



Age-related equations for above- and below-ground biomass of a *Eucalyptus* hybrid in Congo

Laurent Saint-André^{a,*}, Armel Thongo M'Bou^b, André Mabilia^b,
Welcome Mouvondy^b, Christophe Jourdan^c, Olivier Roupsard^d,
Philippe Deleporte^b, Olivier Hamel^a, Yann Nouvellon^b

^aCirad-Forêt, Campus de Baillarguet, TA 10/C, 34398 Montpellier Cedex 5, France

^bUR2PI, BP 1291, Pointe-Noire, Congo

^cCirad-CP, Site de Lavalette, TA 80/01, 34398 Montpellier Cedex 5, France

^dCARFV, BP 231, Espiritu Santo, Vanuatu

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Abstract

A complete set of equations for below- and above-ground biomass of a natural *Eucalyptus* hybrid in Congo was constructed. Heteroscedasticity of data was taken into account by fitting weighted non-linear regressions using maximum likelihood estimates. Stand age was introduced as a complementary variable in the equations for a majority of above-ground compartments and led to improved estimates of biomass. Because of the limited number of sampled trees for below-ground parts, it was not possible to develop the same kind of equations. Simple allometric relationships were then fitted for these components (stumps, large, medium, and fine roots). Additivity was verified and showed no significant deviation except for the youngest stand, where the sum of below- and above-ground biomass equations was preferable to the sum of component equations or to the total biomass equation. This set of equations will now be used to evaluate both the mean and the interval of confidence of biomass content and partitioning within the stands.

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1. Introduction

Biomass equations or volume equations are now widely developed in forestry and agroforestry for both

industrial and scientific purposes. These models have the same objectives: to evaluate some difficult-to-measure tree characteristics from easily collected data such as diameter at breast height (dbh), total height, or tree age. Generally, equations are linear, exponential, allometric, or hyperbolic, and correlations are often very good ($R^2 > 0.8$). For more details, one can refer to the following reviews: Bouchon (1974), Hitchcock

* Corresponding author. Tel.: +33 4 67 59 37 47;
fax: +33 4 67 59 37 33.

E-mail address: standre@cirad.fr (L. Saint-André).

and McDonnell (1979), Pardé (1980), Cailliez (1980), Pardé and Bouchon (1988), and more recently Parresol (1999).

Within the context of carbon sequestration, new applications of these biomass equations are performed. A correct evaluation of carbon storage within the ecosystem is of major importance, especially when these storages are low. It is then necessary to provide an accurate mean biomass but also its confidence interval in order to compare different methods of evaluation (e.g. destructive measurements versus atmosphere–ecosystems exchange) or to compare different stands or silviculture regimes. This implies (i) setting up a representative sampling of the considered ecosystem, (ii) taking the data's heteroscedasticity (non-homogeneous variance among the tree sizes) into account during the fitting process, and (iii) simulating for the whole ecosystem both the mean and the interval of confidence of the biomass estimates. However, up to now, relatively few biomass studies have taken into account the three major difficulties that may occur when building such equations: heteroscedasticity, genericity and additivity. Parresol (1999) proposed a well-documented and explicit review focusing on these three points.

Forty-three thousand hectares of *Eucalyptus* plantations have been established in the coastal plains of Congo for 25 years. A comprehensive study has been conducted since 2001 to evaluate the carbon sequestration for the most planted clone. This natural hybrid pf1 1–41, unknown father \times *Eucalyptus alba* Reinw. ex Blume (from Delwaule, 1988), is the most planted clone (more than 7000 ha from 1978) and the reference one for all research trials is this forest area. The main objective of the comprehensive study is to compare two classical approaches to evaluate carbon storage: a destructive one, through biomass equation and measurement of respiration, and a non-destructive

one obtained from a flux tower and eddy-correlations (Aubinet et al., 2000; Moncrieff et al., 1997a,b). Results dealing with ecosystem respiration can be found in Epron et al. (2004). In the present study, we focused on biomass equations. Working on clonal plantations allowed us to (i) identify the variability of tree biomass when genetic variations are reduced to the minimum, (ii) investigate the variations of biomass equations with stand age or stand maturity. Special attention was paid to model fitting: the objectives were (i) to fit equations for above- and below-ground biomass using weighted regression, and (ii) to evaluate additivity of predicted biomass components. These two points are important before performing simulations on larger scales (stand or region).

2. Material and methods

2.1. Stand selection

The study site is located along the Atlantic coast in the Pointe Noire region (Congo, 4°S, 12°E, 100 m elevation). The mean annual air humidity and air temperature are 85% and 25 °C, respectively, with low seasonal variation (about 2% and 5 °C, respectively). Mean annual precipitation is 1200 mm with a dry season between May and September. Fig. 1 presents the global pattern of the planting schedule in this area. In order to select a wide range of situations, it was decided to sample two stands in the first cycle of plantation (one stand in an old high forest G1, and one stand in an old coppice G2), and four stands in the second cycle (high forest age-series, G3A to G3D). With the exception of G3A, which is an experimental plot in a fertilization trial, all stands were selected within the industrial forest area. Table 1 gives the characteristics of these stands.

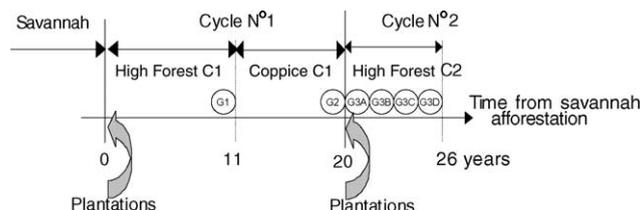


Fig. 1. Planting schedule for the forest area near Pointe-Noire (Congo) and stand sampling. The names of the selected stands are given inside the circles.

Table 1
Description of the selected stands (fit data set and validation data set)

Stand name	Age (months)	Stocking (stems/ha)	Mortality (%)	Basal area (m ² /ha)	Average height (nm)	Nb felled trees	Nb trees with aerial biomass	Nb trees with stump biomass	Nb trees with root biomass	Nb trees with total biomass
Fit data set										
G1	135	666	12	18.7	29.9	16	16	7	4	4
G2	104	709	10	13.3	25.7	12	12	–	–	–
G3A	11	800	0	1.5	4.7	4	4	4	4	4
G3B	27	700	19	4.3	11.2	12	12	12	6	6
G3C	50	709	16	10.0	20.9	12	12	–	–	–
G3D	75	800	7	13.4	23.6	16	14	6	4	4
Stand name	Age (months)	Stocking (stems/ha)	Mortality (%)	Basal area (m ² /ha)	Average height (nm)	Nb felled trees	Nb trees with aerial biomass	Reference		
Validation data set										
V1	88	666	12	14.4	26.5	30	30	Laclau et al. (2000)		
V2	62	666	11	11.2	22.7	12	12	Laclau et al. (2000)		
V3	49	666	16	10.5	20.7	12	12	Laclau et al. (2000)		
V4	24	800	2	6.3	11.0	12	12	Laclau et al. (2000)		
V5	13	666	9	2.0	5.9	12	12	Laclau et al. (2000)		
V6	63	507	5.2	13.1	26.4	12	12	Laclau et al. (2000)		
V7	84	532	–	12.9	26.1	12	12	Bouillet et al. (1998)		
V8	109	507	5.7	16.9	30.2	10	10	Laclau (2001)		
V9	12	532	2.4	–	3.9	10	10	Deleporte, pers. commun.		

2.2. Tree selection

For each stand, between 4 and 16 trees were selected (Table 1) in order to cover the full range of basal area variation within each stand. Trees were selected in plots that satisfied two main criteria: (i) no missing trees to ensure homogeneous and representative growth, and (ii) clean plots to avoid unwanted roots (herbs, shrubs). Because below-ground biomass measurements are tedious and very time-consuming, it was decided to measure only four to six trees in stands G1, G3A, G3B and G3D. Above-ground biomass of these trees was also measured except for two trees in stand G3D.

2.3. Above-ground biomass measurements

The following compartments were considered: stem wood, stem bark, leaves, dead branches and living branches. When felled, the total length of the tree, the height of the first living branch and the crown length were measured. The stem was cut into 1 m sections.

Each part of the tree was weighed in the field. Component biomass was sub-sampled to evaluate the moisture content: we took one 5 cm thick cross-section for each log, about 25% of each branch compartment and 25 leaves by level within the crown (bottom, middle, top). Aliquots were weighed before and after drying at 65 °C to constant weight (about 14 days for the stem and the bark, and 7 days for the other compartments).

2.4. Below-ground biomass measurements

Three different protocols were applied for below-ground biomass evaluation. The first (protocol 1) was designed for the stumps, the second (protocol 2) for the fine and medium roots, and the third (protocol 3) for the largest roots. We extracted both dead and living roots but in this paper we focused only on the living ones.

2.4.1. Stump biomass (protocol 1)

Among the trees sampled for the above-ground biomass, 29 stems were selected for the stump biomass measurement (Table 1). Stumps were defined as the tree part between the above-ground point where

the stem was cut and the below-ground points where the roots could be clearly individualized. Each stump was weighed in the field. Aliquots were sampled in a vertical direction in order to be as representative as possible of the wood density variation. Even if stumps included the woody base of the tree as left after felling, they were classified within the below-ground component because they also included a large part of the root system.

2.4.2. Fine and medium root biomass (protocol 2)

Among the 29 trees sampled for the stump biomass, 18 were selected for the fine and medium root biomass measurement (Table 1). When the previous stand had been harvested, there were one haulage inter-row and one slash inter-row for two normal inter-rows. A Voronoi polygon, which is the elementary space defined by the half distances between the sampled tree and its neighbors (Honda, 1978), was drawn for each tree. A quarter of the polygon area was selected in normal-inter-rows to get an average tree value of root biomass. Excavations were performed manually to a 2 m depth and by soil-auger to a 5 m depth (Fig. 2). Fine and medium roots were sorted manually and by sieving. Eucalypt roots were separated from the other ones according to their texture, color, odor, and elasticity. They were therefore sorted by size (fine root diameter < 5 mm and 5 mm < medium root diameter < 10 mm) and by status (dead or alive). The sorting procedure was performed visually with the help of reference test specimens for which diameters

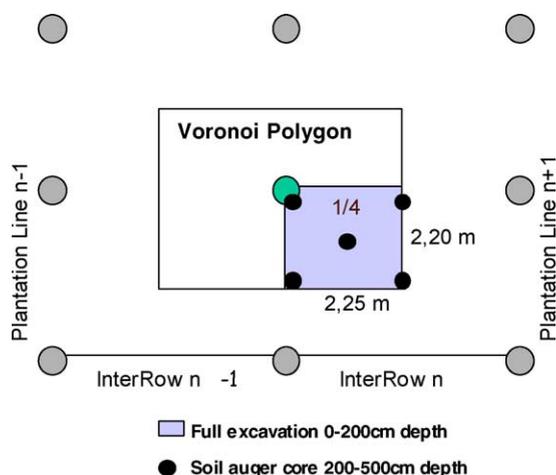


Fig. 2. Protocol for the fine and medium root extraction.

Table 2
Final weighted equations

	Stands used for the calibration	Mean	Error term	R^2	RMSE
Total	G1, G3A, G3B, G3D	$\mu = 5.37 + 235.2d^2h$	$\varepsilon = 12.7(d^2h)^{0.47}$	0.99	9.8
Above-ground	G1, G2, G3A, G3B, G3C, G3D	$\mu = 2.76 + 182.7d^2h$	$\varepsilon = 11.1(d^2h)^{0.64}$	0.99	10.1
Below-ground	G1, G3A, G3B, G3D	$\mu = 38.1(d^2h)^{0.62}$	$\varepsilon = 3.4(d^2h)^{0.46}$	0.98	2.7
Leaves	G1, G2, G3A, G3B, G3C, G3D	$\mu = 0.60 + (5.26 - 0.024age + 565.1 e^{-0.15age})d^2h$	$\varepsilon = 0.5(d^2h)^{0.21}$	0.86	0.4
Dead branches	G1, G2, G3A, G3B, G3C, G3D	$\mu = 0.010age + (11.67 - 0.084age)d^2h$	$\varepsilon = 2.5(d^2h)^{0.44}$	0.22	1.8
Living branches	G1, G2, G3A, G3B, G3C, G3D	$\mu = (7.78 + 1224.1 e^{-0.18age})d^2h$	$\varepsilon = 2.4(d^2h)^{0.57}$	0.77	2.0
Bark	G1, G2, G3A, G3B, G3C, G3D	$\mu = 9.08(d^2h)^{0.72}$	$\varepsilon = 0.7(d^2h)^{0.59}$	0.98	0.5
Stem	G1, G2, G3A, G3B, G3C, G3D	$\mu = 0.22 + (132.4 + 0.27age)d^2h$	$\varepsilon = 10.6(d^2h)^{0.87}$	0.99	8.7
Stump	G1, G3A, G3B, G3D	$\mu = 13.73(d^2h)^{0.70}$	$\varepsilon = 2.2(d^2h)^{0.55}$	0.95	1.7
Large roots	G3B, G3D	$\mu = 1249.8d^{2.52}$	$\varepsilon = 1.9$	0.89	1.9
Medium roots	G1, G3A, G3B, G3D	$\mu = 1.40(d^2h)^{0.46}$	$\varepsilon = 0.3(d^2h)^{0.30}$	0.84	0.3
Fine roots	G1, G3A, G3B, G3D	$\mu = 5.06(d^2h)^{0.30}$	$\varepsilon = 0.7$	0.84	0.7

DM = $\mu + \varepsilon N(0,1)$, follows a normal law of null average and variance equals 1, μ is of the general form $a + b(d^2h)^c$ and $\varepsilon = \sigma(d^2h)^k$. Units: d and h in meter, age in months from the planting date, RMSE in kg/tree. R^2 is dimensionless.

were measured using an electronic caliper. The collected roots were weighed before and after drying at 65 °C to constant weight: about 14 days for the medium roots, and 7 days for the fine roots. Total fine and medium root biomasses (from 0 to 5 m depth) were calculated as follows:

$b_{0-5} = 4 \left(b_{0-2} + \frac{b_{2-5} s_{\text{excavated}}}{s_{\text{soil-auger}}} \right)$, where b_{p1-p2} was the root biomass between $p1$ and $p2$ meter depth. $s_{\text{excavated}}$ and $s_{\text{soil-auger}}$ were the surface area of the excavated area and of the soil-auger cross-section.

2.4.3. Large root biomass (protocol 3)

It was seen in the field that protocol 2 was unsuited to correct evaluation of the large root biomass (diameter > 10 mm) due to the non-homogeneous distribution of the these roots around the tree. This component was then assessed separately. Six additional trees (out of the previous samples, Table 1) were selected, three in stand G3B and three in G3D according to their basal area (low, average, and high). Diameter at breast height and diameter at the base of the tree were recorded. Unfortunately, for these six trees, total height was not measured (Thongo M'bou, 2003). After tree felling, roots were excavated in situ using an air-compressed pistol. Each large root was cut approximately 10 cm from the stump (when it could be differentiated) and excavated until reaching the top end diameter of 1 cm. Roots were weighed in the field. Component biomass was sub-sampled, and weighed before and after drying at 65 °C. Using these

six trees, we fitted a non-linear regression between tree size and the large root biomass (see Table 2). This equation was then used to assess large root biomass of the sampled trees in protocols 1 and 2.

2.5. Validation data set

Twelve data sets, which were previously collected for several biomass and nutrient cycling studies in the same area, were used as validation samples. Only above-ground biomass components were considered (there was a lack of data for the below-ground part of the trees in these data sets). Table 1 gives the characteristics of the selected stands and the associated references. They cover the same range of ages, basal area and mean height than the fit data set, although growth rates are slightly higher.

2.6. General model

The system of equations was written as follows:

$$\begin{aligned}
 y_1 &= f_1(\theta_1, \beta_1) + \varepsilon_1 \\
 y_2 &= f_2(\theta_2, \beta_2) + \varepsilon_2 \\
 &\vdots \\
 y_m &= f_m(\theta_m, \beta_m) + \varepsilon_m
 \end{aligned} \tag{1}$$

where y_j , the biomass of component j , was a function f_j of a set of independent variables θ_j and a set of parameters β_j . Functions f were first assessed individually (see Section 2.7). The system of equations was

thereafter fitted using the SUR regression (Proc MODEL of SAS software, package ETS; SAS, 1990) which fits the component equations all together and takes the cross-equation correlations into account (see Parresol, 2001 for a detailed example of this procedure). Because our data set is unbalanced between the above-ground and the below-ground part, we fitted three systems of equations: the first one with all above-ground compartments, the second one with all below-ground compartments, and the last one with only the sum of biomasses (total above- and below-ground compartments, total tree biomass).

2.7. Individual tree component model

Basic equations were of the following form:

$$\text{Linear model : } y_{s,i,j} = a_{s,j} + b_{s,j}X_{s,i} + \varepsilon_{s,i,j} \quad (2)$$

Non-linear model :

$$y_{s,i,j} = a_{s,j} + b_{s,j}X_{s,i}^{c_{s,j}} + \varepsilon'_{s,i,j} \quad (3)$$

where s represented the stands; $y_{s,i,j}$ the dry matter of tree i for a given component j ; $X_{s,i}$ the independent variable (either d or d^2h ; d and h are, respectively, the diameter at breast height and the total tree height); $a_{s,j}$, $b_{s,j}$, and $c_{s,j}$ the parameters to be estimated; $\varepsilon_{s,i,j}$ and $\varepsilon'_{s,i,j}$ the residual variations not explained by the models. Observations were supposed to be uncorrelated: trees from the same stand were cut as far as possible from one to another and thus reduced the potential competition between them. The error component $\varepsilon_{s,i,j}$ of Eqs. (2) and (3) was supposed to be proportional to X raised to a power k : $E[\varepsilon_{s,i,j}^2] = \sigma_{s,i,j}^2 = \sigma_{s,j}^2 X_{s,i}^{2k_{s,j}}$ (where $\sigma_{s,j}^2$ is the residual variance of the weighted model for the component j). This error component formulation is classically used for biomass equations and the objective is to find the 'optimal' power k to be applied. One way described by Cunia (1964) and Schreuder and Swank (1971) consists in dividing the variable X in classes of equal width and regressing the variance observed in each group to the mean of X . A second solution consists in searching for the value of k that minimized Furnival's index of fit (Furnival, 1961). Lastly, a third solution consists in fitting directly the optimal weight using maximum likelihood procedures (Valentine et al., 1994). Because we did not have enough data to apply the first procedure, we tested the last two.

2.8. Fitting each tree component model

The objective was to find the best model for each compartment. The following steps were performed: (i) fitting the equations stand by stand ("stand models"), (ii) identifying possible variation of parameters between stands, for example $a = f(\text{stand age})$, (iii) fitting a unique model for all the stands ("global model") taking these variations into account and (iv) comparing the "stand model" to the "global model" in order to identify a possible residual stand variation that the global model did not successfully take into account.

Two statistical procedures were used: the first can be performed using the standard package of SAS and an iterative procedure to find the optimal weight using Furnival's index of fit, whereas the second involves proc NLP of SAS software (package OR) to fit simultaneously a model for the mean (e.g. $y_{i,j} = a_j + b_j X_i$ for the linear form) and a model for the variance $\sigma_{i,j}^2 = \sigma_j^2 X_i^{2k_j}$. In all cases, parameters not significantly different from zero were removed and the equation was refitted.

2.8.1. Procedure 1

Linear and non-linear models were fitted using procedures REG and NLIN of SAS Software. Model comparison was based upon the sum of square errors between the estimated and the measured biomass equation (3). When the models did not exhibit the same number of parameters, we used the F -test (Brown and Rothery, 1994). Optimal weight was found using Furnival's index of fit (Furnival, 1961).

2.8.2. Procedure 2

Fittings were performed using proc NLP of SAS software and maximum likelihood (assuming normality) estimations. The following equation was maximized:

$$\text{ML} = -\frac{1}{2} \sum_i \left[\left(\frac{Y_{i,j} - \mu_{i,j}}{\sigma_j X_i^{k_j}} \right)^2 + \log(2\pi) + \log(\sigma_j^2 X_i^{2k_j}) \right] \quad (4)$$

where $\mu_{i,j}$ is the model expression (e.g. $\mu_{i,j} = a_j + b_j X_i$ for the linear form). Parameters to be estimated included those for the model average (a and b) and those for the model variance (σ and k).

Comparisons between models were performed using the Akaike Information Criterion ($\text{AIC} = -2\text{ML} + 2p$) and the Bayesian Information Criterion

($BIC = -2ML + p \log(n)$) where p is the number of parameters of the model and n the number of observations (Akaike, 1973; Schwarz, 1978). When the two criteria led to different results, we chose the model with the fewest parameters.

2.9. Testing the normality of residuals

The normality of the residuals was systematically tested. We used the method proposed by D'Agostino et al. (1990) which tests the normality of a data set (number of observations >20) but also shows in which way the distribution drifts from normality. These tests are based upon the skewness (moment order 3) and the kurtosis (moment order 4) of the tested distribution.

3. Results

3.1. Biomass measurements

Fig. 3 presents the biomass partitioning within the trees of stands G3A, G3B, G3D and G1. The coppice G2 and the mid-term replantation G3C were excluded here (no measured root biomass). There was a clear

trend with stand age. For stand G3A (11-month-old), assimilation organs such as leaves and fine roots represented about 36% of the whole tree biomass, whereas the stem represented only 19%. By contrast for stand G3D (75-month-old), stem wood accounted for 62% of the total biomass whereas assimilation organs represented only 10%. Some compartments exhibited an almost constant proportion over time: bark (4–7%), stump (6–9%), large roots (8–10%) and medium roots (1–2%).

Stand G1 differed from the others by age (it was the oldest stand in our sample) but also by its position in the time schedule from savannah afforestation (first cycle high forest). It is therefore difficult to interpret the observed differences. However, the age effect seems to be predominant. Data for stand G1 were consistent with findings for replanted stands. There was no sudden break in the biomass partitioning between stand G3D (75-month-old) and stand G1 (135-month-old). When considering this continuity, below-ground biomass represented 30% of the total biomass in young trees (11-month-old) and 16% in old trees (135-month-old). The percentages of leaves and fine roots decreased with age. Both seemed to remain quite proportional however.

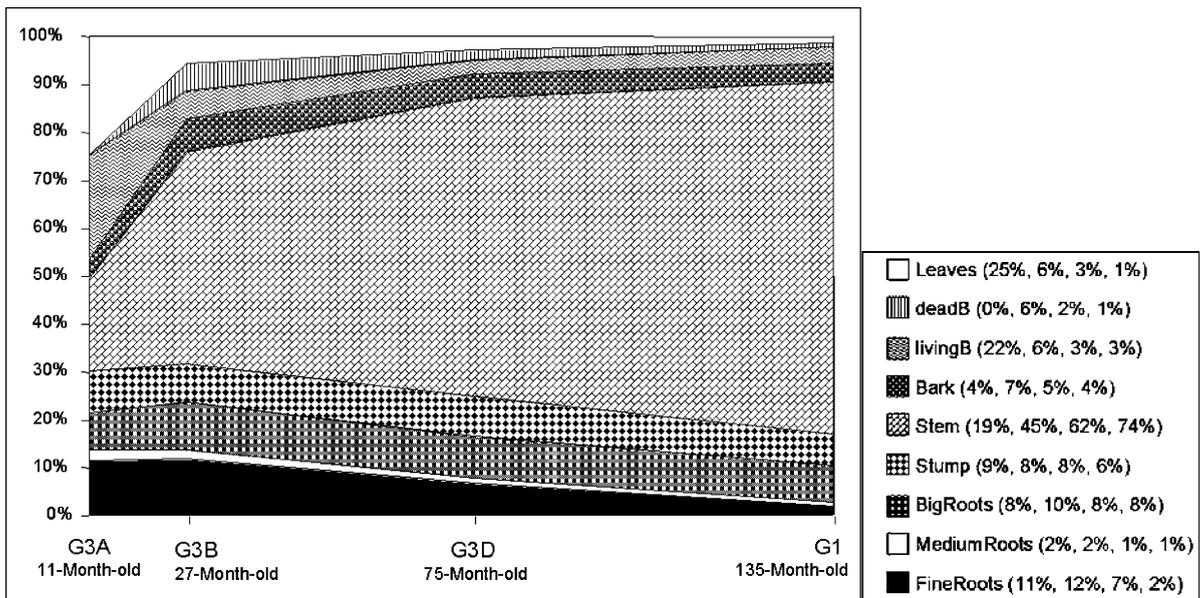


Fig. 3. Average biomass partitioning within the trees for stands G3A, G3B, G3D and G1 (G2 and G3C are not presented: below-ground biomass were not measured in these two stands). Large roots were estimated from the model presented in Table 2. Proportions for components by stands are given inside the brackets.

Fig. 4a and b presents the relationship between the dry matter of both above- and below-ground compartments and the two independent variables: d and d^2h . Relationships were satisfying except for the dead branch biomass which was not very well related to tree size. Trends with d were clearly non-linear whereas those using d^2h might be linear (see stem and total above-ground biomass which exhibited a strong linear relationship). For some compartments (e.g. leaves, dead branches), there was a clear pattern between stands suggesting parameter variation with age and/or stand structure. Even though variances increased with tree dimensions (e.g. stem), heteroscedasticity was not very pronounced. A visual comparison between d and d^2h curves showed that heteroscedasticity was reduced when d^2h was used in the regression for stem, bark, stump, and fine roots.

3.2. Model fitting

Fitting methods 1 and 2 led to very similar results. Except for the large root biomass, models using only d exhibited larger SSE (or lower log-likelihood esti-

mates) than models in d^2h for an equivalent or a higher number of parameters. They were therefore all rejected. An analysis of d^2h models showed that “stand” models always resulted in a lower SSE (or higher log-likelihood estimates) than the “global” models, but they required substantially more parameters. Final equations are presented in Table 2.

3.2.1. Above-ground biomass

Models were considerably improved by the introduction of age in the equations, with the exception of the bark model and, more surprisingly, the total above-ground and the total biomass models (Table 2). In most cases (leaves, living branches and stem), the intercept was fixed and the slope varied with stand age. For the dead branches model, both slope and intercept were found to vary with stand age although the final model was still weak (R^2 equal to 0.22 indicating a large unexplained variation). These parameter variations with stand age are illustrated in Fig. 4a for leaf biomass. The decrease is exponential: young stands exhibits a high slope between leaf biomass and stem size, whereas the oldest ones would

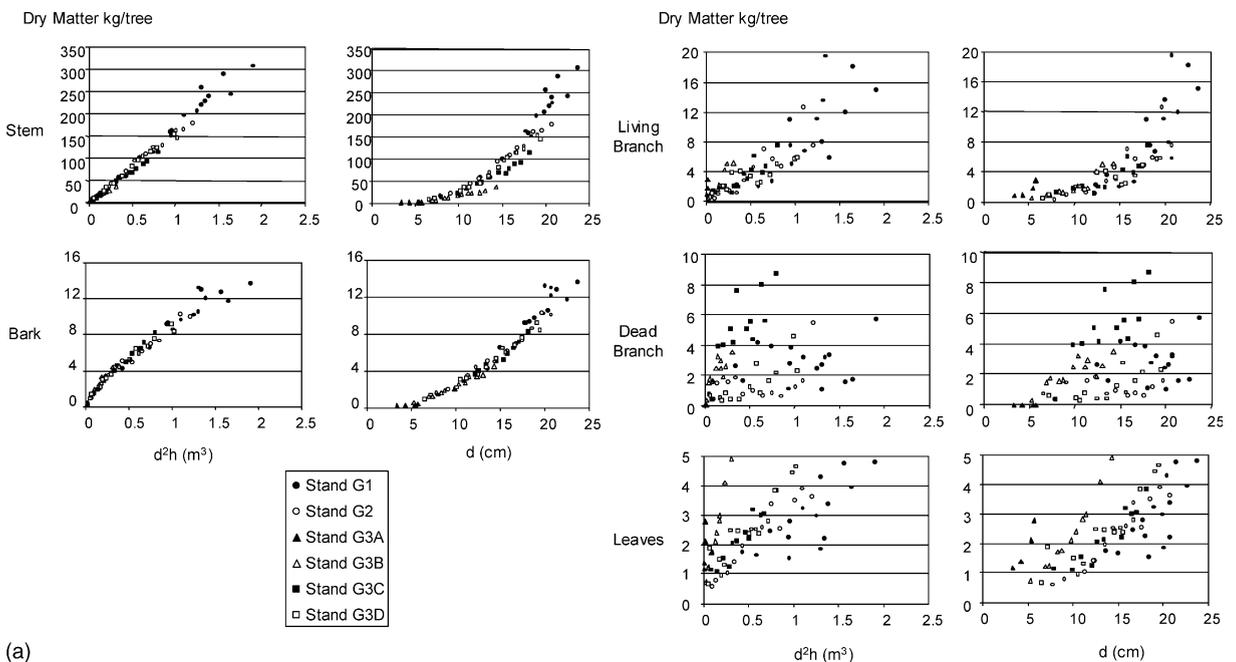


Fig. 4. (a) Above-ground biomass related to d^2h and d for stands G1, G2, G3A, G3B, G3C and G3D. (b) Below-ground biomass related to d^2h and d for stands G1, G3A, G3B, G3D (G2 and G3C are not presented: below-ground biomass were not measured in these two stands). Large roots were only measured in stands G3B and G3D (three fully excavated trees/stand for which only $d_{1,30}$ was available).

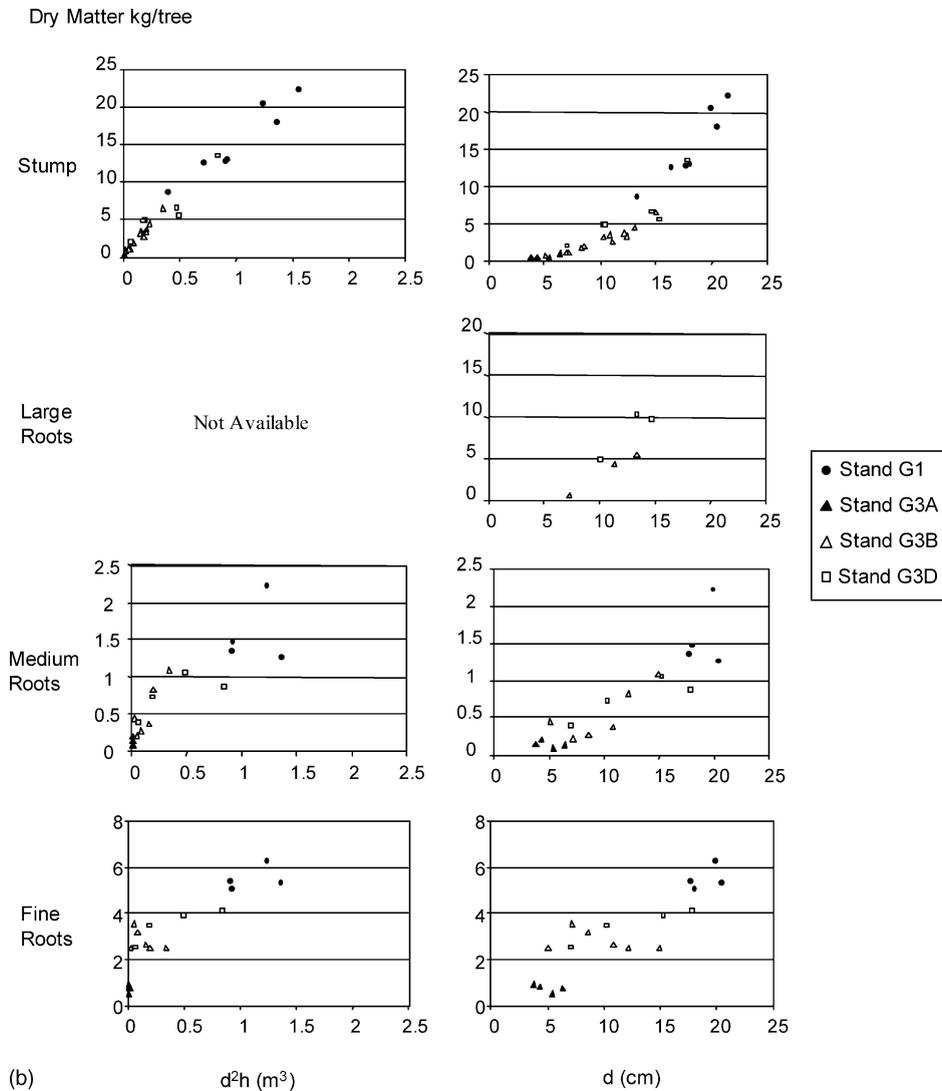


Fig. 4. (Continued).

asymptotically reach a null value (no relationship between trunk size and leaf biomass). It should also be noticed that models are basically linear stand by stand ($DM = a + bd^2h$). The introduction of age was sufficient to take into account all the differences between stands.

Fig. 5 illustrates the differences between the unweighted equation and the weighted one. For each stand (G1, G2, G3A, G3B, G3C, G3D) we plotted the actual data, the fitted curve and the corresponding confidence interval. There was a clear difference in the

confidence interval of estimates. Optimal weights (see Table 2) were found to be completely different from usual practices ($k = 1$, or $k = 2$). A close look at the confidence interval of estimates and the distribution of weighted residuals show that heteroscedasticity was accounted for.

3.2.2. Below-ground biomass

The stand age was not found to improve the stump, fine and medium roots models. This result was expected because the number of trees collected within

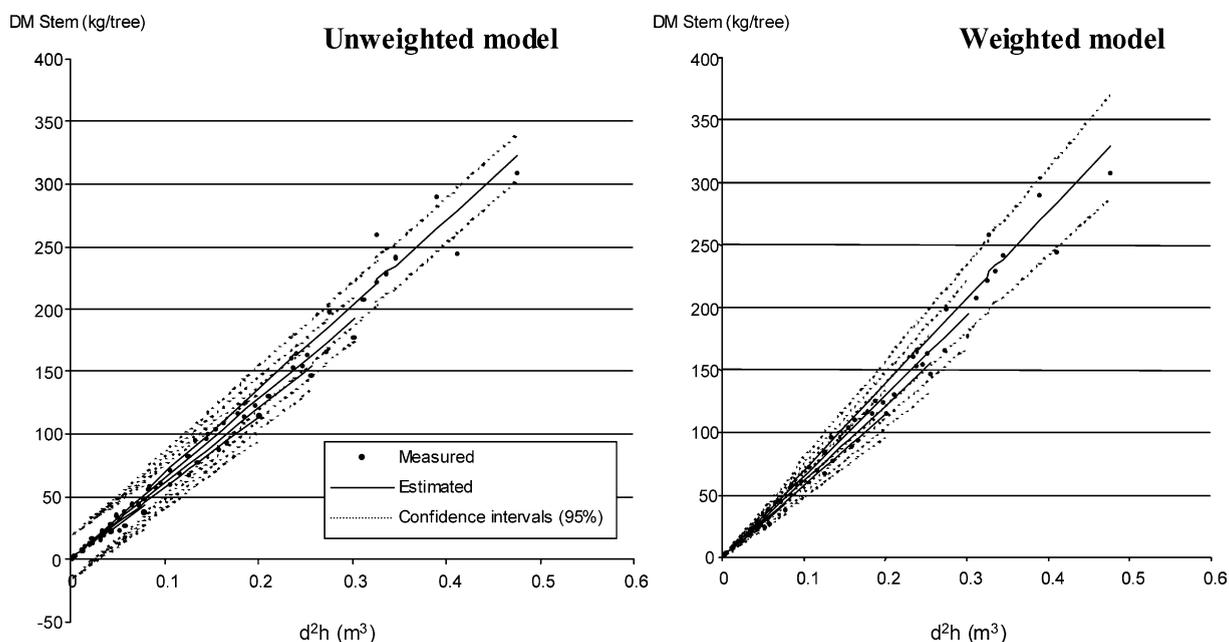


Fig. 5. Measured vs. simulated stem biomass. The 95% interval of confidence is given for each stand by dotted lines.

each stand (4–6 individuals) was not sufficient to obtain the appropriate relationship stand by stand. The resulting global models for the below-ground compartments were then non-linear using only d^2h (Table 2). For the large root biomass, the model was obtained from the six trees of stands G3B and G3D, for which only d was measured (see protocol 3). Due to a low number of observations, weighted regressions were not used for this compartment (Table 2).

3.3. Validation

Models that predict the above-ground biomass were evaluated using the validation data set. Fig. 6 displays a scatterplot of observed versus predicted biomass. The results suggest over-estimation trends for the dead branch, and under-estimation trends for living branch, leaf and bark biomass. Statistics are given in Table 3. The simultaneous F -test for bias, slope = 1 and intercept = 0 recommended by Mayer and Butler (1993), was significant for all compartments ($P < 0.05$). Highest F values were obtained for dead branch and bark biomasses. The slope was significantly greater than 1 for the bark biomass. It was significantly lower than 1 for the stem, the above-ground and the dead branch biomass. The intercept

was significantly different from 0 for the bark biomass. RMSE were, however, of the same magnitude than those found for the fit data set (Table 2). Modeling efficiency (Mayer and Butler, 1993) was close to the maximum value 1, except for the dead branch biomass. When compared to the average values of biomass, mean absolute errors were quite low for the compartments that account for a large part of the total tree biomass (respectively, 7, 6 and 9% for above-ground, stem and bark compartments). The worst estimations were obtained for the dead branches. From these results, above-ground compartment equations were refitted using all available data and procedure 2 (Proc NLP of SAS Software, AIC and BIC information criteria). The resulting equations are given in Table 4. Dead branches, bark and above-ground equations were changed by the addition of the validation sample. Age effect was now introduced in the bark and the above-ground equations. Parameters of the other models were slightly changed but the equations remained the same.

3.4. Additivity

Three estimated values of the total biomass were compared to the actual one (stands G1, G3A, G3B and

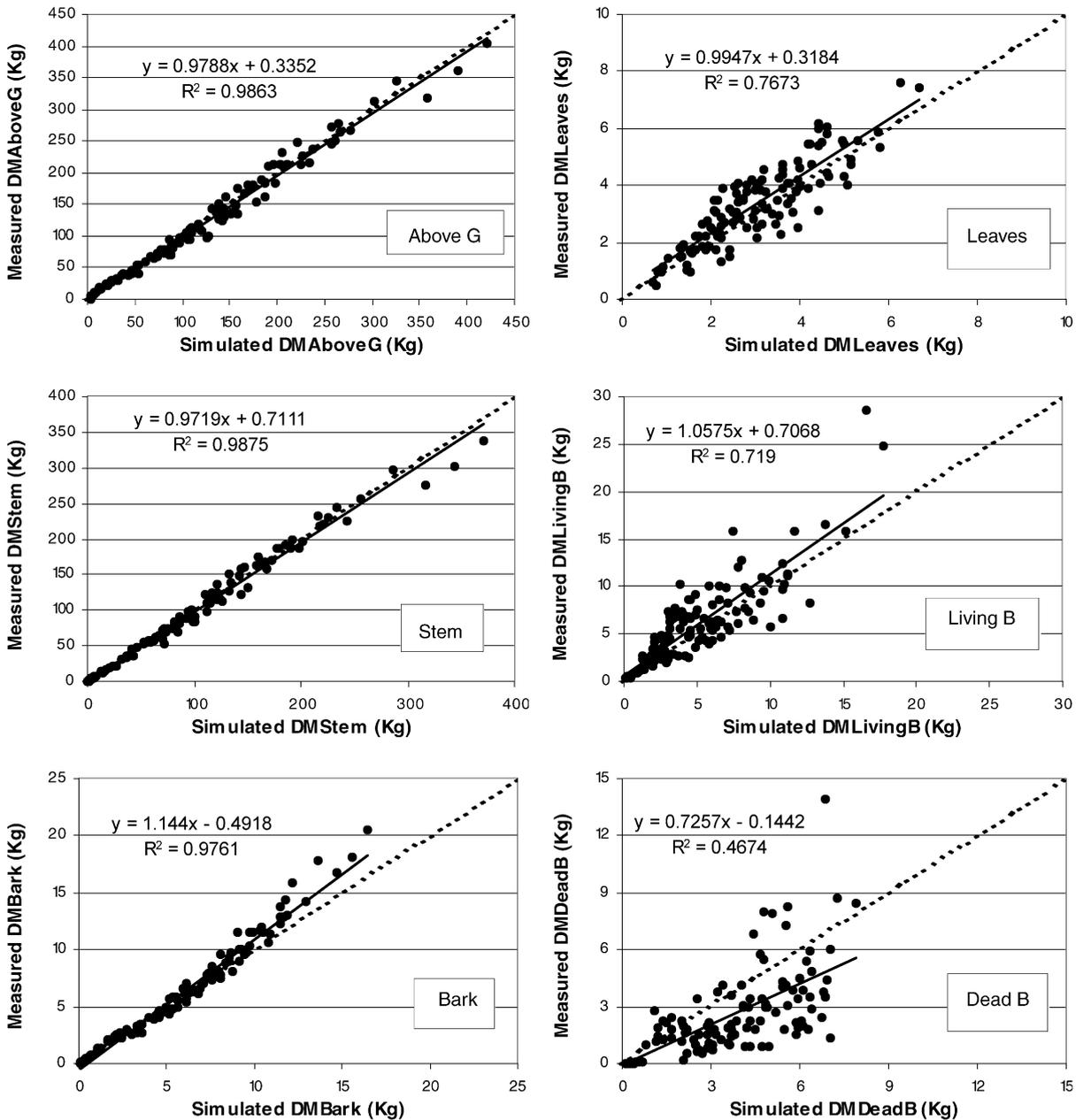


Fig. 6. Simulated compared to measured biomass for the validation sample. Above-ground compartments. The solid line is the regression line. The dotted line is $Y = X$. DM means dry matter (kg).

G3D). T1 was obtained from the total biomass equation, the second one, T2, was obtained from the sum of all compartment equations and the third one, T3, was calculated with the above-ground and the

below-ground equations. Differences ranged from -32 to 18% (average -6%) for T1, from -17 to 31% (average 5%) for T2 and from -18 to 23% (average -1%) for T3. Differences were significant at a 95%

Table 3
Statistics for the whole validation sample

	Stem	Bark	Leaves	Living branches	Dead branches	Above-ground
Number of observations	122	122	122	122	122	122
Mean (observed values)	90.8	6.1	3.3	6.1	2.4	109.9
Mean (simulated values)	92.7	5.7	3.0	5.1	3.5	111.9
Mean Errors	1.9	-0.3	-0.3	-1.0	1.1	2.0
Mean absolute errors (MAE)	5.4	0.6	0.6	1.8	1.6	7.6
Modeling efficiency EF	0.986	0.955	0.722	0.665	0.173	0.985
RMSE	9.3	1.0	0.8	2.6	2.1	11.0
Linear regression						
R^2	0.987	0.976	0.765	0.717	0.463	0.986
Slope ^a	0.97**	1.14***	0.99 ns	1.06 ns	0.73**	0.98*
Intercept ^b	0.71 ns	-0.49***	0.32 ns	0.71 ns	-0.14 ns	0.34 ns
Bias ^c	6.76**	52.67***	11.62***	11.54***	33.16***	4.22*

Units: means and RMSE are given in kg/tree. EF and R^2 are dimensionless. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

^a F -statistic for slope = 1.

^b F -statistic for intercept = 0.

^c F -statistic for slope = 1 and intercept = 0.

confidence level for the first distribution only. A closer look at the error distribution (Fig. 7) shows that this bias was mainly observed for the young stand and the best estimate was provided by T3. Except for this stand, errors were well distributed around zero whatever the procedure used to estimate the total tree biomass and did not exceed 10% of the total tree biomass.

4. Discussion

4.1. Biomass partitioning within the trees

Many published studies have identified the root–shoot ratio (or conversely) of both temperate (Ranger and Gelhaye, 2001) and tropical species (Hase and

Foelster, 1983; Kraenzel et al., 2003; Laclau, 2003). Generally, this ratio decreases progressively with stand age and ranges from 0.5–0.3 for young trees to 0.3–0.15 for old trees. As an example, Hase and Foelster (1983) working on teak species found 0.42 at 4 years of age and 0.20 at 9 years. Kraenzel et al. (2003) also working on teak species found 0.16 at 20 years of age. Similar trends were found by Laclau (2003) for ponderosa pines (0.24 at age 10 compared to 0.16 at age 20). In our cases, observed root–shoot ratios were quite usual and ranged from 0.3 for 1 year of age to 0.16 at 10 years.

4.2. Model construction

The sampling procedure has a great influence on the regression parameters and their reliability. Rennie

Table 4
Final weighted equations for the above-ground compartments

	Mean	Error term	R^2	RMSE
Above-ground	$\mu = 2.08 + (150.9 + 0.28\text{age})(d^2h)^{(0.87 + 0.0012\text{age})}$	$\varepsilon = 9.3(d^2h)^{0.61}$	0.99	8.9
Leaves	$\mu = 0.64 + (50.9 - 0.02\text{age} + 585.3 e^{-0.15\text{age}})d^2h$	$\varepsilon = 0.5(d^2h)^{0.23}$	0.86	0.4
Dead branches	$\mu = (1.52 + 39.5 e^{-0.03\text{age}})d^2h$	$\varepsilon = 1.9(d^2h)^{0.35}$	0.51	1.5
Living branches	$\mu = (7.78 + 1167.9 e^{-0.18\text{age}})d^2h$	$\varepsilon = 2.4(d^2h)^{0.57}$	0.77	2.0
Bark	$\mu = (9.03 + 7.54 e^{-0.05\text{age}})d^2h^{0.76}$	$\varepsilon = 0.6(d^2h)^{0.39}$	0.98	0.5
Stem	$\mu = 0.29 + (127.8 + 0.32\text{age})d^2h$	$\varepsilon = 10.5(d^2h)^{0.88}$	0.99	8.9

$DM = \mu + \varepsilon N(0,1)$, where $N(0,1)$ follows a normal law of null average and variance equals 1, μ is of the general form $a + b(d^2h)^c$ and $\varepsilon = \sigma(d^2h)^k$. Data used for the model calibration (G1, G2, G3A, G3B, G3C, G3D + validation sample). Units: d and h in meters, age in months from the planting date, RMSE in kg/tree. R^2 is dimensionless.

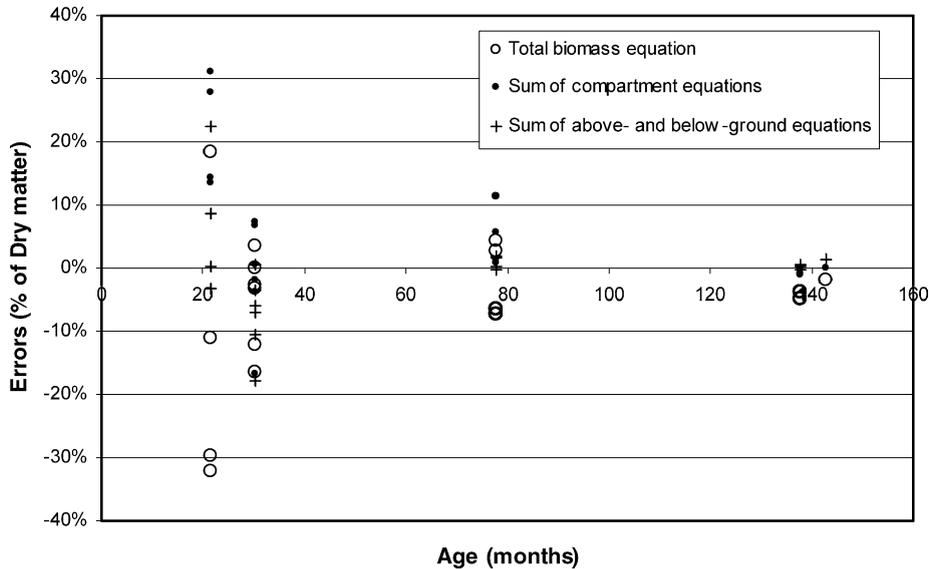


Fig. 7. Distribution of errors for total tree biomass (G2 and G3C are not presented: below-ground biomass was not measured in these two stands).

(1966) gives an accurate description of what should be taken into account. Initially, we planned to sample at least 12 trees within each stand for both above- and below-ground biomass. But owing to the difficulties of excavating and measuring accurately the root system, the number of trees was considerably reduced. Even though we were working on plantations with genetic variability reduced to a minimum (clonal material), this sampling scheme had two main implications: (i) concerning evaluation of the parameters, the number of sampled trees was sufficient for the above-ground biomass, but not for the below-ground biomass for which it was impossible to fit accurate stand-by-stand models; (ii) concerning the reliability of equations (interval of confidences), this number of trees was not sufficient for both above- and below-ground biomass.

The introduction of age in parameters of the basic equations resulted in models that can be interpreted. The total number of parameters of the final equations was quite low (from 2 to 5). The risks of multicollinearity were limited because only two correlated regressors were used (age and d^2h).

Heteroscedasticity was taken into account during the fitting process through weighted functions. We chose this approach after testing of log transformations. It was often noticed that if heteroscedasticity

was reduced by the log transformation, residual errors were still not normally distributed. This was partly due to the remaining heteroscedasticity but also to the non-linear forms of log–log regressions as reported by Návár et al. (2002). Considering these two aspects and the limited number of sampled trees, we then decided to use simple weight functions.

Intercepts were small and, in several cases, not significantly different from zero. We then decided to remove these parameters even if this was not really satisfactory from a biological point of view because trees smaller than 1.5 m high are expected to have a small but non-null biomass.

4.3. Model interpretation

Although numerous studies have been published on stand biomass and its assessment, few of them are strictly devoted to the parameter variation of the allometric relationships with stand age or other factors such as, for example, fertilization.

Zavitkovski (1971), working on young- to medium-aged aspen trees, compared his results to those recorded by Peterson et al. (1970, in Zavitkovski, 1971) in the same species but for twice as old trees. He noticed that for all above-ground compartments the

allometry was different, suggesting that stand age for a given species could have a significant effect on the relationship between biomass and tree dimensions. Williams et al. (2003) studying allometry and biomass of mature plantation *Metasequoia glyptostroboides* in Japan found a statistical difference between their allometric relationship and those elaborated by Satoo (1974, in Williams et al., 2003) for youngest stands of the same species. Bond-Lamberty et al. (2002) introduced age in their equations for both below- and above-ground biomass of six boreal species. But in their study, they used a single form of the log–log relationship for all compartments, and parameters related to stand age were not always significantly different from zero, depending on the considered compartment and species. Conversely, Bradstock (1981), working on a *Eucalyptus grandis* age-series, did not find any age effect on the relationship between biomass and tree size, but the number of felled trees within each stand (4–6) was probably too low for a correct identification. Zohar and Karshon (1984) studied the above-ground biomass of *Eucalyptus camaldulensis* in plantations covering a wide range of age classes (4–35-year-old), densities (400–1700 stems/ha), and climatic conditions (240–600 mm annual rainfall). Unfortunately, they pooled all data and a single regression equation was determined for the whole data set. They do not report possible variations of allometry with stand age, density or climatic conditions.

In our study, model parameters were found to vary clearly with stand age. This is not only the result of a change in tree maturity but rather a combined effect of tree age and tree social status. Let us consider two trees of the same height and diameter but differing in age. They would also exhibit a difference in social status: the youngest tree must be dominant whereas the oldest one is probably suppressed. Both effects, age and social status, lead to an increase in stem biomass for the oldest tree because wood density increases with stand age and the form factor, ratio between stem volume and d^2h , is higher for suppressed trees (Ognouabi and Fouty, 2002 for clone pf1 1–41). Conversely, both effects tend to decrease leaf and living branch biomasses for the oldest and suppressed tree because leaves are closer to the crown periphery as and when the tree grows (Mountou-Nourissier, 1993; Coudurier et al., 1995 for clone pf1 1–41), and

because the crown length is strongly reduced by social status.

For the dead branches, the pattern was found to be much more complex. This result is not surprising because dead-branch biomass depends on physiological process but also on human behavior (uptake for firewood supply), random climatic factors, and insect attacks. This was the only compartment where we could not get an accurate ‘global’ model. Two groups were identified: the first one including stands G3B, G3C and G1 where both intercept and slope of the model varied with the stand age, and the second one for the stands G2 and G3D where the intercept was set to zero. Introducing the validation data set, the model of the second group was found to be the more accurate one, but we did not know the actual cue of such a division.

5. Perspectives and conclusions

In this first study, a complete set of weighted equations for below- and above-ground biomass of a natural *Eucalyptus* hybrid in Congo was constructed. Age was introduced as a supplementary variable in the equations for a majority of above-ground compartments.

Because of the limited number of sampled trees for below-ground biomass, it was not possible to develop the same kind of equations for these compartments (stumps, large, medium and fine roots). Heteroscedasticity of data was taken into account during the fitting process. Additivity was verified and showed no significant deviation except for the youngest stand where the sum of below- and above-ground biomass equations was preferable to the sum of component equations or to the total biomass equation.

These models will now be used to evaluate stand biomass content and partitioning. Theoretically, they are only valid for plantations of the same clone in the same range of site index (middle). However, as stands G2 (coppice) and G3B (lower fertility) did not differ from the others when we took their ages into account, and we are confident in extended use of the above-ground equations on all plantations and coppices of the same clone in this area. For the below-ground equations, we are not so confident and further work should be done, especially for the coppices.

Knowing for each model (i) the interval of confidence of parameters, (ii) the correlation matrix of the parameters, and (iii) the error model, we can use Monte Carlo simulations to calculate both the mean and the interval of confidence for the stand biomass estimates. A study is ongoing on this topic with, in addition, an estimation of the influence of measurement errors (height and dbh) on the estimated values.

Chemical analyses are currently being processed by NIRS techniques to evaluate the carbon content within each compartment. These measurements are necessary to shift from biomass estimates to carbon storage within the stands.

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