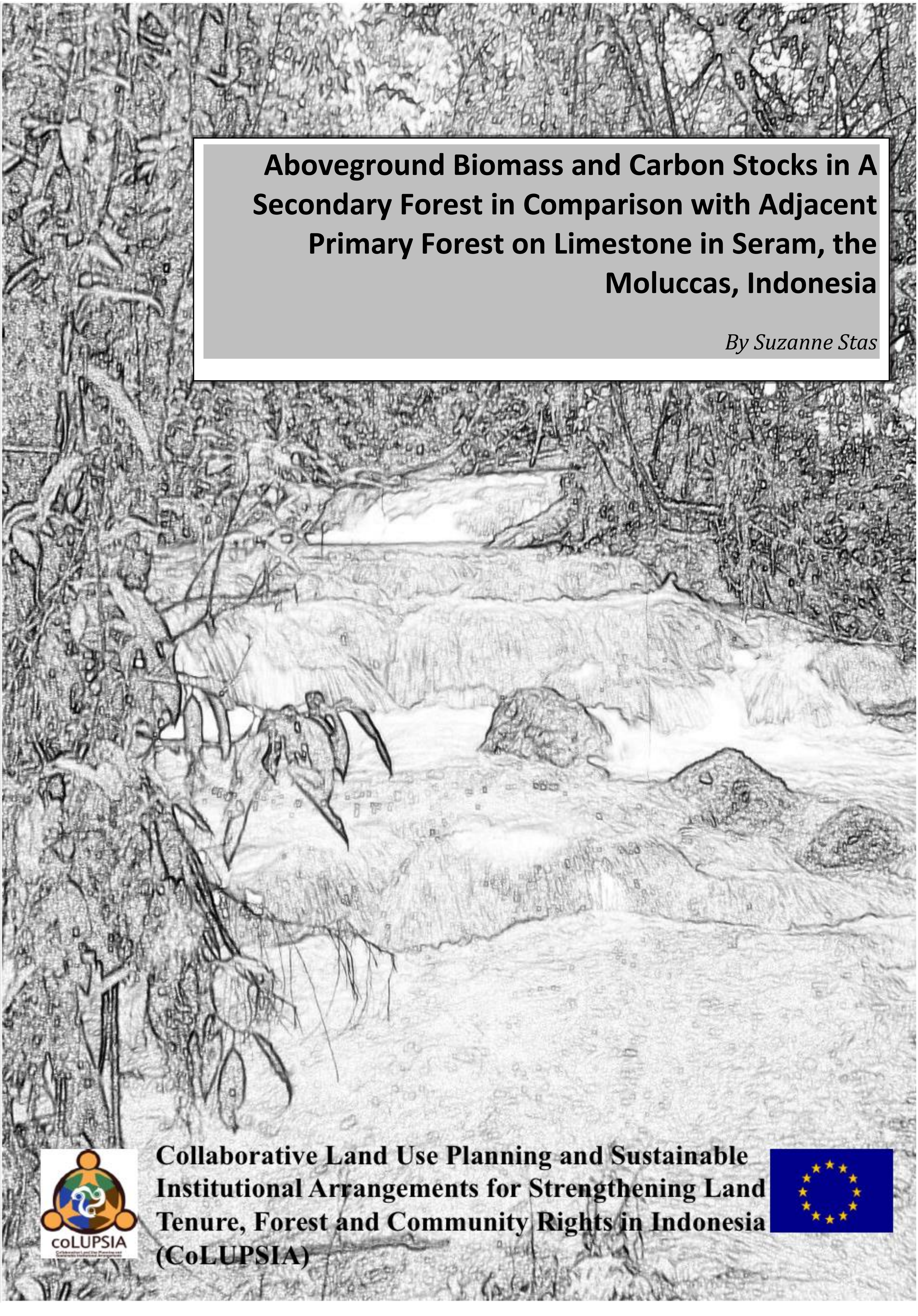

Aboveground Biomass and Carbon Stocks in A Secondary Forest in Comparison with Adjacent Primary Forest on Limestone in Seram, the Moluccas, Indonesia

By Suzanne Stas

Collaborative Land Use Planning and Sustainable Institutional Arrangements for Strengthening Land Tenure, Forest and Community Rights in Indonesia (CoLUPSIA)

This research project was carried out in partial fulfilment of the requirements for the degree of Master of Science in Environmental Biology, specialization Ecology & Natural Resources Management at Utrecht University, the Netherlands. The project took place within the 'Collaborative land use planning and sustainable institutional arrangements for strengthening land tenure, forest and community rights in Indonesia' project (CoLUPSIA). The CoLUPSIA-project is hosted at CIFOR and carried out by CIRAD and partners.

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Abstract

The loss of ecosystem services by deforestation is of global concern. Financial mechanisms such as REDD (reduced emissions from deforestation and forest degradation) are proposed for the conservation of tropical forests. A crucial step in the implementation of REDD is the estimation of national-level carbon emissions from deforestation and degradation and the collection of local biomass and carbon stock data. In this research, the aboveground biomass (AGB) values and associated carbon stocks in a lowland secondary forest will be estimated and compared with an adjacent primary forest, both developed on limestone in Seram, the Moluccas, Indonesia.

Because suitable allometric equations for secondary forests in this region and on limestone were absent, destructive sampling had to be done to determine the AGB in the secondary forest. An allometric equation was developed, in which the AGB can be estimated when tree diameter, height and wood density data are available. This biomass estimate was compared with AGB values that were calculated with existing allometric equations for secondary forests. To calculate the biomass and carbon values in the primary forest, an allometric equation from literature was used.

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

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

The AGB estimate in the secondary forest varied greatly when different existing allometric equations were used. Therefore, this study confirms the importance of choosing suitable allometric equations for each forest type and to consider destructive sampling when suitable equations are absent. We stress that the constructed allometric equation in this study should only be used for old secondary lowland limestone forests in the Moluccas.

Contents

1. Introduction

Tropical rain forests provide many ecosystem services. Ecosystem goods and services are the benefits that humans derive, directly or indirectly, from ecosystem functions. There are numerous ecosystem services, such as climate regulation, water supply and regulation, maintaining biodiversity, carbon storage, pollination and cultural values (MEA, 2005). The loss of these ecosystem services by deforestation and forest degradation is of global concern and particularly important to populations who rely on natural resources for their livelihood.

The carbon storage in forest biomass is been getting increasing attention over the last decades. Deforestation and tropical land-use change lead to significant emissions of greenhouse gases (Fearnside, 2000). In a new international climate agreement it is tried to implement the provision of financial incentives to developing countries to reduce carbon emissions from deforestation and forest degradation (REDD) (Gibbs *et al.*, 2007; Brown & Bird, 2008). This could be realized in a way that countries with high emissions have to compensate it with efforts against deforestation. REDD+ goes a step further, and includes the role of conservation, sustainable management of forests and enhancement of forest carbon stocks (Angelsen *et al.*, 2009). Among the challenges of REDD is estimating national-level carbon emissions from deforestation and degradation (Gibbs *et al.*, 2007). For this, accurate data on forest clearing and carbon storage in these forests for each region are required. Because data on carbon stocks cannot currently be obtained directly over large areas with remote sensing, remotely sensed data should be combined with measurements on the ground (DeFries *et al.*, 2007).

Forests vary in the amount of biomass they contain with climatic and soil conditions. The aboveground 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 by direct or indirect methods. The direct method consists of cutting and weighing the AGB in an established area. This method is destructive and very time-consuming. Therefore, often allometric equations are used for estimating forest biomass. Allometric equations relate the biomass of individual trees to easily obtainable non-destructive 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; Jepsen, 2006; Pearson *et al*., 2005). More accurate biomass estimations will be obtained when region-specific allometric equations will be developed.

The AGB has been estimated for various primary and secondary forests in southeast Asia. Southeast Asian AGB studies in primary forests took place in East-Kalimantan, Indonesia (Yamakura *et al.*, 1986); Central Kalimantan, Indonesia (Brearley *et al.,* 2004); Borneo, southeast Asia (Slik *et al.*, 2010); Sumatra, Indonesia (Laumonier *et al.*, 2010); Sarawak, Malaysia (Proctor *et al.*, 1983); and Peninsular Malaysia (Kato *et al.*, 1978; Okuda *et al.*, 2004; Hoshizaki *et al.*, 2004). For secondary forests, the AGB was estimated for forests in East-Kalimantan, Indonesia (Hashimotio *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, Kenzo *et al.*, 2009b). Even though several studies quantified the AGB in various forest types and areas, the variation and spatial distribution of AGB, and the factors controlling them, at landscape scale 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 & Lugo, 1990; Corlett, 1994; Chokkalingam & de Jong, 2001). According to Chokkalingam & de Jong (2001), secondary forests are *"… 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 of degradation and the degrading intensity.

CoLUPSIA-project

This research project takes place under CIRAD's 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, the Moluccas and Kapuas Hulu, West-Kalimantan. The overall objective of the project is to avoid deforestation and environmental degradation by supporting the development of sustainable institutional arrangements. One of the topics in this project is to make a first step towards payments for ecosystem services. Possible markets for ecosystem services, such as carbon, water, biodiversity and scenic beauty, will be identified. For this, baseline data about these ecosystem services are necessary.

In southeast Asia, most biomass studies took place in the West-Malesia region. Biomass estimates for East-Indonesia are rare and absent for the Moluccas. A considerable part of Seram consists of calcareous soils, however AGB estimates for limestone tropical forests are very rare (only Proctor *et al.* (1983) conducted a comparable ecological study in a primary, limestone forest in Sarawak, Malaysia). The AGB in secondary forests on limestone have not yet been studied. For the implementation of REDD+ in Seram, reference data about biomass and carbon stocks in these limestone forests are necessary.

Objectives

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

The research questions are:
1. What are the aboveground biomass values and carbon stocks in an old secondary limestone forest in Seram, the Moluccas, Indonesia?

2. How do these values differ from an adjacent primary limestone forest?

2. Material & methods

2.1 Site description

Seram, located in the Moluccas, Indonesia, lies between latitudes 02° 46' and 03° 53' south of the equator and covers an area of about 18.000 km^2. Seram's lowlands have a permanently humid tropical climate and mean annual temperatures at sea level vary between 25° to 30°C. Precipitation is generally distributed throughout the year but is affected by the monsoon regimes and mountain ranges. The mountainous terrain runs from east to west through the island, which causes that the northern side has its rainfall peak during the west monsoon, whilst the southern side is wettest during the southeast monsoon (Edwards, 1993). The northern coastal lowlands around Wahai have an annual precipitation between 2000 and 2500 mm with no or weak dry season (Fontanel & 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 represents approximately 10% of Seram (1.860 km^2). The national park includes 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 (Fig. 1). Measurements were carried out in a secondary and primary forest (altitude 50-100 m) on soils developed on limestone, on a slightly hilly terrain. Both forests contained limestone boulders, but the primary forest had a higher coverage of these rocks compared to 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, there remain big uncertainties about the history in the sampled areas. The secondary forest looked degraded on satellite images and was classified as very depleted or over-logged forest in the draft map (Fig. 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 fire-attacked sites remain unclear, but apparently some big standing trees survived the fire. A logging company did some exploration in this area in the mid '90s, but it remains unclear whether they took out trees or not. Around 1999, a logging road was built and local people extracted specific timbers for building material in this area, but probably not in the plot. The fire is considered as the main disturbance in this secondary forest plot. The "primary" forest is most probably undisturbed[1].

2.2 Field measurements

Non-destructive measurements

Two plots of 1 ha (100 x 100 m) in horizontal projection were established, one in a secondary and one in a primary forest. These plots were divided into subplots of 10 x 10 m for easy measurements. In these plots, all living trees ≥ 10 cm diameter at breast height (DBH; at 1.3 m from ground level or 30 cm above buttresses) were tagged and the DBH was measured. The

[1] The nomenclature that is used for undisturbed forests varies in literature. The terminology for these forests varies from primary, mature, undisturbed, old-growth, pristine, virgin and natural forests.

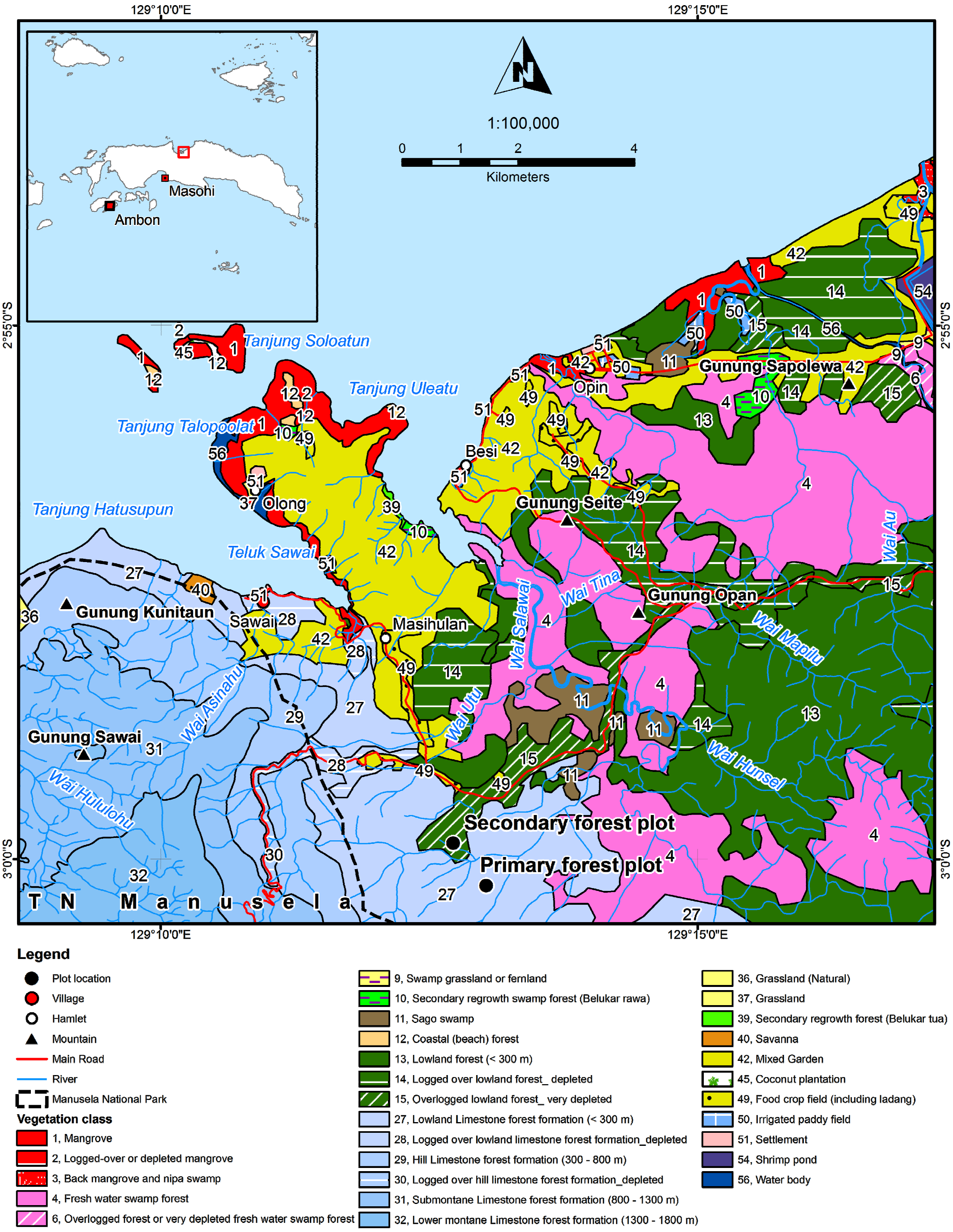

Fig. 1. Vegetation map of Central Seram, the Moluccas, Indonesia (draft by Setiabudi & Laumonier, 2010, CoLUPSIA-project). Measurements were done in a secondary (S 02˚ 59' 51.03"; E 129˚ 12' 43.51") and primary (S 03˚ 00' 14.87"; E 129˚ 13' 01.89") forest plot. Source: 1. Topographic map, Indonesia National Coordinator Agency for Survey and Mapping (Bakosurtanal), 2009; 2. SPOT 5, P/R 329/356, acquisition date 16th January 2009.

point at which diameter measurements were taken was marked with paint. For trees that contained more than one stem ≥ 10 cm DBH, both stems were measured. Botanical samples were collected and local and scientific species names were identified. In the secondary forest, for each tree the total height –from the base of the stem till the top of the tree- was measured with a Haga altimeter. For bended trees or odd shaped stems, an estimation of the height was made. Palms ≥ 10 cm DBH have not been sampled in the plots.

Destructive sampling

Due to the absence of suitable existing allometric equations to estimate the biomass in this secondary forest, destructive sampling was chosen to determine the biomass in this forest type. After the non-destructive measurements (measuring DBH, height and collection of botanical samples), four plots of 10 x 10 m within the 1 ha secondary forest were selected for destructive sampling. These destructive 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). Hereafter we will refer to the vegetation < 10 cm DBH in this plot as the "dense understorey vegetation". In the other three plots, these small trees were (almost) absent and the term "less dense understorey vegetation" refers to the understorey trees in these plots.

All aboveground vegetation in the plots was cut down, as close to ground level as possible. The weight of some remaining buttresses in the field was estimated. Vegetation was separated in trees < 10 cm DBH, trees ≥ 10 cm DBH, lianas, epiphytes, mosses and herbs. These 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 into compartments.

The total fresh weight of the tree compartments was weighed with a hanging scale in the field. Tree compartments from individual trees < 10 cm DBH were combined per subplot; the fresh weight of the tree compartments from trees ≥ 10 cm DBH were weighed per tree. A subsample, or the whole sample if the sample was not too big, from each tree compartment was placed in a field oven (Fig. 2). For each tree compartment, one subsample was derived from trees < 10 cm DBH and one subsample from trees ≥ 10 cm DBH per plot. Subsamples were gathered from the different species occurring in the plots, to cover differences in leaf and wood properties across species. In order to have a representative size of the subsample, it was tried to take at least 25% of the total fresh weight as subsample, but in all cases this was higher than 10%. The fresh weight of these subsamples was determined before placement in the oven. When the subsamples reached constant weight, this was assumed to be oven dry mass and the dry weight of the samples was weighed. 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).

For big stems and large branches, it is not practical to weigh their fresh weight in the field. Often, the oven dry weight is 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 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 (Fig. 3):

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

in which *h* is the height, *R* the radius of the lower base and *r* the radius of the upper base.

Fig. 2. One of the field ovens to dry the subsamples on location.

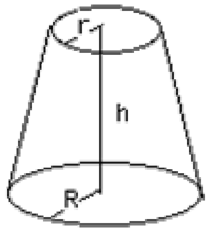

Fig. 3. The three-dimensional shape of a conical frustum.

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 used wood densities will be given in section 2.3.

However, from odd shaped stems for which it was difficult to calculate volumes accurately and big buttresses, the fresh weight of (part of) the stem or buttress was weighed and a woodsample was placed in the oven for dry/fresh weight ratio determination. For these stems, wooddust was collected as well. The aboveground dry weight per tree (for trees ≥ 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 measure tape after the tree was felled, to obtain an indication of the error associated with measuring the height of trees. For each 10 x 10 m subplot within the 1 ha secondary plot, an inventorisation was made whether that plot contained dense or less dense understorey vegetation, to be able 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 in SPSS 18 and the statistical package R.

Structure

The trees in the secondary and primary forest were grouped in DBH-classes of 10 cm interval and the distribution of the diameters in both forest types was compared. Because the DBH distribution was not normal in both forest types and a log-transformation did not improve normality, 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 analysed with calculating Pearson's correlation and fitting a power function. One tree with broken top was excluded from analysis.

Basal areas were calculated for all trees ≥ 10 cm DBH in the secondary and primary forest. The following formula was used:

Tree basal area = Π * $(DBH/2)^2$,

in which DBH is diameter at breast height. Stand basal area was derived by summing the basal areas of individual trees in the plot.

Biomass values in 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 to use 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 & Coomes (2011) showed that missing wood density data can be more accurately estimated with using this worldwide database instead of using local data sets, 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 the other regions where the species is occurring was taken. When the species was not occurring 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 & 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 & 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 also the family was not represented in the database, the mean wood density for southeast Asia (tropical) was taken, which was calculated from the GWD database and has a value of 0.574 g cm^{-3} (Chave *et al.*, 2009).

Construction of site-specific allometric equation

The correlation between AGB and DBH for the trees ≥ 10 cm DBH that were felled during the destructive sampling was assessed by calculating Pearson correlation. We constructed 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 & Hall (1933)):

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

$\ln(AGB) = \alpha + \beta_2 \ln(D^2 H \rho)$, (model II) in which AGB is the aboveground biomass, *D* the trunk diameter, *H* the total tree height and *ρ* the wood specific gravity.

Both equations were used to see which equation gave the best statistical fit for our dataset. The quality of the statistical model was assessed by looking at 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. Besides that, we 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):

$$\text{Error} = 100 * (AGB_{predicted} - AGB_{measured}) / AGB_{measured}$$

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 (Baskerville, 1972). Here was corrected for by multiplying the biomass estimate by the correction factor (CF) (Chave *et al.,* 2005):

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

in which RSE is the residual standard error.

Extrapolation of total AGB to 1 ha secondary forest

The dry weight from the trees ≥ 10 cm DBH, the vegetation < 10 cm DBH and lianas, epiphytes, mosses and herbs from the subplots was extrapolated to the 1 ha-plot. The constructed allometric equation (model I with correction factor) was used to calculate the biomass for all trees ≥ 10 cm DBH. The amount of subplots with dense and less dense understorey vegetation was multiplied with the dry mass of trees < 10 cm DBH in the dense understorey plot and the mean dry mass in the three less dense understorey 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 with 100 (100 subplots). The total AGB in the 1 ha plot was derived by summing the dry weight of trees ≥ 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 ≥ 10 cm DBH in the secondary forest, the constructed allometric equation in this study (model I with correction factor) was used. This estimated biomass value was compared with the AGB calculated with the equations of Kenzo *et al.* (2009a) and Ketterings *et al.* (2001). Kenzo *et al.* (2009a) developed allometric equations for logged-over lowland rainforests with a humid tropical climate in Sarawak, Malaysia. Selective logging for commercial use took place in the forests in the past 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. We used two different formulas: one with only DBH as input parameter; the other with DBH and height as parameters. The allometric equation of Ketterings *et al.* (2001) is constructed for mixed secondary forests in Sumatra, Indonesia. The parameters needed to calculate AGB 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 the AGB in the secondary forest, the constructed allometric equation in this study (model I with correction factor) was used. Also, the calculated AGB values with this equation were compared with the AGB values in the primary forest and converted into carbon estimates.

Biomass values in the primary forest

To estimate the AGB of trees ≥ 10 cm DBH in the primary forest, one of the general allometric equations of Brown was used, which is suitable for tropical primary forests. Brown developed allometric equations for different climatic zones with data from the three main tropical regions. The equation for the moist tropics was used (Brown, 1997, updated by Pearson *et al.*, 2005). Moist regions were defined as areas where rainfall approximately balances potential evapotranspiration (e.g. 1500-4000 mm annual rainfall and a short or no dry season).

The formulas from the used allometric equations from literature can be found in Table 1.

Table 1. The existing allometric equations, inclusive additional information, that are used to estimate the aboveground biomass in the secondary and primary forest. SF = secondary forest; MT = moist tropics; aboveground biomass (AGB) in kg; diameter at breast height (DBH) in cm; height (H) in m; wood specific gravity (WSG) in g cm^{-3}.

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

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

Structure & floristics

The diameter class distribution in both forests showed that most individuals were in the smallest size class (10.0-19.9 cm DBH) and diminishing numbers in the bigger size classes (Fig. 4). The distribution of diameters was the same in the secondary and primary forest (Mann-Whitney U test: $p = 0.846$). The secondary forest ($n = 537$) contained less trees than the primary forest ($n = 657$). The stand basal area for trees ≥ 10 cm DBH in the secondary forest (17.9 m^2 ha^{-1}) was lower than in the primary forest (26.5 m^2 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).

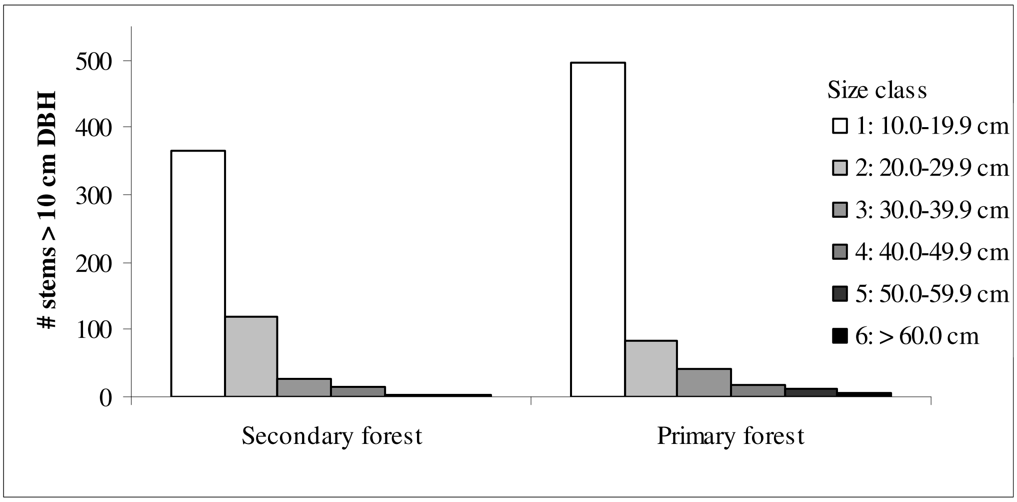

Fig. 4. The population structure in 1 ha secondary and primary forest.

Table 2. Data about the structure in the secondary and primary forest. S.E. = standard error.

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

Height and diameter in the secondary forest had a strong positive correlation (Pearson correlation = 0.720), which means that bigger trees grow taller. A power function between diameter and height was fitted: $Height = 4.409 * DBH^{0.442}$ ($R^2 = 0.479$; regression: $p = 0.000$).

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

The secondary forest contained 54 tree species, in comparison 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 understorey vegetation”.

Biomass values in 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 the different tree compartments. Most weight was lost in the twigs (63%), followed by leaves (60%), branches (44%) and stems (37%).

Table 3. The mean dry/fresh weight ratio and the standard error (S.E.) for leaves, twigs, branches and stems from trees < 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

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^{-3}, in which the units are expressed in oven dry mass per fresh volume (Table 4). For *Casearia glabra, Decaspermum bracteatum* and *Gonocaryum litorale,* an average wood density for the genus level was used. For the other species, a species specific wood density was available and 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 construction 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 can be found in Table 5.

Table 4. Family, species and local names with the corresponding wood specific gravities (WSG; expressed in oven-dry weight per fresh volume) from the felled trees ≥ 10 cm DBH. Wood density values were taken from the Global Wood Density database DRYAD (Zanne *et al.*, 2009).

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

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 ≥ 10 cm DBH that were felled during the destructive sampling in 0.04 ha secondary forest.

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

Aboveground biomass and diameter showed a strong positive correlation (Pearson correlation = 0.875; Fig. 5), which means that bigger trees contain 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^2 and a highly significant regression. After applying the correction factor, model I had an error of 0.1, model II of 0.6 (both overestimations). The stand AGB of the trees ≥ 10 cm DBH in the 1 ha plot with model I (incl. CF) gave a value of 140.7 Mg ha^{-1}; model II (incl. CF) gave an AGB estimate of 136.1 Mg ha^{-1}. For the following AGB estimates in the secondary forest, we chose to work with model I, because of its lower AIC and RSE-value, slightly higher adjusted R^2 and a smaller error between predicted and measured AGB value.

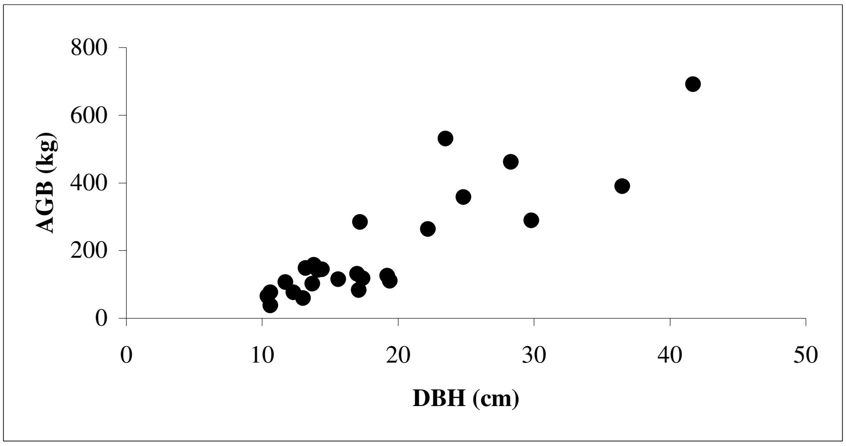

Fig. 5. The relationship between aboveground biomass and diameter for the trees ≥ 10 cm DBH that were felled during the destructive sampling.

Table 6. The constructed allometric equations for the secondary forest. The logarithmic aboveground biomass (AGB; kg) can be predicted by diameter at breast height (DBH; cm), height (H; m) and wood specific gravity (WSG; g cm^{-3}, expressed in oven dry mass per fresh volume). 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^{-3}. The equations are based on data from 25 felled trees. AIC = Akaike Information Criterion; RSE = residual standard error.

Model	AIC	RSE	Adj. R^2	p
I ln(AGB) = -1.9366 + 1.8368 * ln(DBH) + 0.9047 * ln(H) + 1.1645 * ln(WSG)	-92	0.148	0.961	0.000
II ln(AGB) = -1.9946 + 0.9009 * ln(DBH^2 * H * WSG)	-89	0.162	0.953	0.000

Total AGB in 1 ha secondary forest

Table 7 shows the total AGB values in 0.04 ha secondary forest, which includes the biomass of trees < 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. Especially 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, this gave the following AGB values: 140.7 Mg ha^{-1} for trees ≥ 10 cm DBH, 33.4 Mg ha^{-1} for trees < 10 cm DBH and 2.5 Mg ha^{-1} for lianas, epiphytes, mosses and herbs. Summing these values gave a total AGB of 176.5 Mg ha^{-1} in the secondary forest, which is equal to 88.3 Mg C ha^{-1}.

Table 7. Aboveground biomass for different life forms in 0.04 ha secondary forest (obtained from the four destructive sampling plots). DW = oven dry weight.

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
					6343.9

Comparison of biomass estimates from different allometric equations

Fig. 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 among the allometric equations. The allometric equation with only one parameter (DBH) showed a fluent line (Kenzo *et al.*, 2009a: 1); the ones 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 ≥ 10 cm DBH in the secondary forest, calculated with Model I that was constructed in this study, was equal to 140.7 Mg ha^{-1}. This value varied greatly from AGB estimates that were calculated with published allometric equations (Fig. 7). The AGB value, calculated with Kenzo *et al.* (2009a: 1) and Kenzo *et al.* (2009a: 2), was equal to 108.1 Mg ha^{-1} and 70.6 Mg ha^{-1}, respectively. The estimated AGB with the formula of Ketterings *et al.* (2001) was equal to 59.0 Mg ha^{-1}, which is less than half of the biomass value calculated with our site-specific allometric equation.

Biomass values in the secondary vs. primary forest

Fig. 6b shows the relationship between AGB and DBH per tree with the Brown equation (Brown, 1997; updated by Pearson *et al.*, 2005) for the primary forest. The primary forest contained an AGB of 349.9 Mg ha^{-1} (trees ≥ 10 cm DBH), which is 2.5 times higher than the AGB in the secondary forest (140.7 Mg ha^{-1}) (Fig. 7). Converting these biomass estimates into carbon values, the lowland, limestone secondary forest contained a carbon stock of 70.3 Mg ha^{-1} and the adjacent primary forest of 175.0 Mg ha^{-1}.

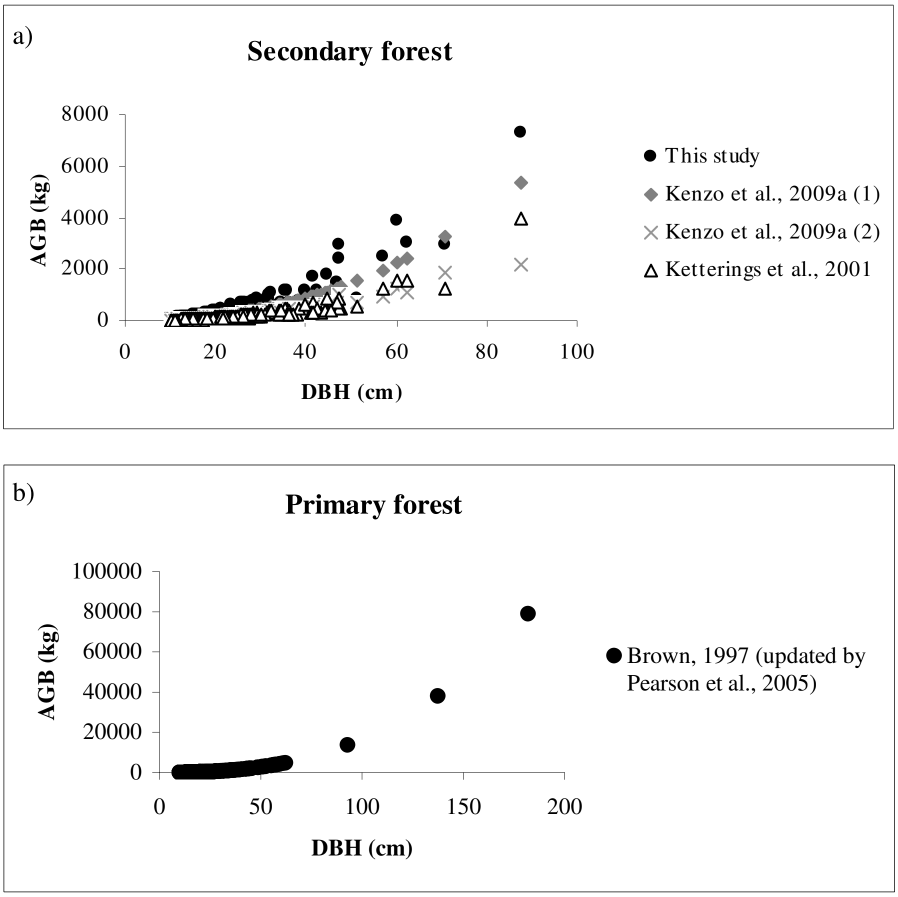

Fig. 6. Relationships between AGB and DBH per tree for the secondary (a) and primary (b) forest by using the constructed allometric equation in this study and published allometric equations.

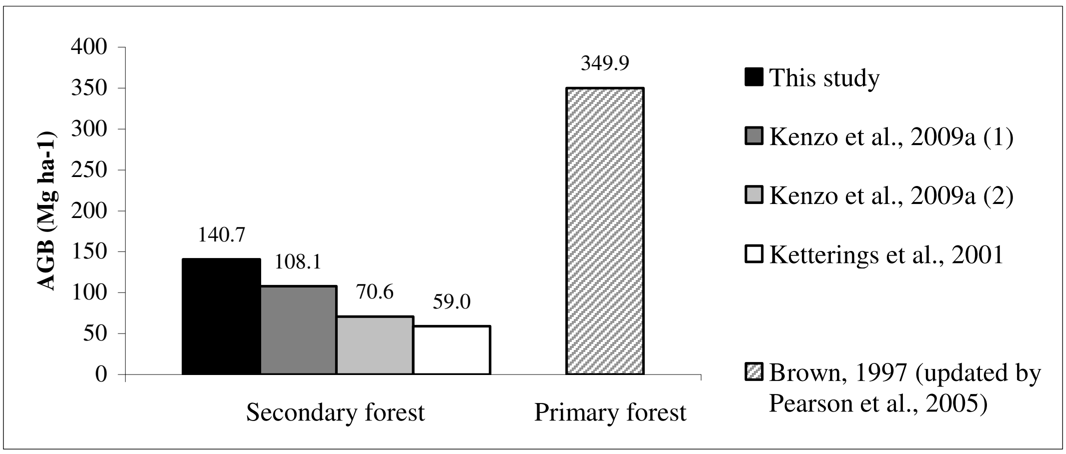

Fig. 7. The aboveground biomass values for trees ≥ 10 cm DBH in 1 ha secondary and primary forest when various allometric equations are used.

4. Discussion

In this study, the aboveground biomass values and carbon stocks in a secondary forest were calculated and compared with an adjacent primary forest on limestone in Seram, the Moluccas, Indonesia. In the secondary forest, destructive sampling was carried out and a site-specific allometric equation was constructed to estimate the 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.

Structure

The diameter distribution in both the secondary and primary forest showed a population with 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 between both 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 less stems ≥ 10 cm DBH compared to the primary forest, but the mean and median DBH were very comparable. The biggest tree was found in the primary forest and the stand basal area of the primary forest was higher compared to 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 & Lugo, 1990). With age, total stem density decreases, while the number of trees > 10 cm DBH, individual tree diameter and stand basal area increases. Even though the primary forest in this study contained bigger trees and more individuals in the bigger size classes, the higher number of individuals ≥ 10 cm DBH in the primary forest, particularly in the smallest size class, has led that the mean and median in both forests were very similar.

Destructive sampling and biomass values in the secondary forest

During the destructive sampling, samples of all tree compartments were dried in field built ovens, because laboratories to dry plant samples are absent in Seram. However, small plant materials had the risk of falling through the holes of the chicken wire, which was used to cover the stem-platform in the ovens. Using this rudimentary equipment can have led to a small bias in the dry/fresh weight ratios, which means that the reduction in weight can not totally be 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 constructed allometric equation in this study was used to calculate the AGB in the 1 ha secondary plot. Because destructive sampling is very labour intensive, this often leads to a small amount of felled trees and especially 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 constructed in this study was used. With the application of the formula of Kenzo *et al.* (2009a: 1 and 2) and Ketterings *et al.* (2001), respectively, 15 and 6 trees fell outside the DBH-range. For the primary forest, 1 tree was bigger than the maximum DBH-range when Brown’s equation (1997, updated by Pearson *et al.,* 2005) was used. The biomass of those big trees can not be estimated accurately.

In this study it was found that 20.1% of the total AGB in the secondary forest was allocated in other life forms than trees ≥ 10 cm DBH. For primary forests, it is often assumed that the understorey accounts for an insignificant fraction of the total AGB in an area. However, for secondary forests, which have often a more open canopy and higher light levels close to the ground, the understorey can be a substantial part of the total AGB. Lugo (1992) found earlier that the AGB of understorey 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).

Comparison with biomass values in southeast Asia

In this research, we found an AGB of 140.7 Mg ha^{-1} in the secondary forest, compared to 349.9 Mg ha^{-1} in the primary forest, both on calcareous soils in Seram, the Moluccas, 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 AGB recovery 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 fires (lightly disturbed stand, LDS). In 1997, fourteen years after the fire, the AGB of trees ≥ 10 cm DBH in the HDS, MDS, and LDS was 117, 280 and 315 Mg ha^{-1}, respectively, which is considerably lower compared to biomass values in the original forest in that area (> 400 Mg ha^{-1}*)*. The magnitude and extent of the fire in our study is unknown, but our AGB estimate (140.7 Mg ha^{-1}) lies in between the value for a heavily and moderately disturbed stand and closest to the AGB estimate for a heavily disturbed stand. However, we studied the secondary forest almost 30 years after the main disturbance (fire), which means that our forest had double the recovery time compared to the studied secondary forests in Toma *et al.* (2005). This, together with a different studied forest type, can explain the differences in biomass between our secondary forest and the stands in Toma *et al*.

Total AGB, including understorey vegetation, in 10-12-year-old fallow forests (after fire, logging and shifting cultivation) in East-Kalimantan varied from 45-56 Mg ha^{-1} (Hashimotio *et al.*, 2000). Almost all of the study area was burned in the fire. The vegetation height varied from 7-14 m, the maximum DBH was 22.5 cm and the secondary forest was dominated by three pioneer species. The forest studied by Hashimotio *et al.* (2000) was in an earlier successional stage compared to our secondary forest, which is reflected in the lower AGB values found by Hashimotio *et al*.

Slik *et al.* (2008), who studied the AGB recovery up to 6.5 years after low intensity surface fires in East-Kalimantan, found that AGB was greatly reduced by fire and showed no, or only limited, recovery with time since fire. Also, during that same period, no significant recovery of the pre-fire species composition took place, which indicates that regeneration of burned forests takes a considerable amount of time. Slik *et al.* (2008) state that it is unknown how long it will take for burned forests to reach their pre-fire condition and therefore 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^{-1}) is comparable to the biomass value in a primary lowland limestone rainforest in Sarawak, Malaysia. In that forest, Proctor *et al.* (1983) found a total AGB of 380 Mg ha^{-1}, in which also the mass of epiphytes, lianas and other life forms is included. However, Proctor *et al.* (1983) calculated the AGB with the use of a volume-formula and an average wood density value from literature, which are both questionable. Old-growth forests in Borneo, which are dominated by dipterocarps, showed considerably higher AGB values, a mean of 457 Mg ha^{-1} (trees with DBH ≥ 10 cm; Slik *et al.*, 2010) and 486 Mg ha^{-1} (trees with DBH ≥ 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 studied forests in Borneo and the Moluccas. Even though the study of Laumonier *et al.* (2010) was also carried out in dipterocarp forests (Sumatra, Indonesia), they found a comparable AGB value for trees ≥ 10 cm DBH, i.e. a mean of 361 Mg ha^{-1}.

However, biomass values at landscape level can show a considerable amount of variability and therefore it is not always accurate to compare biomass estimates from different sample sizes. Slik *et al.* (2010) and Laumonier *et al.* (2010) analysed 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 with a general allometric equation. However, Brown *et al.* (1989) stress that one must be cautious in applying equations intended for the tropics as a whole to any specific region. Destructive sampling has not yet been carried out in primary limestone forests. Often, destructive sampling takes place in cooperation with industrial logging companies. However, logging companies work rarely in limestone forests. Therefore, it is hard to find suitable conditions to perform destructive sampling in limestone forests.

Biomass and vegetation studies in 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 how the structure and floristics in these forests differ from forests on other soil types.

Biomass values in secondary vs. primary forests

The estimated AGB and carbon values in the secondary forest, with a recovery time of almost thirty years after fire, were 2.5 times lower compared to the values in the primary forest. This is due to a lower density of stems ≥ 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 in the LDS (originally dipterocarp forest) with the AGB values in primary, dipterocarp forests in the region. The LDS contained 315 Mg ha^{-1}, while primary forests contained 481 to 542 Mg ha^{-1}, which means that the secondary forest contained approximately 1.5 times less AGB compared to the primary forests. Toma *et al.* (2005) estimated 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.

Comparison of applying different allometric equations

Results obtained in this study and elsewhere (e.g. Chave *et al.*, 2004; Jepsen, 2006; Kenzo *et al.*, 2009a; Pearson *et al*., 2005) show that the choice of allometric equation is of great importance, because biomass estimates are highly sensitive to the choice of allometric equation. 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 literature. Kenzo *et al*. (2009a) developed different formulas to calculate the AGB for logged-over rainforests in Sarawak, Malaysia. One formula has only DBH as input parameter, the other equation estimates AGB by combining DBH and height data. Even though both formulas are based on AGB data from the same felled trees and are constructed for the same forests, the AGB estimates for the secondary forest in this study differed greatly with the use of these two equations. The AGB estimated with the formula of Ketterings *et al.* (2001) was less than half of the AGB calculated with the site-specific allometric equation.

5. Conclusions & recommendations

The aboveground biomass (AGB) and carbon stocks from trees ≥ 10 cm DBH in the old secondary limestone forest (140.7 Mg ha^{-1}; 70.3 Mg C ha^{-1}) were 2.5 times lower than the values in the adjacent primary forest (349.9 Mg ha^{-1}; 175.0 Mg C ha^{-1}) in Seram, the Moluccas, Indonesia.

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

When also the biomass of trees < 10 cm DBH and lianas, epiphytes and small understorey plants was included, the secondary forest contained a total AGB of 176.5 Mg ha^{-1}. As much as 20% of the total AGB stock was found in other life forms than trees ≥ 10 cm DBH. Because secondary forests contain generally many small stems, it is recommended to include understorey biomass values in total AGB estimates for secondary forests.

The biomass values in the secondary forest varied greatly when different existing allometric equations were used, which shows that allometric equations are very site- and forest type-specific. Therefore, we stress the importance of choosing suitable allometric equations for each forest type. The constructed allometric equation in this study should only be used for old secondary lowland limestone forests in the Moluccas (but the equation is probably applicable to other regions in southeast Asia with comparable climate conditions as well). Parameters should be used in the same units and the formula is only suitable for the ranges mentioned in the text. A broader diameter range and a bigger sample size for the allometric equation are recommended. Besides that, it is recommended to consider destructive sampling for other secondary forest types and primary limestone forests.

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