

Estimation of root biomass based on excavation of individual root systems in a primary dipterocarp forest in Pasoh Forest Reserve, Peninsular Malaysia

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(Accepted 16 January 2010)

Abstract: Precise estimation of root biomass is important for understanding carbon stocks and dynamics in tropical rain forests. However, limited information is available on individual root masses, especially large trees. We excavated 121 root systems of various species (78) and sizes (up to 116 cm in dbh), and estimated both above- and below-ground biomass in a lowland primary dipterocarp forest in the Pasoh Forest Reserve, Peninsular Malaysia. A tree census was conducted in four research plots (each 0.2 ha) and stand-level biomass was estimated. We examined relationships between tree size parameters and masses of coarse roots (roots ≥ 5 mm in diameter) and derived a dbh-based allometric equation. The amounts of coarse roots that were lost during excavation were corrected. Coarse-root biomass before and after correction for lost roots was estimated to be 63.8 and 82.7 Mg ha⁻¹, indicating that significant amounts of roots (23%) were lost during the sampling. We also estimated the biomass of small root (<5 mm) by applying pipe-model theory. The estimate, 13.3 Mg ha⁻¹, was similar to another estimate of small roots, 16.4 Mg ha⁻¹, which was obtained directly by the soil-pit sampling method. Total below-ground (BGB) and above-ground biomass (AGB) was estimated to be 95.9 and 536 Mg ha⁻¹, respectively. The biomass-partitioning ratio (BGB/AGB) was about 0.18. In conclusion, the dbh-based allometric equation for coarse roots developed in this study, which kept good linearity even including the data of larger trees, might be useful for evaluating below-ground carbon stocks in other stands of similar forest (old-growth dipterocarp) in South-East Asia.

Key Words: allometry, biomass allocation, dipterocarp, fine roots, lost roots, primary tropical rain forest

INTRODUCTION

Tropical rain forests of South-East Asia have potentially larger biomasses than other tropical forest ecosystems (Brown *et al.* 1989, Cairns *et al.* 1997, Cannell 1982), and these forests may also serve as carbon sinks, as suggested for tropical forests in other regions (Chave *et al.* 2008, Malhi & Phillips 2004, Phillips *et al.* 1998, 2002). However, the role of tropical forests as carbon sinks or sources is still under debate, because of the variation in

data and methods that have been used to assess their carbon pools and dynamics (Clark 2004).

Biomass estimation of tropical rain forests in South-East Asia has been carried out intensively in Peninsular Malaysia and Borneo (Hoshizaki *et al.* 2004, Kato *et al.* 1978, Kira 1978, Okuda *et al.* 2004, Yamakura *et al.* 1986). However, most of these previous studies assessed only above-ground biomass. Studies of tree roots in tropical regions have mainly focused on the biomass and production of fine roots (Jaramillo *et al.* 2003, Röderstein *et al.* 2005), and with few exceptions (Hozumi *et al.* 1969, Kenzo *et al.* 2009, Ogawa *et al.* 1965, Sierra *et al.* 2007) have rarely examined root mass at the individual

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tree level. The lack of knowledge concerning below-ground total biomass (i.e. including structural coarse roots) remains common to tropical rain forests worldwide (Chave *et al.* 2005, Clark *et al.* 2001a, b), especially for larger trees. Thus, there is a need for a reliable method for estimating root biomass to quantify carbon balances in tropical rain-forest ecosystems.

The characterization of allometric relationships between the masses of plant organs (leaves, stems and roots) and size-related variables (e.g. stem diameter and height) is a fundamental step for estimating forest biomass, net primary production, and carbon dynamics (Chave *et al.* 2005, Kira & Shidei 1967, Tierney & Fahey 2007). Kato *et al.* (1978) first applied allometric methods to the estimation of above-ground biomass in the tropical rain forest at the Pasoh Forest Reserve in Malaysia. They reported that the data obtained from larger trees dominated the shape of the allometric equation (i.e. regression slope and intercept) and biomass estimates. This implies that extrapolation derived from a small dataset without sampling larger trees is likely to cause substantial over- or under-estimation of stand-level biomass. Similar problems might arise in root biomass estimation. The measurement of individual root masses by digging out whole root systems is very laborious and sometimes requires heavy machines. Furthermore, even if roots are excavated carefully, it is difficult to avoid losses of roots that are broken during the excavation. Thus, subsequently derived allometric equations that ignore the amount of missing roots, may considerably underestimate root biomass, especially for large trees (Niklas 2003, 2005; Niklas & Enquist 2002). Therefore, to estimate root biomass precisely, there is a need to correct for the amount of lost roots.

One possible approach to correct for lost roots is to measure the diameters of all lost roots at the position of each broken end after excavating a root system. Then, if a significant relationship between the diameter and dry mass can be derived for a sample of lost roots, we may calculate the total mass of lost roots for individual trees. A similar correction method for lost roots has already been applied to some forest types, such as teak (*Tectona grandis*) plantations (Hiratsuka *et al.* 2005) and temperate conifer (*Pseudotsuga menziesii*) forest (Santantonio *et al.* 1977).

Fine-root biomass is generally assessed using area-based sampling techniques, such as soil coring, excavating soil pits and monolith extraction (Claus & George 2005, Jackson *et al.* 1997, Yanai *et al.* 2006). These methods require use of a certain number of sampling points to reflect the heterogeneous distribution of fine roots (Vogt & Persson 1991), and fine-root biomass has rarely been assessed at the individual level, due to technical difficulties. Alternatively, the fine-root mass of individual trees may be estimated from theoretical calculations. For example, the pipe-model theory of tree

architecture suggests that the total cross-sectional area of branches remains constant at each branching level in several tree species (Shinozaki *et al.* 1964). This means that the sum of sectional areas of daughter branches is likely to be the same as that of a mother branch. If this rule of branching pattern applies to tree root systems, the total cross-sectional area of branching roots should be equal to the sectional area of the mother root at the root-stem base (or at other stem positions, such as breast height) (Richardson & Dohna 2003). This model may provide an alternative way of estimating root masses, including smaller roots (i.e. fine roots), without destructive sampling, although its applicability in forest ecosystems has not been validated sufficiently yet.

The main objective of the present study was to develop an allometric equation for coarse-root mass and estimating total root biomasses in a primary lowland dipterocarp forest in Malaysia. For this purpose, we excavated the root systems of a large number of trees, covering almost the whole size range of existing trees, including canopy trees. The amounts of roots that were broken and lost during the excavation were corrected, and their relative proportion was evaluated. Small-root mass of individual trees was estimated by applying pipe-model theory, and its applicability to stand-level estimation was evaluated by comparing the result: it yielded with another estimate of small-root biomass. In this paper, we discuss the methodological advantages and limitations of estimating coarse-root mass, focusing on the allometric equation. We also discuss the characteristics of biomass and partitioning between above- and below-ground parts of the study forest by comparing the patterns in other old-growth tropical rain forests.

METHODS

Study site

The study site was located in Compartment 47 (2°59'N, 102°18') in the Pasoh Forest Reserve, Negeri Sembilan (c. 110 km south-east of Kuala Lumpur), Peninsular Malaysia. The Pasoh forest reserve is the most intensively investigated site of primary lowland dipterocarp forest in South-East Asia (Ashton *et al.* 2003, Hoshizaki *et al.* 2004, Kato *et al.* 1978, Kira 1969, 1978; Kira & Shidei 1967, Kochummen *et al.* 1990, Manokaran *et al.* 1991, Okuda *et al.* 2003). More than 800 tree species are present in the reserve (Kochummen *et al.* 1990, Manokaran *et al.* 1991), including large specimens of Dipterocarpaceae and Leguminosae species, such as *Dipterocarpus cornutus* and *Koompassia malaccensis*, up to c. 50 m tall. In this paper, nomenclature follows Kochummen (1997). Annual rainfall averages approximately 2000 mm, with a range of 1700–3200 mm (Kochummen *et al.* 1990).

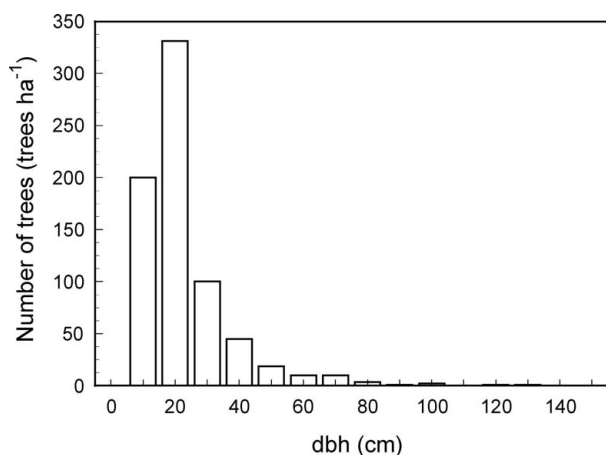


Figure 1. Frequency distribution of the dbh of trees in the four census plots (P1–P4). These plots were established before logging in a primary lowland dipterocarp forest at Compartment 47 in the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia.

Compartment 47 is located on a west-facing slope (150–500 m asl). Most previous studies in the Reserve have been conducted in the lower part of Compartment 22 (about 4 km from our site), where the terrain is rather flat, and is underlain by Triassic sediments and some granite (Ashton *et al.* 2003). The major soil type at the study site is Ultisol (Soil Survey Staff 2006), and its fertility is generally low in the study site; available P ranges from 0.3 to 3.9 mg kg⁻¹ in the top 20 cm, and less than 0.5 mg kg⁻¹ in deeper soils according to Yamashita *et al.* (2003).

Field measurements and sampling

Four permanent research plots (P1–P4; each 20 × 100 m) were established in Compartment 47. In each plot, size parameters of all living trees (breast height stem diameter, dbh > 5 cm) were measured in 2004. Figure 1 shows that dbh frequencies peaked at values between 20–30 cm (mean = 17.8 cm) and the maximum was about 121 cm.

We selected 121 sample trees within Compartment 47 with stem diameters ($D_{0.3}$ or dbh) ranging from 0.5 to 116 cm (Appendix 1). Some tree sampling was carried out in December 2004, but most was done in January, February and September 2005. Both above- and below-ground components of 99 individuals were weighed, but only roots of 22 other individuals (mainly larger trees) were measured, because their above-ground parts had already been commercially harvested. Prior to the logging, however, we measured the dbh and height (H) of these 22 individuals. In total, the sample trees (excluding three non-identified trees) represented 78 species, and the acquired data were divided into a set for trees with dbh ≥ 2.5 cm ($n = 54$) and a set for smaller trees (dbh < 2.5 cm, $n = 67$), representing 43 and 35 species, respectively.

The number of sampled trees per species was mostly less than three, but was higher for the following four species: *Anaxagorea javanica* ($n = 12$), *Alangium ebenaceum* ($n = 4$), *Dacryodes rugosa* ($n = 4$) and *Rinorea anguifera* ($n = 4$). The sample also contained various life forms, including emergent, main canopy and understorey trees. The largest sample tree (dbh = 116 cm, $H = 50$ m) was a dipterocarp (*Dipterocarpus cornutus*, Figure 2a).

In this study, roots were divided into the two size groups, coarse root and small root. Coarse roots (i.e. structural roots), which were defined as roots exceeding 5 mm in diameter, were excavated manually or using a power shovel (Figure 2). They were washed using a water pressure pump and brushes, then weighed using spring balances (measurement range = 5–100 kg), except for the two largest trees (Figure 2), the stumps of which were so large that they were weighed using a 500-kg tension meter (Nagaki Seiki Co Ltd, Osaka Japan) after division into smaller pieces. Subsamples (100–300 g) were taken from each component and dry/fresh mass ratios were determined after oven-drying at 85 °C to constant weight for 7 d or more; longer durations (maximum = 14 d) were applied for subsamples (mostly stems and roots) of relatively large trees. The maximum depth of tap roots was about 4 m, which was recorded for the second-largest individual, *Sindora coriacea* (Figure 2b).

To correct for losses of coarse roots that were broken and lost during the root excavation, we selected 16 individuals with different a wide range of sizes (dbh = 3.0–26.1 cm) from the sample trees. Diameters of all lost roots of these selected trees were measured at each broken end (see crosses in Figure 3). Then, dry masses of some selected roots were measured by tracing them as far as possible towards their tips, retrieving them and weighing them, as above.

Small-root (less than 5 mm in diameter) biomass was estimated by using the two different methods; hereafter, the term ‘small roots’ included so-called fine roots (i.e. <2 mm) but also slightly larger roots (2–5 mm). One approach was calculation by applying pipe-model theory (Shinozaki *et al.* 1964). Another method was direct estimation by sampling soil-pits. In this method, five 2-m-deep soil-pits were made using a mechanical excavator in the Compartment 47 in February and October 2005. A form of square pillar (5 cm × 5 cm × 200 cm) was sampled from each soil profile. Every soil block was carefully washed with tap water, and small roots were extracted carefully from the soil by hand (Oliveira *et al.* 2000). Dry mass of these roots was determined after oven-drying at 65 °C for 72 h.

As for above-ground biomass, each component (stems, branches and leaves) of the sample trees, fresh mass was measured separately. Then, its dry mass was determined using each corresponding dry/fresh mass ratio in the same manner for coarse roots.

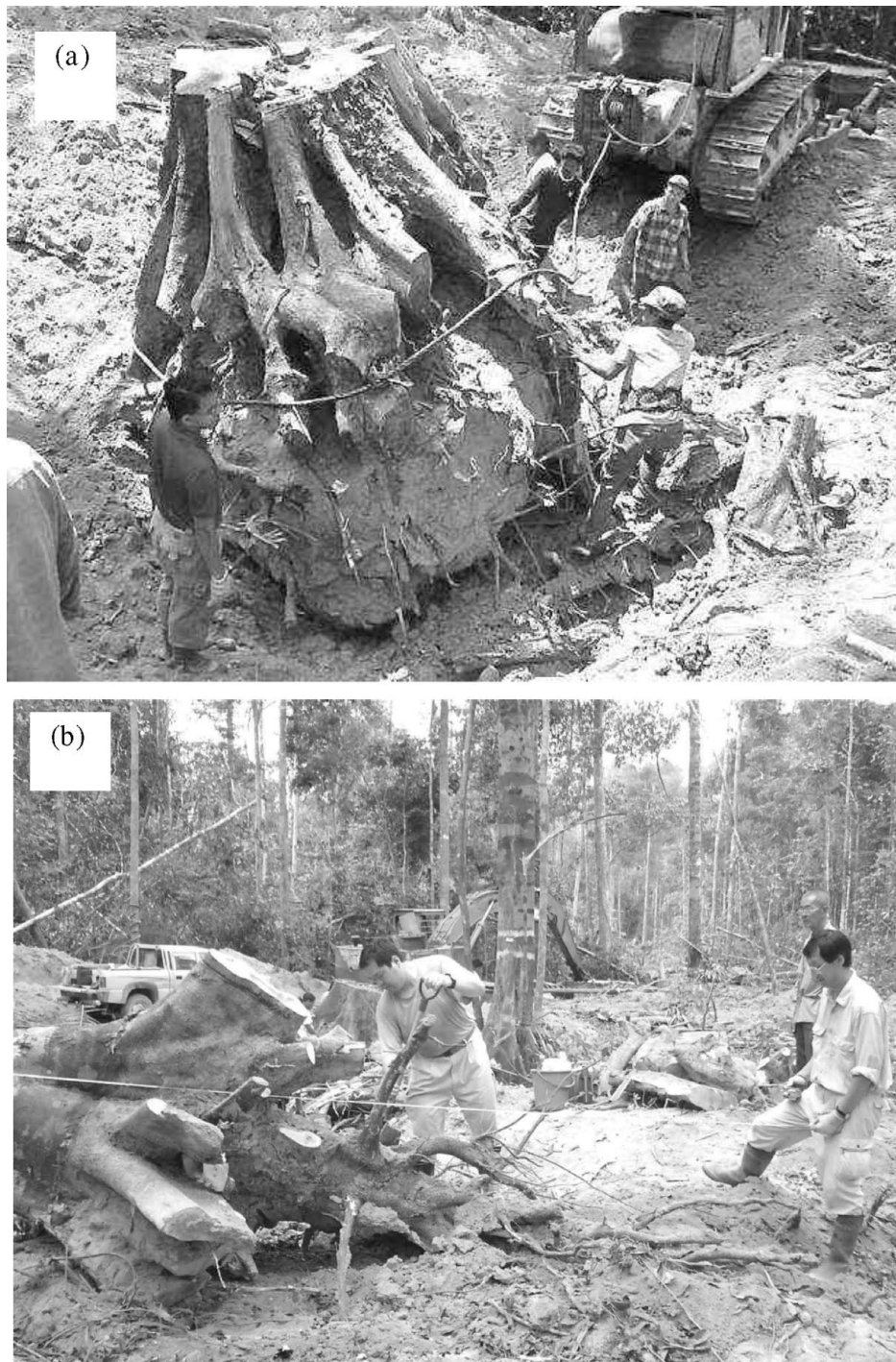


Figure 2. Two examples of root systems for the largest tree and the deepest-rooted tree excavated in the study forest on February 2005. The largest sample tree, *Dipterocarpus cornutus*, shows unclear and shallow (less than 2 m in depth), but many lateral coarse roots expanded horizontally (up to c. 10 m) (a). The deepest-rooted tree, *Sindora coriacea*, has a taproot reaching 4 m depth (b). This site is a primary lowland dipterocarp forest immediately after selective logging at Compartment 47 in the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia.

Data analysis

Above- and below-ground biomasses in the four census plots were estimated primarily by deriving corresponding size-mass allometric equations, except for small roots. In this study, the main targets for biomass estimation were

large trees (dbh > 5 cm). Here, we describe the principle of the allometric method and a common form of regression analysis.

Size-mass allometry is generally expressed as a power-form equation: $Y = aX^b$, where X is an appropriate size variable, Y is a dependent mass variable, a is a

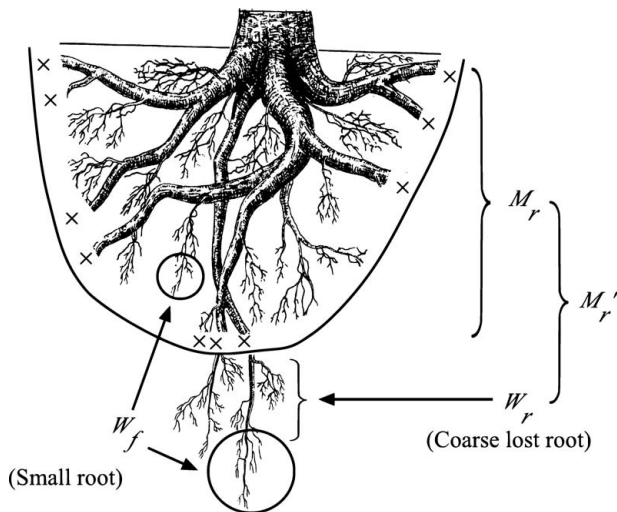


Figure 3. Illustration of definitions of root components (and their abbreviations) used to estimate root masses of individual trees. M_r : dry mass of coarse roots (>5 mm in diameter), including part of the tree stump, which was directly weighed just after root system excavation (i.e. root mass before correcting for the amount of lost roots). W_r : dry mass of coarse roots that were broken and lost during root excavation. W_f : dry mass of small roots (<5 mm). M_r' : total mass of coarse roots after correction for lost roots (i.e. $M_r + W_r$). The crosses show the positions of breakage for each lost root, where diameter (d_r) was measured to examine relationship between the diameter and dry mass of sampled lost roots. (Redrawn from Karizumi 1979.)

normalization constant, and b is a scaling exponent (Ogawa *et al.* 1965). An extended power-form equation may also be used (e.g. for estimating tree height): $1/Y = 1/aX^b + 1/Y_{max}$, where Y_{max} indicates the upper limit of dependent variable Y . In the present paper, all allometric relationships between size dimensions and dry masses were approximated by ordinary least-square regression (OLS) after the parameters (X , Y) were log-transformed. Coefficients of the regression (a , b) were calculated using the Delta Graph 5.7 software package (Red Rock Software Inc.). A correction factor (CF) was applied to the a -value of each regression, which was required for correcting systematic bias due to log-transformation (Sprugel 1983). The significance of each regression was tested by calculating the coefficient of determination (r^2). Results of two allometric regressions were compared by analysis of covariance (ANCOVA).

RESULTS

Estimation of coarse-root biomass

First, we examined allometric relationships between stem diameters and dry masses of coarse roots (M_r) before correcting for lost roots, using the data obtained from all sample trees ($n = 121$). The equation is given by:

$$M_r = aD^b \quad (1)$$

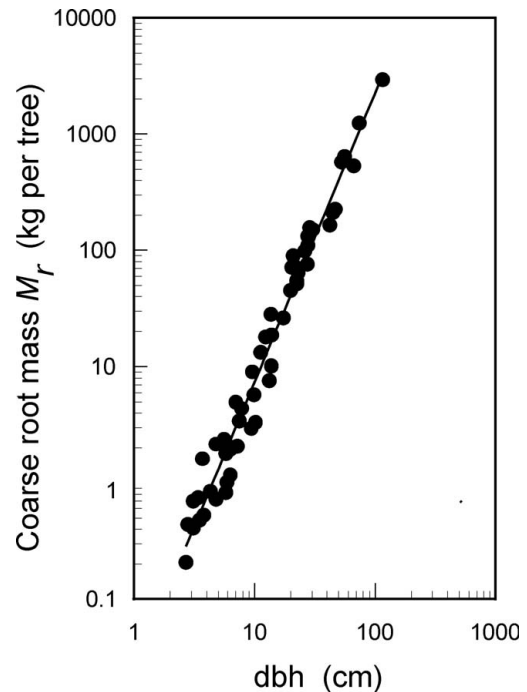


Figure 4. Allometric relationship between dbh and dry mass of coarse roots (M_r) before correction for lost roots of the sample trees ($n = 54$, $dbh \geq 2.5$ cm). See Eq. (1) in Table 1 for the regression coefficients and other statistics.

where D indicates stem diameters measured at different heights (dbh , D_0 , $D_{0.3}$). The analysis indicated that M_r was significantly correlated with dbh for individuals with $dbh \geq 2.5$ cm ($r^2 = 0.970$; $n = 54$) (Figure 4; see Eq. 1 in Table 1). Thus, for the larger trees, the dbh -based allometric equation (Eq. 1) was selected as a basic equation for estimating their coarse-root biomass before correction for lost roots. For smaller trees (<2.5 cm), however, dbh was a less-good predictor for M_r ($r^2 = 0.334$) (Figure 5a; Eq. 1-1 in Table 1) than stem diameters measured at lower positions, such as $D_{0.3}$ ($r^2 = 0.741$) (Figure 5b; Eq. 1-2) and D_0 ($r^2 = 0.795$) (Figure 5c; Eq. 1-3).

Second, the amount of coarse roots that was lost was corrected in a similar way to that proposed by Santantonio *et al.* (1977). Some coarse roots with different diameters ($n = 27$) were selected randomly from the sample trees of various species and sizes. The relationship between the breakage end diameter (d_r) and dry mass (m_r) of these sampled lost roots was approximated by the following allometric equation:

$$m_r = a d_r^b \quad (2)$$

As shown in Figure 6, the relationship was highly significant ($r^2 = 0.912$; see Eq. 2 in Table 1).

If we measure diameters of all broken lost roots (d_r) for each sample tree, the total mass of lost roots (W_r) of an individual tree can be estimated using Eq. (2). However,

Table 1. Coefficients and other allometric statistics ($Y = aX^b$) used for estimating coarse root biomass. See text for the definition of each abbreviation of size parameters (X). The regression intercept (a) is the value after applying the correction factor. All regressions were significant ($P < 0.01$). Root biomass was measured in a primary lowland dipterocarp forest at Compartment 47 in the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia.

Eq. no.	Variables		Coefficients		Sample size		dbh of trees (cm)
	Y (kg per tree)	X (cm)	a	b	r^2	n	
1 Coarse root (no correction)	M_r	dbh	0.026	2.49	0.970	54	≥ 2.5
1-1	M_r	dbh	0.079	1.04	0.334	53	< 2.5
1-2	M_r	$D_{0.3}$	0.030	1.95	0.741	67	< 2.5
1-3	M_r	D_0	0.018	2.12	0.795	62	< 2.5
2 Sample lost root	m_r	d_r	0.040	2.23	0.912	27	
3 Lost root	W_r	dbh	0.000	3.42	0.907	16	2.0–26.0
4 Coarse root (after correction)	M_r'	dbh	0.023	2.59	0.976	54	≥ 2.5

collecting such data is extremely laborious. Therefore, we measured diameters of all broken and lost roots only for the 16 selected individuals as mentioned above, although these sample trees were relatively small (dbh < 26.1 cm). The diameter of each lost root of these sample trees was measured, at the breakage point on the retained root system (d_r , see crosses in Figure 3), using a steel measure or digital calliper to ± 0.1 mm. In total, 1032 lost roots were measured. As summarized in Figure 7, d_r ranged up to about 50 mm, but was mostly less than 15–16 mm.

For each of the 16 sample trees, the total lost-root mass (W_r) was calculated using Eq. (2). In the calculation, lost roots that were smaller than the defined threshold for small roots (5 mm diameter) were excluded, since the mass of small roots at the individual-tree level was estimated separately using a different method. There was a significant relationship between W_r and dbh (Figure 8; $r^2 = 0.907$; $n = 16$) (Table 1), which was given by the following allometric equation:

$$W_r = a \text{ dbh}^b. \quad (3)$$

Thus, the biomass of coarse missing roots was obtained by applying Eq. (3) to the census data for each plot.

We also derived an allometric equation for estimating coarse-root mass after correction for lost roots, although the equation was not used for estimating stand-level biomass. From Eq. (3), W_r of the other sample trees was estimated, then the dry mass of coarse roots after lost-root correction (M_r') was calculated as the sum of M_r and W_r for the 54 sample trees. The allometric relationship between dbh and M_r' , given by the following equation, was also highly significant ($r^2 = 0.976$; Table 1):

$$M_r' = a \text{ dbh}^b. \quad (4)$$

Estimation of small-root biomass

Small-root biomass at the stand level was estimated by applying the pipe-model theory (Shinozaki *et al.* 1964), according to which the total cross-sectional area of branching roots is expected to be equal to that of the mother root. If the diameter of such a mother root is replaced by that measured at the stem-root base (dbh), the assumption can be expressed by the following

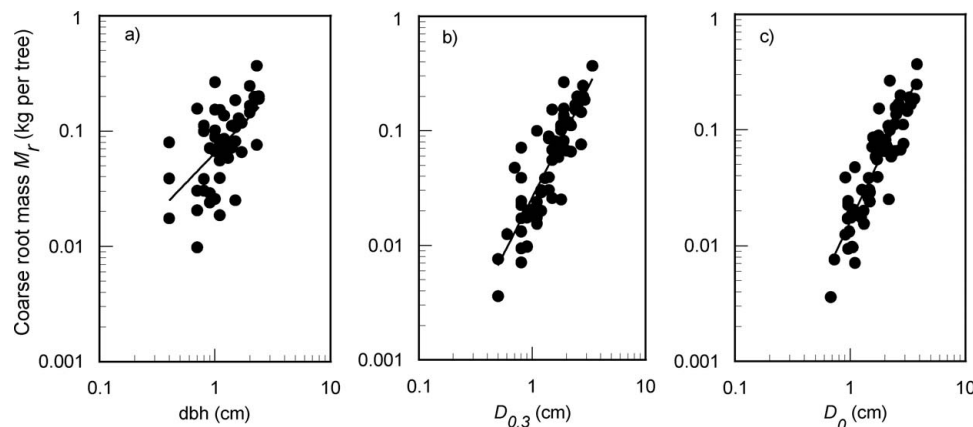


Figure 5. Allometric relationships between the dry mass of coarse roots (M_r) and three stem size parameters: dbh (a), $D_{0.3}$ (b), and D_0 (c) for smaller sample trees (dbh < 2.5 cm). See Eqs (1-1), (1-2) and (1-3) in Table 1 for the coefficients of each regression.

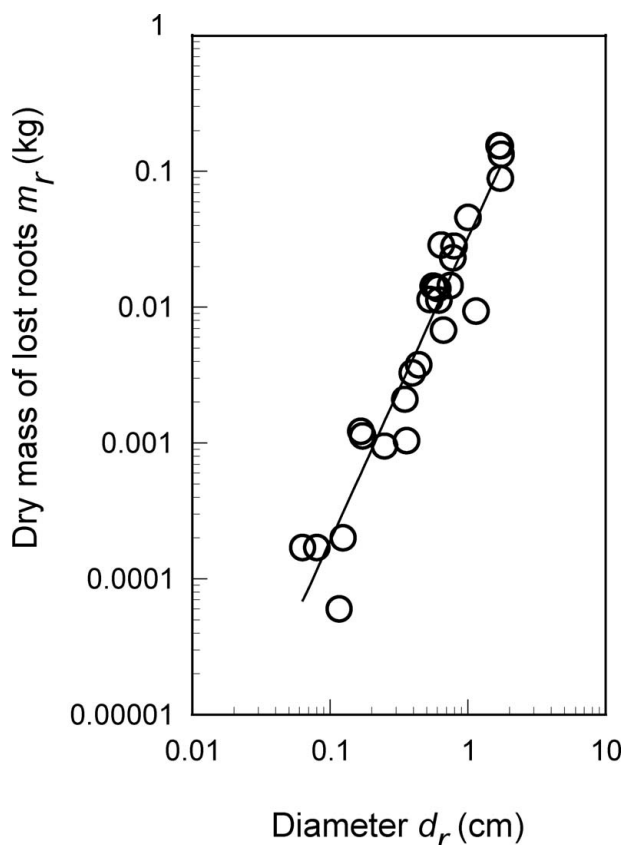


Figure 6. Relationship between diameter (d_r) and dry mass (m_r) of the lost roots ($n = 27$) obtained from 16 sample trees. See Eq. (2) in Table 1 for the regression coefficients and other statistics.

equation:

$$N_r(d_f/2)^2\pi = (\text{dbh}/2)^2\pi, \quad (5)$$

where N_r is the total number of branching roots per tree and d_{fi} is the basal diameter of one root. In this model approach, the d_f value was fixed at 5 mm (i.e. a threshold of diameter for small roots as defined in this study) so that

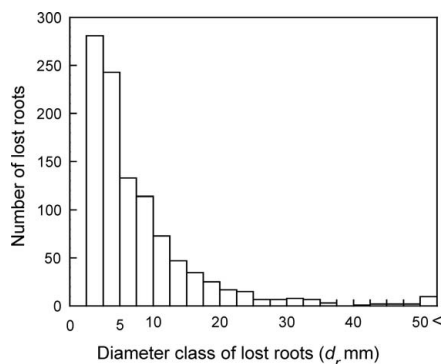


Figure 7. Frequency distribution of diameters of lost roots. The diameter (d_r) was measured at breakage points (see crosses in Figure 3) of all lost roots of the 16 sampled root systems. Here, absolute numbers of roots in each diameter class are shown by pooling the data for all measured missing roots ($n = 1032$).

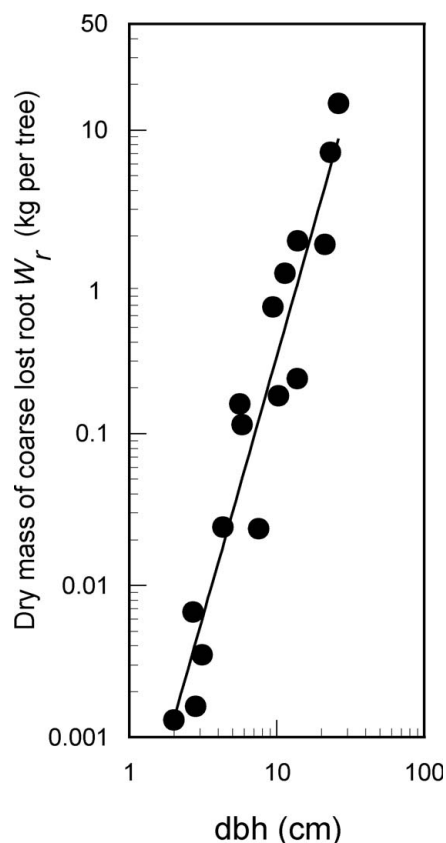


Figure 8. Relationship between dbh and dry mass of coarse lost roots (W_r) for the sample trees ($n = 16$). See Eq. (3) in Table 1 for the regression coefficient.

the total number of these roots per tree was calculated simply as a ratio of the two diameters (i.e. $N_r = \text{dbh}^2/d_r^2$). A constant value was also established for the dry mass of a small root (Figure 6, *c.* 8.5 g per root), from the $d_r - m_r$ relationship (Eq. 2). Hence, the total mass of small roots per tree (W_f) could be calculated simply by multiplying N_r by this constant dry mass of one root. The small-root biomass in each census plot could then be estimated as the sum of W_f for all target-size trees ($\text{dbh} > 5$ cm).

Estimation of above-ground biomass

For above-ground components of biomass, several size-mass allometric equations were established during the 1970s IBP (International Biological Programme) project, based on measurements of large numbers of trees harvested in the lowland dipterocarp forests in the Pasoh Forest Reserve (Hoshizaki *et al.* 2004, Kato *et al.* 1978). In the present study, we re-established these allometric relationships, based on data from our original set of sample trees ($n = 33$). The biomasses of woody parts (stems plus branches) and leaves were estimated separately using

Table 2. Coefficients and other allometric statistics used for estimating the biomass of above-ground components. Equation 7 is a linear allometric equation ($Y = a X^b$), while other equations (6, 8) approximate the allometric relationships by an extended power-form ($1/Y = 1/aX^b + 1/Y_{max}$, for details see text). The regression intercept (a) is the value after applying the correction factor. All regressions were significant ($P < 0.01$). These biomass was measured in a primary lowland dipterocarp forest at Compartment 47 in the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia.

Eq. no.	Variables		Coefficients			Sample size	
	Y	X	a	b	Y_{max}	r^2	n
6 Tree height	H (m)	dbh (cm)	1.61	1.00	69	0.925	55
7 Stem plus branch	M_{sb} (kg per tree)	dbh^2H (cm ³)	0.036	1.01	–	0.993	33
8 Leaf	M_l (kg per tree)	M_{sb} (kg per tree)	0.108	0.75	105	0.651	33

corresponding allometric equations. The forms of these equations were the same as those derived in the IBP studies. A combined size parameter (dbh^2H) was used for the allometry of above-ground woody parts (M_{sb} ; stem plus branch mass), and M_{sb} was used for the allometry of leaf mass (M_l), as follows:

$$1/H = 1/(a \text{ dbh}) + 1/H_{max}, \quad (6)$$

$$M_{sb} = a(\text{dbh}^2H)^b, \quad (7)$$

$$1/M_l = 1/a M_{sb}^b + 1/M_{lmax}. \quad (8)$$

In these equations, H_{max} in Eq. (6) and M_{lmax} in Eq. (8) indicate asymptotic values (or upper limits) of tree height and leaf mass, respectively (Table 2). We did not measure heights of some sample trees and estimated them using Eq. (6) based on data derived from 55 sample trees.

Biomass and biomass allocation

Table 3 summarizes estimates of above- and below-ground biomass in the four research plots. The primary estimate of coarse-root biomass based on Eq. (1), i.e. the sum of M_r before correction for lost roots, ranged

from 52.3 to 77.8 Mg ha⁻¹ (mean = 63.8 Mg ha⁻¹). The amount of lost roots estimated using Eq. (3), i.e. sum of W_r , ranged from 15.3 to 25.0 Mg ha⁻¹ (mean = 18.9 Mg ha⁻¹). Summing the mean M_r and W_r values gave a total estimate of coarse-root biomass of c. 83 Mg ha⁻¹. The biomass of lost roots, as a proportion of total coarse-root biomass, was about 23%.

The estimates of small-root biomass obtained from the pipe-model approach ranged from 11.1 to 15.0 Mg ha⁻¹ (mean = 13.3 Mg ha⁻¹) (Table 3). The values fell within the range of small-root biomass, 10.0 to 23.5 Mg ha⁻¹ (mean = 16.4 Mg ha⁻¹), which was obtained from the soil-pit sampling method. Consequently, the total below-ground biomass (BGB), defined as the sum of coarse roots after correction for lost roots and small roots by the pipe-model method, ranged between 78.7 and 118 Mg ha⁻¹ (mean = 95.9 Mg ha⁻¹). The percentages of coarse and small roots were about 86% and 14% of BGB, respectively.

Estimates of above-ground total biomass (AGB) ranged between 436 and 648 Mg ha⁻¹ (mean = 536 Mg ha⁻¹) (Table 3). The woody parts (stems plus branches) comprised 99% of AGB. The ratio of total below-ground to total above-ground biomass (BGB/AGB) did not differ greatly among the four plots (mean = 0.18), despite large variation in stand total biomass.

Table 3. Estimates of above- and below-ground biomass and AGB/BGB ratio of four research plots. The values of small root biomass indicate the estimates by the pipe-model method. Below-ground total biomass (BGB) is the sum of coarse root biomass after lost roots correction and small root biomass by the pipe-model method. Four plots (P1–P4) were established before logging in a primary lowland dipterocarp forest at Compartment 47 in the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia.

Plot	Above ground (Mg ha ⁻¹)			Below ground (Mg ha ⁻¹)				Stand Total		
	Stem & Branch	Leaf	Above-total AGB	Coarse root		Total	Small root	Below-total BGB	Total (Mg ha ⁻¹)	BGB/AGB B/A
				No correction	Lost roots					
P1	536	6.3	542	63.7	17.8	81.5	14.0	95.5	638	0.18
P2	642	5.8	648	77.8	25.0	103	15.0	118	766	0.18
P3	432	4.9	436	52.3	15.3	67.6	11.1	78.7	515	0.18
P4	513	5.7	519	61.2	17.6	78.8	13.0	91.8	611	0.18
Mean	531	5.7	536	63.8	18.9	82.7	13.3	95.9	632	0.18
SD	87	0.6	87	10.6	4.2	14.7	1.7	16.2	103	0.00

DISCUSSION

Methodological advantages and limitations

In this study size–mass allometric equations were first developed for estimating coarse-root biomass in a lowland dipterocarp forest, based on measurements of over 100 root systems. In South-East Asia, tree root mass has been directly examined in several tropical forest systems, including seasonal rain forest in Cambodia (Hozumi *et al.* 1969) and evergreen forest in Thailand (Ogawa *et al.* 1965). However, the largest trees sampled in the previous studies were relatively small; the maximum dbh of the trees sampled by Hozumi *et al.* (1969) and Ogawa *et al.* (1965) was 25.8 and 15.1 cm, respectively. The numbers of root-excavated trees examined were also limited ($n = 8$ and 3, respectively). In contrast, our data cover almost the entire range of tree sizes (dbh = 0.5–116 cm) likely to be encountered in typical old-growth dipterocarp forest in the study region. Notably, the diameter of the largest excavated *Dipterocarpus cornutus* individual was close to the maximum stem diameters recorded in the four plots. For instance, the maximum dbh recorded in a 6-ha census plot of the Forest Reserve was *c.* 125 cm (Niiyama *et al.*, unpubl. data) and the dbh of the largest tree examined in the 1970s IBP study of the allometry of above-ground parts, mentioned above, was *c.* 102 cm (Kato *et al.* 1978).

The accuracy of forest biomass estimates inevitably depends on both the quality and quantity of data used for developing size–mass allometric equations. Kato *et al.* (1978) reported that allometric regressions between size parameters (e.g. dbh²*H*) and the dry mass of above-ground components (e.g. stems), derived from abundant sample data ($n = 156$; maximum dbh = 102 cm) in the dipterocarp forest of Pasoh, showed high correlation with good linearity plotted on a log–log scale. Our data also showed high correlations and linearity, not only for above-ground components, but also for coarse roots (Eq. 1), and for trees of all sizes, including emergent trees. These findings suggest that the allometric equations developed in our study may be based on sufficiently accurate data from sufficiently large samples to provide robust estimates of biomass.

Another factor that may affect the accuracy of root biomass estimates is associated with sampling errors; coarse roots are broken and lost during root-system excavation. We estimated the amount of such lost roots and found that their proportion was significant (about 23% of total coarse roots). Attempts to apply a similar correction method for lost roots have already been made in an old forest of Douglas fir (*Pseudotsuga menziesii*) (Santantonio *et al.* 1977). The cited authors reported that the proportion of roots of the three largest trees they examined (dbh = 94–135 cm) that were lost

during root excavation amounted to 10.8–15.7% of the total root mass (fresh weight). The proportions are somewhat smaller than those we found. However, both studies suggest that coarse-root biomass is likely to be substantially underestimated, if there is no correction for roots missed during root sampling.

The correction method for lost roots involved making a proportional adjustment to estimated root masses, based on observed relationships between the diameters and dry masses of the lost roots of sampled root systems, and between dbh and total mass of lost roots at the individual-tree level. We anticipated that the proportion of roots missed during sampling might generally be larger for large trees than for smaller ones. Accordingly, the slope of Eq. (3), i.e. the coefficient *b* of the allometric equation linking dbh and the mass of lost roots (W_r) was significantly larger (3.42 versus 2.49) than the slope of Eq. (1), i.e. the coefficient *b* of the allometric equation linking dbh and the mass of coarse roots before correction for lost roots (M_c ; $P < 0.001$, ANCOVA). The difference suggests that the relative proportion of lost roots is not constant and tends to increase considerably with increases in tree size. To confirm this possibility, however, our correction method needs to be further improved by adding more data. This is because we only examined the diameter distribution of lost roots for a relatively small number of trees.

Small-root biomass was assessed by the two different approaches: theoretical calculation and soil-pit sampling method. Prior to the present study, Yamashita *et al.* (2003) reported that small-root biomass (<5 mm in diameter) was estimated to be about 9.7 Mg ha⁻¹ using a soil-coring method ($n = 15$, each 0–20 cm depth) in a 6-ha plot established within the Pasoh Forest Reserve. The estimates are somewhat smaller than those of small-root biomass (mean = 16.4 Mg ha⁻¹) in our study stand (Compartment 47) which were also obtained by exhaustive sampling of five soil pits (0–200 cm depth). However, our theoretical estimate of small-root biomass based on the pipe-model (13.3 Mg ha⁻¹) is close to and within the range of these values obtained using the direct sampling method. This concurrence provides at least some support for the key assumption; that the area-preserved branching pattern is applicable to tree root systems, as used for the calculation of small root mass at the individual level in our model approach (i.e. Eq. 5).

Richardson & Dohna (2003) tested the rule of constant total area branching using data on root systems of Douglas fir (*Pseudotsuga menziesii*) trees. Their results suggested that branching patterns differed somewhat by individual size, but the rule of constant total area was maintained. We have also examined branching patterns of roots of several tropical species, and confirmed that their root systems are likely to follow the rule of constant total area (Niiyama *et al.*, unpubl. data). However, tropical

trees display various types of root-system structures (Jenik 1976, Pavlis & Jenik 2000) and branching patterns may differ between species. Thus, more evidence is required to establish that the rule of constant total area root branching in various species can be generally applied to the estimation of fine-root biomass in tropical rain forests.

Carbon stocks and allocation in old-growth dipterocarp forest

Compared with other tropical forests, the above-ground total biomass (AGB) in the old-growth dipterocarp forest (536 Mg ha^{-1}) we examined here is much larger than that reported for seasonal rain forests ($<c. 300 \text{ Mg ha}^{-1}$) in South-East Asia or South America. Our estimate falls in the upper range of AGB of old-growth evergreen rain forests ($c. 400\text{--}650 \text{ Mg ha}^{-1}$) (Hozumi *et al.* 1969, Kira 1978; see also reviews by Clark *et al.* 2001b, Houghton *et al.* 2001, Yamakura *et al.* 1986). The below-ground total biomass (BGB) of our study forest (95.9 Mg ha^{-1}) also seems to be relatively large for tropical forests, although little comparable information is available on coarse-root biomass obtained using the allometric method.

BGB/AGB ratios of tropical forests have been reviewed using published data and several mean values have been suggested: for example, about 0.19 (Jackson *et al.* 1996) and 0.24 (Cairns *et al.* 1997). The BGB/AGB we obtained for our dipterocarp forest (0.18) is very similar to, or slightly smaller than, these global-scale mean values. Furthermore, these review studies indicate that the BGB/AGB ratio varies depending on the absolute biomass value. For example, according to data presented in the two articles (Cairns *et al.* 1997, Chave *et al.* 2005), the ratio is about 0.14 for stands with relatively high biomass ($n = 7$; $\text{AGB} > 300 \text{ Mg ha}^{-1}$), while it is up to 0.19 if data are obtained from stands of lower biomass ($n = 12$; $\text{AGB} > 200 \text{ Mg ha}^{-1}$). Since our old-growth forest has relatively high biomass ($\text{AGB} > 500 \text{ Mg ha}^{-1}$), the relatively low BGB/AGB ratio is consistent with this postulated pattern of above- and below-ground biomass partitioning in tropical rain forests. However, it should also be noted that soil fertility is generally low in the study forest (Yamashita *et al.* 2003) and the reason why relatively little carbon is allocated to roots in this forest, despite the paucity of nutrients in the soil, is unclear.

During the IBP study of the 1970s mentioned above, the coarse-root biomass of the old-growth dipterocarp forest in the Pasoh Forest Reserve was estimated by assuming that it was equivalent to 10% of AGB (Kira 1969). Small-root biomass (roots $< 1 \text{ cm}$ in diameter) was also estimated using a soil-core sampling method (Kato *et al.* 1978, Kira 1978). According to the IBP estimates, the BGB/AGB ratio of the investigated site was about 0.14; substantially lower than the BGB/AGB ratio (0.18) obtained in the

present study. The research plots for tree censuses used in the IBP study and ours were not identical. However, both stands were similar in terms of tree density and size structure. Furthermore, the estimate of small-root biomass of the IBP plots ($c. 20 \text{ Mg ha}^{-1}$) is close to that of our study stand ($c. 16 \text{ Mg ha}^{-1}$; pipe-model method). Thus, the discrepancy in BGB/AGB ratio is mainly due to the lower assumed proportional mass of coarse roots (10% of AGB) used in the IBP study; if the revised allometric equation for coarse-root mass (Eq. 4) is applied to the IBP census data (Kira & Yoneda, pers. comm.), BGB/AGB becomes close to 0.18.

Allometric scaling has long been a debated topic in biology (Enquist *et al.* 1998, West *et al.* 1997), but recent theoretical advances provide insights in the partitioning pattern of plant organs (Enquist & Niklas 2001, 2002; Niklas 2003). The WBE (West–Brown–Enquist) theory predicts that both AGB and BGB are proportional to $\text{dbh}^{8/3}$, and that tree height is proportional to $\text{dbh}^{2/3}$ in various forest communities. Our results of corresponding allometric equations, which were based on the dataset of an old-growth tropical rain forest, do not support the prediction well. Thus, re-evaluation of such a general allometric theory may be required by gathering more datasets of various forest types.

Concluding remarks

We found that the dbh-based allometric equations for coarse-root mass before correction for lost roots (Eq. 1) gave a good fit to the data we acquired, even including data for some emergent trees and a wide range of species. From a practical viewpoint, our equation may be useful for evaluating below-ground carbon stocks in other stands of old-growth dipterocarp forests in South-East Asia, especially in cases where long-term tree census data are available, but only above-ground carbon stocks have been evaluated as yet (Hoshizaki *et al.* 2004, Kato *et al.* 1978, Kira 1978, Okuda *et al.* 2004, Yamakura *et al.* 1986). Use of our allometric equation for coarse roots may then allow the evaluation of time trends of forest carbon stocks in both above- and below-ground parts. For this purpose, a revised equation (Eq. 4), in which the amount of lost coarse roots is incorporated, seems more appropriate than the primary allometric equation derived without the correction (Eq. 1).

In this study, we did not estimate the biomass of relatively small individuals ($\text{dbh} < 5 \text{ cm}$) in the census plots, since smaller trees may contribute only a small proportion of total biomass in old-growth tropical rain forests (Yamakura *et al.* 1986). Our analysis indicated that the D_0 -based allometric equations for coarse-root mass (Eq. 1–3) provide the best model for smaller individuals, rather than equations based on other size parameters (dbh , $D_{0.3}$). If necessary, the equation can be used for estimating carbon stocks in such smaller

trees. However, not only smaller trees but also other plant species (e.g. palms, lianas and herbaceous species) may be important components of total carbon stocks in tropical forests (Clark *et al.* 2001a, b). This, and other relevant issues, should be further addressed by collecting sample data and applying specific methods of biomass estimation to these other components.

ACKNOWLEDGEMENTS

We thank the Forestry Department of Negeri Sembilan for permission to use the logging site for our study. We profoundly thank the late Professors K. Yoda and H. Ogawa for encouraging our studies in Pasoh, and Drs T. Kira and T. Yoneda for providing us the original census and sampling data obtained in the IBP project. We also thank Drs T. Okuda and Rahim Nik for their leadership and efforts on NIES/FRM/UPM projects. We appreciate valuable comments on an early version of the manuscript from Drs Y. Kiyono, Y. Chiba, T. Sato, S. Saito and Y. Niiyama. We thank Drs Y. Maruyama, H. Tanouchi, N. Ohsawa, S. Sasaki, S. Noguchi, N. Adachi, M. Ichikawa, S. Nishimura and T. Yagihashi for their kind support during our field study in Malaysia. We also greatly thank reviewers for their helpful comments and suggestions to improve the manuscript. This study was funded by the Ministry of Environment, Japan through the Global Environmental Research Program (grant nos. E-3, E-4 and S-1), and was supported in part by a Grant-in-Aid for Scientific Research (No. 19255012) from the Ministry of Education, Culture, Sports, Science and Technology in Japan.

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Appendix 1. Size dimensions and dry mass of each component of the sample trees (n = 121) used for biomass estimation. *D*₀, *D*_{0.3}, and dbh are stem diameters at ground level, 0.3 m height and breast height (1.3 m), respectively. Tree height (*H*) was directly measured after felling for some sample trees (n = 69). *Root* indicates dry mass of coarse roots before lost roots correction (n = 54), and *S & B* indicates mass of stem plus branch (n = 33). Sample trees are listed by order of species name and dbh. All sample trees were measured in a primary lowland dipterocarp forest at Compartment 47 in the Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia.

Species	Size				Dry mass		
	<i>D</i> ₀ (cm)	<i>D</i> _{0.3} (cm)	dbh (cm)	<i>H</i> (m)	Root (kg)	<i>S & B</i> (kg)	Leaf (kg)
<i>Aglai cordata</i>	2.0	1.9	1.5	2.9	0.082	0.326	0.030
<i>Aglai forbesii</i>			22.4	19.7	55.1		
<i>Aglai forbesii</i>			30.4	28.7	151	880	27.3
<i>Aglai odoratissima</i>			28.8	22.0	157		
<i>Alangium ebenaceum</i>	1.0	0.9	0.4	1.4	0.017	0.050	0.021
<i>Alangium ebenaceum</i>	2.7	2.0	1.0	2.1	0.067	0.224	0.024
<i>Alangium ebenaceum</i>		11.4	11.3	16.9	13.2	67.7	1.35
<i>Alangium ebenaceum</i>	1.0	0.8		1.2	0.022	0.032	0.016
<i>Alphonsea elliptica</i>			19.9	22.4	45.2		
<i>Alphonsea maingayi</i>	1.5	1.3	0.8	1.6	0.038	0.100	0.033
<i>Alphonsea maingayi</i>	2.2	1.1	0.8	2.5	0.100	0.120	0.016
<i>Anaxagorea javanica</i>	1.3	1.2	0.7	1.7	0.030	0.055	0.012
<i>Anaxagorea javanica</i>	1.0	0.9	1.1	1.6	0.019	0.039	0.020
<i>Anaxagorea javanica</i>	2.0	1.6	1.2	2.5	0.065	0.173	0.031
<i>Anaxagorea javanica</i>	2.1	1.7	1.3	3.1	0.069	0.260	0.026
<i>Anaxagorea javanica</i>	2.3	1.7	1.3	3.0	0.059	0.245	0.050
<i>Anaxagorea javanica</i>	1.9	1.7	1.4	3.0	0.072	0.223	0.048
<i>Anaxagorea javanica</i>	2.9	2.2	1.4	3.3	0.111	0.515	0.096
<i>Anaxagorea javanica</i>	3.6	2.9	1.5	3.0	0.185	0.516	0.044
<i>Anaxagorea javanica</i>	3.1	2.7	2.0	3.6	0.145	0.674	0.059
<i>Anaxagorea javanica</i>	3.4	2.5	2.0	3.4	0.166	0.625	0.101
<i>Anaxagorea javanica</i>	3.8	2.8	2.0	3.9	0.247	0.738	0.066
<i>Anaxagorea javanica</i>	4.7	4.0	3.5	5.6	0.479	2.05	0.261
<i>Anaxagorea javanica</i>	6.8	5.3	4.8	6.9	0.726	5.06	0.504
<i>Anisoptera laevis</i>	3.8	3.4	2.3	3.0	0.369	0.807	0.042
<i>Anisoptera laevis</i>			27.8	24.1	110		
<i>Aporusa falcifera</i>	1.0	0.8		0.7	0.013	0.019	0.004
<i>Aporusa microstachya</i>	1.7	1.4	1.1	1.9	0.039	0.120	0.032
<i>Aporusa miqueliana</i>	1.8	1.5	1.1	2.0	0.153	0.146	0.039
<i>Aporusa miqueliana</i>	2.6	2.4	2.1	4.0	0.168	0.931	0.054
<i>Aporusa nigricans</i>	1.7	1.6	1.3	3.9	0.058	0.307	0.005
<i>Aporusa prainiana</i>		2.1	1.7	3.6	0.118	0.517	0.092
<i>Ardisia crassa</i>	1.0	0.8		0.9	0.009	0.017	0.005
<i>Ardisia sp. 2</i>	1.7	1.5	1.1	2.7	0.055	0.185	0.028
<i>Atuna elata</i>	2.7	2.5	2.2	5.3	0.199	0.771	0.097
<i>Barringtonia pendula</i>	5.7	4.8	3.7	5.1	1.62	2.15	0.024
<i>Buchanania sessifolia</i>	3.3	2.6	2.4	4.9	0.190	0.854	0.124
<i>Calophyllum dioscurii</i>			13.3	18.9	7.61		
<i>Casearia sp.</i>	0.0	6.8	6.2	9.5	2.05	13.9	0.734
<i>Dacryodes rostrata</i>	1.4	1.5	1.0	2.1	0.026	0.105	0.012
<i>Dacryodes rostrata</i>	8.7	7.6	7.2	12.6	2.07	15.7	0.745
<i>Dacryodes rugosa</i>	1.5	1.4	0.8	2.7	0.030	0.139	0.020
<i>Dacryodes rugosa</i>		3.9	3.4	7.0	0.748		
<i>Dacryodes rugosa</i>		5.0	4.3	7.5	0.849	5.30	0.435
<i>Dacryodes rugosa</i>	0.7	0.5		0.6	0.004	0.007	0.003
<i>Diospyros apiculata</i>	1.1	1.0	0.7	1.6	0.020	0.038	0.006
<i>Diospyros buxifolia</i>	3.6	3.4	3.1	7.2	0.410	2.67	0.094
<i>Diospyros latisejala</i>	7.5	7.1	6.3	12.2	1.95	17.2	1.02
<i>Diospyros penangiana</i>	2.2	1.8	1.0	1.9	0.101	0.196	0.019
<i>Dipterocarpus costulatus</i>			66.7	40.4	534	6100	72.0
<i>Dipterocarpus costulatus</i>			116	50.0	2945		
<i>Drypetes pendula</i>			42.2	33.4	165		
<i>Eugenia sp.</i>		14.4	13.7	20.3	28.1	176	5.11
<i>Eurycoma longifolia</i>	9.7	8.2	7.5	14.5	3.43	19.9	0.421
<i>Ganua sp. 1</i>	8.4	7.2	6.3	12.3	1.17	12.1	1.29
<i>Ganua sp. 1</i>				27.5	20.3	76.0	
<i>Gironniera nervosa</i>	1.1	0.8		1.3	0.007	0.024	0.009

Appendix 1. Continued.

<i>Gironniera parvifolia</i>	7.6	6.7	5.9	13.2	1.01	10.1	0.442
<i>Gironniera parvifolia</i>	11.8	10.8	10.2	14.9	3.32	42.2	0.641
<i>Glycosmis chlorosperma</i>	1.5	1.1	0.9	2.7	0.024	0.148	0.019
<i>Gonocaryum gracile</i>	2.2	1.9	1.0	2.1	0.266	0.241	0.012
<i>Homalium dictyoneurum</i>		8.6	7.0	12.1	4.96		
<i>Homalium longifolium</i>		5.3	5.8	7.9	1.79	6.47	0.362
<i>Hopea dryobalanoides</i>		10.0	9.4	11.5	2.96	30.2	3.42
<i>Hopea dryobalanoides</i>			9.9	19.0	5.75		
<i>Ilex macrophylla</i>		1.6	1.1	2.6	0.081	0.164	0.036
<i>Ixora</i> sp.	1.5	1.2	0.9	2.8	0.029	0.118	0.018
<i>Knema furfuracea</i>	2.5	2.2	1.7	3.5	0.066	0.537	0.062
<i>Koompassia malaccensis</i>			53.0	46.2	578	5800	10.9
<i>Lithocarpus curtisii</i>	0.0	6.5	5.9	10.6	1.88	11.1	0.695
<i>Lithocarpus encleisacarpus</i>			9.6	15.9	9.06		
<i>Lithocarpus wallichianus</i>	1.6	1.4	1.2	2.9	0.086	0.224	0.041
<i>Macaranga lowii</i>		3.0	2.8	5.0	0.440	1.18	0.074
<i>Melanochyla</i> sp. 1	1.3	1.1		0.9	0.017	0.037	0.010
<i>Memecylon megacarpum</i>		3.2	2.7	4.0	0.207	1.78	0.367
<i>Mesua ferrea</i>	1.7	1.6	1.1	3.8	0.069	0.288	0.045
<i>Microdesmis casearifolia</i>	1.8	1.4	1.0	2.0	0.089	0.140	0.052
<i>Mitrephora maingayi</i>	1.6	0.8	0.9	1.0	0.071	0.032	0.013
<i>Monocarpia marginalis</i>	1.1	0.9		1.0	0.010	0.026	0.009
<i>Myristica cinnamomea</i>	2.9	2.7	2.3	4.8	0.076	0.944	0.128
<i>Neoscortechinia kingii</i>		27.9	26.1	25.8	98.5	719	7.18
<i>Neoscortechinia kingii</i>		31.8	27.7	28.5	132	902	6.60
<i>Nothaphoebe umbelliflora</i>			17.4	26.0	26.3		
<i>Ochanostachys amentacea</i>			56.0	33.9	644		
<i>Parashorea densiflora</i>			4.8	9.2	2.16		
<i>Payena lucida</i>	2.2	1.8	1.5	4.2	0.108	0.400	0.027
<i>Payena lucida</i>		7.4	5.6	7.9	2.38	8.89	0.387
<i>Phaeanthus ophthalmicus</i>	1.3	1.1		1.2	0.015	0.031	0.008
<i>Polyalthia cinnamomea</i>		2.8	2.4	4.9	0.201	1.17	0.092
<i>Polyalthia sumatrana</i>		1.6	1.2	2.0	0.070	0.136	0.023
<i>Ptychopyxis costata</i>	1.8	1.5	1.0	1.9	0.068	0.120	0.015
<i>Ptychopyxis costata</i>	2.5	1.9	1.2	2.4	0.136	0.205	0.011
<i>Quercus gemelliflora</i>			44.8	35.9	212		
<i>Rinorea anguifera</i>	2.5	1.9	0.7	2.0	0.156	0.198	0.006
<i>Rinorea anguifera</i>	0.9	0.6		0.7	0.013	0.011	0.002
<i>Rinorea anguifera</i>	1.0	0.8		0.9	0.024	0.022	0.006
<i>Rinorea anguifera</i>	1.1	0.7		1.1	0.047	0.023	0.004
<i>Ryparosa acuminata</i>			20.4	21.8	71.3		
<i>Santiria apiculata</i>			12.4	15.2	18.0	128	4.01
<i>Santiria apiculata</i>	0.7	0.5		1.1	0.008	0.014	0.007
<i>Santiria</i> sp.	1.0	0.8		1.2	0.017	0.028	0.004
<i>Saprosma scortechinii</i>	2.2	1.8	1.5	2.3	0.025	0.341	0.024
<i>Sarcotheca griffithii</i>			13.9	17.8	18.7		
<i>Scaphium macropodium</i>	2.1	1.8	1.3	1.8	0.073	0.189	0.007
<i>Schoutenia accrescens</i>			21.0	22.9	89.8		
<i>Shorea lepidota</i>			46.8	35.0	226	2090	32.9
<i>Shorea macroptera</i>			13.8	16.2	10.1	57.2	2.55
<i>Shorea macroptera</i>	1.3	1.2		1.2	0.020	0.040	0.010
<i>Shorea maxwelliana</i>	2.8	2.4	1.0	2.0	0.153	0.292	0.031
<i>Sindora coriacea</i>			74.0	38.4	1250		
<i>Xanthophyllum affine</i>			22.5	18.5	51.6		
<i>Xanthophyllum eurhynchum</i>	2.4	1.8	0.8	2.1	0.112	0.244	0.010
<i>Xanthophyllum eurhynchum</i>	5.8	4.1	3.1	4.6	0.699	2.27	0.143
<i>Xerospermum noronhianum</i>	0.9	0.8	0.4	1.6	0.039	0.045	0.005
<i>Xerospermum noronhianum</i>		1.9	1.6	3.1	0.129	0.362	0.052
<i>Xerospermum noronhianum</i>		23.7	21.1	19.0	74.5	419	11.2
Unknown	1.9	1.7	0.4	1.7	0.080	0.081	0.002
Unknown	1.0	0.9	0.7	1.5	0.010	0.062	0.002
Unknown	4.1	3.9	3.8	5.1	0.529	2.04	0.251
Unknown	7.1	6.1	5.8	10.2	0.828	12.7	0.483
Unknown		26.4	23.0	19.3	64.2	552	5.42