Forest Ecology and Management 260 (2010) 1873–1885

Contents lists available at ScienceDirect

Forest Ecology and Management

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

# Allometric equations for biomass estimations in Cameroon and pan moist tropical equations including biomass data from Africa

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ARTICLE INFO

*Article history:*
Received 5 June 2010
Received in revised form 18 August 2010
Accepted 19 August 2010

*Keywords:*
Biomass
Cameroon
Moist tropical forests
Tree allometry

ABSTRACT

Moist tropical forests in Africa and elsewhere store large amounts of carbon and need accurate allometric regressions for their estimation. In Africa the absence of species-specific or mixed-species allometric equations has lead to broad use of pan moist tropical equations to estimate tree biomass. This lack of information has raised many discussions on the accuracy of these data, since equations were derived from biomass collected outside Africa.

Mixed-species regression equations with 71 sample trees using different input variables such as diameter, diameter and height, product of diameter and height, and wood density were developed to estimate total aboveground biomass and biomass of leaves and branches for a Cameroon forest. Our biomass data was added to 372 biomass data collected across different moist tropical forests in Asia and South America to develop new pan moist tropical allometric regressions. Species-specific and mixed-species height diameter regression models were also developed to estimate heights using 3833 trees.

Using only diameter as input variable, the mixed-species regression model estimates the aboveground biomass of the study site with an average error of 7.4%. Adding height or wood density did not improve significantly the estimations. Using the three variables together improved the precision with an average error of 3.4%. For general allometric equations tree height was a good predictor variable. The best pan moist tropical equation was obtained when the three variables were added together followed by the one which includes diameter and height. This study provides height diameter relationships and wood density of 31 species. The pan moist tropical equation developed by Chave et al. (2005), estimates total aboveground biomass across different sites with an average error of 20.3% followed by equations developed in the present study with an average error of 29.5%.



## 1. Introduction

Climate change during the last decades has increased the need of information on the amount of forest biomass in different regions for climate policy definition. This requires reliable estimations of carbon pools in forest ecosystems (Brown, 2002; Wirth et al., 2003; Joosten et al., 2004). The estimation of above and below ground biomass pools is of great importance for the characterization of structure and function of ecosystems (Chave et al., 2003). The information on biomass amounts helps not only to understand energy accumulation within forest ecosystems, but also serves as an ecological indicator for sustainability (Aboal et al., 2005). Reliable information on the amount of forest biomass is also useful for implementing REDD (Reducing Emissions from Deforestation and Forest Degradation) policy recently introduced in the Kyoto Protocol. These estimates can also help to assess forest productivity, carbon pools, and carbon sequestration in biomass components including roots, trunk, branches and leaves (Návar, 2009).

One of the major sources of uncertainty in estimating the amount of biomass is the lack of reliable regression equations which can convert the parameters measured directly in the field, such as diameter and height, to aboveground biomass estimates. General and site specific allometric equations have been developed from biomass of mixed tropical species (Dawkins, 1961; Ogawa et al., 1965; Brown et al., 1989; Overman et al., 1994; Brown, 1997; Araújo et al., 1999; Nelson et al., 1999; Chambers et al., 2001; Keller et al., 2001; Ketterings et al., 2001; Chave et al., 2005; Basuki et al., 2009). No allometric equation for biomass estimations has been developed so far specifically for African tropical forests. For biomass estimations in African forests, general allometric equations derived from data collected outside Africa are often used (e.g. Brown et al., 1989; Chave et al., 2005). Even if covariance analyses show for these equations that there is no detectable effect of continents, their practical use should be restricted to large scales, global and regional com-

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0378-1127/$ – see front matter © 2010 Published by Elsevier B.V.
doi:10.1016/j.foreco.2010.08.034

parisons. Their application to particular species on specific sites should be limited. One of the constraints of some of these equations is that they include only diameter at limited range and exclude height. Before using allometric equations, their validity within a particular area needs to be tested (Crow, 1978; Brown et al., 1989; Houghton et al., 2001; Chave et al., 2001, 2005). If regression equations take into account dbh across the entire tree species range, the tree height and the specific wood density, they can provide more accurate biomass estimates (Cole and Ewel, 2006; Litton and Kauffman, 2008).

The most accurate method to determine tree biomass is the destructive method, which requires felling of trees and measurement of tree components. This method is labour intensive and time consuming and is in most cases restricted to small trees at small scales (Ketterings et al., 2001; Li and Xiao, 2007). Harvesting trees requires in general special authorization which is not often easy to acquire. It also draws attention of local population who in many cases ask for compensation for trees harvested in their locality. Therefore, biomass studies are very costly and consequently only few datasets are available. The use of regression equations allows estimating the total aboveground biomass of trees as well as of different components (root, stem, branches, and leaves) with easily measured parameters such as diameter (Kershaw and Maguire, 1995; Monserud and Marshall, 1999; Návar et al., 2002; Porté et al., 2002; Xiao and Ceulemans, 2004; Northup et al., 2005; Bullock and Heath, 2006; Fehrmann and Kleinn, 2006). Different species on the same site may have different tree heights, wood densities, architecture resulting consequently in different allometric relationships (Chave et al., 2003). The development of regression equations for single dominant or most used species and for mixed-species is important for forests inventory data which are composed of a multitude of species (Návar, 2009).

The objectives of this paper therefore are to (1) use destructive biomass data to develop allometric equations for estimating the amount of tree biomass in Campo-Ma'an area; (2) select the most important species of our study site and develop individual diameter tree height relationships for these species, as well as general diameter tree height relationships for mixed-species; (3) develop pan moist tropical allometric equations with the Campo-Ma'an biomass data and those of Brown (1997), Araújo et al. (1999), Nelson et al. (1999) and Ketterings et al. (2001); (4) evaluate the accuracy of existing pan moist tropical allometric equations.

## 2. Material and methods

### 2.1. Study site

The study was conducted in Cameroon within the Campo-Ma'an area which is located between latitudes 2°10′–2°52′N and longitudes 9°50′–10°54′E. It is an area of 772 066 ha, incorporating a National Park (264 064 ha, 34%), a protected forest (11 968 ha, 1.6%), a forest management zone with five logging concessions (241 809 ha, 31.4%), an agro-forestry area where local population have controlled access for multi-purpose uses (196 155 ha, 25.5%), a rubber and an oil plantation (57 750 ha, 7.5%) and a coastal area (320 ha). The Campo-Ma'an forest is bordered in the western part by the Atlantic Ocean and in the southern part by the river Ntem and Equatorial Guinea. Most of the land is covered by lowland tropical moist forests that extend from Southeast Nigeria to Gabon and the Mayombe area in Congo (Letouzey, 1968, 1985). The area is marked by outstanding biological diversity, with Atlantic biafran, Atlantic littoral, mixed Atlantic, semi-caducifoliated, subtropical mountain, degraded and swamp forests. It is situated on the Precambrian shield constituted of metamorphic and old volcanic rocks. Metamorphic rocks such as gneisses, migmatites, schists and quartzites dominate the geologic underground in the area. Sedimentary rocks of the Cretaceous can also be found in the Campo basin. The topography ranges from undulating to rolling in the lowland area and, to steeply dissect in the more mountainous areas. The western part of the park, which reaches the coast, is generally flat, with altitudes ranging between 0 m and 300 m. In the eastern part, which is quite mountainous, the altitude varies between 400 m and 1100 m and the rolling and steep terrain has more variable landscape (Tchouto, 2004). The climate is typical equatorial with two distinct dry seasons (December–February and June–August) and two wet seasons (March–May and September–November). The average annual rainfall generally ranges between 2950 mm/year in the coastal area in the western part to 1670 mm/year in the eastern part. The average annual temperature is about 25 °C and there is little variation between seasons and years. The hydrography of the area shows a dense pattern with many rivers, small river basins, fast-flowing creeks and rivers in rocky beds containing many rapids and small waterfalls. The main rivers are Ntem, Lobe, Bongola, Biwome, Ndjo'o, Mvila and Nye'ete.

### 2.2. Sampling and measurements

#### 2.2.1. Biomass data

Biomass data were obtained from felled trees collected in 2000 during the main dry season in three sample plots of 10 m × 10 m (Ibrahima et al., 2002). Before felling, species name of trees were identified and the diameter at breast height (dbh) and height were measured. All trees less than 50 cm in the sample plot were felled except one tree with dbh of 79 cm. Trees were felled at ground level with machete or chainsaw according to tree size and split into fractions as shown in the sketch below. The branches, twigs and leaves were separated from the trunk. Sawdust was also collected, weighted and added to the value of each category. Each category was put in a tarpaulin of 2 m × 2 m which was folded and weighted with a weighting scale (maximum weight 100 kg). Sub-samples of each category were collected, weighted fresh in the field with an electronic balance (maximum weight 3 kg). They were oven dried in the lab at 60 °C to obtain the moisture content. The moisture content (MC) of samples enables to deduce the MC in each section of the tree. Hence, it was then possible to obtain dry mass of each section of trees using the formula dry weight = fresh weight – moisture weight.

71 trees were used for development of site specific allometric equations for estimation of total aboveground biomass of mixed-species and for estimation of biomass of leaves and branches (cf. Appendix A).

To develop pan moist tropical equations including Cameroon (Africa) biomass data, we selected biomass data of moist tropical forests collected in different countries and continents from literature (Brown, 1997; Araújo et al., 1999; Nelson et al., 1999; Ketterings et al., 2001). Brown (1997) reported 169 tree biomass data including only diameter collected from Para Brazil, South Asia (Indonesia and Cambodia). Among this data, the location of 42 trees was not specified. Araújo et al. (1999) provided biomass data of 127 trees ranging from 10 cm to 138 cm including diameter and height collected in the state of Para, Brazil. Nelson et al. (1999) reported 27 total aboveground biomass data with trees ranging between 2 cm and 27 cm collected from Central Amazon. Ketterings et al. (2001) reported total above ground biomass data of 29 trees with dbh ranging from 7.6 cm to 48.1 cm including tree height and wood specific density collected in a moist forest, Indonesia.

#### 2.2.2. Height diameter data

The data was collected from three different land uses namely the National Park, the Managed area (concession forests) and the Agro-forest area including community forests and open access for-

**Table 1**
31 tree species selected from a total of 145 species, 3738 trees (dbh ≥ 10 cm) based on their ranking according to the importance value index (IVI) and commercial use.

| Case no. | Rank | Name | Abundance (*N*/ha) | Frequency (%) | Dominance ($m^2$/ha) | IVI |
|---|---|---|---|---|---|---|
| 1 | 1 | Edip | 25.38 | 100 | 1.25 | 17.28 |
| 2 | 2 | Oveng meki | 13.77 | 80 | 0.89 | 11.03 |
| 3 | 3 | Mekimekulu | 15.00 | 76 | 0.63 | 10.16 |
| 4 | 4 | Kankee | 16.00 | 88 | 0.41 | 9.85 |
| 5 | 5 | Mbazoa Afum | 13.08 | 68 | 0.59 | 9.12 |
| 6 | 6 | Ebap tom | 8.46 | 84 | 0.49 | 7.49 |
| 7 | 7 | Abem | 6.08 | 60 | 0.78 | 7.31 |
| 8 | 8 | Assam | 7.62 | 88 | 0.49 | 7.27 |
| 9 | 9 | Mfang | 5.31 | 52 | 0.73 | 6.59 |
| 10 | 10 | Assas | 10.62 | 52 | 0.32 | 6.56 |
| 11 | 11 | Minsi | 8.54 | 80 | 0.28 | 6.43 |
| 12 | 12 | Asseng | 6.69 | 48 | 0.56 | 6.19 |
| 13 | 13 | Ekang | 4.69 | 28 | 0.74 | 5.76 |
| 14 | 14 | Atjek kribi | 5.00 | 72 | 0.34 | 5.28 |
| 15 | 15 | Ngon | 3.08 | 72 | 0.47 | 5.21 |
| 16 | 16 | Mvomba | 5.62 | 64 | 0.28 | 4.97 |
| 17 | 18 | Bidou | 1.46 | 28 | 0.78 | 4.83 |
| 18 | 19 | Okweng ele | 6.00 | 56 | 0.26 | 4.82 |
| 19 | 21 | Omang | 2.92 | 60 | 0.35 | 4.27 |
| 20 | 26 | Padouk | 1.08 | 48 | 0.50 | 3.95 |
| 21 | 29 | Moambe jaune | 3.46 | 64 | 0.17 | 3.74 |
| 22 | 30 | Andok | 3.46 | 64 | 0.16 | 3.67 |
| 23 | 33 | Niove | 2.15 | 64 | 0.20 | 3.39 |
| 24 | 34 | Oyang | 2.62 | 48 | 0.16 | 2.95 |
| 25 | 35 | Emien | 1.15 | 40 | 0.31 | 2.92 |
| 26 | 36 | Azobe | 0.85 | 32 | 0.38 | 2.92 |
| 27 | 37 | Ekaba | 3.62 | 20 | 0.22 | 2.81 |
| 28 | 41 | Enak | 2.85 | 48 | 0.07 | 2.62 |
| 29 | 46 | Tali | 0.85 | 32 | 0.25 | 2.31 |
| 30 | 47 | Mevini | 2.00 | 48 | 0.05 | 2.23 |
| 31 | 55 | Akom/Limba | 0.92 | 12 | 0.21 | 1.63 |
| 32–145 | | Other | 97.23 | | 8.52 | 124.41 |
| | | Total | 287.54 | | 21.83 | 300.00 |

est areas. In each land use eight plots of 20 m × 250 m representing in total 24 plots (12 ha) were used to assess tree species in the different vegetation types present in this area. One plot of 100 m × 100 m (1 ha) was assessed in a concession forest in the eastern part of the study area. In each of the 24 plots, a subplot of 5 m × 20 m was included. In the plots, all trees with dbh ≥ 10 cm were measured. The parameters recorded were species name, dbh, total height, stem quality and the geographical coordinates *x* and *y*. In 5 m × 20 m subplot in each of the 24 plots, all trees with dbh between 5 cm and 10 cm were additionally recorded including species name, dbh, and total height.

For species which could not be identified directly on the field, voucher of the species were collected for species identification in the National Herbarium. The tree diameter was measured at 1.30 m height from the soil for all trees without buttresses and at 0.30 m height from the end of the buttresses or aerial roots. The tree height was measured with the SUUNTO height meter for all open trees with good visibility of the top and was estimated when it was not possible to see the top of the tree. To avoid over or under estimation of trees with poor visibility, a measurement was firstly made on an easily measurable border tree which helped to adjust height estimates.

In total 3833 trees with diameter ranging from 5 cm to 170 cm were selected for this study. We used the Importance Value Index (IVI) developed by Curtis and McIntosh (1951), to choose species for development of species-specific tree height allometric equations. According to this index, tree species in a given ecosystem can be classified in terms of their importance in that ecosystem. IVI evaluated according to the equation *IVI = relative abundance + relative dominance + relative frequency,* where abundance is the number of individuals (*N*/ha), dominance the basal area ($m^2$/ha) and frequency the percentage of plots in which a species is represented. 31 species out of 145 belonging to 17 families were selected for the development of species-specific height ∼ diameter regression equations. The selection criteria were the ranking based on IVI and the commercial value of species (Table 1).

To determine the specific wood density, 4–5core samples were collected for each species. The fresh volume of each sample was estimated using the Archimedes principle which states that at about 4 °C a solid immersed in water experiences an upward force equal to the weight of the water it displaces. The wood sample was oven dried during 48 h at 75 °C and weighted using an electronic balance. The specific wood density was calculated as oven dry weight divided by fresh volume. Our values seem to be similar to those of Brown (1997) but lower compared to values of Gerard et al. (2009) (Table 2).

### 2.3. Data analysis and modelling

The mathematical model for biomass studies which is most commonly used has the form of a power function (Zianis and Mencuccini, 2004; Pilli et al., 2006) because it has long been noted that a growing plant maintains the weight proportion between different parts (West et al., 1997, 1999). This function assumes the form $M = aD^b$ (Niklas, 1994; Kaitaniemi, 2004; Pilli et al., 2006) where $a$ and $b$ are the scaling coefficients, $D$ the diameter at breast height and $M$ the total weight of aboveground dry biomass of a tree. In most cases the variability of $D$ explained largely the variability of $M$. This correlation makes $D$ a good predictor for $M$. The most comprehensive approach to describe universal allometric scaling was presented by West et al. (1997, 1999), Brown and West (2000), Enquist (2002) and Niklas (1994, 2004). Their model commonly known as WBE model derives mainly from fractal geometry. Their fractal model predicts that aboveground biomass $M$ scales against stem diameter $D$, $a$, $b$ value of 2.67 ($M \sim D^{8/3}$). Zianis and Mencuccini (2004) using a world-wide list of 279 biomass allometric equations showed that this value should rather be closed to 2.36 and varies with species, stand age, site quality, climate, and stock-

**Table 2**
Wood dry density (g cm$^{-3}$) of selected tree species. For each species, local or commercial name, scientific name and family name and its density from three different sources are reported. A: Campo-Ma'an; B: Brown, 1997; C: Gerard et al., 2009.

| No. | Name | Scientific name | Family | Density (g cm$^{-3}$) | | |
|---|---|---|---|---|---|---|
| | | | | A | B | C |
| 1 | Edip | Strombosia tetrandra | Olacaceae | 0.76 | 0.63 | – |
| 2 | Oveng meki | Dialium pachyphyllum Harms | Caesalpiniaceae | – | – | – |
| 3 | Mekimekulu | Sabicea capitellata | Rubiaceae | 0.66 | – | – |
| 4 | Kankee | Allophylus africanus | Sapindaceae | – | – | – |
| 5 | Mbazoa Afum | Strombosia pustulata | Olacaceae | 0.74 | – | – |
| 6 | Ebap tom | Santiria trimera | Burseraceae | 0.53 | 0.53 | – |
| 7 | Abem (Ebiara) | Berlinia bracteosa | Caesalpinioideae | 0.55 | 0.60 | 0.70 |
| 8 | Assam/Rikio | Uapaca guineensis | Euphorbiaceae | 0.68 | 0.60 | – |
| 9 | Mfang (Eyoum) | Dialium pachyphyllum | Caesalpinioideae | 0.96 | 0.83 | 0.94 |
| 10 | Assas | Macaranga hurifolia | Euphorbiaceae | 0.26 | 0.40 | – |
| 11 | Minsi | Calpocalyx dinklagei | Mimosaceae | – | 0.66 | – |
| 12 | Asseng (Parasolier) | Musanga cecropioides | Moraceae | – | 0.23 | – |
| 13 | Ekang (Miama) | Calpocalyx heitzii | Mimosaceae | 0.78 | 0.66 | – |
| 14 | Johimbe (Atjek kribi) | Pausinystalia johimbe | Rubiaceae | 0.83 | – | – |
| 15 | Ngon (Eveuss) | Klainedoxa gabonensis | Irvingiaceae | 0.70 | 0.87 | 1.06 |
| 16 | Mvomba | Xylopia quintasii | Annonaceae | 0.51 | 0.70 | – |
| 17 | Bidou (Ozouga) | Saccoglotis gabonensis | Humiriaceae | 0.57 | 0.74 | 0.89 |
| 18 | Okweng ele | Hymenostegia afzeli | Caesalpiniaceae | 0.78 | 0.78 | – |
| 19 | Omang (Alep) | Desbordesia glaucescens | Irvingiaceae | 0.59 | – | 1.05 |
| 20 | Padouk (Mbel) | Pterocarpus soyauxii | Papilionoideae | 0.75 | 0.61 | 0.79 |
| 21 | Moambe jaune (Mfo) | Enanthia chlorantha | Annonaceae | 0.53 | 0.42 | – |
| 22 | Andok | Irvingia gabonensis | Irvingiaceae | – | 0.71 | – |
| 23 | Niove (M'bonda) | Staudtia kamerunensis | Myristicaceae | 0.80 | 0.75 | 0.88 |
| 24 | Oyang | Xylopia aethiopica | Annonaceae | 0.71 | 0.50 | – |
| 25 | Emien (Ekouk) | Alstonia congensis | Apocynaceae | 0.51 | 0.33 | 0.36 |
| 26 | Azobe (Okoga/Bongossi) | Lophira alata | Ochnaceae | 0.92 | 0.87 | 1.06 |
| 27 | Ekaba (Ekop ribi) | Tetraberlinia bifoliolata | Caesalpinioideae | – | 0.54 | 0.62 |
| 28 | Enak | Anthonotha macrophylla | Cealsapiniaceae | 0.70 | 0.78 | – |
| 29 | Tali (Elon) | Erythrophleum ivorensis | Caesalpinioideae | 0.82 | 0.72 | 0.91 |
| 30 | Mevini (Ebene) | Diospyros crassiflora | Ebenaceae | 0.84 | 0.82 | 0.90 |
| 31 | Akom/Limba | Terminalia superba | Combretaceae | 0.36 | 0.45 | 0.54 |

ing of stands. The value of $b$ is between two and three in most cases.

To account for the heteroscedasticity of data (variance increases with increasing diameter or height of trees), the standard method for estimating the coefficients $a$ and $b$ is through the least-square regression of log-transformed data for $D$ and $M$ with the value of $M$ obtained from destructive sample trees, i.e. $\ln(M) = \ln(a) + b\ln(D)$. This transformation introduces a systematic bias on the original scale that is generally corrected with a correction factor $CF$ depending on the residual standard error ($RSE$) (Finney, 1941; Baskerville, 1972; Yandle and Wiant, 1981; Sprugel, 1983; Madgwick and Satoo, 1975) according to $CF = \exp(RSE^2/2)$. Height prediction on the original scale, for example $\exp(\ln(a) + b\ln D)$ is multiplied by $CF$ (>1) to correct underestimation. The larger the RSE, the more uncertain regression models predict biomass values, and the larger the correction factor (Chave et al., 2005).

For biomass estimations, models (1)–(14) were tested. In these models, $M$ represents the total weight of aboveground dry biomass, $D$ the diameter at breast height, $H$ the total height and $\rho$ the specific wood density of a tree.

Linear models from Brown et al. (1989):

$$M = a + bD + cD^2 \quad (1)$$

Transformed nonlinear models from Brown et al. (1989):

$$\ln(M) = a + b\ln(D) \quad (2)$$

$$\ln(M) = a + b\ln(D^2H) \quad (3)$$

$$\ln(M) = a + b\ln(D^2H\rho) \quad (4)$$

Models from Chave et al. (2005):

$$\ln(M) = a + b\ln(D) + c\ln(H) + d\ln(\rho) \quad (5)$$

$$\ln(M) = a + b\ln(D) + c(\ln D)^2 + d(\ln D)^3 + b\ln(\rho) \quad (6)$$

Other models:

$$\ln(M) = a + b\ln(DH) \quad (7)$$

$$\ln(M) = a + b\ln(D) + c\ln(H) \quad (8)$$

$$\ln(M) = a + b\ln(D) + c\ln(\rho) \quad (9)$$

$$\ln(M) = a + b\ln(D^2H) + c\ln(\rho) \quad (10)$$

$$\ln(M) = a + b\ln(D) + c\ln(D^2H) + d\ln(\rho) \quad (11)$$

$$\ln(M) = a + b\ln(D) + c\ln(D^2H\rho) \quad (12)$$

$$\ln(M) = a + b\ln(D^2\rho) + c\ln(H) \quad (13)$$

$$\ln(M) = a + b(\ln D)^2 + c(\ln D)^3 + d\ln(D^2H) + b\ln(\rho) \quad (14)$$

First, we develop equations using only diameter as predictor. Then we stepwise include height and density and analyze their effects on the predictive quality of models. For each of the models tested, the following indicators of goodness of fit are reported:

- Adjusted $R^2$: corrects the coefficient of determination by accounting for an increasing number of independent variables.
- Residual standard error of estimate (RSE): square root of the residual variance around the regression function.
- Akaike Information Criterion (AIC): measure of goodness of fit of a regression model proposed by Akaike (1974). The regression equation with the lowest AIC value is the best estimator. $AIC = 2k - 2\ln(L)$ where $k$ is the number of parameters in the regression model, $L$ the likelihood of the data under the according regression model.

All the models listed above were tested. The best ones depending on the number of variables (diameter, height, wood density) included were selected based on the residual standard error, the

**Table 3**
Allometric equations for estimations of total aboveground biomass (*M*), biomass of leaves and of branches in Campo-Ma'an. *a*, *b* and *c* are the model's fitted parameters; *N* the sample size; RSE is the residual standard error of the estimate; Adj $R^2$ is the coefficient of determination, *D* range the diameter range of the trees analyzed, AIC the Akaike Information Criterion and the average value of relative errors in percentage.

| Equation type | *a* | *b* | *c* | *N* | RSE | Adj. $R^2$ | *D* (cm) | AIC | % |
|---|---|---|---|---|---|---|---|---|---|
| *Total biomass* | | | | | | | | | |
| 1. $\ln(M)=a+b\ln(D)$ | −1.8967 | 2.1135 | | 68 | 0.278 | 0.9089 | 1–10 | 46 | 7.8 |
| 2. $\ln(M)=a+b\ln(D)$ | −2.1079 | 2.3278 | – | 71 | 0.330 | 0.9562 | 1–79 | 48 | 7.4 |
| 3. $\ln(M)=a+b\ln(D^2H)$ | −3.0788 | 0.9066 | – | 71 | 0.328 | 0.9561 | 1–79 | 47 | 7.3 |
| 4. $\ln(M)=a+b\ln(D)+c\ln(\rho)$ | −1.9644 | 2.3382 | 0.3579 | 71 | 0.325 | 0.9575 | 1–79 | 48 | 7.0 |
| 5. $\ln(M)=a+b(\ln D)^2+c\ln(D^2H)+\beta\ln(\rho)$[a] | −2.3325 | 0.1651 | 0.6620 | 71 | 0.291 | 0.9659 | 1–79 | 34 | 3.4 |
| *Leaves* | | | | | | | | | |
| 6. $M=a+bD+cD^2$ | −0.1009 | 0.0626 | 0.0027 | 71 | 0.129 | 0.9976 | 1–79 | −83 | −15.8 |
| 7. $\ln(M)=a+b\ln(D)$ | −4.2028 | 1.6144 | | 71 | 0.686 | 0.708 | 1–79 | 156 | −13.7 |
| *Branches* | | | | | | | | | |
| 8. $M=a+bD+cD^2$ | 7.1585 | −3.0711 | 0.1912 | 71 | 2.874 | 0.9994 | 1–79 | 357 | −10.2 |
| 9. $\ln(M)=a+b\ln(D)$ | −4.8605 | 2.3754 | | 71 | 0.909 | 0.7496 | 1–79 | 192 | −58.7 |

[a] $\beta=0.1309$.

adjusted $R^2$ and the AIC. To validate these best models, we compare the mean, total, minimum and maximum biomass of measured trees with estimations of the different equations and also with their average value of the relative errors $100(M_{pi}-M_i)/M_i$ where $M_{pi}$ is the predicted dry weight of tree *i*, $M_i$ its observed dry weight.

Regression equations including height may improve significantly the models. To develop relationships of height as a function of diameter, we tested three models (van Laar and Akça, 1997 ((15) and (17)); Korsun, 1948 (16)):

$$\ln(H)=a+b\ln(D) \tag{15}$$

$$\ln(H)=a+b\ln(D)+c\ln(D^2) \tag{16}$$

$$\ln(H)=a+\frac{b}{D} \tag{17}$$

The best model was selected based on the residual standard error and was used to develop the species-specific relationship between height and diameter.

All data were analyzed with statistical software STATISTCA 9.

## 3. Results

### 3.1. Mixed-species allometric equations of the study site

We tested model (2) with only diameter (1–79 cm) as explanatory variable (Fig. 1). Then we included the height and tested its effect with diameter. Finally, we tested the effect of the three variables diameter height and wood density together in the models. The mixed-species allometric equations for biomass estimation are summarized in Table 3. The simple allometry $\ln(M)=-1.8967+2.1135\ln(D)$ (dbh range between 1 cm to 10 cm) or $\ln(M)=-2.1079+2.3278\ln(D)$ (dbh range 1–79 cm) seem to be good predictors of total aboveground biomass. The introduction of total height (model 3) did not improve the accuracy of the result with a RSE of 0.328 and an adjusted $R^2$ of 0.9561 and an AIC of 47. The wood density (model 9) provides a better fit with an adjusted $R^2$ of 0.9575, a RSE of 0.325 and an AIC of 48. Putting the three variables together (model 14) gives the best fit with an adjusted $R^2$ of 0.9659, a RSE of 0.291 and an AIC of 34.

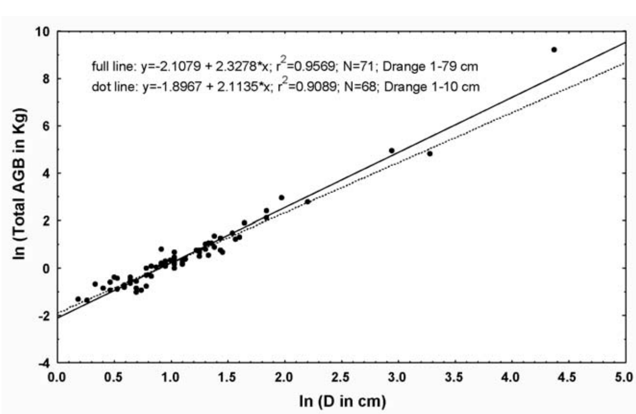


**Fig. 1.** Regression between the logarithm of total aboveground biomass in kg and the logarithm of diameter at breast height (*D*) in cm of 71 trees from our study site.

To test the consistency of fits, we added 20 trees which were not included in the development of the estimators and compared the values directly measured in the field for all trees (91) with estimations of our models. The result confirms simple model 2 to be a good estimator at the study site with an average error of 7.4%. Adding the three variables improved the fit with an average error of 3.4%. To estimate the biomass of branches and leaves, we tested two models 1 and 2. Model 1 $M=-0.1009+0.0626\,D+0.0027\,D^2$ seems to be a good predictor of leaves biomass with a RSE of 0.129 an adjusted $R^2$ of 0.9976. Model 2 seems to give a poorer estimator $\ln(M)=-4.2028+1.6144\ln(D)$ for leaves with an adjusted $R^2$ of 0.708 and an AIC of 156. The comparison of measured biomass with estimated biomass shows that model 2 is the best estimator with an average error of −13.7%; the average error of model 1 is −15.8%. Model 1 gives a good estimator for branches $M=7.1585+-3.0711D+0.1912D^2$ with a $R^2$ of 0.994. The comparison of measured and estimated biomass with the two estimators confirm model 1 as the best fit for branches with an average error of −10.2%.

### 3.2. General allometric equations for moist tropical forests

The data used to develop general allometric equations for moist tropical forests include our data and others originating from South America and Asia (Fig. 2). Since inventory data do not always include diameter, height and wood density, we tested the effects of each of these variables (Fig. 3). The best equation including only diameter $\ln(M)=-2.1801+2.5624\ln(D)$ uses 443 trees with diameter ranging from 1 cm to 148 cm. This equation has a RSE of 0.444 and an adjusted $R^2$ of 0.9671 (Table 4). The best allometric equation including diameter and height obtained with equation $\ln(M)=-3.2249+0.9885\ln(D^2H)$ uses 274 trees with diameters ranging from 1 cm to 138 cm. This equation has a RSE of 0.443 and an adjusted $R^2$ of 0.9710. Several models were tested to check the effect of inclusion of wood density. The equation $\ln(M)=-2.4733+0.2893(\ln D)^2-0.0372(\ln D)^3+0.7415\ln(D^2H)+0.2843\ln(\rho)$ (model 14) gives the best fit with three variables with a RSE of 0.437, an adjusted $R^2$ of 0.9717 and an AIC of 334. For validation of the models we compared the results of directly

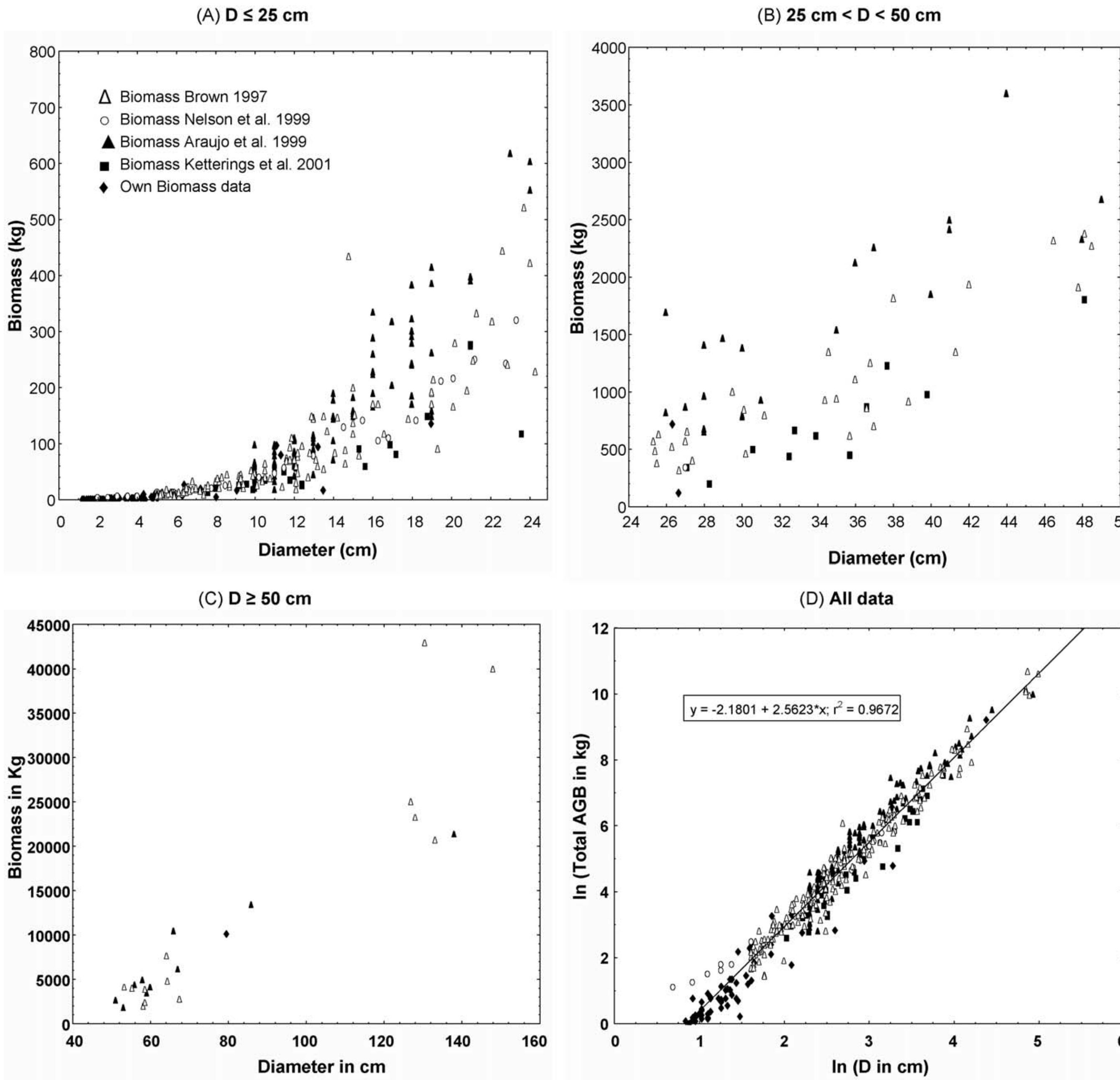


**Fig. 2.** Scatter plot showing the biomass from Brown, 1997, Nelson et al., 1999, Araújo et al., 1999, Ketterings et al., 2001 and our own biomass data. Graph A shows biomass data for $D \leq 25$ cm. Graph B shows biomass data diameter at breast height between 25 cm and 50 cm. Graph C shows biomass data with $D \geq 50$ cm. Graph *D* shows the regression between the logarithm of total aboveground biomass in kg and the logarithm of diameter at breast height (*D*) in cm for all trees.

**Table 4**

General or pan tropical allometric equations for estimations of total aboveground biomass in moist tropical forests. *a*, *b*, *c* and *d* are the model's fitted parameters; *N* the sample size; RSE is the residual standard error of the model; Adj $R^2$ is the coefficient of determination, *D* range the diameter range of the trees used and AIC the Akaike Information Criterion. Data are from Araújo et al. (1999), Nelson et al. (1999), Ketterings et al. (2001) and this paper input. Eq. (2) included these data and also data from Brown (1997).

| Equation type | *a* | *b* | *c* | *d* | *N* | RSE | Adj. $R^2$ | *D* range | AIC |
|---|---|---|---|---|---|---|---|---|---|
| 1. $\ln(M) = a + b\ln(D)$ | −2.2057 | 2.5841 | – | – | 274 | 0.483 | 0.9653 | 1–138 | 383 |
| 2. $\ln(M) = a + b\ln(D)$ | −2.1801 | 2.5624 | – | – | 443 | 0.444 | 0.9671 | 1–148 | 542 |
| 3. $\ln(M) = a + b\ln(D^2H)$ | −3.2249 | 0.9885 | – | – | 274 | 0.443 | 0.9710 | 1–138 | 335 |
| 4. $\ln(M) = a + b\ln(D) + c(\ln D)^2 + d(\ln D)^3 + \beta^{a}\ln(\rho)$ | −1.3774 | 1.3919 | 0.5477 | −0.0725 | 274 | 0.471 | 0.9670 | 1–138 | 375 |
| 5. $\ln(M) = a + b(\ln D)^2 + c(\ln D)^3 + d\ln(D^2H) + \beta^{*}\ln(\rho)$ | −2.4733 | 0.2893 | −0.0372 | 0.7415 | 274 | 0.437 | 0.9717 | 1–138 | 334 |

[a] 4. $\beta$ is 0.3529; 5. $\beta$ is 0.2843.

**Table 5**
Average errors in percentage (%) of published pan moist tropical equations and this paper input general equations. Published regressions are from Brown et al. (1989), (Brown 2 and Brown 3), Brown (1997), (Brown 1) and Chave et al. (2005). *D*, *H* and $\rho$ are the input parameters for regressions, which stands for diameter, height and wood density.

| Site | Brown 1 (*D*) | Brown 2 (*D*, *H*) | Brown 3 (*D*, *H*, $\rho$) | Chave. (*D*, *H*, $\rho$) | General 1 (*D*) | General 2 (*D*, *H*) | General 3 (*D*, *H*, $\rho$) |
|---|---|---|---|---|---|---|---|
| Para Amazone | −17.2 | −10.9 | 5.0 | −12.3 | −4.3 | 1.3 | 1.2 |
| Asia | 65.5 | 54.2 | 54.9 | 28.7 | 91.7 | 75.5 | 76.5 |
| Central Amazone | −10.3 | −6.4 | −9.9 | −29.6 | 2.4 | 4.5 | −1.9 |
| Africa | 29.5 | 31.3 | 60.8 | 10.7 | 42.8 | 39.9 | 38.4 |

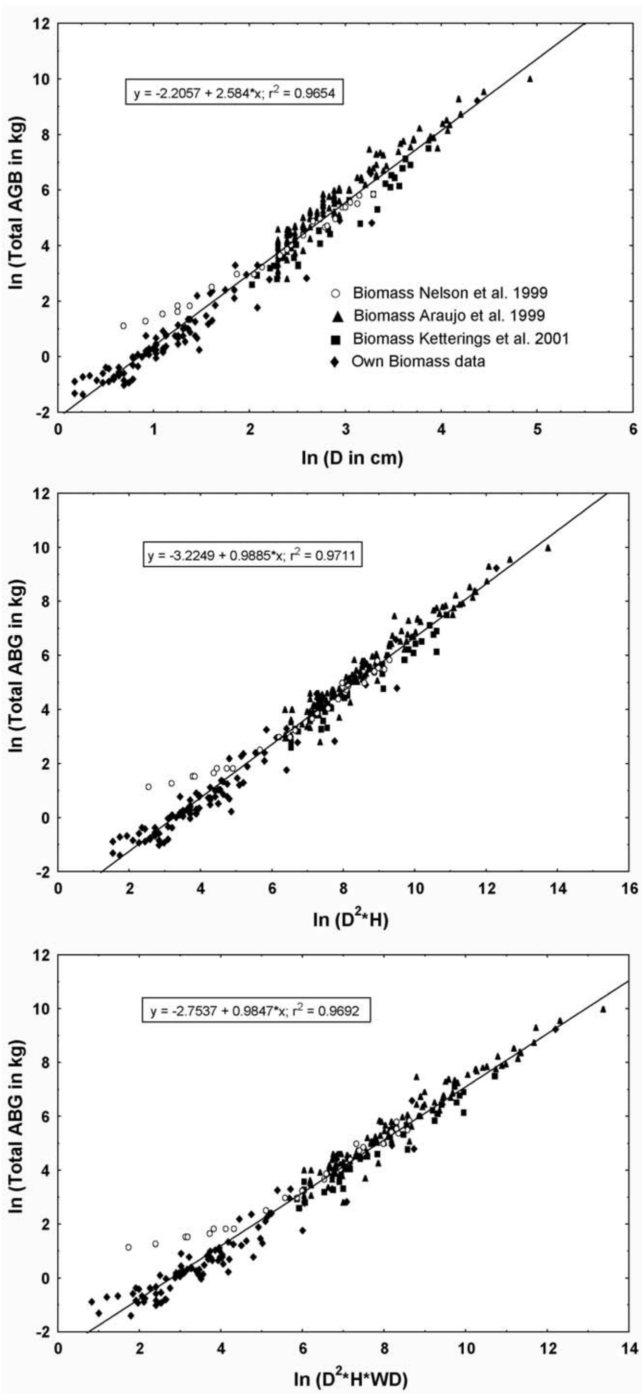


**Fig. 3.** Regression between the logarithm of total aboveground biomass and the logarithm of diameter at breast height in cm (upper graph); the logarithm of product of diameter and height in m (middle graph); the logarithm of product of square diameter, height and wood density (g cm$^{-3}$). Biomass data do not include data from Brown, 1997.

measured biomass with estimates of selected models in different locations across countries and continents (Table 5). General allometric equation with 3 variables (Model 14) confirms to be the best estimator with an average error of 29.5% reaching an average error of only 1.2% at Para Amazone. It is followed by model 3 containing two variables (diameter and height) with an average error of 30.3%. The model 2 with only one variable (diameter) gives a poor estimator for general allometric equation with an average error of 35.3%.

Brown et al. (1989), Brown (1997) and Chave et al. (2005) studied pan moist tropical allometric equations for large scale biomass estimations. Their equations have been widely used in moist tropical forests in areas where no specific equations for biomass estimations was developed. We selected two equations from Brown et al. (1989), one from Brown (1997) and one from Chave et al. (2005). The first equation of Brown et al. (1989) $M = \exp(-3.1141 + 0.9719 \ln(D^2H))$ was developed with 168 trees with dbh ranging from 5 cm to 130 cm with destructive biomass data collected in Cambodia, Brazil and Indonesia. The second equation $M = \exp(-2.4090 + 0.9522 \ln(D^2H\rho))$ was developed with 94 trees with dbh ranging from 5 cm to 130 cm. The equation of Brown (1997) $M = \exp(-2.134 + 2.530 \times \ln(D))$ was developed for moist forests with 170 trees ranging from 5 cm to 148 cm. The equation of Chave et al. (2005) $M = \exp(-2.977 + \ln(D^2H\rho))$ was developed from 1505 trees with dbh ranging from 5 cm to 156 cm collected from moist tropical forests in Brazil, French Guiana, India, Indonesia, Venezuela and Malaysia. To compare published equations with the one developed in this study, we estimated the average error made by each equation at different locations and continents. The result is summarized in Table 5. The equation of Chave et al. (2005) is the best estimator across continent and site with an average error of 20.3% and was directly followed by our general Eq. (3) of this study with 29.5%. Equation with only two variables (diameter and height) of Brown et al. (1989) estimates much better biomass across site than equation with three variables (Table 5). The dataset used (168 trees for equation with two variables and only 94 trees for equation with three variables) for the development of these equations should be a reason of this difference.

### 3.3. *Height regression equations*

The results of our biomass allometric equations study shows that the introduction of height in the allometric equation ameliorates the precision. To determine the relationship between height and diameter for our selected trees species, we tested three models 15–17 which have been reported by different authors to give good fit of height diameter relationship. The results are summarized in Table 6. The simple equation from model 15 $\ln(H) = 1.05 + 0.63 \ln(D)$ estimates better the relationship between the two variables with a correlation coefficient of 0.79 and a RSE of 0.294. For the development of specific allometric relationship between height and diameter for selected species, we used therefore model 15 as model estimator. The results of estimators for selected 31 species are summarized in Table 7. *b* values of allometric equations have a mean of 0.66 with 95% of values ranging between 0.56 and 0.83. *a* values of the allometric equations have a mean of 1.01 with 95% of val-

**Table 6**
Result of regression analysis for the different models tested for estimation of the relationship between tree height and diameter. *a*, *b* and *c* are the model's fitted parameters, S.E. *a*, S.E. *b*, S.E. *c* the standard error for *a*, *b* and *c*; R.S.E. is the residual standard error of the estimate, *R* the correlation coefficient and *N* the sample size.

| Equation type | *a* | *b* | *c* | *N* | R.S.E. | *R* | *D* range | AIC |
|---|---|---|---|---|---|---|---|---|
| $\ln(H)=a+b\ln(D)$ | 1.0506 | 0.6347 | – | 3833 | 0.294 | 0.7895 | 5–170 | 1497 |
| $\ln(H)=a+b\ln(D)+c\ln(D^2)$ | 1.0082 | 0.4931 | 0.2163 | 3833 | 0.294 | 0.7898 | 5–170 | 1499 |
| $\ln(H)=a+b/D$ | 3.6100 | −11.2056 | – | 3833 | 0.321 | 0.7426 | 5–170 | 2171 |

ues ranging between 0.72 and 1.51. *Xylopia aethiopica* (Oyang) has extreme values, *b* above 1 (1.04) and *a* 0.13 the lowest. Analysis of scatter plot shows a linear regression of negative slope between *b* and *a*, $b=1.0053-0.3348a$, with adjusted $R^2$ of 0.88 and RSE of 0.494 (Fig. 4a).

## 4. Discussions

### 4.1. Site specific mixed-species regressions

Several studies have attempted to study site specific allometric regressions for different species. The study of Nelson et al. (1999) with 132 trees in Central Amazon showed that simple model with only diameter as input is a good estimator which estimates biomass of mixed-species only with an average error of 19.8%. Including the height ameliorates just very little the precision with an average error of 17.7%. Including diameter, height and wood density has resulted in their study to much better precision with an average error of 14%. The study of Overman et al. (1994) with 54 mixed tree species in an Amazon rain forest found a relative higher average error of 25.6% for biomass estimations with only diameter as input. Adding height had just little effect with an average error of 24.3%. The three variables diameter, height and wood density dropped the precision of the measurement to 11.2%.

In this study, considering only diameter as input variable estimates the biomass of the study site with an average error of only 7.4%. Adding height to diameter has not improved the regression precision. Diameter and wood density together have improved slightly the accuracy with an average error of 7%. The three input variables together have improved significantly the accuracy with an average error of 3.4%. This study provides species-specific allometric relationship for height (Table 7) and also data of wood density (Table 2) for 31 species. This can be used to improve the estimations of biomass. Knowing that larger dataset provides best fit, we added the 20 trees used to test consistency and at it increases trees above 10 cm from three to eight trees. The best fit was based on these 91 trees. When only diameter is the input variable, the allometric equation recommended is $M=\exp(-1.9967+2.3924\ln(D))$. When diameter and height are available the regression recommended is $M=\exp(-2.9946+0.9317\ln(D^2H))$. In case diameter and wood density are available, the regression equation suggested is $M=\exp(-1.8623+2.4023\ln(D)-0.3414\ln(\rho))$. In case diameter, height and wood density are all available the equation suggested is $M=\exp(-2.4360+0.1399(\ln D)^2+0.7373\ln(D^2H)+0.2790\ln(\rho))$. In case heights and wood densities are not available in our site or similar, height diameter relationships summarized in Tables 6 and 7 and densities in Table 2 can be used. The mean value of densities was 0.64 g $cm^{-3}$ and can be used in our site or similar site when there is no data.

In the dataset of 71 trees, only three trees were above 10 cm. With the log transformation, the distance between biggest and small trees is remarkably reduced as one can see in Fig. 1. There-

**Table 7**
Height regression model $\ln(H)=a+b\ln(D)$ for selected species of our study site. *a* and *b* are the model's fitted parameters, S.E. *a*, S.E. *b* the standard error for *a* and *b*; R.S.E. is the residual standard error of the estimate, *R* the correlation coefficient and *N* the sample size.

| Species name | *a* | *b* | S.E. *a* | S.E. *b* | R.S.E | *R* | *N* | *D* range |
|---|---|---|---|---|---|---|---|---|
| Edip | 1.49 | 0.46 | 0.072 | 0.024 | 0.199 | 0.74 | 312 | 5–75 |
| Oveng meki | 1.04 | 0.65 | 0.097 | 0.032 | 0.236 | 0.84 | 174 | 5–125 |
| Mekimekulu | 1.11 | 0.59 | 0.088 | 0.031 | 0.213 | 0.81 | 198 | 5–63 |
| Kankee | 0.58 | 0.83 | 0.118 | 0.044 | 0.191 | 0.82 | 179 | 5–50 |
| Mbazoa Afum | 0.92 | 0.72 | 0.078 | 0.027 | 0.165 | 0.91 | 163 | 5–67 |
| Ebap tom | 0.78 | 0.74 | 0.108 | 0.036 | 0.184 | 0.90 | 98 | 5–50 |
| Abem | 0.39 | 0.83 | 0.207 | 0.059 | 0.291 | 0.85 | 77 | 10–78 |
| Assam | 0.58 | 0.82 | 0.114 | 0.038 | 0.205 | 0.92 | 87 | 5–80 |
| Mfang | 0.51 | 0.84 | 0.145 | 0.043 | 0.225 | 0.93 | 63 | 10–100 |
| Assas | 0.93 | 0.70 | 0.102 | 0.036 | 0.159 | 0.87 | 127 | 5–45 |
| Minsi | 1.32 | 0.52 | 0.138 | 0.050 | 0.237 | 0.71 | 110 | 5–54 |
| Asseng | 1.33 | 0.54 | 0.196 | 0.059 | 0.229 | 0.71 | 83 | 9–80 |
| Ekang | 1.63 | 0.46 | 0.152 | 0.043 | 0.182 | 0.83 | 54 | 12–89 |
| Atjek kribi | 0.49 | 0.89 | 0.156 | 0.051 | 0.207 | 0.92 | 55 | 5–70 |
| Ngon | 0.84 | 0.72 | 0.235 | 0.066 | 0.236 | 0.88 | 36 | 11–110 |
| Mvomba | 0.98 | 0.76 | 0.216 | 0.071 | 0.275 | 0.80 | 67 | 10–52 |
| Bidou | 1.74 | 0.53 | 0.483 | 0.115 | 0.289 | 0.74 | 19 | 18–170 |
| Okweng Ele | 1.30 | 0.53 | 0.156 | 0.053 | 0.220 | 0.76 | 75 | 5–48 |
| Omang | 1.44 | 0.55 | 0.236 | 0.071 | 0.298 | 0.78 | 39 | 5–83 |
| Padouk | 0.83 | 0.73 | 0.506 | 0.125 | 0.365 | 0.85 | 15 | 8–140 |
| Moambe jaune | 0.69 | 0.82 | 0.235 | 0.079 | 0.235 | 0.86 | 39 | 10–46 |
| Andok | 0.56 | 0.77 | 0.322 | 0.104 | 0.248 | 0.76 | 43 | 12–45 |
| Niove | 0.95 | 0.68 | 0.228 | 0.072 | 0.249 | 0.88 | 29 | 5–100 |
| Oyang | 0.13 | 1.04 | 0.204 | 0.066 | 0.163 | 0.96 | 24 | 10–47 |
| Emien | 0.82 | 0.63 | 0.380 | 0.102 | 0.322 | 0.88 | 13 | 11–95 |
| Azobe | 1.49 | 0.60 | 0.364 | 0.094 | 0.329 | 0.90 | 12 | 5–110 |
| Ekaba | 1.13 | 0.65 | 0.248 | 0.081 | 0.285 | 0.77 | 47 | 10–83 |
| Enak | 1.14 | 0.55 | 0.244 | 0.088 | 0.186 | 0.76 | 30 | 5–52 |
| Tali | 0.90 | 0.69 | 0.337 | 0.094 | 0.328 | 0.91 | 13 | 6–105 |
| Mevini | 0.88 | 0.67 | 0.269 | 0.101 | 0.229 | 0.79 | 29 | 5–43 |
| Akom/Limba | 1.56 | 0.45 | 0.314 | 0.088 | 0.269 | 0.85 | 12 | 10–90 |

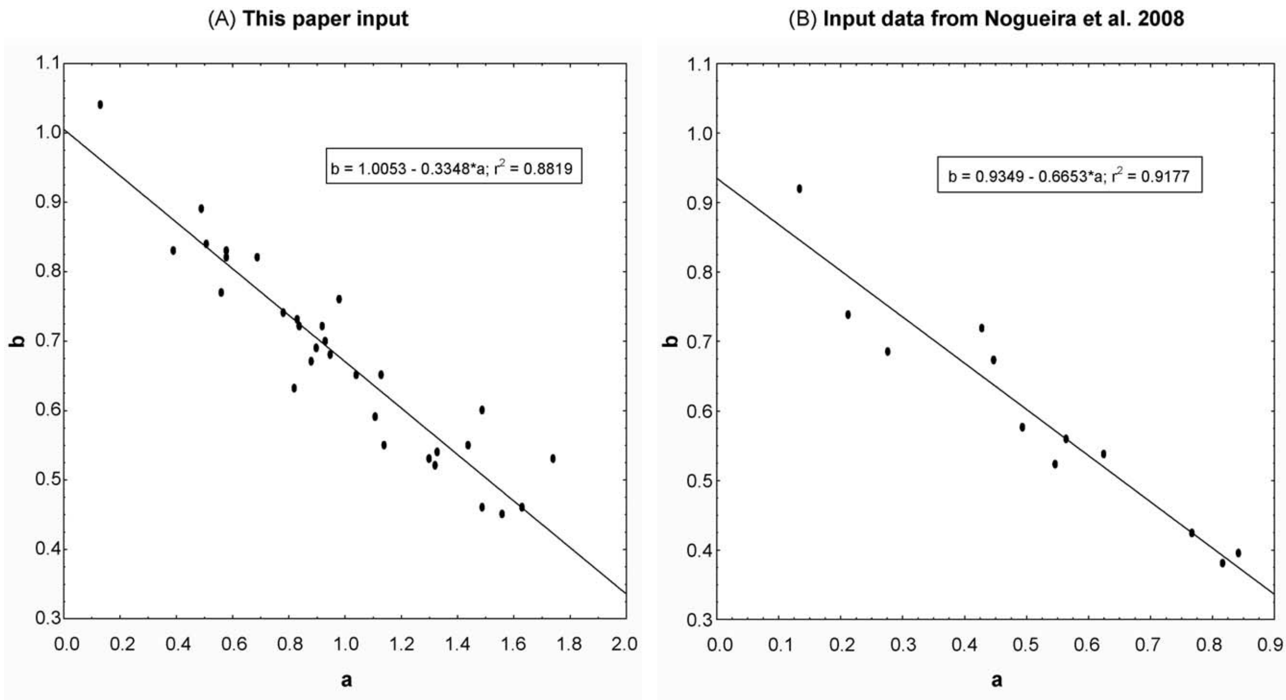


**Fig. 4.** Scatter plot showing the relationship between *b* and *a* in the height diameter allometric equation with the model $\ln(H) = a + b\ln(D)$.

fore, the three biggest trees in diameter are less extreme after transformation. The few big trees help to calibrate the relationship at upper range. This can be viewed also in the scatter plot in Fig. 1. This argument has been supported by Chave et al. (2001) which stated that the biomass values of the smallest trees strongly affect the coefficients in the allometric between *M* and *D*. This argument was strongly discussed by Zianis and Mencuccini (2004) who showed that "valid estimates for the scaling coefficients in relationship between *M* and *D* can be obtained from only two values of *D* and the corresponding *M*". Nevertheless, more data at upper diameter range are needed for consistency of the allometry for bigger trees.

The regression equations of branches and leaves elaborated in this study constitute an additional improvement for estimations of biomass when inventory data provide information on trunk volume as it is in many cases. The relation $M = \rho \times V$ can enable to derive the biomass of trunk and the regression equations of branches and leaves to estimate their biomass. The sum of the three assortments gives the total aboveground of a tree. The expansion factor ratio of total biomass to biomass of the trunk was also estimated for each tree (Appendix A). The mean expansion factor for all trees is 1.22. It can also be used as alternative to convert bole volume from inventory data to total aboveground biomass. In this case the diameter range should be between 1 cm and 79 cm.

This study also confirms the value of *b* to be between 2 and 3 in the relationship $M = aD^b$ as predicted in many studies (West et al., 1997, 1999; Brown and West, 2000; Enquist, 2002; Niklas, 1994, 2004; Zianis and Mencuccini, 2004). In the relationship $H = aD^b$, this study found the value of *b* to be between 0.10 and 1 with a mean value close to 0.66. *b* and *a* are linked with a linear relationship with negative slope which is −0.3348 in the present study. The study of Nogueira et al. (2008) publishes 12 regression equations between height and diameter $H = aD^b$. The analysis of values between *b* and *a* confirms the tendency of linear relationship of negative slope with a value −0.6653 in their case (Fig. 4b). The mean value of *b* in the study of Nogueira et al. (2008) is 0.59 with a range between 0.38 and 0.92 which is similar to the results found in this study.

### 4.2. Pan moist tropical regressions

Different authors have attempted to develop general allometric equations which can be used irrespective of site, regions or continent. In practise, when there are species-specific regression equations at a given location, it is always advisable to use them. In case of absence of species-specific regressions at a site, mixed-species regressions are the most suitable. General allometric equations are recommended only in case of lack of these equations. Since existing allometric equations developed so far have not included data from Africa, many discussions have been raised concerning their validity in Africa.

We gathered biomass data from different locations (Asia, South America and our own data) and use them to develop general allometric regressions which include data from Africa. We tested many models and selected the best one for different input variables. The analysis of average errors (Table 5) shows that the equation of Chave et al. (2005) is the best estimator at different locations. This should be attributed to the large input data set used for the development of this equation. It was difficult to make a general conclusion or classification of general allometric equations. The scatter plot showing errors made by general equations in estimating biomass data at different locations (Fig. 5) suggests using these equations at a specific site only on special conditions with care. Before using these allometry regressions, it is necessary to calibrate the relation with at least 5–20 biomass tree data from real measurement at the specific site. With these additional site specific data, it can be checked which of the published allometric relationship is suitable for the study site. General allometric regressions developed in this paper with three variables diameter, height and wood density reduces the errors of the estimator. Therefore, we recommend using equation of Chave et al. (2005) or the one developed in this study with three variables in case there is no biomass data to test consistency of different estimators.

If diameter, height and wood density are available in forest inventory data, the best general allometry developed in

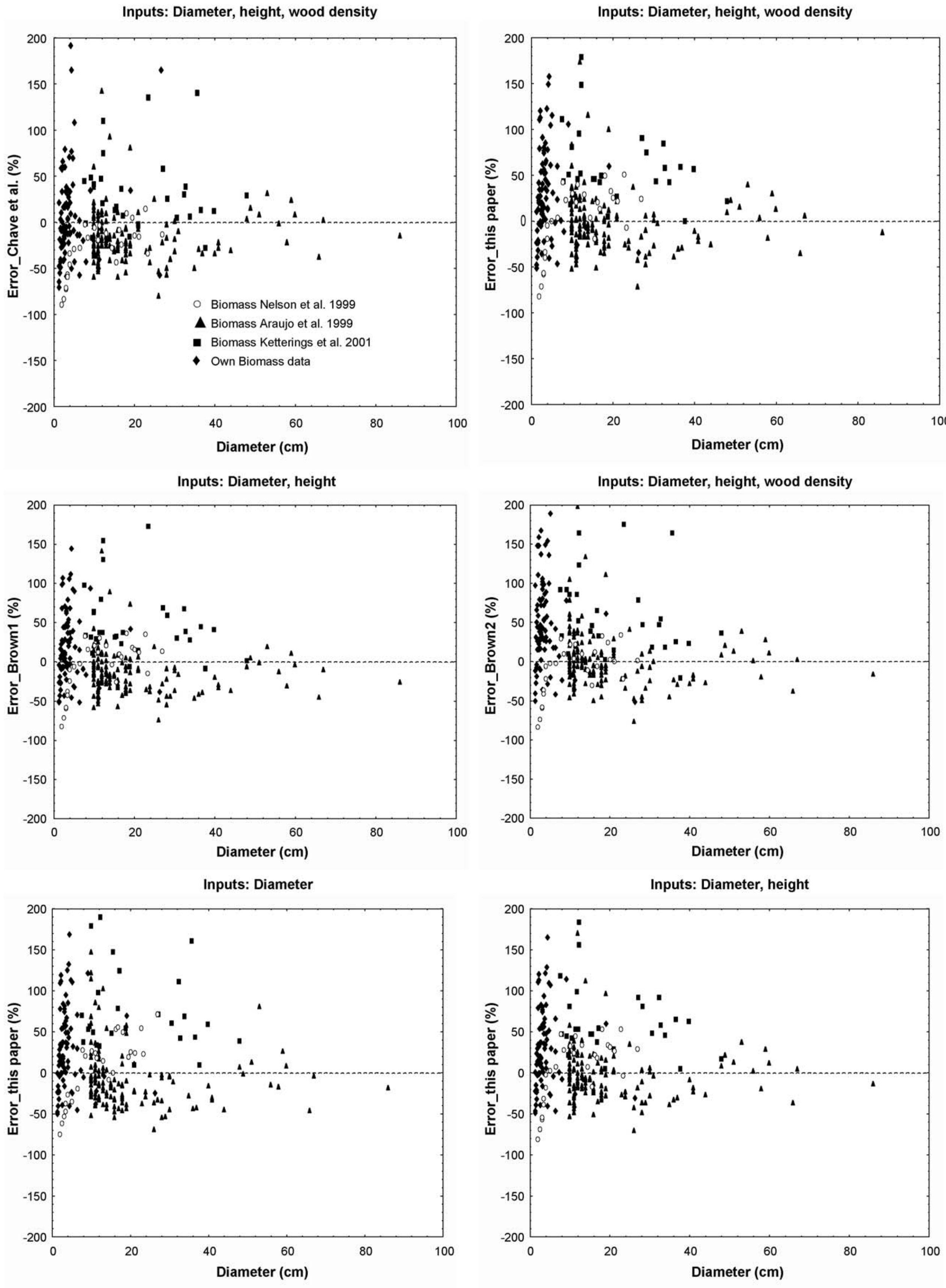


**Fig. 5.** Error of three published pan moist tropical equations and three equations of this paper to predict total aboveground biomass from different data source. Tendency to underestimate or overestimate is indicated by the distance above or below 0% line.

this research is $M = \exp(-2.3778 + 0.2893(\ln D)^2 - 0.0372(\ln D)^3 + 0.7415\ln(D^2H) + 0.2843\ln(\rho))$. If diameter and height are available in forest inventory data, the best general allometry proposed by this work is $M = \exp(-3.1268 + 0.9885\ln(D^2H))$. If diameter and wood density are available in forest inventory data, the best general allometry developed here is $M = \exp(-1.2665 + 1.3919\ln(D) + 0.5477(\ln D)^2 - 0.0725(\ln D)^3 + 0.3529\ln(\rho))$. If only diameter is available in forest inventory data, the best general allometry is $M = \exp(-2.0815 + 2.5624\ln(D))$. Height has shown to be a good explanatory variable across site; therefore general allometric incorporating at least diameter and tree height should be preferred.

## 5. Conclusions

Mixed-species regression equations provide good estimates of total aboveground biomass of the Campo-Ma'an forest when using only diameter as input variable with an average error of only 7.4%. Including height in the model has not improved the precision of the model and having the three variable diameter, height and wood density has improved the precision to 3.4%. This study has provided wood density (Table 2) and species-specific allometric relationship between height and diameter (Table 7) for 31 tree species. They can be used to improve estimations of total aboveground biomass. The regression equations of branches and leaves developed in this study can also be used to estimate total aboveground biomass when inventory data provide estimates of volumes or biomass of trunk of trees.

It should be kept in mind when using allometric equations that many sources of errors are possible. The sources of bias which can create additional errors are the range of observations, the bias of logarithm transformation and data source. The regressions should not be applied beyond the range of observations used to develop the model. Because the distance between for instance 0.1, 1, 10, 100, 1000, 10 000 are the same in the logarithm scale, the transformation stretches the smaller trees and compresses the bigger ones. Using logarithm units rather than observation units minimizes the distance of observed values (Nelson et al., 1999). This can be viewed comparing Fig. 2a, b and c with d. Many authors state that this bias can be corrected by using the correction factor $CF = \exp(RSE^2/2)$ (Saldarriaga et al., 1988; Chave et al., 2005; Stow et al., 2006). The correction factor of regression equations should be introduced to minimize this bias when back transforming to the normal value for biomass (kg) or heights (m). In many cases of forest inventories, tree diameters and heights are obtained through eye estimations of skilled workers. This can be a source of errors which needs to be considered when applying regression equations.

In the absence of species-specific allometric equations or mixed-species allometric equations at a given site, general allometric equations for moist forests are an appropriate alternative. Although allometric equation developed by Chave et al. (2005) seems to estimate much better aboveground biomass at various sites with an average error of 20.3%, followed by the best one developed in this study, it was difficult to draw a general conclusion for the best pan moist tropical allometric equations. It is necessary to have some true biomass values to test and select the general allometric equation which fits much better on the study site. This study provides different pan moist tropical allometric equations which can be used depending on the type of data available.

## Acknowledgements

The biomass data collection was financed by the European commission and the Tropenbos International. Under the grant WWFCCPO/KZ/GRANT/FY09/020/TNM/GAN/nep WWF Kudu Zombo has supported all other field data collection. The authors give special thanks to these institutions and extend their gratitude to Katholisher Akademischer Ausländer Dienst (KAAD) and also to Ulrich Stiftung foundation for their financial assistance. We also extend our special thank to Prof. Dr. Alexander Knohl for his comments for the improvement of this study.

## Appendix A. Biomass data of Campo-Ma'an

For each tree, the local name, the dry wood density, the diameter, the height and the corresponding value of biomass for leaves, branches, trunk, total and expansion factor are reported. The expansion factor is the ratio total biomass to trunk biomass.

| No. | Local name | Density ($g\,cm^{-3}$) | Diameter (cm) | Height (m) | Leaves (Kg) | Branches (kg) | Trunk (kg) | Total (kg) | Expansion factor |
|---|---|---|---|---|---|---|---|---|---|
| 1 | akendeng | 0.64 | 4 | 6.4 | 0.13 | 0.22 | 3.49 | 3.85 | 1.10 |
| 2 | ako ele | 0.65 | 1.6 | 3.8 | 0.07 | 0.03 | 0.44 | 0.55 | 1.24 |
| 3 | ako ele | 0.65 | 3 | 5.4 | 0.16 | 0.07 | 1.12 | 1.35 | 1.20 |
| 4 | awonog | 0.5 | 3.1 | 5.5 | 0.11 | 0.06 | 1.27 | 1.44 | 1.13 |
| 5 | awonog | 0.5 | 6.3 | 8.3 | 0.36 | 0.43 | 7.40 | 8.19 | 1.11 |
| 6 | awonog | 0.5 | 2.8 | 5.2 | 0.16 | 0.17 | 1.24 | 1.57 | 1.27 |
| 7 | awonog | 0.5 | 3.9 | 6.3 | 0.28 | 0.32 | 2.16 | 2.75 | 1.28 |
| 8 | awonog | 0.5 | 3.5 | 5.9 | 0.08 | 0.10 | 1.42 | 1.60 | 1.13 |
| 9 | awonog | 0.5 | 2.2 | 4.6 | 0.02 | 0.05 | 0.66 | 0.72 | 1.09 |
| 10 | awonog | 0.5 | 2.3 | 4.7 | 0.06 | 0.10 | 0.92 | 1.08 | 1.18 |
| 11 | awonog | 0.5 | 3.7 | 6.1 | 0.09 | 0.13 | 2.53 | 2.74 | 1.08 |
| 12 | azobe | 1.08 | 2.8 | 5.2 | 0.06 | 0.06 | 1.80 | 1.93 | 1.07 |
| 13 | dabema | 0.73 | 1.7 | 3.9 | 0.01 | 0.07 | 0.32 | 0.41 | 1.26 |
| 14 | ebene | 1.05 | 1.3 | 3.4 | 0.01 | 0.01 | 0.23 | 0.25 | 1.08 |
| 15 | ebene | 1.05 | 1.8 | 4.1 | 0.05 | 0.06 | 0.33 | 0.44 | 1.34 |
| 16 | ebene | 1.05 | 4.2 | 6.6 | 0.06 | 0.04 | 2.04 | 2.14 | 1.05 |
| 17 | edon | 0.64 | 2 | 4.3 | 0.02 | 0.02 | 0.52 | 0.56 | 1.08 |
| 18 | ekong | 0.59 | 2.5 | 4.9 | 0.08 | 0.03 | 1.11 | 1.22 | 1.10 |
| 19 | ekong | 0.59 | 3.5 | 5.9 | 0.05 | 0.02 | 2.02 | 2.09 | 1.04 |
| 20 | ekong | 0.59 | 2.6 | 5 | 0.05 | 0.02 | 0.99 | 1.07 | 1.08 |
| 21 | ekong | 0.59 | 1.2 | 3.2 | 0.01 | 0.00 | 0.25 | 0.27 | 1.05 |
| 22 | ekong | 0.59 | 3.8 | 6.2 | 0.19 | 0.07 | 2.57 | 2.83 | 1.10 |
| 23 | ekong | 0.59 | 2.5 | 4.9 | 0.07 | 0.10 | 0.94 | 1.11 | 1.17 |
| 24 | ekop naga | 0.68 | 5.2 | 7.4 | 0.37 | 0.99 | 5.11 | 6.48 | 1.27 |
| 25 | endon | 0.64 | 2.2 | 4.6 | 0.08 | 0.11 | 0.78 | 0.97 | 1.24 |
| 26 | endon | 0.64 | 1.7 | 3.9 | 0.04 | 0.04 | 0.58 | 0.65 | 1.13 |
| 27 | endon | 0.64 | 4.2 | 6.6 | 0.19 | 0.18 | 3.10 | 3.47 | 1.12 |
| 28 | essang afan | 0.64 | 2.2 | 4.6 | 0.09 | 0.14 | 0.73 | 0.96 | 1.31 |

Appendix A (*Continued* )

| No. | Local name | Density (g cm$^{-3}$) | Diameter (cm) | Height (m) | Leaves (Kg) | Branches (kg) | Trunk (kg) | Total (kg) | Expansion factor |
|---|---|---|---|---|---|---|---|---|---|
| 29 | etup ngon | 0.64 | 3 | 5.4 | 0.02 | 0.07 | 1.10 | 1.18 | 1.08 |
| 30 | etup ngon | 0.64 | 2.6 | 5 | 0.20 | 0.23 | 0.88 | 1.31 | 1.49 |
| 31 | etup ngon | 0.64 | 2.8 | 5.2 | 0.29 | 0.22 | 0.99 | 1.50 | 1.52 |
| 32 | eveus | 0.87 | 2.8 | 5.2 | 0.09 | 0.08 | 0.97 | 1.14 | 1.17 |
| 33 | ewolet | 0.47 | 26.7 | 18.8 | 3.18 | 58.00 | 59.73 | 120.92 | 2.02 |
| 34 | ilomba | 0.5 | 9.1 | 10.2 | 0.60 | 0.99 | 14.39 | 15.98 | 1.11 |
| 35 | kanda | 0.7 | 3.5 | 5.9 | 0.04 | 0.01 | 1.87 | 1.91 | 1.02 |
| 36 | keka afan | 0.64 | 2 | 4.3 | 0.12 | 0.05 | 0.20 | 0.36 | 1.84 |
| 37 | keka afan | 0.64 | 2 | 4.3 | 0.05 | 0.04 | 0.33 | 0.42 | 1.28 |
| 38 | keka afan | 0.64 | 1.8 | 4.1 | 0.04 | 0.09 | 0.34 | 0.47 | 1.39 |
| 39 | keka afan | 0.64 | 2.6 | 5 | 0.07 | 0.16 | 1.07 | 1.30 | 1.21 |
| 40 | keka afan | 0.64 | 2.7 | 5.1 | 0.15 | 0.18 | 1.02 | 1.35 | 1.32 |
| 41 | keka afan | 0.64 | 1.9 | 4.2 | 0.02 | 0.04 | 0.62 | 0.68 | 1.11 |
| 42 | keka afan | 0.64 | 2.3 | 4.7 | 0.07 | 0.06 | 0.57 | 0.70 | 1.22 |
| 43 | keka afan | 0.64 | 3.8 | 6.2 | 0.13 | 0.21 | 1.37 | 1.71 | 1.25 |
| 44 | keka afan | 0.64 | 3.4 | 5.8 | 0.10 | 0.22 | 1.79 | 2.11 | 1.18 |
| 45 | keka afan | 0.64 | 2.4 | 4.8 | 0.13 | 0.16 | 0.71 | 1.00 | 1.41 |
| 46 | keka afan | 0.64 | 3.7 | 6.1 | 0.15 | 0.17 | 1.83 | 2.15 | 1.18 |
| 47 | keka afan | 0.64 | 2.5 | 4.9 | 0.11 | 0.14 | 0.95 | 1.21 | 1.27 |
| 48 | keka afan | 0.64 | 3.0 | 5.4 | 0.10 | 0.11 | 0.95 | 1.16 | 1.22 |
| 49 | Koffi afan | 0.64 | 1.7 | 3.9 | 0.11 | 0.07 | 0.50 | 0.68 | 1.36 |
| 50 | mbe mvaa | 0.64 | 3.0 | 5.4 | 0.02 | 0.14 | 1.05 | 1.21 | 1.15 |
| 51 | mfang mvanda | 0.52 | 1.9 | 4.2 | 0.07 | 0.04 | 0.40 | 0.51 | 1.26 |
| 52 | mfo | 0.55 | 3.5 | 5.9 | 0.49 | 0.35 | 1.13 | 1.98 | 1.74 |
| 53 | mfo | 0.55 | 4.3 | 6.7 | 0.06 | 0.05 | 1.85 | 1.96 | 1.06 |
| 54 | miasmigomo | 0.64 | 2.1 | 4.4 | 0.03 | 0.04 | 0.33 | 0.39 | 1.19 |
| 55 | minsii | 0.83 | 1.9 | 4.2 | 0.04 | 0.05 | 0.48 | 0.58 | 1.20 |
| 56 | minsii | 0.83 | 2.5 | 4.9 | 0.15 | 0.06 | 1.95 | 2.16 | 1.11 |
| 57 | minsii | 0.83 | 1.5 | 3.7 | 0.03 | 0.02 | 0.38 | 0.43 | 1.12 |
| 58 | minsii | 0.83 | 2.8 | 5.2 | 0.05 | 0.02 | 0.90 | 0.96 | 1.07 |
| 59 | minsii | 0.83 | 5.0 | 7.3 | 0.08 | 0.39 | 3.20 | 3.67 | 1.15 |
| 60 | niove | 0.93 | 4.7 | 7.0 | 0.17 | 0.21 | 3.93 | 4.31 | 1.10 |
| 61 | nom ovoe | 0.64 | 1.4 | 3.5 | 0.04 | 0.11 | 0.36 | 0.51 | 1.40 |
| 62 | nom sikong | 0.64 | 2.2 | 4.6 | 0.09 | 0.07 | 0.30 | 0.45 | 1.53 |
| 63 | okekela | 0.64 | 7.2 | 9.0 | 0.29 | 0.84 | 17.86 | 18.99 | 1.06 |
| 64 | ossang mevini | 0.73 | 1.6 | 3.8 | 0.03 | 0.05 | 0.30 | 0.39 | 1.28 |
| 65 | ossang mevini | 0.73 | 2.8 | 5.2 | 0.05 | 0.08 | 1.15 | 1.28 | 1.12 |
| 66 | Owoe | 0.55 | 6.3 | 8.3 | 0.34 | 2.66 | 7.81 | 10.81 | 1.38 |
| 67 | Owoe | 0.55 | 4.0 | 6.4 | 0.18 | 0.26 | 1.93 | 2.37 | 1.23 |
| 68 | Owoe | 0.55 | 4.8 | 7.1 | 0.03 | 0.03 | 3.22 | 3.28 | 1.02 |
| 69 | rikio | 0.65 | 2.6 | 5.0 | 0.07 | 0.02 | 1.13 | 1.22 | 1.08 |
| 70 | sangomo | 0.65 | 19.0 | 15.5 | 2.78 | 4.68 | 129 | 136 | 1.06 |
| 71 | tali | 0.90 | 79.4 | 35.0 | 22.03 | 969 | 9054 | 10 045 | 1.11 |

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