indonesia. The Yamakura model, which was developed for a DBH range of 4.5–130 cm, uses DBH and H to formulate predictions for each tree component (*i.e.*, stems, branches, and leaves). The Basuki model, which was developed for a DBH range of 6–200 cm, uses DBH and WD to predict AGB. The Niiyama model, which is an allometric regression equation for BGB, is based on the tropical lowland dipterocarp forests in Pasoh (The Malay Peninsula, Malaysia). It was developed for a DBH range of 2.5–116 cm and uses DBH to predict BGB. The Suwarna model comprises allometric regression equations for the tropical peat swamp forests in Riau (Sumatra, Indonesia). They were developed to make predictions for each component of a tree (*i.e.*, stems, branches, twigs, leaves, and BGB). AGB in the Yamakura and Suwarna models is defined as the sum of the biomasses of stem, branches (and twigs), and leaves. None of these four models recorded hollow trees. To compare our biomass data and the predicted biomass, the present tree data (DBH, H, WD) were substituted into the previous model equations.

**Statistical analysis**

Allometric analysis was used to describe the differences in DBH–H and DBH–biomass relationships for the forest types. Logarithmically transformed values of H, AGB, and BGB were regressed against DBH or $\mathrm{DBH}^2\times\mathrm{H}$. The effects of forest type on tree size and biomass were analyzed using ANCOVA (with DBH or $\mathrm{DBH}^2\times\mathrm{H}$ as covariates).

For hollow trees, the product of hollow volume ($m^3$) and measured WD ($\mathrm{Mg\,m^{-3}}$) were calculated to estimate the biomass lost due to hollow formation. When sampled tree have brittle heart in the central cores, WD was compared between sapwood and brittle heart by student's t-test.

Table 4. Wood density of sampled trees in hollow size measurement in Alan Batu forest (PC2).

| Species | DBH (cm) | Wood density ($Mg m^{-3}$) Sapwood and heartwood Mean ± SD | Brittle heart Mean ± SD |
|---|---|---|---|
| *Combretocarpus rotundatus* | 40.7 | 0.624 ± 0.046 | – |
| *Litsea gracilipes* | 21.0 | 0.394 ± 0.012 | – |
| *Shorea albida* (*Alan Batu*) | 19.1 | 0.576 ± 0.020 | 0.386 ± 0.014 |
| *Shorea albida* (*Alan Batu*) | 70.2 | 0.644 ± 0.033 | – |
| *Shorea albida* (*Alan Batu*) | 62.9 | 0.563 ± 0.047 | – |
| *Shorea albida* (*Alan Batu*) | 47.7 | 0.587 ± 0.034 | – |
| *Shorea albida* (*Alan Bunga*) | 22.5 | 0.349 ± 0.038 | 0.349 ± 0.038 |

n = 3. Brittle heart was defined as a fuzzy end grain at cross section when a log was cut by chainsaw (see Figure 1d).

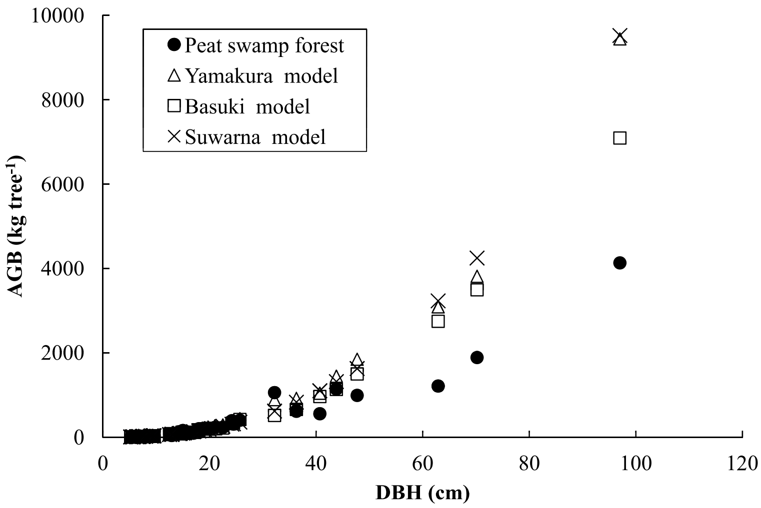


Fig. 2. Comparison of DBH–AGB (kg tree$^{-1}$) [diameter at breast height – aboveground biomass] relationships between tropical peat swamp forest trees sampled in this study [Sarawak] and predictions of previously published models for tropical rain and peat swamp forests. Model parameters and site indices are detailed in Table 3.

## RESULTS

### Biomasses of individual trees

A total of 44 trees were selected (12 in PC1, 27 in PC2, and 5 in PC3) with DBH ranging from 5.2 to 110.8 cm and H ranging from 7.1 to 49.4 m; the trees belonged to 14 different species. Biomasses obtained by destructive sampling ranged from 7.1 to 4148.0 kg tree$^{-1}$ (AGB) and from 1.0 to 1343.4 kg tree$^{-1}$ (BGB) (Tables 1,2). The BGB sampling loss was estimated at 9.4 and 7.3%, 8.3% on average, of the whole BGB for DBH 25.7 cm and 43.8 cm trees, respectively.

### Hollow size

Hollows were checked and WD were measured in seven trees ranging from 19.1 to 70.2 cm in DBH. Hollows were found in four trees with DBH exceeding 40 cm (Table 2). Hollows passed through the primary stems (Fig. 1b, c) and ranged in volume from 0.23 to 1.08 $m^3$ (Table 2). These values corresponded to 42.3 ± 12.9% (mean ± SD) of stem volume (range: 23.3−51.9%). Hollow trees were identified as *S. albida* (Batu) and *Combretocarpus rotundatus*. A specimen of *Litsea gracilipes* measuring 21.0 cm in DBH had a partly hollow stem.

Measured WD ranged from 0.349 to 0.644 $Mg\,m^{-3}$ (Table 4). A small *S. albida* (Batu) tree measuring 19.1 cm

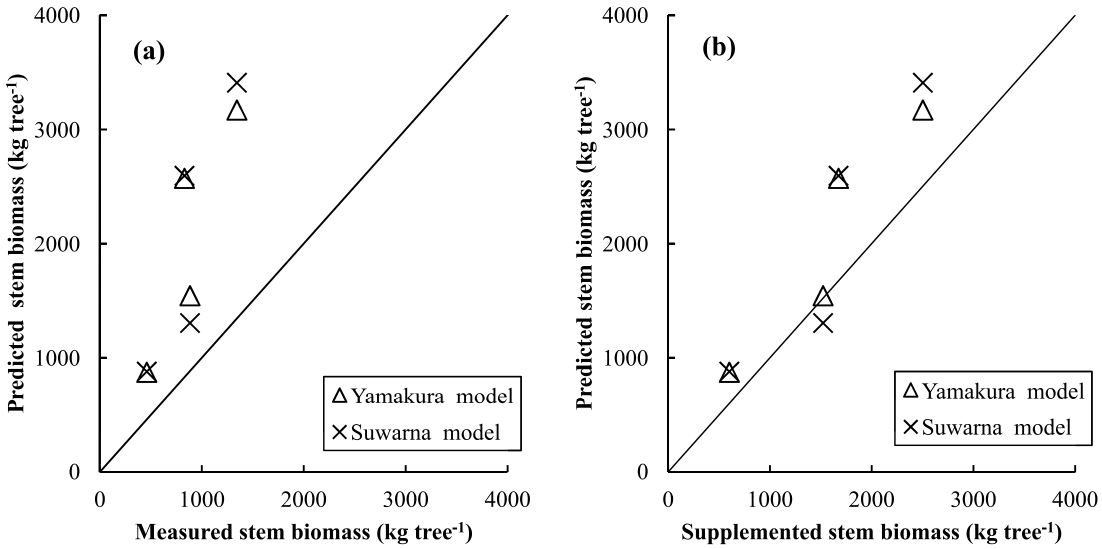


Fig. 3. Relationships between hollow tree stem biomasses and model-predicted stem biomasses: (a) measured stem biomass, (b) "supplemented" stem biomass (measured stem biomass plus biomass lost to cavity formation calculated from hollow volume and measured wood density [WD]). The line represent y = x.

in DBH had brittle heart sectors in its central core (Fig. 1d). The brittle heart measured 0.16 $m^3$ (Table 2) and occupied 45.6% of the stem volume. WD of brittle heart was significantly different from the sapwood ($t(4) = 13.657$, $P < 0.01$). The stem of a *S. albida* (Bunga) tree measuring 22.0 cm in DBH was made up entirely of brittle heart wood. This form of wood was not found in other trees that were sampled. The estimated biomass loss calculated from hollow volume × measured WD ranged from 125.9 to 1113.4 kg $tree^{-1}$, occupying 56.8 ± 24.1% of the whole AGB.

## Relationships between DBH with above- and belowground biomass

When DBH were ≥ 40.7 cm, the Basuki, Yamakura, and Suwarna models produced larger AGB (the average AGB overestimation of these models was 1604.5 ± 1601.1 kg $tree^{-1}$, reaching a maximum of 5386.0 kg for *S. albida* [Batu] with a DBH of 97.0 cm; Fig. 2). Fig. 3 shows the effect of biomass loss caused by hollows in four trees on the stem biomass predicted using previous stem biomass models (Yamakura and Suwarna models). "Supplemented" stem biomass values provided in Fig. 3 are supplemented by biomass losses to hollows (calculated from hollow volume and measured WD). All the models had overestimated measured stem biomass (Fig. 3a), but the difference was reduced when supplemented stem biomass was taken into account (Fig. 3b) (the average difference between measured stem biomass and predicted stem biomass was 1164.4 ± 743.4 kg $tree^{-1}$; the average difference between supplemented stem biomass and predicted stem biomass was 468.5 ± 441.5 kg $tree^{-1}$).

When DBH was ≥ 60 cm, the Niiyama and Suwarna models produced larger BGB (the average overestimate for these models were 889.0 ± 1285.2 kg $tree^{-1}$, reaching a maximum of 3197.0 kg $tree^{-1}$ for a specimen of *S. albida* [Batu] with a DBH of 110.8 cm, Fig. 4). Trees in this DBH class belonged to *S. albida* (Bunga) and *S. albida* (Batu).

The DBH-H relationships did not differ among the forest types ($P < 0.05$). Size- biomass relations ($DBH^2 \times H$–AGB and $DBH^2 \times H$–BGB) were significantly different among the forest types (for AGB, intercepts of PC1 and PC2 were higher than that of PC3 [$P < 0.01$]; for BGB, slopes of PC1 and PC2 were different [$P < 0.05$]).

## Development of allometric equations

With the highest adjusted coefficients of determination ($R_{adj}^2$), lowest AIC and FI, Model 2 and 6 were selected as the most accurate for AGB and BGB, respectively (Table 5). When predicted variables were matched, the models including $[\ln(DBH)]^2$ as a predictor variable (Models 2 and 6) had higher $R_{adj}^2$, lower AIC and FI than the other models (Model 1 and 5) (Tables 5).

When predictor variable numbers were equal to or fewer than those of earlier models, the AGB values predicted by Model 3 (DBH and H included as predictor variables), Model 4 (DBH and WD included as predictor

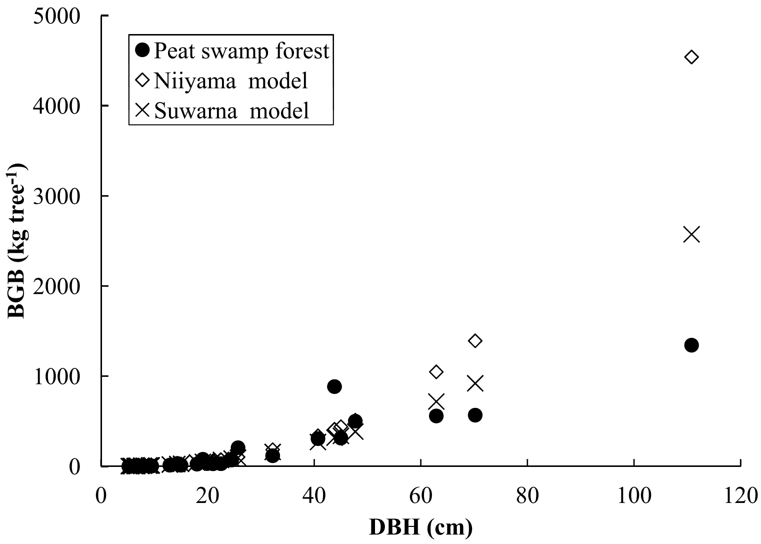


Fig. 4. Comparison of DBH–BGB (kg tree$^{-1}$) [diameter at breast height – belowground biomass] relationships between the tropical peat swamp forest trees sampled in this study (Sarawak) and predictions of previously published models for tropical rain and peat swamp forests. Model parameters and site indices are detailed in Table 3.

Table 5. Coefficients and allometric models used for estimating dry weights of aboveground biomass.

| Models | a | DBH b | H c | WD d | DBH$^2$ e | Adjusted $R^2$ | CF | AIC | FI |
|---|---|---|---|---|---|---|---|---|---|
| Aboveground biomass (n = 41) | | | | | | | | | |
| Model 1 | −2.3785 | 1.7078 *** | 0.9704 * | 0.6389 ns | | 0.9677 | 1.0487 | 25.65 | 0.00313 |
| Model 2 | −3.4804 | 3.0581 *** | 0.6242 ns | 0.6405 ns | 0.2015 ** | 0.9717 | 1.0425 | 21.05 | 0.00293 |
| Model 3 | −3.8903 | 3.1700 *** | 0.5108 ns | | 0.2013 ** | 0.9704 | 1.0444 | 21.99 | 0.00300 |
| Model 4 | −3.1574 | 3.7215 *** | | 0.4931 ns | 0.2618 ** | 0.9699 | 1.0452 | 22.74 | 0.00303 |
| Model 5 | −1.4927 | 2.2250 *** | | | | 0.9615 | 1.0581 | 30.92 | 0.00342 |
| Model 6 | −3.5339 | 3.7146 *** | | | 0.2529 ** | 0.9694 | 1.0459 | 21.99 | 0.00305 |
| Belowground biomass (n = 32) | | | | | | | | | |
| Model 1 | −4.0218 | 2.2177 *** | 0.5784 ns | 1.1541 ns | | 0.9521 | 1.1334 | 52.25 | 0.02437 |
| Model 5 | −4.2149 | 2.6109 *** | | | | 0.9508 | 1.1373 | 51.31 | 0.02466 |
| Model 6 | −6.1049 | 3.9957 *** | | | 0.2322 ns | 0.9544 | 1.1267 | 49.81 | 0.02378 |

Adjusted $R^2$, adjusted coefficients of determination; CF, correction factor; AIC, Akaike information criterion; FI, Furnival index. Significance levels: ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

variables) and Model 6 (DBH as a predictor variable) were less biased than the Yamakura (DBH and H as predictor variables), Basuki (DBH and WD as predictor variables) and Suwarna (DBH as the predictor variable) models (Fig. 5a). Similarly, BGB predicted by Model 6 (DBH as the predictor variable) was less biased than the Niiyama and Suwarna models (DBH as the predictor variable) (Fig. 5b).

## DISCUSSION

### Characteristics of tree biomass and the effect of hollows on tree biomass estimation in a Sarawak peat swamp forest

AGB data were obtained for trees ranging in DBH from 5.2 to 97.0 cm and BGB data for trees ranging in DBH from 5.2 to 110.8 cm (Tables 1,2). BGB values may contain sampling loss of around 8.3% on average. These data cover

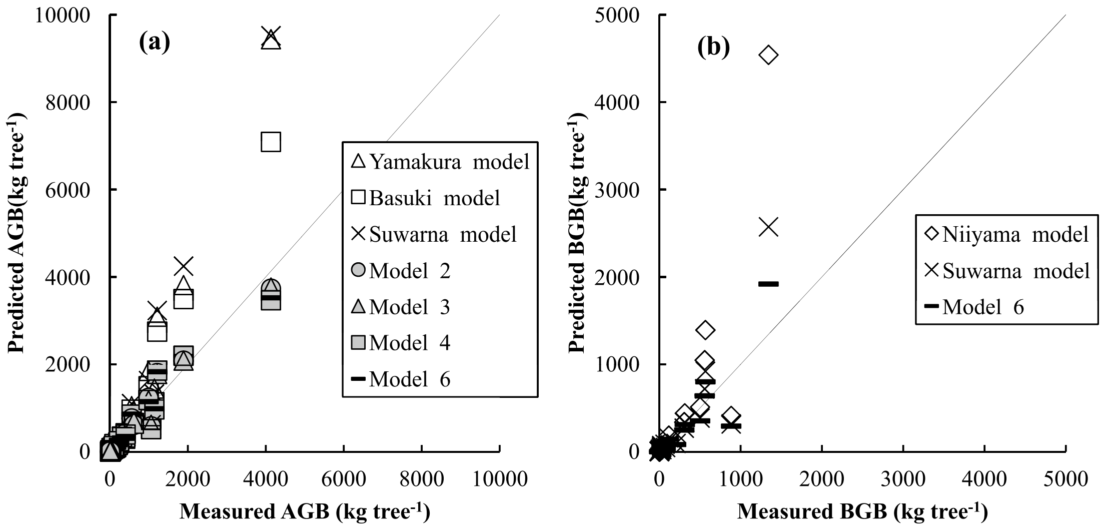


Fig. 5. Relationships between measured biomass and predicted biomass calculated from a smaller number of predictor variables: (a) AGB [aboveground biomass] (kg tree$^{-1}$), (b) BGB [belowground biomass] (kg tree$^{-1}$). The line represent y = x.

almost the entire range of tree sizes likely to be encountered in the study region. The trees with the largest DBH were close to the maximum DBH class (114.6–191.0 cm; Whitmore 1975) in the Sarawak peat swamp forests. These measured biomasses (AGB and BGB) and hollow sizes obtained through destructive sampling will provide valuable data for future studies of tropical peat swamps.

DBH-biomass relations are different among forest types. Measured AGB increased with DBH, but at a lesser rate than the predictions of previously published models for tropical rainforests and Indonesian peat swamp forests (Fig. 2). Among hollow trees, those with a DBH exceeding 40 cm had pipe-like cavities passing through the primary stems (Fig. 1a-c). On average, hollows of these large individuals accounted for 42.3% of the whole stem volume (range: 22.3 –51.9%). Our findings are similar with previous observations; large *S. albida* trees that are dominant or co-dominant in the Sarawak peat swamp forests were reported to have hollow stems (Anderson 1972, Tropical Agriculture Research Center 1977). It was also found that *C. rotundatus* trees, which grow in peat swamps throughout Sarawak (Anderson 1972), also have hollow stems. It is likely that substantial numbers of these large trees have hollows and the presence of these cavities will certainly affect the estimations of forest biomass. In other forest types, the occurrence of hollow trees would cause little error in wood volume estimation. Nogueira et al. (2006) reported that tree hollows in central Amazonia have little effect on total stem volume per unit forest area (effect size: 0.7%). Wormington and Lamb (1999) also found that most Australian eucalyptus trees become partially hollow upon reaching the 90–100 cm DBH size class; however, hollow diameters in these trees were only in the range of 1–10 cm and large hollow trees were considered rare. In contrast, it was found that, in the Sarawak peat swamp forests, the occurrence of hollows accounts for the estimation errors in biomass by using previously published models without considering the influence of hollow. The three earlier models *i.e.* Yamakura, Basuki, and Suwarna tested against the empirical data had overestimated the biomass of trees with DBH ≥ 40 cm (Fig. 2). AGB overestimations were particularly distinct for hollow trees (Fig. 3a). On the other hand, overestimations decreased when biomass loss to cavity formation were considered (Fig. 3b).

The tendency of the measured BGB to increase with DBH was less than predictions of previously published BGB models without considering the influence of hollow, especially for trees with DBH exceeding 60 cm (Fig. 4). These large trees were identified as *S. albida*. While cavity volume was not measured in the stumps, it was observed that the hollows actually extended to ground level (Fig. 1c). Thus, biomass loss to cavity formation also occurred in stumps. With the very low bulk density and the low availability of soil mineral nutrients, as in the peat swamps, the trees form extensive root systems to stabilize the large aboveground parts on the spongy soil and also to capture nutrients. We predict that irregular DBH–BGB relations to be caused by a combination of positive and negative effects on root biomass, such as root growth and hollow expansion. According to predicted BGB by the Niiyama and Suwarna models (which uses DBH to predict BGB), BGB increases constantly with DBH, causing the modeled biomasses of large trees to be overestimated (Fig. 4).

To accurately estimate biomass, specific models reflecting the morphological characteristics of trees are required for tropical peat swamp forests. Brittle heart was found in a *S. albida* (Batu) tree without a hollow cavity; the DBH of this specimen was 19.1 cm (Fig. 1d), and the brittle heart occupies 45.6% of the stem volume. The WD of the brittle heart was significantly lower than the WD of the sapwood ($P < 0.05$; Table 4). Since many tropical trees have brittle heart in the central cores (Takada and Kikata 1984), biomass estimation models for swamp forest trees without hollows must also be carefully chosen.

## Allometric equations for a peat swamp forest in Sarawak

Model 2 and Model 6 were selected as the best models for estimating AGB and BGB, respectively (Table 5). These models were the second order polynomial regression models with an assumption that DBH-biomass relations are non monotonic. Our models with the small number of predictor variables were more suitable for the peat swamp forest than previous models (Fig. 5a,b). We developed models that included one (only DBH: Model 6) or two (DBH and H, or WD: Model 3 and 4) parameters as predictor variables for estimating AGB. When treetops are easily distinguished, it is better to select models that include H as a predictor variable which improves the accuracy of biomass estimates. If the forest is multi-layered and treetops are difficult to distinguish, it is better to select models without H to avoid errors in field measurements. When dominant tree species are easily identifiable, it is best to select models that include WD. No differences were detected in DBH–H relationships among forest types, but this was not the case for $DBH^2 \times H$–biomass relationships. Our models also need to be further refined by examining the differences among forest types and by collecting more biomass and morphological data.

The allometric models from this study are the first that are specific to tropical peat swamp forests where hollow trees are not rare. Our models are based on biomass data obtained by destructive sampling in a logged-over peat swamp forest. Thus, our allometric models are generally useful for the logger-over peat swamp forests in Sarawak. Tropical peat swamp forests of Southeast Asia occur in the lowlands of eastern Sumatra, Sarawak, Brunei, the Malay Peninsula, southwestern New Guinea, and the southern Philippines etc. However, the occurrence of hollow has been reported only in Sarawak. This distribution of trees with cavities requires further confirmation by empirical study.

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