Forest Ecology and Management 259 (2010) 505–513

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Landscape-scale variation in the structure and biomass of the hill dipterocarp forest of Sumatra: Implications for carbon stock assessments

Yves Laumonier [a,*], Andreas Edin [b,1], Markku Kanninen [b,1], Agung W. Munandar [c,2]

[a] *Environment and Societies Department, UR 36, Center International for Research on Agronomy and Development (CIRAD), Montpellier, France*
[b] *Center for International Forestry Research (CIFOR), Bogor, Indonesia*
[c] *Direktorat Perencanaan Kawasan Hutan, Direktorat Jenderal Planologi Kehutanan – Ministry of Forestry, Jakarta, Indonesia*

A R T I C L E I N F O

Article history:
Received 12 August 2009
Received in revised form 4 November 2009
Accepted 8 November 2009

Keywords:
Carbon stocks
Above-ground biomass
Landscape-scale variation
Tropical rain forest
Hill dipterocarp forest
Sumatra

A B S T R A C T

One of the first steps in estimating the potential for reducing emissions from deforestation and forest degradation (REDD) initiatives is the proper estimation of the carbon components. There are still considerable uncertainties about carbon stocks in tropical rain forest, coming essentially from poor knowledge of the quantity and spatial distribution of forest biomass at the landscape level.

We evaluate the influence of site and topography on forest structure, biomass and carbon stock over a forested landscape in Sumatra. Sixteen sites were selected across a landscape of ca. 1000 km^2, and within each site, a network of small 0.1 ha plots was laid down perpendicular to the major topographical gradient. Structural parameters for trees with diameter bigger or equal to 10 cm and major life forms were recorded for each plot. The total sampled area was 70.2 ha.

The above-ground biomass (AGBM) in the 16 sites ranged from 271 $\pm$ 19 to 478 $\pm$ 38 Mg ha^{-1}, with a mean of 361 $\pm$ 7 Mg ha^{-1}. This value is similar to the global 'tropical wet forest' estimate of Keith et al. (2009), but 23% higher than the biome default value given in the IPCC (2006) guidelines. Plots on acid tuff were the most distinctive in having fewer and smaller trees, with a resulting low AGBM. The number of stems was low, but the average tree diameter was larger on the nutrient-rich young volcanic andesitic soils. Landscape-scale variability of forest structure and dynamics was considerable. Within sites, there was little variation of mean height or mean diameter of the trees, but significant differences in stem density, basal area and AGBM between land facets. Both topography and geology appeared to affect the dynamics and the biomass of the forest.

At the same time, our findings confirm the need for caution in extrapolating data from small plots to larger spatial scales when estimating carbon stocks for a given forest type or a region. Our results for C stock values for Sumatra lowland and hill dipterocarp forests (135–240 Mg ha^{-1}, with a mean of 180 Mg ha^{-1}) showed higher variability in C stock values at landscape level than generally reported in the literature. Based on our results, stratified sampling is recommended for biomass and carbon estimation. Within an error range of 6–8% of the AGBM, a minimum area of 4–6 ha should be sufficient to estimate biomass with satisfactory accuracy at the landscape scale. Networks of several small plots across landscape are preferable to fewer larger plots, providing that the sampling is representative of the land facets in the area.

1. Introduction

The loss of ecological services provided by tropical rain forests (TRFs), together with the reduced availability of renewable resources, is of global concern. As a result of an increased awareness of climate change, the UNFCCC provides a common global framework for all parties to combat global warming, one that recognizes the critical role of these forests. TRFs play an important role in the global carbon cycle, and there are increasing concerns about their conversion being major sources of greenhouse gases (carbon dioxide, methane and nitrous oxide) (Kanninen et al., 2007; Nabuurs et al., 2007).

The Thirteenth Session of the Conference of Parties (COP 13) to the UNFCCC in Bali in December 2007 produced a roadmap for reducing emissions from deforestation and forest degradation (REDD). Among the issues of the "readiness" for REDD initiatives are the availability of good quality reference data, and a fair distribution of payments for ecosystem services among those responsible for deforestation. One challenge of REDD is to quantify

* Corresponding author at: Center for International Forestry Research (CIFOR), P.O. BOX 6596, JKPWB, Jakarta 10065, Indonesia. Tel.: +62 251 8622622/+33 467 59 37 61; fax: +62 251 8622100/+33 467 59 39 09.
E-mail addresses: y.laumonier@cgiar.org, yves.laumonier@cirad.fr (Y. Laumonier), a.edin@cgiar.org (A. Edin), m.kanninen@cgiar.org (M. Kanninen), awe@dephut.go.id (A.W. Munandar).
[1] Tel.: +62 251 8622622; fax: +62 251 8622100.
[2] Tel.: +62 21 573 0212; fax: +62 21 572 0216.

0378-1127/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2009.11.007

nations' carbon emissions from deforestation and forest degradation. For this, better information on deforestation rates (derived from remote sensing) and carbon stocks and storage is still needed (Gibbs et al., 2007). As far as remote sensing studies are concerned, the assessment of the long-term global trend in tropical forest areas and deforestation rates is far from being error-free (Grainger, 2008). Accurate estimation of the carbon stocks of the reference case is a basic step in the process of REDD, but data on carbon stocks cannot currently be obtained directly over large areas from remote sensing (DeFries et al., 2007). This requires quantifying above-ground biomass on the ground. For forest carbon stocks, many studies have already emphasized the need to develop specific biomass models for each region and forest type (Brown et al., 1989; Brown, 1992; Brown and Iverson, 1992; Segura and Kanninen, 2005), and that caution should be exercised when using general models of total above-ground biomass in carbon projects (Noble et al., 2000). The Intergovernmental Panel on Climate Change (IPCC, 2006) gives a biome default value of 146 Mg C ha^{-1} for the 'tropical wet forest', but there are still considerable uncertainties about carbon stocks in such an environment, which makes current estimates of carbon source from changes in tropical land use to the atmosphere inaccurate and imprecise. This uncertainty comes from, among others, poor knowledge of the quantity and spatial distribution of forest biomass at landscape-level, often extrapolated from very small forest plots.

The AGBM of a number of South East Asian vegetation types has been studied – secondary forests and regrowth (Hashimotio et al., 2000; Ketterings et al., 2001; van Noordwijk et al., 2002; Brearley et al., 2004; Jepsen, 2006); mangroves (Komiyama et al., 1988; Kusmana et al., 1992); peat swamps (Brady, 1997); and Kerangas[3] forest (Bruenig, 1974) – but very few old-growth, well-drained lowland and hill TRF sites (Kato et al., 1978 in Pasoh, Malaysia; Yamakura et al., 1986 in East Kalimantan; Kohyama et al., 1989 in Ulu Gadut, West Sumatra; and more recently, Samalca, 2007 and Basuki et al., 2009 in Berau, East Kalimantan). The studies of old-growth, well-drained lowland and hill TRFs are unduly low when one considers the large extent covered by such forests. More measurements of biomass across the region are needed, especially to get better understanding of its variation and distribution within the forest landscape, and of the factors, such as soil type, geology, and topographic position, affecting variations in forest structure.

The aim of this study was to evaluate the influence of site (geology/geomorphology) and topographic positions (within-the-site-variation) on forest structure, above-ground biomass and carbon stocks over a large (800–1000 km^2) landscape of old-growth tropical rain forest in South and Central Sumatran Hill Dipterocarp rain forest area. The original data for this study were collected in the late 1990s in the context of a landscape-scale ecological study of the Sumatran tropical rain forest, aimed at providing recommendations for conservation and forest management.

2. Study sites and the methods used

The sample plots were located within the ecological zones and forest types defined by Laumonier et al. (1986) and Laumonier (1997) for Sumatra. The sampling was planned to be representative of the larger landscape, trying to cover and encompass the diversity of geology, soil types, watersheds, and main topographic positions within the hill forest zone.

We used a stratified systematic sampling design across the major environmental gradients for the area (geology and elevation). The total forest area was first stratified using satellite images combined with data on climate (one bioclimatic zone, mean temperature of the coldest month $\geq$20 °C, mean annual rainfall between 2500 and 3500 mm with a few areas receiving up to 4000 mm, mean number of dry months $\leq$2), topography (one elevation zone between 300 and 800 m, with moderate to steep slopes, usually less then 150 in length and sometimes less then 50 m), and 16 geologies (in the absence of soil maps). Such pre-stratified study sites were taken to be homogeneous in term of environmental variables relevant to vegetation, and the sites for forest sampling were selected within these strata. The 16 Hill Evergreen Rain Forest sites (sensu Whitmore, 1984) represent a total of 70.2 ha sampled over a range of geological/geomorphology situations (young and old volcanic, sedimentary, metamorphic) rocks across a landscape of 800–1000 km^2 (Fig. 1 and Table 1).

Within each site, 2.6–6 ha of forest were sampled using a network of small 0.1 ha survey plots laid down approximately every 100 m along transects perpendicular to the major topographical gradient. Positioned in this way, forest sample plots covered a whole range of land facets, which are defined here in terms of their topographic position (valley bottom, lower slope, mid-slope, upper slope, ridge). Such a design maximizes the habitat range of data collected and is considered to be more suitable for extrapolation to landscape level and modeling purpose (Grace et al., 1995; Laurance et al., 1999). This design also helps to separate the effects of soil type according to topographic position on different geologies.

In each plot, diameter at breast height (DBH) $\geq$10 cm (measured at 1.3 m or above buttresses or trunk anomalies) was measured for each tree, as well as the height of the first branch, measured using a Haga altimeter. Height measurements are difficult in TRF. Using the same team of surveyors and often calibrating and checking measurements with the help of the tree climbers collecting botanical samples, we estimated typical error to be less than 5 m for the tall trees and less than 1 for the shorter ones. The contribution of the major life forms in the forest structure (trees and shrubs estimated crown projection cover) and number of standing palms, screwpines, bamboos, rattans and other climbers) was also recorded (Table 2). Altogether 702 plots were sampled and 34 988 individual trees representing 1233 morphospecies measured.

In the absence of destructive sampling measurements for Sumatra, we choose to use the equation for the Moist Tropics (Brown, 1997, updated in Pearson et al., 2005) to estimate the above-ground biomass (AGBM) of the trees:

$$\mathrm{AGBM} = \exp(-2.289 + 2.649 \times \ln \mathrm{DBH}^{-0.021} \times \ln \mathrm{DBH}^2) \qquad (1)$$

where DBH is the diameter at breast height. This allometric model is a generic one, based on data from the three main tropical regions. An alternative would have been to use the allometric model developed by Yamakura et al. (1986), based on destructive sampling measurements in Indonesian Borneo lowland forest. The Yamakura data set actually has been used by Brown and colleagues in both their original model and the updated version. The biomass values obtained by using the Eq. (1) were converted into C by multiplying them by 0.5.

To calculate the relationship between the sampling intensity (number of plots) and standard error of the mean AGBM, we used 1000 bootstrapped recalculations of the mean AGBM using sub-samples (with replacement) of between 25 and 700 plots.

3. Results

3.1. Variation of forest structure and biomass within sites

In general, variation in mean height and mean DBH of the trees within each site did not exceed 10% of the overall site means.

[3] Tropical formations of very diverse forest associations from tall to low closed forest with a xeromorph and sclerophyll physiognomy on sandy soils; known also rather incorrectly as "Heath forest", because the physiognomy of the degraded forms reminds that of the European heaths.

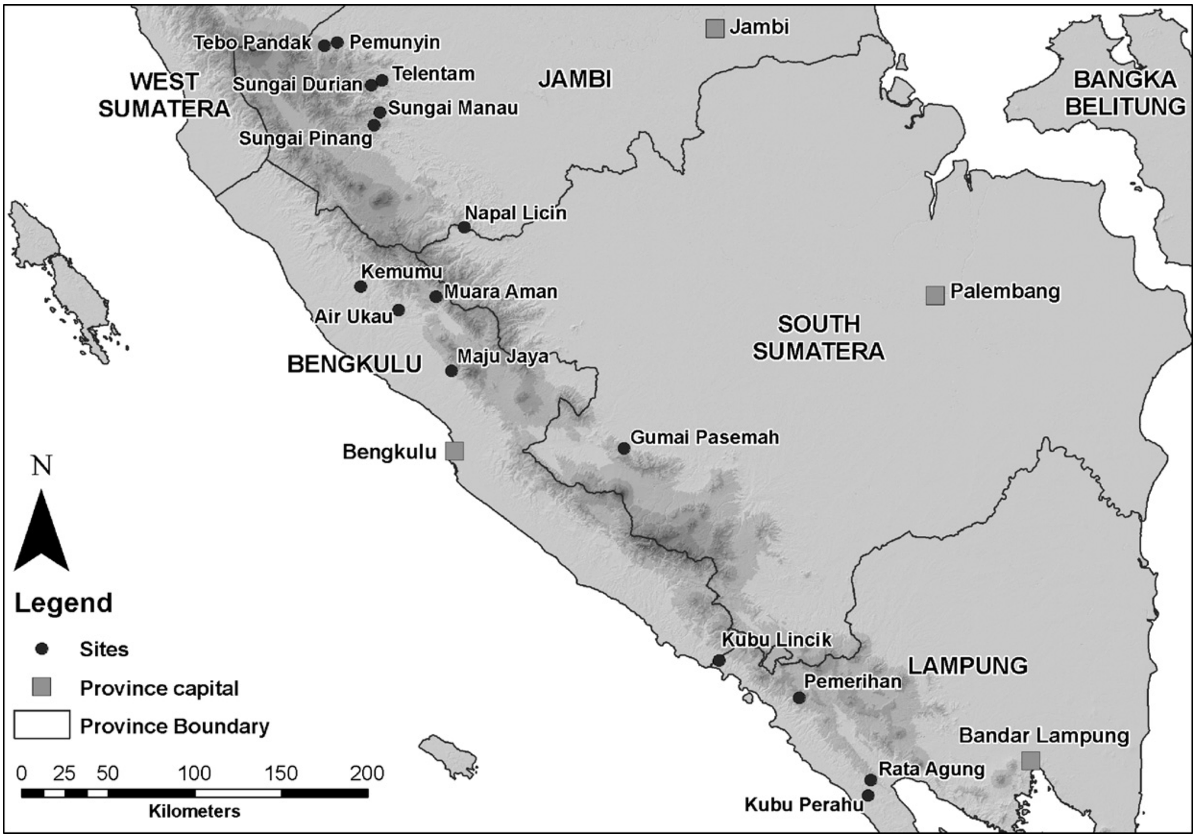

Fig. 1. Research sites in the provinces of Bengulu, Jambi, Lampung, and South Sumatra. For site coordinates, see Table 1.

However, more significant differences (as high as factor 2–3) were observed in stem density (number of trees ha^{-1}), BA (m^2 ha^{-1}) and AGBM (Mg ha^{-1}) between land facets (Fig. 2). In most cases, the lowest values occurred for plots in valley bottoms and the highest for plots on flat, large ridges. The AGBM was as low as 208 ± 49 Mg ha^{-1} (10 plots, in total 1 ha) for some forests in valleys and lower slopes on acid tuffs substratum, and as much as 654 ± 97 Mg ha^{-1} (12 plots, total 1.2 ha) in very dense forests on large ridges of young volcanic material.

Crown coverage per layer (mean% crown cover per strata) was not affected by topographical position, and it had no obvious pattern. The total crown coverage per land facet was higher (closed canopies) on ridges and valleys than on slopes. The density (number of trees ha^{-1}) of saplings and small trees was affected by topographical position, with higher numbers of saplings and small trees on slopes. This was also the case for liana and rattans for most of the sites. Epiphytes were usually more abundant in plots on lower slopes and in valleys.

3.2. Variation of forest structure and biomass between sites

Box plot analysis of the data between sites showed more variation in stem density and mean height than with biomass (Fig. 3).

Estimates of the density of trees (number of trees ha^{-1}) and of their contribution to total AGBM varied among sites by almost a factor of 2. The AGBM at the 16 sites ranged from 271 ± 19 to 478 ± 38 Mg ha^{-1}, with a mean of 361 ± 7 Mg ha^{-1} (Table 3). At the

Table 1
Study site locations, total area sampled, and physiography of the site (one climatic zone).

Site code	Site	Province	Latitude	Longitude	Area sampled (ha)	Altitude range (m)	Geology
1	Tebo Pandak	Jambi	1°41′19″	101°35′31″	3.3	400–550	Young andesite
2	Pemunyin	Jambi	1° 40′23″	101°39′37″	2.6	350–550	Granite
3	Sungai Durian	Jambi	1° 53′38″	101°50′13″	4.5	300–600	Sandstone (mainly)
4	Telentam	Jambi	1°52′11″	101°53′32″	4.5	300–600	Old andesite
5	Sungai Pinang	Jambi	2°06′13″	101°51′01″	4.3	300–600	Young andesite
6	Sungai Manau	Jambi	2°02′07″	101°52′52″	4.5	350–650	Granites (mainly)
7	Napal Licin	South Sumatra	2°38′08″	102°19′06″	4.5	400–550	Old andesite
8	Kemumu	Bengkulu	2°56′33″	101°46′54″	4.5	350–650	Andesitic
9	Muara Aman	Bengkulu	2°59′44″	102°10′13″	4.5	500–800	Metasediment
10	Air Ukau	Bengkulu	3°03′58″	101°58′34″	4.5	300–350	Granite (mainly)
11	Maju Jaya	Bengkulu	3°22′55″	102°15′00″	4.5	300–500	Andesitic
12	Gumai Pasemah	South Sumatra	3°47′06″	103°08′39″	4.5	350–550	Sandstone
13	Kubu Lincik	Lampung	4°53′15″	103°38′17″	4.5	400–600	Andesitic
14	Pemerihan	Lampung	5°05′00″	104°03′11″	4.5	250–350	Acid Tuff
15	Rata Agung	Lampung	5°30′38″	104°25′26″	6.0	300–450	Andesitic
16	Kubu Perahu	Lampung	5°35′21″	104°24′36″	4.5	600–800	Basalt to andesitic

Table 2
Recorded variables in the plots.

Variable	Explanation
Emergent trees	Crown cover of emergent trees (DBH ≥ 50 cm)
Upper canopy	Crown cover for trees (30 ≤ DBH < 50 cm)
Lower canopy	Crown cover for trees (10 ≤ DBH < 30 cm)
Pole trees	Crown cover trees (DBH < 10 cm and height > 4 m)
Sapling	Crown cover trees (DBH < 10 cm and height < 4 m)
Shrubs	Crown cover shrubs (1.5 m ≤ height < 4 m)
Palm	Number of palms
Pandan	Number of pandans
Rotan solitary	Number of solitary rattans
Rotan cluster	Number of cluster of rattans
Liana <5 cm	Number of climbers DBH < 5 cm
Liana ≥5 cm	Number of climbers DBH ≥ 5 cm
Bamboo	Number of bamboos
Epiphytes	Code of abundance of epiphytes (0 none to 4 very abundant)

general landscape level, valleys and lower slopes have the smallest AGBM value of 315 ± 12 Mg ha^{-1}, slopes average 354 ± 9 Mg ha^{-1}, and ridges attain 436 ± 20 Mg ha^{-1}. The frequency distribution of AGBM values across the sites showed peaks in values in the 300–330 and 390–420 Mg ha^{-1} ranges (Fig. 4). Classically, for undisturbed forest, the highest number of trees occurs in the lowest diameter classes, giving a reverse J-shaped distribution. This was the case for the sites sampled here (Fig. 5a). In contrast, most of the AGBM was concentrated in the DBH range from 20 to 69.9 cm (Fig. 5b), accounting for 59.5% of the total AGBM. Larger trees (DBH ≥ 70 cm) cm) comprised 33% and smaller trees (10 ≤ DBH ≤ 19.9 cm) constituted 7.5% of the total AGBM, respectively.

Plots on acid tuff supported fewer and smaller trees, on average, than most other sites, and a correspondingly low basal area and estimated AGBM. Plots on nutrient-rich soils derived from young andesitic rocks had fewer stems compared with other sites, but larger average tree diameter (Table 3).

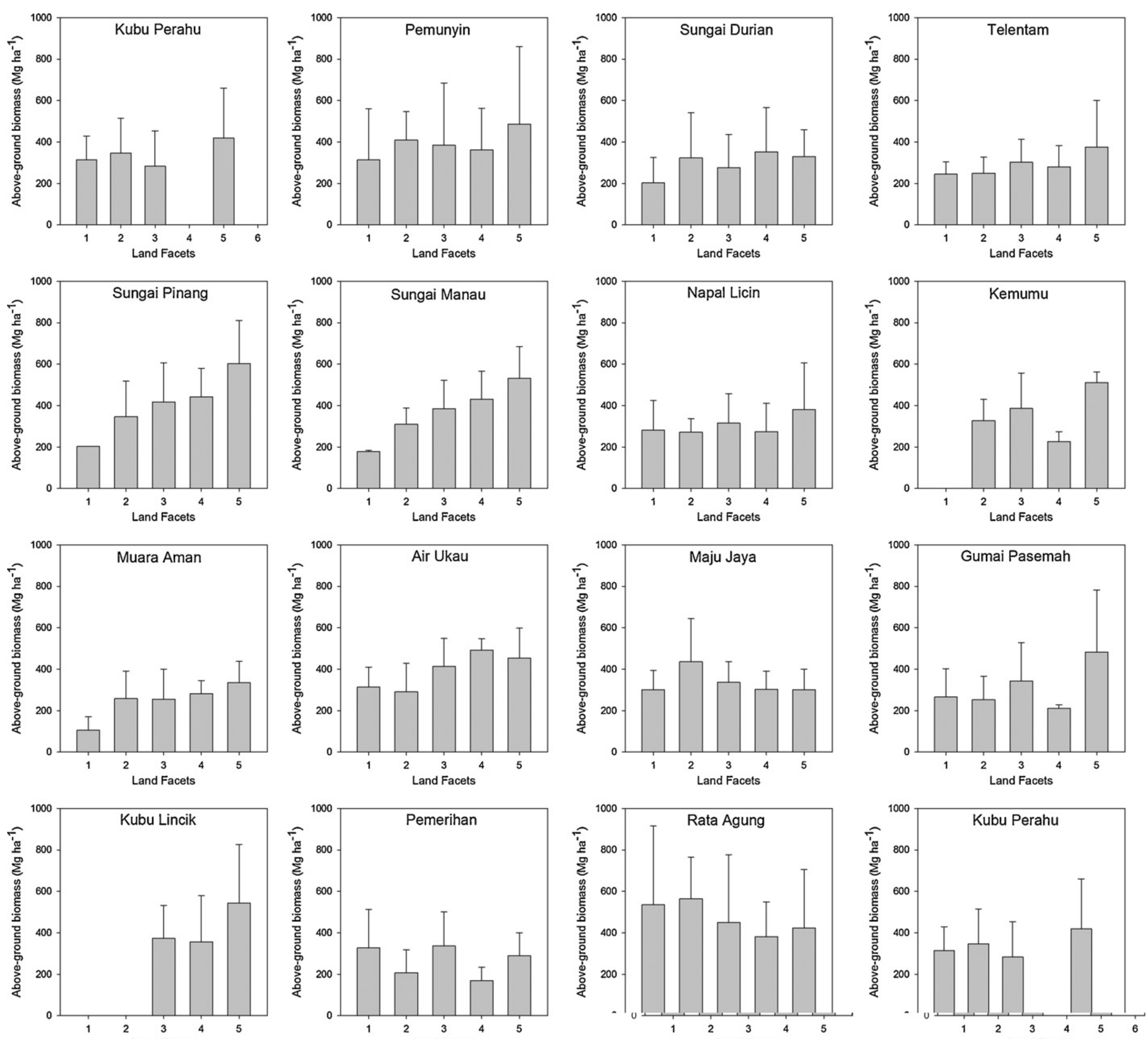

Fig. 2. Above-ground biomass (Mg ha^{-1}) in different land facets 1–5 (1 = valley bottom; 2 = lower slope; 3 = mid-slope; 4 = upper slope; 5 = ridge) and sites. Bars indicate standard error of the mean.

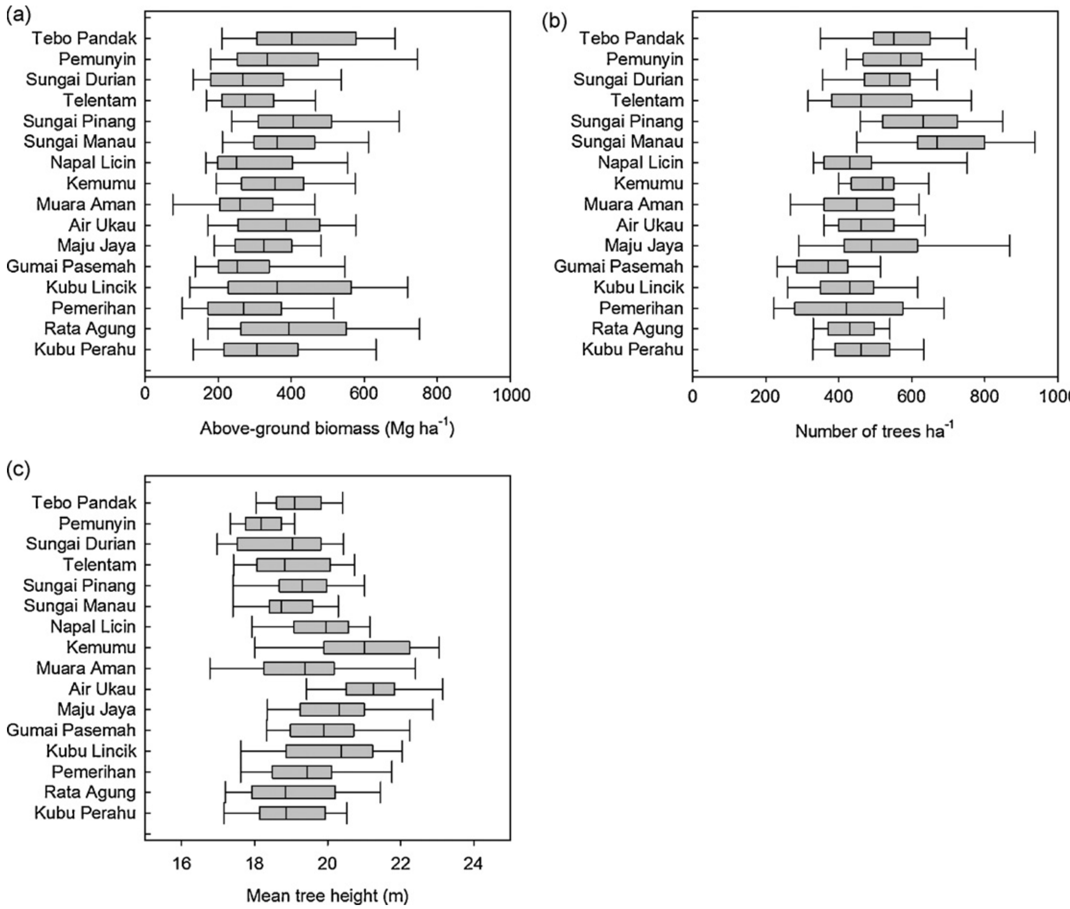

Fig. 3. (a) Above-ground biomass (Mg ha^{-1}). (b) Number of trees per ha. (c) Mean tree height (m) across the 16 sites. The boundaries of the box indicates the 25th and 75th percentiles, a line within the box marks the median. Error bars above and below the box indicate the 10th and 90th percentiles, respectively.

For tree-crown cover per stratum and life form proportion among sites, no clear pattern emerges in relation to geology (Table 4). Generally speaking, crown cover is smaller on sandstone, acid tuff and old weathered andesitic material. The densest canopy cover is on young andesitic and granites substrata.

3.3. Small trees and other life form contribution

The differences between sites in canopy cover per strata are large enough to suggest significant differences in LAI which could in turn produce differences in AGBM. The contribution to the AGBM of

Table 3

Forest structure and above-ground biomass (AGBM) (Mg ha^{-1}) (mean ± SEM) per site[a,b].

Site code	Site	Mean N stems/ha	Mean height (m)	Mean basal area/ha (m^2)	Mean total AGBM (Mg ha^{-1})	Mean AGBM 10–30 cm (Mg ha^{-1})	Mean AGBM 30–50 cm (Mg ha^{-1})	Mean AGBM >50 cm (Mg ha^{-1})
1	Tebo Pandak	584 ± 26	21.3 ± 0.2	40.8 ± 2.7	477.7 ± 38.0	81.9 ± 4.0	105.1 ± 6.7	290.7 ± 35.7
2	Pemunyin	586 ± 29	20.0 ± 0.2	35.6 ± 3.3	415.6 ± 51.7	81.3 ± 4.8	91.1 ± 9.8	243.2 ± 48.1
3	Sungai Durian	531 ± 22	20.6 ± 0.2	28.1 ± 1.7	304.8 ± 24.9	77.3 ± 3.3	87.7 ± 7.0	139.8 ± 22.0
4	Telentam	502 ± 24	20.9 ± 0.2	28.0 ± 1.7	307.8 ± 22.8	69.7 ± 3.6	85.6 ± 5.5	152.5 ± 20.9
5	Sungai Pinang	635 ± 22	21.2 ± 0.1	38.4 ± 1.8	428.0 ± 24.9	88.7 ± 3.7	107.8 ± 8.4	231.5 ± 21.3
6	Sungai Manau	698 ± 25	20.8 ± 0.1	37.3 ± 1.7	391.2 ± 21.2	97.2 ± 3.9	120.7 ± 7.0	173.2 ± 18.0
7	Napal Licin	458 ± 20	21.8 ± 0.2	27.3 ± 1.6	308.3 ± 22.4	60.2 ± 3.4	74.6 ± 5.1	173.5 ± 20.2
8	Kemumu	513 ± 15	22.9 ± 0.2	33.7 ± 1.6	373.0 ± 22.6	71.5 ± 2.5	102.7 ± 7.4	198.9 ± 20.6
9	Muara Aman	453 ± 19	21.0 ± 0.1	26.1 ± 1.5	271.2 ± 18.7	66.9 ± 3.5	99.8 ± 7.7	104.5 ± 15.0
10	Air Ukau	479 ± 17	23.2 ± 0.1	33.1 ± 1.6	377.0 ± 22.2	61.4 ± 3.0	108.4 ± 6.5	207.1 ± 20.1
11	Maju Jaya	548 ± 29	22.0 ± 0.1	31.7 ± 1.5	335.6 ± 18.3	74.6 ± 4.7	118.3 ± 9.9	142.8 ± 15.6
12	Gumai Pasemah	359 ± 15	21.9 ± 0.2	26.6 ± 1.8	300.5 ± 24.7	51.0 ± 2.2	81.4 ± 5.5	168.0 ± 21.7
13	Kubu Lincik	439 ± 19	22.1 ± 0.2	32.8 ± 2.3	395.6 ± 33.0	58.4 ± 2.7	73.6 ± 7.2	263.7 ± 30.4
14	Pemerihan	432 ± 25	21.5 ± 0.2	25.6 ± 1.8	284.2 ± 22.9	54.3 ± 3.6	73.1 ± 4.2	156.8 ± 19.9
15	Rata Agung	436 ± 10	20.9 ± 0.2	33.7 ± 1.9	445.1 ± 33.8	56.9 ± 1.7	64.9 ± 3.1	323.2 ± 32.8
16	Kubu Perahu	469 ± 17	20.9 ± 0.2	30.3 ± 2.0	351.2 ± 29.7	62.2 ± 2.6	85.1 ± 6.1	203.8 ± 26.9
	Overall mean	504 ± 6	21.4 ± 0.04	31.7 ± 0.5	360.6 ± 7.2	69.1 ± 1.0	91.9 ± 1.8	199.7 ± 6.6

[a] Based on woody stems ≥10 cm DBH or diameter above buttress.

[b] Estimated above-ground biomass (AGBM) (Mg ha^{-1}) is calculated from the diameter of individual trees using the updated tropical moist allometric equation by Brown (1997). Data are standardized to a per hectare basis. Data are means ± SEM.

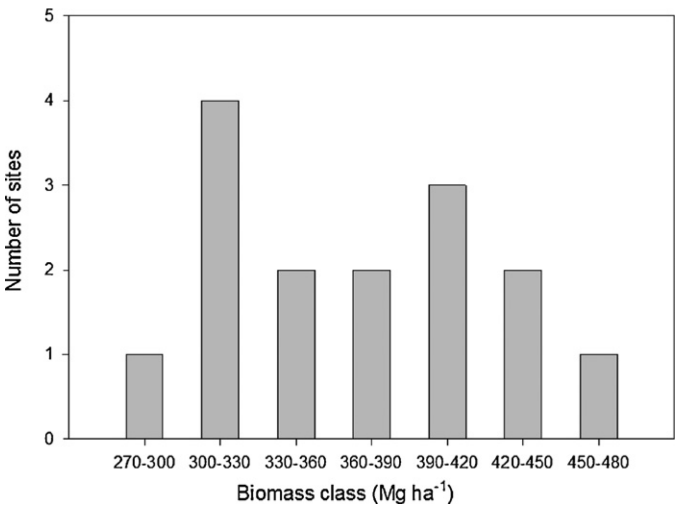

Fig. 4. Number of sites by groups of measured plot above-ground biomass values (Mg ha^{-}).

smaller trees (diameter between 3 and 9.9 cm) was calculated for a lowland dipterocarp rainforest in the same area to be around 5% of the total above-ground biomass (Laumonier, 1997).

The average number of palms (mainly *Oncosperma horridum*) varies from 4 to 77 individuals per ha, and screwpine trees from 0 to 92 stems per ha. These species rarely reach 10 cm in diameter and contribute little to total AGBM compared with trees when using a 10 cm diameter cut-off. Ferns and rattans seem to be more abundant on volcanic and granite derived soils. The average number of big climbers (diameter above 5 cm) varied from 3 to 38 per ha, and from 5 to 68 per ha for the small lianas. The contribution of lianas to the total AGBM for these forest types was also small.

4. Discussion

4.1. Landscape-scale variability and extrapolation from plot to landscape for C assessment

We have shown considerable landscape-scale variability in forest structure and dynamics. Both topographic situation and

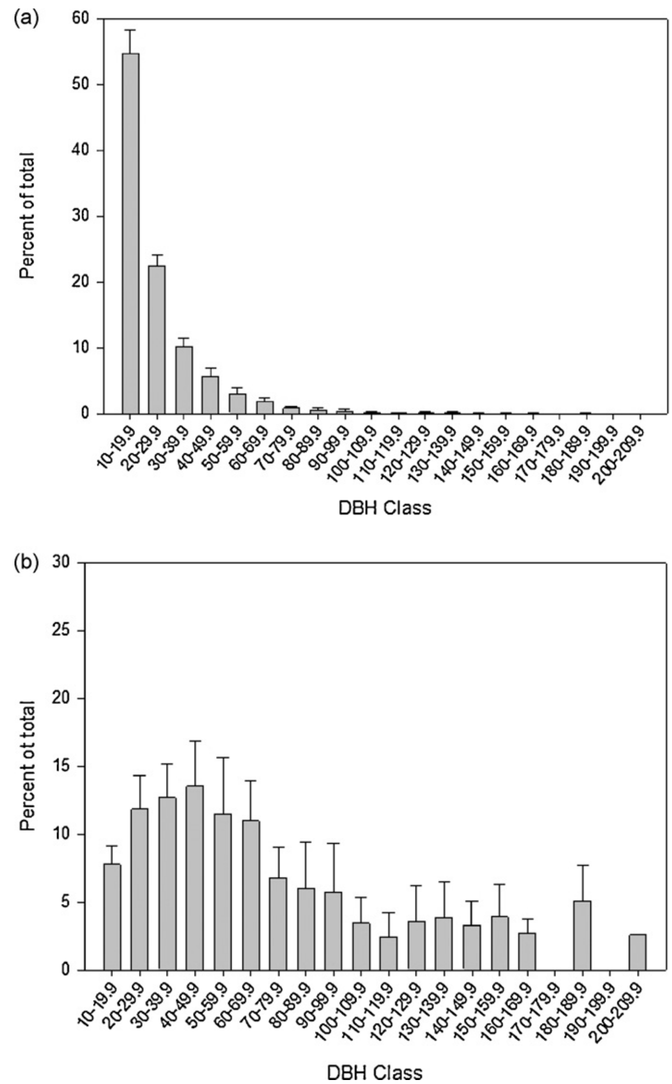

Fig. 5. Frequency distribution (per cent of total) of: (a) number of trees in DBH classes and (b) above-ground biomass per DHB class.

Table 4
Forest structure: tree cover and life forms per site.

	Site[a]															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Cover %																
Emergent	51	48	31	38	48	51	38	51	38	47	43	43	44	37	44	38
Upper canopy	54	71	51	52	51	50	46	60	56	56	35	56	46	45	51	28
Lower canopy	61	50	62	55	67	73	23	18	27	45	22	36	55	22	27	22
Pole trees	43	27	17	26	73	66	12	17	21	31	20	26	43	19	35	23
Sapling	27	23	7	10	22	24	6	14	20	17	6	15	37	16	42	33
Shrub	10	10	5	15	15	10	10	10	5	5	5	15	5	10	10	15
Number/ha																
Palm >4 m	45	14	2	22	17	26	8	34	2	1	2	4	24	9	9	19
Palm <4 m	27	–	35	1	42	–	10	43	19	8	2	13	41	5	5	28
Pandan >4 m	12	14	–	–	1	9	1	31	1	1	1	2	1	–	2	–
Pandan <4 m	39	–	14	–	57	1	52	61	18	53	12	7	6	–	10	3
Fern >150 cm	6	–	–	5	30	–	6	39	20	5	17	2	9	–	9	–
Solitary rattan	73	60	1	1	8	5	43	–	1	–	2	14	45	10	51	97
Rattan clump	28	26	26	21	4	5	–	1	58	68	44	1	–	–	–	–
Liana >5 cm	18	24	5	9	3	5	5	38	3	8	21	3	7	4	14	20
Liana <5 cm	69	66	17	30	15	27	14	54	22	18	56	5	18	26	25	46
Epiphytes	17	15	16	17	22	23	–	8	5	7	2	11	–	–	2	1

[a] *Sites:* 1 = Tebo Pandak; 2 = Pemunyin; 3 = Sungai Durian; 4 = Telentam; 5 = Sungai Pinang; 6 = Sungai Manau; 7 = Napal Licin; 8 = Kemumu; 9 = Muara Aman; 10 = Air Ukau; 11 = Maju Jaya; 12 = Gumai Pasemah; 13 = Kubu Lincik; 14 = Pemerihan; 15 = Rata Agung; 16 = Kubu Perahu.

geology (and the soil derived from it) appear to affect the structural variables of the forest such as stem number, BA and AGBM. Higher stem density, especially higher sapling density, occurs on steep slopes. Land facets affect the dynamics and the biomass of the forest (turn-over higher on slope), and this will have an obvious influence on the carbon cycle. Similar results have been reported from South America (Clark and Clark, 2000). AGBM is much higher on ridges than in valleys and lower slopes which may seem surprising since nutrients accumulate down slope. A possible explanation for the higher tree biomass on ridges could be the greater amount of light and better drainage.

For the non-swamp tropical rain forests of Sumatra the only available figure for C stock in the literature is 254 Mg ha^{-1}, where 80% of that value comes from living trees (203.2 Mg ha^{-1}), 10% from dead wood, and 10% from top soil (Hairiah and Sitompul, 2000 referred to by Murdiyarso et al., 2002). This number is based on one sample plot of 0.04 ha, a tiny sample. Our results for the same area show a much larger range of carbon stock values at the landscape level for this forest type (135–240 Mg C ha^{-1}, with a mean of 180 Mg C ha^{-1}).

4.2. Recommend sampling at landscape level, and requirement for sufficient sample size for biomass estimation

Small plots have the advantage of allowing replication. Distributed over a large landscape, they allow assessment of the landscape variation. Nevertheless the minimum area to be inventoried has to be standardized. A bootstrap resampling test on the effect of sample size on the standard error of AGBM showed that sampling an area of 10 ha overall will allow above-ground biomass to be estimate to within 5.5% (Fig. 6). If one aims for an error level of 6–8%, a minimum area of 4–6 ha (e.g. 40–60 plots of 0.1 ha each) should be sampled to estimate biomass with that accuracy.

4.3. Comparisons with other studies in the Malesian region

The results obtained in this study can be compared with other published values in the biogeographic region of Malesia (Table 5). Other than Okuda et al. (2004), who applied Kato model to the 50 ha Pasoh plot, and Samalca (2007), who sampled 7 ha, most published results are based on small sample plots, often below 1 ha

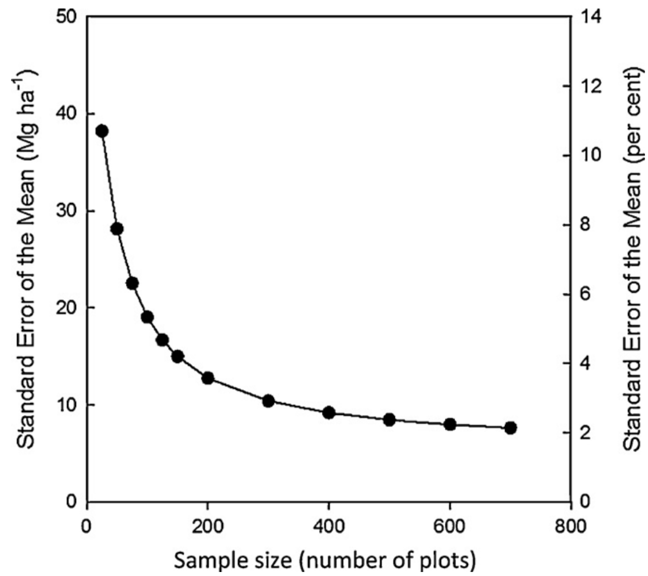

Fig. 6. Effect of sample size (number of plots) on standard error of mean of estimated above-ground biomass (in Mg ha^{-1} and per cent) based on 1000 bootstrapped recalculations of above-ground biomass using sub-samples of 25–700 plots.

and even as low as 0.04 ha. This makes generalization and extrapolation of the results questionable. For instance, in our data set and sampling design, the AGBM values when extrapolated from a single 0.1 ha sample plot would vary between 37.4 and 1513 Mg ha^{-1}. If we combine ten 0.1 ha plots to form a one hectare plots (a common plot size choice in many TRF studies), the variability is still high, with values ranging from 220 to 700 Mg ha^{-1}.

A key concern for implementing any REDD initiative is how precise the measurements are. Chave et al. (2004) have shown that one of the most important sources of error currently relates to the choice of allometric model. Efforts to standardize biomass estimation methods in the region become even more important when so many REDD initiatives are likely to emerge. Our data set was also used with other allometric models developed in SE Asia (Kato et al., 1978, Pasoh, Malaysia, and Yamakura et al., 1986,

Table 5
Published above-ground biomass AGBM (Mg ha^{-1}) values for the lowland and hill dipterocarp forest of the Malesian biogeographic region compared to our results.

Location	Number of plots	Plot size (ha)	Mean AGBM (Mg ha^{-1})	Diameter limit (cm)	Reference	Model used[a]	Applied to our data set AGBM (Mg ha^{-1})
Sebulu, East Kalimantan, Indonesia	1	1	486	≥10	Yamakura et al. (1986)	1	355.8
Berau, East Kalimantan, Indonesia	143	0.05	328	≥10	Samalca (2007)	7	378.5
Ulu Gadut, West Sumatra, Indonesia	1	1	380–405	≥8	Kohyama et al. (1989)	1	355.8
Pasirmayang, Jambi, Sumatra, Indonesia	2	0.02	406	≥5	Hairiah and Sitompul (2000) in Murdiyarso et al. (2002)	5	377.7
Pasirmayang, Jambi, Sumatra, Indonesia	1	6	320–400	≥10	Laumonier (1997)	1	355.8
Batang Ule, Jambi, Sumatra, Indonesia	1	3	390–420	≥10	Laumonier (1997)	1	355.8
Barito Ulu, Central Kalimantan, Indonesia	3	0.25	358	≥10	Brearley et al. (2004)	6	297.1
Pasoh, Malaysia	1	0.1	655	≥4.5	Kato et al. (1978)	2	388.7
Pasoh, Malaysia	1	0.2	465	≥4.5	Kato et al. (1978)	2	388.7
Pasoh, Malaysia	1	0.2	431	≥4.5	Kira (1978)	3	484.1
Pasoh, Malaysia	1	50	310	≥5	Okuda et al. (2004)	2	388.7
Ulu Segama Forest Reserve, Malaysia	5	0.1	349	≥10	Tangki and Chappell (2008)	4	368.1
Ulu Segama Forest Reserve, Malaysia	5	0.1	506	≥10	Tangki and Chappell (2008)	4	368.1
Mulu, Sarawak, Malaysia	1	1	650	≥10	Proctor et al. (1983)	6	297.1
South-Central Sumatra, Indonesia	702	0.1	360.6	≥10	This study	8	360.6

W = weight; W_S = weight of stems; W_B = weight of branches; W_L = weight of leaves; D = diameter; H = height; BA = basal area.

[a] *Models used*: (1) $W = W_S + W_B + W_L$ ($W_S = 2.903 \times 10^{-2}(D^2H)^{0.9813}$; $W_B = 0.1192 \times W_S^{1.059}$; $W_L = 9.146 \times 10^{-2}(W_S + W_B)^{0.7266}$), (2) $W = W_S + W_B + W_L$ ($W_S = 0.313(0.1D^2H)^{0.9733}$; $W_B = 0.136W_S^{1.070}$; $W_L = ((0.124W_S^{0.794})^{-1} + 125^{-1})^{-1}$, (3) $W = W_S + W_B + W_L$ ($W_S = 0.313(0.1D^2H)^{0.9733}$; $W_B = 0.316W_S^{1.070}$; $W_L = ((0.124W_S^{0.794})^{-1} + 125^{-1})^{-1}$, (4) $W = e^{(-2.134 + 2.530 \ln(D))}$, (5) $W = 0.092 \times D^{2.60}$, (6) $W = \text{volume}(H \times BA \times 0.5) \times 0.6$, (7) $W = e^{(-1.2495 + 2.3109 \ln(D))}$, (8) $W = \exp(-2.289 + 2.649 \ln(D) \times 0.021 \ln(D)^2)$.

Sebulu, East Kalimantan), all calibrated with destructive sampling, and results compared. These indicate that Yamakura's models gave figures similar to ours based on Brown's adapted Moist Tropical Forest equation (355 Mg ha^{-1} using Yamakura model against our 360 Mg ha^{-1}, less than 1.5% difference). Considering the difficulty, time constraint and additional error introduce by including height measurements, it would seem to be easier, in the absence of destructive sampling, to use the adapted Brown equation instead.

5. Conclusion

Our study provides the most comprehensive estimate presently available for AGBM at a landscape level in the South and Central Sumatra hill zone. Biomass in the hill dipterocarp forests of South and Central Sumatra is high, averaging 361 Mg ha^{-1} (270–480) for trees with diameter above 10 cm. The lowest values are for forests on acid tuff or very steep slopes, the highest on young volcanic formations. The biomass values of the present study are within the range of similar TRF studies across meso-landscape scale (see for instance Laurance et al., 1999, AGBM of 318 Mg ha^{-1}; Nascimento and Laurance, 2002, AGBM of 325 Mg ha^{-1} for Amazonia). It is about 16% higher than the value given for the Pasoh 50 ha plot in Peninsular Malaysia by Okuda et al. (2004). It is rather similar (5% higher) to the 'tropical wet forest' estimate of Keith et al. (2009), but 23% higher than the biome default value given by IPCC (2006).

Caution is definitely needed when extrapolating data from small plots to larger spatial scales for purposes of calculating carbon stocks in a given forest type or a region. This statement may seem trivial for ecologists and biologists acquainted with sampling issues, but surprisingly many published values replicated in text books and reports originate from very small sample plots (see Table 5). Biomass can vary by a factor of 2 over forest sites in a 1000 km^2 area. A single hectare plot is considered insufficient and stratified sampling is recommended within ecological zones (one forest type) before establishing the plot network (GOFC-GOLD, 2008). Our study showed the importance of even more detailed eco-floristic zoning prior to sampling if one expects to capture landscape-scale variation in forest stands. In such a case, a network of small plots across landscape (e.g. 20 plots of 0.2 ha each) is preferable to four 1 ha plots, providing that the sampling covers representative areas of the different land facets. In addition, some plots in the network must be established permanently for proper monitoring of the changes of carbon stocks. One possible explanation for the variation encountered at landscape scale may be that the landscapes sampled varied greatly in soil chemistry and texture, linked to the physiography of the site. This is being investigated further, together with the distribution of the dominant tree species in the region.

Acknowledgements

This research was financially supported by the Commission of the European Communities, the National Forest Institute (UK) and the Center International for Research on Agronomy and Development (CIRAD). The authors thank the staff of the regional forest inventory and land use planning divisions (BIPHUT-Palembang) of the Indonesian Ministry of Forestry for help in collecting data in the field. The authors thanks Peter Frost for reviewing, editing and commenting on the manuscript. The authors would also like to thank Daniel Murdiyarso and one anonymous referee for valuables comments and suggestions.

References

Basuki, T.M., van Laake, P.E., Skidmore, A.K., Hussin, Y.A., 2009. Allometric equations for estimating the above-ground biomass in tropical lowland Dipterocarp forests. For. Ecol. Manage. 257, 1684–1694.

Brady, M.A., 1997. Organic matter dynamics of coastal peat deposits in Sumatra, Indonesia. PhD Thesis. University of British Columbia, 259 pp.

Brearley, F.Q., Prajadinata, S., Kidd, P.S., Proctor, J., Suriantata, 2004. Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. For. Ecol. Manage. 195, 385–397.

Brown, S., Gillespie, A., Lugo, A.E., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. Forest Sci. 35, 881–902.

Brown, S., Iverson, L.R., 1992. Biomass estimates for tropical forests. World Resour. Rev. 4 (3), 366–383.

Brown, S., 1992. Measuring carbon in forests: current status and future challenges. Environ. Pollut. 116, 363–372.

Brown, S., 1997. Estimating biomass and biomass change of tropical forests: a primer. FAO Forestry Paper 134, Rome, 55 pp.

Bruenig, E.F., 1974. Ecological Studies in Kerangas Forests of Sarawak and Brunei. Borneo Literature Bureau for Sarawak Forest Department, Kuching, 237 pp.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., Perez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. Philos. Trans. R. Soc. Lond. B 359, 409–420.

Clark, D.B., Clark, D.A., 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Manage. 137, 185–198.

DeFries, R., Achard, F., Brown, S., Herold, M., Murdiyarso, D., Schmlamadinger, B., deSouza Jr., C., 2007. Earth observations for estimating greenhouse gas emissions form deforestation in developing countries. Environ. Sci. Policy 10, 385–394.

Gibbs, H.K., Brown, S., Niles, J.O., Foley, J.A., 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. Environ. Res. Lett. 2, 1–13.

GOFC-GOLD, 2008. Reducing greenhouse gas emissions from deforestation and degradation in developing countries: a sourcebook of methods and procedures for monitoring, measuring and reporting. GOFC-GOLD Report Version COP13-2, GOFC-GOLD Project Office. Natural Resources Canada, Alberta, Canada, 108 pp.

Grace, J., Lloyd, J., McIntyre, J., Miranda, A.C., Meir, P., Miranda, H.S., Nobre, C., Moncrieff, J., Massheder, J., Malhi, Y., Wright, I., Gash, J., 1995. Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992–1993. Science 270, 778–780.

Grainger, A., 2008. Difficulties in tracking the long-term global trend in tropical forest area. PNAS 105 (2), 818–823.

Hashimotio, T., Kojima, K., Tange, T., Sasaki, S., 2000. Changes in carbon storage in fallow forests in the tropical lowlands of Borneo. For. Ecol. Manage. 126, 331–337.

IPCC, 2006. In: Eggleston, H.S., Buendia, L., Miwa, K., Ngara, T., Tanabe, K. (Eds.), Intergovernmental Panel on Climate Change Guidelines for National Greenhouse Gas Inventories. Vol. 4 Agriculture, Forestry and Other Land Use. IGES, Kanagawa, Japan. , [online]http://www.ipcc-nggip.iges.or.jp/public/2006gl/vol4.html.

Jepsen, M.R., 2006. Above-ground carbon stocks in tropical fallows, Sarawak, Malaysia. For. Ecol. Manage. 225, 287–295.

Kanninen, M., Murdiyarso, D., Seymour, F., Angelsen, A., Wunder, S., German, L., 2007. Do Trees Grow on Money? The implications of deforestation research for policies to promote REDD. In: Forest Perspectives No 4, Center for International Forestry Research (CIFOR), Bogor, Indonesia, 61 pp.

Kato, R., Tadaki, Y., Ogawa, H., 1978. Plant biomass and growth increment studies in Pasoh forest. Malay. Nat. J. 30 (2), 211–224.

Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. PNAS 106, 11635–11640.

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

Kira, T., 1978. Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. In: Tomlinson, P.B., Zimmermann, M.H. (Eds.), Tropical Trees as Living Systems. Cambridge University Press, pp. 561–590.

Kohyama, T., Hotta, M., Ogino, K., Syahbuddin, Mukhtar, E., 1989. Structure and dynamics of forest stands in Gunung Gadut, West Sumatra. In: Hotta, M. (Ed.), Diversity and Plant–Animal Interaction in Equatorial Rain Forest. Sumatra Nature Study, Kagoshima University, pp. 33–47.

Komiyama, A., Moriya, H., Prawiroatmodjo, S., Toma, T., Ogino, K., 1988. Forest as an ecosystem, its structure and function: 2. Primary productivity of mangrove forest. In: Ogino, K., Chihara, M. (Eds.), Biological System of Mangroves: A Report of East Indonesia Mangrove Expedition 1986. Ehime University, Japan, pp. 97–106.

Kusmana, C., Sabiham, S., Abe, K., Watanabe, H., 1992. An estimation of above ground tree biomass of a mangrove forest in East Sumatra, Indonesia. TROPICS 1, 243–257.

Laumonier, Y., Purnadjaja, Setiabudi, 1986. International Map of the Vegetation. "Central Sumatra" (1:1. 000. 000) Institut de la Carte Internationale de la Végétation (ICIV)/BIOTROP SEAMEO Center, Toulouse, France/Bogor.

Laumonier, Y., 1997. The Physiography and Vegetation of Sumatra. Kluwer Academic, Dordrecht, 223 pp.

Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P., Lovejoy, T.E., Rankin de Merona, J.M., Chambers, J.Q., Gaston, C., 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. For. Ecol. Manage. 118, 127–138.

Murdiyarso, D., van Noordwijk, M., Wasrin, U.R., Tomich, T.P., Gillison, A.N., 2002. Environmental benefits and sustainable land-use options in the Jambi transect, Sumatra. J. Veg. Sci. 13, 429–438.

Nabuurs, G.J., Masera, O., Andrasko, K., Benitez-Ponce, P., Boer, R., Dutschke, M., Elsiddig, E., Ford-Robertson, J., Frumhoff, P., Karjalainen, T., Krankina, O., Kurz, W.A., Matsumoto, M., Oyhantcabal, W., Ravindranath, N.H., Sanz Sanchez, M.J., Zhang, X., 2007. Forestry. In: Metz, B., Davidson, O.R., Bosch, P.R., Dave, R., Meyer, L.A. (Eds.), Climate Change 2007: Mitigation. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge. , [online]http://www1.ipcc.ch/ipccreports/ar4-wg3.htm.

Nascimento, F.E.M., Laurance, W.F., 2002. Total above-ground biomass in central Amazonia rainforests: a landscape-scale study. For. Ecol. Manage. 168, 311–321.

Noble, I., Apps, M., Houghton, R., Lashof, D., Makundi, W., Murdiyarso, D., Murray, B., Sombroek, W., Valentini, R., 2000. Implications of different definitions and generic issues. In: Watson, R., Noble, I., Bolin, B., Ravindranath, N.H., Verardo, D., Dokken, D. (Eds.), Land Use, Land Use Change, and Forestry. A Special Report to IPCC. Cambridge University Press, Cambridge, pp. 53–118.

Okuda, T., Suzuki, M., Numata, S., Yoshida, K., Nishimura, S., Adachi, N., Niiyama, K., Manokaran, N., Hashim, M., 2004. Estimation of aboveground biomass in logged and primary lowland rainforests using 3-D photogrammetric analysis. For. Ecol. Manage. 203, 63–75.

Pearson, T., Walker, S., Brown, S., 2005. Sourcebook for Land Use, Land-Use Change and Forestry Project. Winrock International and the BioCarbon Fund of the World Bank, 64 pp.

Proctor, J., Anderson, J.M., Chai, P., Vallack, H.W., 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. J. Ecol. 71, 237–260.

Samalca, I.K., 2007. Estimation of forest biomass and its error. A case in Kalimantan, Indonesia. MSc Thesis. ITC, Enschede, The Netherlands, 84 pp.

Segura, M., Kanninen, M., 2005. Allometric models for tree volume and total aboveground biomass in a tropical humid forest of Costa Rica. BIOTROPICA 37, 2–8.

Tangki, H., Chappell, N.A., 2008. Biomass variation across selectively logged forest within a 225-km^2 region of Borneo and its prediction by Landsat TM. For. Ecol. Manage. 256, 1960–1970.

van Noordwijk, M., Rahayu, S., Hairiah, K., Wulan, Y.C., Farida, A., Verbist, B., 2002. Carbon stock assessment for a forest-to-coffee conversion landscape in Sumber-Jaya (Lampung, Indonesia): from allometric equations to land use analysis. Sci. Chin. C (45 Suppl.), 75–86.

Whitmore, T.C., 1984. Tropical Rain Forest of the Far East, 2nd edition. Clarendon Press, Oxford, 352 pp.

Yamakura, T., Hagihara, A., Sukardjo, S., Ogawa, H., 1986. Aboveground biomass of tropical rain forest stands in Indonesian Borneo. Vegetatio 68 (2), 71–82.