



# **Above-ground biomass and carbon stocks in a secondary forest in comparison with adjacent primary forest on limestone in Seram, the Moluccas, Indonesia**

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Cover photo by Suzanne M. Stas

Performing destructive sampling in a secondary forest on limestone in Seram, in the Moluccas in eastern Indonesia. The weight of the tree compartments was determined in the field using a hanging scale.

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# 1. Introduction

Tropical rainforests provide a wide range of ecosystem services. Ecosystem goods and services are the benefits that humans derive, directly or indirectly, from ecosystem functions. Ecosystem services of tropical rainforests include climate regulation, water supply and regulation, maintenance of biodiversity, carbon storage, pollination and cultural values, among others (MEA 2005). The loss of these ecosystem services due to deforestation and forest degradation is of global concern and of particular importance to rural populations that rely on natural resources for their livelihoods.

Carbon stored in forest biomass has been increasingly attracting attention in recent decades, as deforestation and tropical land-use change lead to significant emissions of greenhouse gases (Fearnside 2000). A new international climate mechanism was proposed with the aim of providing financial incentives to developing countries to reduce carbon emissions from deforestation and forest degradation; this mechanism was called REDD (Gibbs et al. 2007; Brown and Bird 2008). The idea was that countries with high emissions would have to compensate for those emissions by making efforts to reduce deforestation. The evolution of REDD into REDD+ took the scheme a step further by including the role of conservation, sustainable forest management and enhancement of forest carbon stocks (Angelsen et al. 2009). A major technical challenge for REDD+ is the estimation of national-level carbon emissions from deforestation and forest degradation (Gibbs et al. 2007). For this, accurate data on forest clearing and carbon storage in forests are required for each region. Data on carbon stocks cannot be obtained directly over large areas with remote sensing, so it is necessary to combine remotely sensed data with measurements on the ground (DeFries et al. 2007).

The amount of biomass that forests contain varies with climatic and soil conditions. The above-ground biomass (AGB) present in trees generally accounts for the greatest fraction of total living biomass in a forest (Brown 1997). The amount of AGB in a region can be estimated either directly or indirectly. The direct method consists of cutting and weighing the AGB in an established area. However, as this method is destructive and very time-consuming, allometric

equations from the literature are often used to estimate forest biomass. Allometric equations relate the biomass of individual trees to easily obtainable nondestructive measurements, such as diameter, height and wood density. It has been demonstrated that choosing suitable allometric equations for each forest type is of great importance, because biomass and associated carbon estimates are highly sensitive to the choice of allometric equation (Chave et al. 2004; Pearson et al. 2005; Jepsen 2006).

AGB has been estimated for various primary and secondary forests in Southeast Asia. Studies on AGB in primary forests in Southeast Asia were conducted in East Kalimantan, Indonesia (Yamakura et al. 1986); Central Kalimantan, Indonesia (Brearley et al. 2004); Borneo, Malaysia, Indonesia and Brunei (Slik et al. 2010); Sumatra, Indonesia (Laumonier et al. 2010); Sarawak, Malaysia (Proctor et al. 1983); and Peninsular Malaysia (Kato et al. 1978; Hoshizaki et al. 2004; Okuda et al. 2004). For secondary forests, AGB was estimated for forests in East Kalimantan, Indonesia (Hashimoto et al. 2000; Toma et al. 2005), Central Kalimantan, Indonesia (Brearley et al. 2004), Sumatra, Indonesia (Ketterings et al. 2001) and Sarawak, Malaysia (Jepsen 2006; Kenzo et al. 2009a, b). Even though several studies quantified AGB in various forest types and areas, the variation and spatial distribution of AGB at landscape scale, and the factors controlling them, are still poorly understood (Laumonier et al. 2010; Slik et al. 2010).

The destruction of primary forests worldwide has led to an expansion of the area of secondary forests and increasing interest in the role, structure and function of these forests (Brown and Lugo 1990; Corlett 1994; Chokkalingam and de Jong 2001). Chokkalingam and de Jong (2001, 21) define secondary forests as “forests regenerating largely through natural processes after significant human and/or natural disturbance of the original forest vegetation at a single point in time or over an extended period, and displaying a major difference in forest structure and/or canopy species composition with respect to nearby primary forests on similar sites.” Secondary forests are generally classified based on the cause and intensity of degradation.



## 1.1 CoLUPSIA

This research was conducted as part of the CIRAD project “Collaborative Land Use Planning and Sustainable Institutional Arrangements for Strengthening Land Tenure, Forest and Community Rights in Indonesia” (CoLUPSIA). The project focuses on Seram in Maluku Province and Kapuas Hulu in West Kalimantan Province. The overall objective of the project is to avoid deforestation and environmental degradation by supporting the development of sustainable institutional arrangements. One of the aims of this project is to take the first step toward establishing a payment for ecosystem services scheme. Possible markets for ecosystem services, such as carbon, water, biodiversity and scenic beauty, will be identified. For this, baseline data on these ecosystem services are necessary.

In Southeast Asia, most biomass studies were conducted in the West Malesia region. Biomass estimates are rare for East Indonesia and completely nonexistent for the Moluccas. A part of Seram

consists of calcareous soils; however, AGB estimates for tropical forests on limestone are very rare (only Proctor et al. (1983) have conducted a comparable ecological study in a primary forest on limestone in Sarawak, Malaysia). AGB in secondary forests on limestone has not yet been studied. To implement REDD+ in Seram, reference data on biomass and carbon stocks in these limestone forests are necessary.

## 1.2 Objectives

The objectives of this study were to estimate the AGB and carbon stocks in an old secondary forest and to examine how these values differ from those for an adjacent primary forest on limestone in Seram, the Moluccas, Indonesia.

The research questions are as follows:

1. What are the above-ground biomass values and carbon stocks in an old secondary forest on limestone in Seram, the Moluccas, Indonesia?
2. How do these values differ from those for an adjacent primary forest on limestone?

## 2 Material and methods

### 2.1 Site description

Seram, an island in the Moluccas archipelago in eastern Indonesia, lies between latitudes  $02^{\circ}46'$  and  $03^{\circ}53'$  south of the equator and covers an area of about 18,000 km<sup>2</sup>. Seram's lowlands have a permanently humid tropical climate, and mean annual temperatures at sea level vary between 25 °C to 30 °C. Precipitation is generally distributed throughout the year but is affected by monsoon regimes and mountain ranges. Mountains run through the island from east to west; as a result, the northern side has its rainfall peak during the west monsoon and the southern side is wettest during the southeast monsoon (Edwards 1993). Annual precipitation in the northern coastal lowlands around Wahi is between 2000 and 2500 mm, with a weak or no dry season (Fontanel and Chantefort 1978). The "drier" season is from May to October, when monthly rainfall seldom exceeds 100 mm (Edwards 1993).

Manusela National Park, located in the central part of the island, is the largest protected area in the Moluccas and covers approximately 10% of the land area of Seram (1860 km<sup>2</sup>). The national park encompasses a broad range of altitudes and vegetation types from coastal mangroves to mountain vegetation. The forests of Seram have been influenced by humans for many thousands of years and in almost all coastal areas, primary forest has been replaced by cultivated land, together with secondary forest (Ellen 1985).

Field sites are in lowland forests in the north of Seram near the hamlet Masihulan (Figure 1). Measurements were carried out in a secondary forest and a primary forest (altitude 50–100 m) on soils developed on limestone, on slightly hilly terrain. Both forests contain limestone boulders, but the primary forest has more of these rocks than the secondary forest. Data were collected between April and June 2011.

Information from local people was used to determine the history of the forests. However, substantial uncertainties about the history in the sampled areas remain. The secondary forest appeared on satellite images to be degraded and was classified in the draft

map as very depleted or over-logged forest (Figure 1). This secondary forest experienced a natural fire in 1982 during the dry season. However, the magnitude and duration of the fire and the exact locations of burned sites remain unclear, although apparently some large standing trees survived the fire. A logging company did some exploration in this area in the mid-1990s, but it remains unclear whether or not it extracted any timber. Around 1999, a logging road was built and local people extracted in this area specific timbers as building materials, but probably not from the study plot. Fire is considered the main disturbance in this secondary forest plot. The "primary" forest is most probably undisturbed. Note that the nomenclature for undisturbed forests used in the literature varies. These forests are variously termed primary, mature, undisturbed, old-growth, pristine, virgin and natural forests.

### 2.2 Field measurements

#### 2.2.1 Nondestructive measurements

Two plots, each 1 ha (100 × 100 m) in horizontal projection, were established, one in a secondary forest and one in a primary forest. These plots were divided into subplots of 10 × 10 m for easy measurement. In these plots, all living trees  $\geq 10$  cm diameter at breast height (dbh; at 1.3 m from ground level or 30 cm above the buttresses) were tagged and the dbh was measured. The point at which diameter measurements were taken was marked with paint. For trees that had more than one stem of  $\geq 10$  cm dbh, all stems of that size were measured. Botanical samples were collected and local and scientific species names were identified. In the secondary forest, the total height of each tree (from the base of the stem to the top of the tree) was measured using a Haga altimeter. For trees with bent or oddly shaped stems, the height was estimated. Palms  $\geq 10$  cm dbh in the plots were not sampled.

#### 2.2.2 Destructive sampling

As suitable allometric equations to estimate the biomass in this secondary forest were not available, destructive sampling was chosen as a means of determining the biomass in this forest type. Following the nondestructive measurements

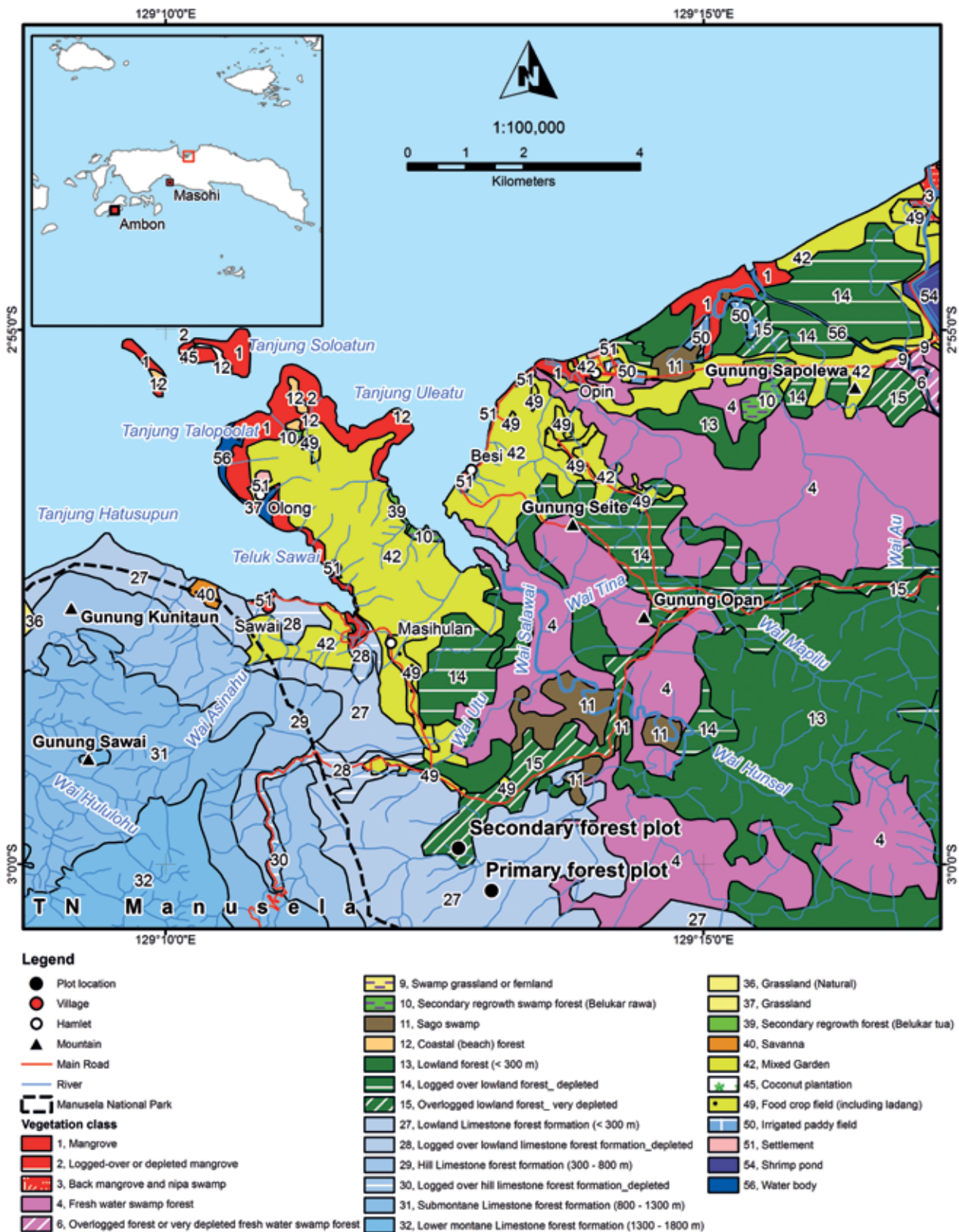


Figure 1. Vegetation map of Central Seram, the Moluccas, Indonesia (Setiabudi and Laumonier, 2010, CoLUPSIA). Measurements were made in a secondary (S 02°59'51.03"; E 129°12'43.51") and primary (S 03°00'14.87"; E 129°13'01.89") forest plot.

Sources: Topographic map: Indonesian National Coordination Agency for Survey and Mapping (Bakosurtanal) (2009); SPOT 5, P/R 329/356, acquisition date: 16 January 2009.

(measuring dbh and height and collecting botanical samples), four plots of 10 × 10 m within the 1 ha secondary forest were selected for destructive sampling. These four plots represented the mosaics of different successional stages of the vegetation within the 1 ha secondary forest plot. One of the selected destructive-sampling plots contained many small trees (<10 cm dbh). We refer to the vegetation <10 cm dbh in this plot as “dense understory vegetation”. The other three plots had almost no such small trees, and the term “less dense understory vegetation” refers to the understory trees in these plots.

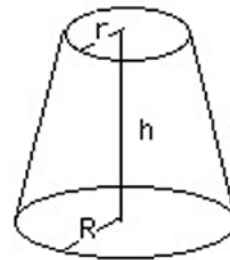
All above-ground vegetation in the plots was cut down, as close to the ground as possible. The weight of some remaining buttresses in the field was estimated. Vegetation was separated into: trees <10 cm dbh, trees ≥ 10 cm dbh, lianas, epiphytes, mosses and herbs. Trees and shrubs were further divided into leaves, twigs, branches and stems (tree compartments). Lianas were divided into leaves and stems; epiphytes, mosses and herbs were not further divided.

The total fresh weight of the tree compartments was weighed in the field using a hanging scale. Tree compartments from individual trees <10 cm dbh were combined per subplot; the fresh weight of the tree compartments from trees ≥10 cm dbh was measured for each tree separately. A subsample from each tree compartment (or the whole sample if the sample was not too big) was placed in a field oven (Figure 2). For each tree compartment, one subsample was derived for each plot from trees <10 cm dbh and one subsample from trees ≥10 cm dbh. Subsamples were gathered from the various species occurring in the plots to account for differences in leaf and wood properties across species. To ensure the size of the subsample was representative, we aimed to take at least 25% of the total fresh weight as a subsample; in all cases this was higher than 10%. The fresh weight of these subsamples was determined before they were placed in the oven. When the subsamples reached a constant weight, they were assumed to be oven dry mass and the dry weight of the samples was determined. A dry/fresh weight ratio for each subsample was calculated and these ratios were multiplied by the total fresh weight of the corresponding tree compartments in the plot to determine the total dry weight of the leaves, twigs, branches and stems (Overman et al. 1994).



**Figure 2.** One of the field ovens used to dry the subsamples on location.

Photo: Suzanne M. Stas, 2011.



**Figure 3.** The three-dimensional shape of a conical frustum.

It is not practical to measure the fresh weight of big stems and large branches in the field. Therefore, the oven dry weight is often derived in the following way (Overman et al. 1994; Brown 1997; Ketterings et al. 2001). For stems ≥10 cm dbh and large branches, the diameter was measured at every meter to calculate the volume of each meter length of log. For this, the formula for calculating the volume ( $V$ ) of a conical frustum was used (Figure 3):

$$V = 1/3 \pi h (R^2 + Rr + r^2),$$

where  $h$  is the height,  $R$  the radius of the lower base and  $r$  the radius of the upper base.

To obtain the oven dry weight, this volume was multiplied by the wood density (in oven dry mass per unit of fresh volume) of the species, derived from

the DRYAD Global Wood Density (GWD) database (Zanne et al. 2009). Further explanation about the wood densities used is given in Section 2.3.

However, for oddly shaped stems, for which it was difficult to calculate volumes accurately, and for big buttresses, the fresh weight of (part of) the stem or buttress was weighed and a wood sample was placed in the oven to determine the dry/fresh weight ratio. For these stems, wood dust was collected as well. The above-ground dry weight per tree (for trees  $\geq 10$  cm dbh) was derived by summing the dry mass of the leaves, twigs, branches and stem.

The height of each tree was re-measured with a measuring tape after the tree was felled, to obtain an indication of the error associated with measuring the height of trees. For each  $10 \times 10$  m subplot within the 1 ha secondary forest plot, an inventory was made of whether that plot contained dense or less dense understory vegetation, in order to extrapolate the biomass values of trees  $< 10$  cm dbh to the total 1 ha plot.

## 2.3 Data analysis

Statistical analyses were carried out using SPSS 18 and the statistical package R.

### 2.3.1 Structure

Trees in both the secondary and primary forest were grouped into dbh classes of 10 cm intervals and the distribution of the diameters in the two forest types was compared. However, the dbh distribution was not normal in either forest type and a log-transformation did not improve normality, so a Mann–Whitney U test was used to compare the diameter distribution in the forest types. The relationship between dbh and height in the secondary forest was analyzed by calculating Pearson's correlation and fitting a power function. One tree with a broken top was excluded from the analysis. Basal areas were calculated for all trees  $\geq 10$  cm dbh in the secondary and primary forests. The following formula was used:

$$\text{Tree basal area} = \pi (\text{dbh} / 2)^2,$$

where dbh is diameter at breast height. The stand basal area was derived by summing the basal areas of individual trees in the plot.

### 2.3.2 Biomass values for the secondary forest

#### Wood densities

Wood density data from the GWD database (Zanne et al. 2009) were used to calculate the dry weight of big stems and large branches after destructive sampling and as parameters in biomass equations for the secondary forest. Wood density data are often available for only a subset of species. Missing wood densities are usually estimated by averaging the wood densities of other species within the same genus or family. Slik (2006) showed that 72.5% of the variation in species-specific wood densities can be explained by genus wood-specific gravity for Indonesian tree species. Flores and Coomes (2011) showed that missing wood density data can be more accurately estimated using this worldwide database rather than local datasets, mostly because of the larger sample size. If the species occurred in the GWD database, the wood density was taken as listed in the database. A species with multiple records in the database was given the (mean) value for Southeast Asia (tropical); when the value for Southeast Asia (tropical) was not available, a mean value from other regions where the species occurs was taken. When the species did not appear in the database, the average of the genus to which that species belongs was taken. When the genus was not in the list, the family average of the species was taken. The average of all species in that genus or family across the world was taken, because Flores and Coomes (2011) showed that correlations between observed and estimated wood densities strongly decreased when a subset was used instead of the complete GWD database. Flores and Coomes (2011) calculated a relative error of 16% when missing wood densities were estimated by averages within genera and 24% within families, using the GWD database. If the family was not represented in the database either, the mean wood density for Southeast Asia (tropical) was taken. It was calculated using data in the GWD database at a value of  $0.574 \text{ g cm}^{-3}$  (Chave et al. 2009).

#### Development of site-specific allometric equation

The correlation between AGB and dbh for the trees  $\geq 10$  cm dbh that were felled during the destructive sampling was assessed by calculating Pearson's correlation. We developed two mixed-species equations for the secondary forest. Chave et al. (2005) compared a number of models commonly used in the forestry literature to estimate AGB and selected a few models based on their mathematical

simplicity and their applied relevance. Using the linear models function of the R software, parameters for our forest type were fitted for the following models (selected by Chave et al. (2005), but the more general model was first proposed by Schumacher and Hall (1933)):

$$\ln(\text{AGB}) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho) \quad (\text{model I})$$

$$\ln(\text{AGB}) = \alpha + \beta_2 \ln(D^2 H \rho), \quad (\text{model II})$$

where AGB is the above-ground biomass,  $D$  is the trunk diameter,  $H$  is the total tree height and  $\rho$  is the wood-specific gravity.

Both equations were used to determine which gave the best statistical fit for our dataset. The quality of the statistical model was assessed using the Akaike information criterion (AIC), residual standard error (RSE), adjusted  $R^2$  and significance value ( $p$ ). The best statistical model minimizes the values of AIC and RSE, has a high adjusted  $R^2$  and a low  $p$ -value. We also evaluated the performance of the regression model by calculating the deviation of the predicted (using the model) versus measured (weighed) total AGB via the following formula (Chave et al. 2005):

$$\text{Error} = 100 \times (\text{AGB}_{\text{predicted}} - \text{AGB}_{\text{measured}}) / \text{AGB}_{\text{measured}}$$

The models can in principle be used to estimate tree AGB, as long as their residuals are normally distributed. These equations calculate the AGB of individual trees. Summation of the AGB values of the trees is the biomass estimate for the stand.

The log-transformation of the data contains a bias in the final biomass estimation. We corrected for this by multiplying the biomass estimate by the correction factor (CF) (Baskerville 1972):

$$\text{CF} = \exp(\text{RSE}^2/2),$$

where RSE is the residual standard error.

### Extrapolation of total AGB to 1 ha secondary forest

The dry weight of trees  $\geq 10$  cm dbh, vegetation  $< 10$  cm dbh and lianas, epiphytes, mosses and herbs from the subplots was extrapolated to the 1 ha plot. The allometric equation developed (model I with CF) was used to calculate the biomass for all trees  $\geq 10$  cm dbh. The number of subplots with dense and less dense understory vegetation was multiplied by the dry mass of trees  $< 10$  cm dbh in the dense understory

plot and the mean dry mass in the three less dense understory plots, respectively. To extrapolate the dry weight of the lianas, epiphytes, mosses and herbs from the destructive plots to the whole 1 ha plot, the mean dry value from the destructive plots was multiplied by 100 (100 subplots). The total AGB in the 1 ha plot was derived by summing the dry weight of trees  $\geq 10$  cm dbh, trees  $< 10$  cm dbh, lianas, epiphytes, mosses and herbs.

### Comparison of biomass estimates from different allometric equations

To calculate the biomass of the trees  $\geq 10$  cm dbh in the secondary forest, the allometric equation developed in this study (model I with CF) was used. This estimated biomass value was compared with the AGB calculated using the equations of Kenzo et al. (2009a) and Ketterings et al. (2001). Kenzo et al. (2009a) developed allometric equations for logged-over lowland rainforests in a humid tropical climate in Sarawak, Malaysia. At their study site, selective logging for commercial use had taken place in the previous 20 years. The forests mainly contained late-successional and pioneer tree species. The forest canopy of the sampled areas was almost closed and some of the canopy trees had reached heights of approximately 40 m. For our site we used two formulas: one with only dbh as input parameter and the other with dbh and height as parameters. The allometric equation of Ketterings et al. (2001) was developed for a secondary regrowth forest mixed with rubber in Sumatra, Indonesia. The parameters needed to calculate AGB using that equation can be estimated from the site-specific power relationship between height and diameter and from wood density data at the site.

In the further calculations for AGB in the secondary forest, the allometric equation developed in this study (model I with CF) was used. In addition, the AGB values calculated using this equation were compared with the AGB values for the primary forest and converted into carbon estimates.

### 2.3.3 Biomass values for the primary forest

To estimate the AGB of trees  $\geq 10$  cm dbh in the primary forest, one of the general allometric equations developed by Brown (1997) was used, as it is suitable for tropical primary forests. Brown developed allometric equations for different climatic zones using data from the three main tropical regions. The equation for moist tropics was used (Brown 1997, updated by Pearson et al. 2005). Moist regions were defined as areas where rainfall approximately balances potential



**Table 1. Allometric equations from the literature, with additional information, used to estimate above-ground biomass in the secondary and primary forests.**

Site	Forest type	Regression	n	dbh-range	Reference
Sarawak, Malaysia	SF	$AGB = 0.1525 \times dbh^{2.34}$	30	1.0–44.1 cm	Kenzo et al. 2009a: (1)
Sarawak, Malaysia	SF	$AGB = 0.1083 \times (dbh^2 \times H)^{0.80}$	30	1.0–44.1 cm	Kenzo et al. 2009a: (2)
Sumatra, Indonesia	SF	$H = k \times dbh^c$ $AGB = 0.11 \times WSG \times dbh^{2+c}$	29	7.6–48.1 cm	Ketterings et al. 2001
World moist tropics	MT	$AGB = \exp(-2.289 + 2.649 \times \ln dbh - 0.021 \times \ln dbh^2)$	170	5–148 cm	Brown 1997, updated by Pearson et al. 2005

Notes: SF = secondary forest; MT = moist tropics; above-ground biomass (AGB) in kg; diameter at breast height (dbh) in cm; height (H) in m; wood-specific gravity (WSG) in  $g\ cm^{-3}$ .

evapotranspiration (e.g., 1500–4000 mm annual rainfall and a short or no dry season).

The formulas from the allometric equations from the literature that were used are given in Table 1.

### 2.3.4 Conversion of biomass estimates into carbon values

Carbon values for the forests were derived by multiplying the obtained biomass values by 0.5 (Pearson et al. 2005).



# 3 Results

## 3.1 Structure and floristics

The diameter class distribution in the two forests showed that most individuals were in the smallest size class (10.0–19.9 cm dbh), with numbers getting smaller for the bigger size classes (Figure 4). The distribution of diameters was the same in the secondary and primary forests (Mann–Whitney U test:  $p = 0.846$ ). The secondary forest ( $n = 537$ ) contained fewer stems  $\geq 10$  cm dbh than the primary forest ( $n = 657$ ). The stand basal area for trees  $\geq 10$  cm dbh in the secondary forest ( $17.9 \text{ m}^2 \text{ ha}^{-1}$ ) was smaller than that in the primary forest ( $26.5 \text{ m}^2 \text{ ha}^{-1}$ ). The mean and median dbh were very similar in both forest types. The tree with the biggest diameter was found in the primary forest (182.0 cm dbh) (Table 2).

Height and diameter in the secondary forest had a strong positive correlation (Pearson’s correlation = 0.720), which means that the thicker the tree, the greater the height. A power function between diameter and height was fitted:  $\text{Height} = 4.409 \times \text{dbh}^{0.442}$  ( $R^2 = 0.479$ ; regression:  $p = 0.000$ ).

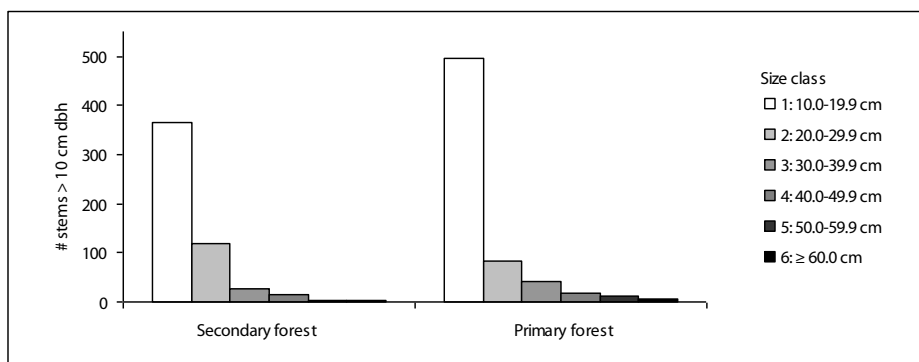
The height of trees  $\geq 10$  cm dbh in the secondary forest varied from 6 to 40 m. The mean absolute error in measuring heights was 1.1 m, which was underestimated in 53.8% of cases and overestimated in 46.2%.

The secondary forest contained 54 tree species, compared with 59 species in the primary forest. In the secondary forest, the most abundant species were *Decaspermum bracteatum* (Myrtaceae), *Mallotus penangensis* (Euphorbiaceae), *Syzygium lineatum* (Myrtaceae), *Meliosma pinnata* (Sabiaceae) and *Elaeocarpus sphaericus* (Elaeocarpaceae). In the primary forest, the species *Aglaia sapindina* (Meliaceae), *Leptonychia glabra* (Sterculiaceae), *Myristica lancifolia* (Myristicaceae), *Elaeocarpus sphaericus* (Elaeocarpaceae) and *Mallotus penangensis* (Euphorbiaceae) had the highest abundance. These five most abundant species in the primary forest occurred also in the secondary forest. Part of the secondary plot contained many small trees of the secondary species *Lunasia amara* (Rutaceae), previously referred to as “dense understory vegetation”.

**Table 2. Data on the structure of the secondary and primary forests.**

	Secondary forest	Primary forest
n	537	657
Stand basal area ( $\text{m}^2 \text{ ha}^{-1}$ )	17.9	26.5
Mean DBH $\pm$ S.E. (cm)	$18.3 \pm 0.4$	$18.6 \pm 0.5$
Median DBH (cm)	15.0	14.4
Max DBH (cm)	87.5	182.0

Note: S.E. = standard error.



**Figure 4. The population structure in 1 ha of secondary forest and primary forest.**

## 3.2 Biomass values for the secondary forest

The dry/fresh weight ratios for the tree compartments were calculated for trees <10 cm dbh and trees ≥10 cm dbh separately and per subplot. Table 3 shows the mean dry/fresh weight ratios for the subsamples of each tree compartment. Most weight was lost in the twigs (63%), followed by leaves (60%), branches (44%) and stems (37%).

### 3.2.1 Site-specific allometric equation

With the destructive sampling, a total of 25 trees ≥10 cm dbh were cut down, in the range of 10.4–41.7 cm dbh and 10.3–23.6 m height. These trees represented 10 species, 9 genera and 7 families and wood-specific gravity ranged from 0.320 to 0.730 g cm<sup>-3</sup>, in which the units are expressed in oven dry mass per fresh volume (Table 4). For *Casearia glabra*, *Decaspermum bracteatum* and *Gonocaryum litorale*, the average wood density for the genus level was used. For the other species, a species-specific wood density was available and was used. Four of the five most abundant species in the 1 ha secondary plot occurred also in the destructive sampling plots (for trees ≥10 cm dbh) and were included in the development of the allometric equation. Detailed information about the 25 trees ≥10 cm dbh that were felled during the destructive sampling and used to fit the parameters in the regression model is given in Table 5.

AGB and diameter showed a strong positive correlation (Pearson's correlation = 0.875; Figure 5), which means that bigger trees contained more biomass. The data from Table 5 were used to estimate the parameters in the allometric models for the secondary forest (Table 6). Both models gave a very good fit, which means they had a high adjusted R<sup>2</sup> and a highly significant regression. After applying the CF, model I had an error of 0.1 and model II an error of 0.6 (both overestimations). The stand AGB of the trees ≥10 cm dbh in the 1 ha plot with model I (including the CF) gave a value of 140.7 Mg ha<sup>-1</sup>; model II (including the CF) gave an AGB estimate of 136.1 Mg ha<sup>-1</sup>. For the following AGB estimates in the secondary forest, we chose to work with model I, because of its lower AIC and RSE, slightly higher adjusted R<sup>2</sup> and a smaller error between predicted and measured total AGB value for the felled trees.

Table 3. The mean dry/fresh weight ratio and the standard error (S.E.) for leaves, twigs, branches and stems from trees <10 cm and ≥10 cm dbh in the four subplots.

	Dry/fresh weight ratio	
	Mean	S.E.
Leaves	0.40	0.02
Twigs	0.37	0.02
Branches	0.56	0.02
Stems	0.63	0.01

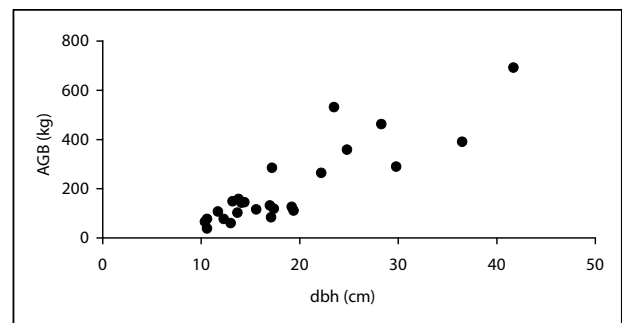


Figure 5. Relationship between above-ground biomass and diameter for the trees ≥10 cm dbh that were felled during the destructive sampling.

### 3.2.2 Total AGB in 1 ha secondary forest

Table 7 shows the total AGB values for 0.04 ha of secondary forest, which includes the biomass of trees ≥10 cm and <10 cm dbh, lianas, epiphytes, mosses and herbs. Most biomass was allocated in trees ≥10 cm dbh. However, as much as 20.1% of the total AGB stock was found in other life forms. In particular, trees <10 cm dbh contained a substantial part of the biomass values. For trees ≥10 cm dbh, 67.7% of the dry biomass was allocated in stems, 27.7% in branches, 1.5% in twigs and 3.1% in leaves. For trees <10 cm dbh, this allocation was as follows: 70.4% in stems; 17.8% in branches; 3.0% in twigs and 8.8% in leaves.

When the dry weight biomass values from the destructive sampling plots were extrapolated to the 1 ha secondary forest plot, the following AGB values resulted: 140.7 Mg ha<sup>-1</sup> for trees ≥10 cm dbh, 33.4 Mg ha<sup>-1</sup> for trees <10 cm dbh and 2.5 Mg ha<sup>-1</sup> for lianas, epiphytes, mosses and herbs. Summing these values gave a total AGB of 176.5 Mg ha<sup>-1</sup> for the secondary forest, which is equal to 88.3 Mg C ha<sup>-1</sup>.

**Table 4. Family, species, local name and the corresponding wood-specific gravity (WSG; expressed in oven-dry weight per fresh volume) from felled trees  $\geq 10$  cm dbh.**

Family	Species	Local name	WSG ( $\text{g cm}^{-3}$ )
Meliaceae	<i>Aglaia sapindina</i>	Wapane	0.420
Flacourtiaceae	<i>Casearia glabra</i>	-	0.627
Myrtaceae	<i>Decaspermum bracteatum</i>	Kayu merah daun halus	0.722
Elaeocarpaceae	<i>Elaeocarpus sphaericus</i>	Mataharihale	0.327
Euphorbiaceae	<i>Glochidion perakense</i>	Tombe tombe hutan	0.550
Cardiopteridaceae	<i>Gonocaryum litorale</i>	Kopi hutan	0.662
Flacourtiaceae	<i>Homalium foetidum</i>	Samar	0.730
Euphorbiaceae	<i>Mallotus multiglandulosus</i>	Kapor	0.442
Euphorbiaceae	<i>Mallotus penangensis</i>	Wasu wate	0.590
Sabiaceae	<i>Meliosma pinnata</i>	Wasa heli	0.320

Note: Wood density values were taken from the Global Wood Density database DRYAD (Zanne et al. 2009).

**Table 5. Diameter at breast height (dbh), height (H) (measured after felling), wood-specific gravity (WSG) and biomass data, expressed in oven dry weight (DW), for the 25 trees  $\geq 10$  cm dbh that were felled during the destructive sampling in 0.04 ha secondary forest.**

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

**Table 6. Allometric equations developed for the secondary forest. The logarithmic above-ground biomass (AGB; kg) can be estimated using diameter at breast height (dbh; cm), height (H; m) and wood-specific gravity (WSG; g cm<sup>-3</sup>, expressed in oven dry mass per fresh volume).**

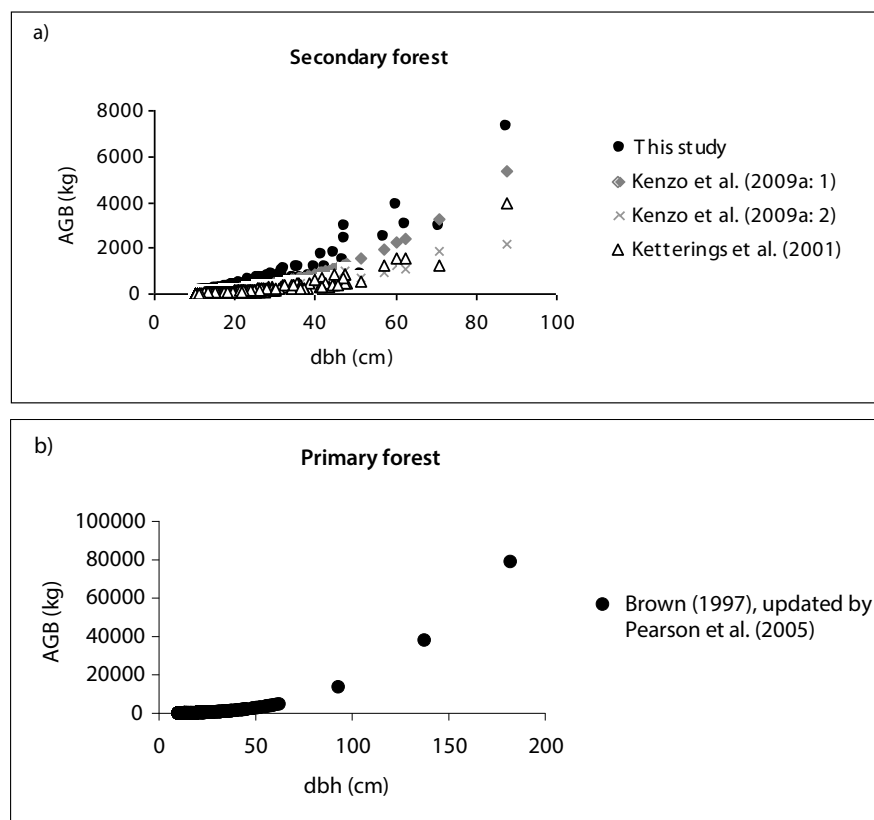
Model	AIC	RSE	Adj. R <sup>2</sup>	p
I $\ln(\text{AGB}) = -1.9366 + 1.8368 \times \ln(\text{dbh}) + 0.9047 \times \ln(H) + 1.1645 \times \ln(\text{WSG})$	-92	0.148	0.961	0.000
II $\ln(\text{AGB}) = -1.9946 + 0.9009 \times \ln(\text{dbh}^2 \times H \times \text{WSG})$	-89	0.162	0.953	0.000

Notes: Range in dbh: 10.4–41.7 cm; range in H: 10.3–23.6 m; range in WSG: 0.320–0.730 g cm<sup>-3</sup>. The equations are based on data from 25 felled trees. AIC = Akaike information criterion; RSE = residual standard error.

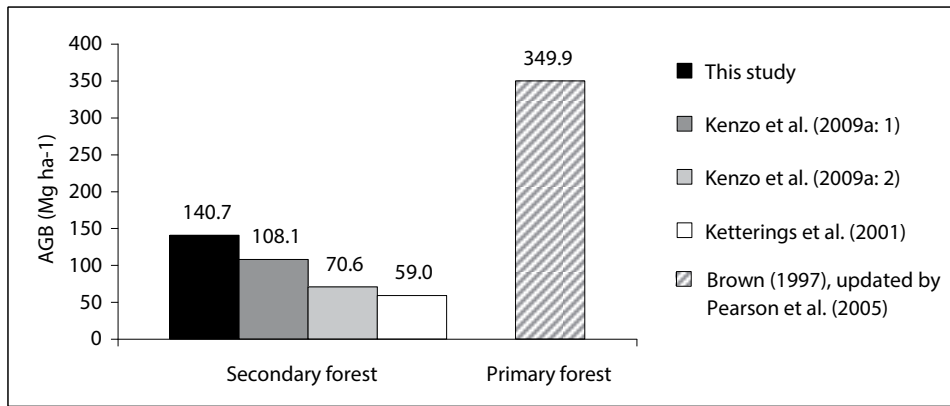
**Table 7. Above-ground biomass for different life forms in 0.04 ha secondary forest (obtained from the four destructive sampling plots).**

Life form	DW stems (kg)	DW branches (kg)	DW twigs (kg)	DW leaves (kg)	Total DW (kg)
Trees ≥10 cm dbh	3433.6	1406.7	74.5	154.7	5069.5
Trees <10 cm dbh	826.6	209.7	35.7	102.9	1174.9
Lianas	67.5	-	-	9.3	76.8
Epiphytes	-	-	-	-	18.2
Mosses & herbs	-	-	-	-	4.5
<b>Total AGB</b>					<b>6343.9</b>

Notes: DW = oven dry weight; AGB = above-ground biomass.



**Figure 6. Relationship between above-ground biomass (AGB) and diameter at breast height (dbh) per tree for the secondary (a) and primary (b) forest determined using the allometric equation developed in this study and allometric equations from the literature.**



**Figure 7.** The above-ground biomass values for trees  $\geq 10$  cm dbh in 1 ha secondary and primary forest when various allometric equations are used.

### 3.2.3 Comparison of biomass estimates from different allometric equations

Figure 6a shows the relationship between AGB and dbh per tree with the different allometric equations for secondary forests. All equations showed an exponential relationship, but the AGB estimates varied between them. The allometric equation with only one parameter (dbh) showed a fluent line (Kenzo et al. 2009a: 1); those based on several input parameters (dbh, height and wood-specific gravity) had a scattered relationship (this study; Kenzo et al. 2009a: 2; Ketterings et al. 2001).

The AGB from trees  $\geq 10$  cm dbh in the secondary forest, calculated using model I as developed in this study, was equal to  $140.7 \text{ Mg ha}^{-1}$ . This value varied greatly from the AGB estimates that were calculated using published allometric equations (Figure 7). The AGB values calculated using Kenzo et al. (2009a: 1) and Kenzo et al. (2009a: 2) were equal to  $108.1 \text{ Mg ha}^{-1}$  and  $70.6 \text{ Mg ha}^{-1}$ ,

respectively. The AGB estimated using the formula of Ketterings et al. (2001) was equal to  $59.0 \text{ Mg ha}^{-1}$ , which is less than half of the biomass value calculated using our site-specific allometric equation.

### 3.3 Biomass values for the secondary vs. primary forest

Figure 6b shows the relationship between AGB and dbh per tree for the primary forest using the Brown equation (Brown 1997, updated by Pearson et al. 2005). AGB in the primary forest was calculated as  $349.9 \text{ Mg ha}^{-1}$  (trees  $\geq 10$  cm dbh), which is 2.5 times higher than the AGB calculated for the secondary forest ( $140.7 \text{ Mg ha}^{-1}$ ) (Figure 7). Converting these biomass estimates into carbon values gives a carbon stock of  $70.3 \text{ Mg ha}^{-1}$  for the lowland secondary forest on limestone and a carbon stock of  $175.0 \text{ Mg ha}^{-1}$  for the adjacent primary forest.

# 4 Discussion

In this study, the AGB values and carbon stocks in a secondary forest were calculated and compared with those for an adjacent primary forest on limestone in Seram, in the Moluccas in eastern Indonesia. In the secondary forest, destructive sampling was carried out and a site-specific allometric equation was developed to estimate AGB in this forest type. Existing allometric equations were used for comparisons of biomass estimates in the secondary forest and to estimate the biomass in the primary forest.

## 4.1 Structure

The diameter distribution in both the secondary and the primary forest showed that the populations included many more juveniles than adults. This reverse J-shaped curve is typical for an uneven-aged mixed forest and is commonly found in old-growth forests in an equilibrium state. The similar diameter distribution in the two forest types shows that the population structure in the old secondary forest has already recovered. However, the most abundant species in the secondary and primary forest differed.

In this study, the secondary forest had fewer stems  $\geq 10$  cm dbh than the primary forest, but the mean and median dbh were very similar. The biggest tree was found in the primary forest and the stand basal area of the primary forest was larger than that of the secondary forest. Secondary forests are generally characterized by a high total stem density but low density of trees  $>10$  cm dbh; short trees with small diameters; and low basal area (Brown and Lugo 1990). With age, total stem density decreases, whereas the number of trees  $>10$  cm dbh, individual tree diameter and stand basal area increase. Even though the primary forest in this study contained bigger trees and more individuals in the bigger size classes, the higher number of individuals  $\geq 10$  cm dbh in the primary forest, particularly in the smallest size class, has led that the mean and median were very similar in the two forests.

## 4.2 Destructive sampling and biomass values for the secondary forest

During the destructive sampling, samples of all tree compartments were dried in field-built ovens, because of the absence of laboratories to dry plant samples in Seram. However, there was the risk that small plant materials would fall through the holes in the chicken wire used to cover the stem platform in the ovens. Using this rudimentary equipment may have led to a small bias in the dry/fresh weight ratios, in which case the reduction in weight cannot be totally attributed to a loss in water content.

This study and many others (e.g., Brown 1997; Overman et al. 1994) found that tree AGB was strongly correlated with trunk diameter. The allometric equation developed in this study was used to calculate AGB in the 1 ha secondary plot. The labor-intensive nature of destructive sampling tends to result in only a small number of trees being felled; in particular, trees in the bigger size classes are poorly represented. Seventeen trees in the secondary forest were bigger than the maximum dbh range when the allometric equation developed in this study was used. With the application of the formula developed by Kenzo et al. (2009a: 1 and 2) and Ketterings et al. (2001), respectively, 15 and 6 trees fell outside the dbh range. One tree in the primary forest was bigger than the maximum dbh range when Brown's equation (1997, updated by Pearson et al. 2005) was used.

In this study, it was found that 20.1% of the total AGB in the secondary forest was in life forms other than trees  $\geq 10$  cm dbh. In primary forests, it is often assumed that the understory accounts for an insignificant fraction of the total AGB in an area. However, for secondary forests, which often have a more open canopy and higher light levels close to the ground, the understory can be a substantial part of the total AGB. Lugo (1992) found that the AGB of understory plants (dbh  $<4$  cm) can be up to 30% of the total AGB of secondary forests. For 9–12-year-old secondary forests, on average 76% of the AGB  $>5$  cm dbh was allocated in trees  $>10$  cm dbh and 24% consisted of stems 5–10 cm dbh (Lawrence 2005).

### 4.3 Comparison with biomass values across Southeast Asia

In this research, we found the secondary forest to have AGB of 140.7 Mg ha<sup>-1</sup> compared with 349.9 Mg ha<sup>-1</sup> in the primary forest, both on calcareous soils in Seram, in the Moluccas in eastern Indonesia.

Several studies have assessed the biomass of young secondary forests in Southeast Asia, up to 14 years after disturbance. However, biomass estimates for old secondary forests are lacking. Toma et al. (2005) studied the post-fire recovery in AGB in a dipterocarp forest in East Kalimantan after wild fires in 1982–1983. Sites with varying levels of logging and fire damage were studied: a heavily disturbed stand (HDS), where most of the large trees were logged before the fires and the fire damage was heavy; intermediate levels of logging and fire damage (moderately disturbed stand, MDS); and low damage both by logging and by fires (lightly disturbed stand, LDS). In 1997, 14 years after the fire, the AGB of trees  $\geq 10$  cm dbh in the HDS, MDS and LDS was 117, 280 and 315 Mg ha<sup>-1</sup>, respectively, which was considerably lower than biomass values for the original forest in that area ( $>400$  Mg ha<sup>-1</sup>). The magnitude and extent of the fire in our study are not known, but our AGB estimate (140.7 Mg ha<sup>-1</sup>) lies in between the values for a HDS and MDS, and closer to the AGB estimate for a HDS. However, we studied the secondary forest almost 30 years after the main disturbance (fire), which means that our forest had double the recovery time of the secondary forests studied by Toma et al. (2005). This, together with the difference in the type of forest studied can explain the differences in biomass between our secondary forest and the stands described by Toma et al.

Total AGB, including understory vegetation, in 10–12-year-old fallow forests (after fire, logging and shifting cultivation) in East Kalimantan was found to vary from 45 to 56 Mg ha<sup>-1</sup> (Hashimoto et al. 2000). In that study, almost all of the study area had been burned in the fire. The vegetation height varied from 7 to 14 m, the maximum dbh was 22.5 cm and the secondary forest was dominated by three pioneer species. The forest studied by Hashimoto et al. (2000) was in an earlier successional stage than our secondary forest, which is reflected in the lower AGB values found in their study.

Slik et al. (2008) studied the AGB recovery up to 6.5 years after low-intensity surface fires in East Kalimantan and found that AGB was greatly reduced by fire and had shown no, or only limited, recovery since fire. In addition, during that same period, no significant recovery of the pre-fire species composition occurred, which indicates that regeneration of burned forests takes a considerable amount of time. Slik et al. (2008) stated that it is unknown how long it takes burned forests to reach their pre-fire condition and they stress the importance of long-term monitoring of disturbed forests.

The amount of biomass found in the primary forest in our study (349.9 Mg ha<sup>-1</sup>) is comparable to the biomass value found for a lowland primary rainforest on limestone in Sarawak, Malaysia (Proctor et al. 1983). In that forest, Proctor et al. (1983) found a total AGB of 380 Mg ha<sup>-1</sup>, which includes the mass of epiphytes, lianas and other life forms. However, they calculated the AGB with a volume formula and an average wood-density value from the literature, both of which are questionable. In other studies, old-growth forests in Borneo, which are dominated by dipterocarps, showed considerably higher AGB values: a mean of 457 Mg ha<sup>-1</sup> (trees with dbh  $\geq 10$  cm; Slik et al. 2010) and 486 Mg ha<sup>-1</sup> (trees with dbh  $\geq 10$  cm; Yamakura et al. 1986). The dipterocarp family consists of huge canopy and emergent trees (Ashton 1982; Whitmore 1984) and most biomass is stored in these large trees. The absence of dipterocarps on limestone can explain the observed difference in AGB in the forests studied in Borneo and the Moluccas. Even though the study by Laumonier et al. (2010) was also carried out in dipterocarp forests (Sumatra, Indonesia), they found a comparable AGB value for trees  $\geq 10$  cm dbh, that is, a mean of 361 Mg ha<sup>-1</sup>.

However, biomass values at landscape level can vary considerably and a comparison of biomass estimates from different sample sizes is not always accurate. Slik et al. (2010) and Laumonier et al. (2010) analyzed 247 and 70 ha, respectively, and calculated a mean AGB for the area. The sample size of all the other studies in primary forests was equal to 1 ha. Laumonier et al. (2010) found that within an error range of 6–8% of the AGB, a minimum sample area of 4–6 ha is needed to estimate biomass with satisfactory accuracy at the landscape scale.



The AGB in the primary forest in this study was estimated using a general allometric equation. However, Brown et al. (1989) stressed a need for caution when applying equations intended for the tropics as a whole to any specific region. Destructive sampling has not yet been carried out in primary forests on limestone. Often, destructive sampling takes place in cooperation with industrial logging companies. However, logging companies rarely work in forests on limestone, which makes it difficult to find suitable conditions for performing destructive sampling in such forests.

Biomass and vegetation studies on limestone forests are very rare. Limestone karsts have high species diversity and often contain high levels of endemism (Clements et al. 2006). However, there are still many uncertainties concerning how the structure and floristics in these forests differ from forests on other soil types.

#### 4.4 Biomass values for secondary vs. primary forests

The estimated AGB and carbon values for the secondary forest, with a recovery time of almost 30 years after fire, were 2.5 times lower than the values for the primary forest. This is due to a lower density of stems  $\geq 10$  cm dbh, lower stand basal area and the occurrence of smaller trees in the secondary forest.

Different degrees of disturbance result in forests with different AGB values and lower values are associated with more human or natural disturbance. Toma et al. (2005) compared their AGB value for a LDS (originally dipterocarp forest) with the AGB values for primary dipterocarp forests in the region. The LDS contained  $315 \text{ Mg ha}^{-1}$ , while primary forests contained  $481\text{--}542 \text{ Mg ha}^{-1}$ , which means that the secondary forest contained approximately 1.5 times less AGB than the primary forests. Toma et al. (2005) estimated that it would have taken more than

100 years for the LDS to attain the level of AGB present in primary forests in the region.

Brearley et al. (2004) compared a 55-year-old secondary rainforest (fallow after farming) with the adjacent, undisturbed, primary forest in Central Kalimantan, Indonesia. The mean AGB of the old secondary forest was 74% of the primary forest, which was not significantly different. However, there were still major differences in the floristics and species diversity.

#### 4.5 Comparison of results with different allometric equations

Results obtained in this study and elsewhere (e.g., Chave et al. 2004; Pearson et al. 2005; Jepsen 2006; Kenzo et al. 2009a) show that the choice of allometric equation is of great importance, because biomass estimates are highly sensitive to the equation used. Chave et al. (2004) quantified types of uncertainty that could lead to error in estimating the AGB and found that the most important source of error was related to the choice of the allometric model. The estimated AGB for the secondary forest in this study varied greatly with the use of different allometric equations, developed for secondary forests, from the literature. Kenzo et al. (2009a) developed two formulas to calculate the AGB for logged-over rainforests in Sarawak, Malaysia: one formula has dbh as the only input parameter, and the other estimates AGB by combining dbh and height data. Even though both formulas are based on AGB data from the same felled trees and were developed for the same forests, the AGB estimates for the secondary forest in this study differed greatly depending on which of these two equations was used. The AGB estimated using the formula of Ketterings et al. (2001) was less than half of that calculated using the site-specific allometric equation.

## 5 Conclusions and recommendations

The above-ground biomass (AGB) and carbon stocks from trees  $\geq 10$  cm dbh in an old secondary forest on limestone ( $140.7 \text{ Mg ha}^{-1}$ ;  $70.3 \text{ Mg C ha}^{-1}$ ) were 2.5 times lower than the values for an adjacent primary forest ( $349.9 \text{ Mg ha}^{-1}$ ;  $175.0 \text{ Mg C ha}^{-1}$ ) in Seram, the Moluccas, Indonesia.

The AGB in the secondary forest in this study differs from published biomass values for secondary forests in other areas within the region, because the type and intensity of disturbance, recovery time and original forest type are non-uniform. The AGB value for the primary forest is comparable to the value found for another primary forest on limestone in Southeast Asia. However, ecological studies in tropical forests on limestone are very rare and more studies in this forest type are recommended, as are comparisons with adjacent forests on other soil types.

When the biomass of trees  $< 10$  cm dbh, lianas, epiphytes and small understory plants was included, the total AGB for the secondary forest was  $176.5 \text{ Mg ha}^{-1}$ . As much as 20% of the total AGB stock was

found in life forms other than trees  $\geq 10$  cm dbh. Because secondary forests generally contain many small stems, it is recommended that understory biomass values be included in total AGB estimates for secondary forests.

The biomass values for the secondary forest varied greatly depending on the allometric equation used, which shows that allometric equations are highly specific to the site and forest type. Therefore, we stress the importance of choosing suitable allometric equations for each forest type. The allometric equation developed in this study should be used only for old secondary lowland forests on limestone in the Moluccas. Parameters should be used in the same units and the formula is suitable only for the ranges mentioned in the text. A broader diameter range and a bigger sample size for the allometric equation are recommended. It is also recommended that destructive sampling be considered for other secondary forest types and primary forests on limestone.

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The loss of ecosystem services due to deforestation is of global concern. Financial mechanisms such as REDD+ (reducing emissions from deforestation and forest degradation) have been proposed as ways to support the conservation of tropical forests. Crucial steps in the implementation of REDD+ are to estimate national-level carbon emissions from deforestation and forest degradation and to collect data on local biomass and carbon stocks. In this research, above-ground biomass (AGB) values and associated carbon stocks in a lowland secondary forest are estimated and compared with those in an adjacent primary forest, both growing on limestone in Seram, the Moluccas, Indonesia.

Suitable allometric equations for secondary forests in this region and on limestone were not available, so destructive sampling was necessary to determine the AGB in the secondary forest. An allometric equation was developed that makes it possible to estimate the AGB when tree diameter, height and wood density data are available. This biomass estimate was compared with AGB values that were calculated using existing allometric equations for secondary forests. To calculate the biomass and carbon values for the primary forest, an allometric equation from the literature was used.

The AGB for trees  $\geq 10$  cm dbh in the secondary forest ( $140.7 \text{ Mg ha}^{-1}$ ) was 2.5 times lower than that in the primary forest ( $349.9 \text{ Mg ha}^{-1}$ ). Converting these biomass estimates into carbon stocks gave a value of  $70.3 \text{ Mg ha}^{-1}$  for the secondary forest and  $175.0 \text{ Mg ha}^{-1}$  for the primary forest. The AGB estimate for the secondary forest differs from published values for other areas within the region, because age, type of disturbance and original forest type are non-uniform. The AGB value for the primary forest is comparable to that found in a biomass study conducted in a Malaysian primary limestone forest, but lower than those found in primary forests in Borneo that are dominated by dipterocarps. Ecological limestone studies in the tropics are very rare and more studies of this forest type, and comparisons with adjacent forests on different soil types, are recommended.

When the biomass of understory vegetation and other life forms was included, the total AGB in the secondary forest was equal to  $176.5 \text{ Mg ha}^{-1}$ . As much as 20% of the total AGB was found in life forms other than trees  $\geq 10$  cm dbh. Because secondary forests generally contain many small stems, it is recommended that understory vegetation be included in total AGB estimates for secondary forests.

The AGB estimate in the secondary forest varied greatly depending on which of the existing allometric equations was used. Therefore, this study confirms the importance of choosing suitable allometric equations for each forest type and the need to consider destructive sampling when suitable equations are not available. We stress that the allometric equation developed in this study should be used only for old secondary lowland limestone forests in the Moluccas.

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