

UvA-DARE (Digital Academic Repository)

Evaluation of regression models for above-ground biomass determination in Amazon rain forest

Overman, J.P.M.; Witte, H.J.L.; Saldarriaga, J.G.

Publication date 1994

Published in Journal of Tropical Ecology

Link to publication

Citation for published version (APA):

Overman, J. P. M., Witte, H. J. L., & Saldarriaga, J. G. (1994). Evaluation of regression models for above-ground biomass determination in Amazon rain forest. *Journal of Tropical Ecology*, *10*, 207-218.

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: https://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

UvA-DARE is a service provided by the library of the University of Amsterdam (https://dare.uva.nl)



Evaluation of Regression Models for Above-Ground Biomass Determination in Amazon Rainforest

Johannes Petrus Maria Overman; Hendrik Johannes Louis Witte; Juan Guillermo Saldarriaga

Journal of Tropical Ecology, Vol. 10, No. 2. (May, 1994), pp. 207-218.

Stable URL:

http://links.jstor.org/sici?sici=0266-4674%28199405%2910%3A2%3C207%3AEORMFA%3E2.0.CO%3B2-O

Journal of Tropical Ecology is currently published by Cambridge University Press.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/cup.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Evaluation of regression models for above-ground biomass determination in Amazon rainforest

JOHANNES PETRUS MARIA OVERMAN,* HENDRIK JOHANNES LOUIS WITTE* and JUAN GUILLERMO SALDARRIAGA†

*Hugo de Vries Laboratory, Faculty of Biology, University of Amsterdam, Kruislaan 318, 1098 SM Amsterdam, the Netherlands.

† Tropenbos-Colombia Programme, A.A. 036062, Santafé de Bogotá, Colombia.

ABSTRACT. In a mature lowland 'terra firme' forest near Araracuara in Colombia, a study was conducted to determine the above-ground biomass by means of regression analysis. Dry weight, DBH (i.e. stem diameter at 1.3 m above ground level, or just above buttresses if these surpassed 1.3 m in height), total height and specific wood density were measured on 54 harvested trees, chosen in a 'selected random' manner. Nine different regression models were evaluated for statistical correctness, accuracy of the estimates and for practical use. The logarithmically transformed models with DBH², and DBH² × height as independent variables appeared to be the only models meeting the above criteria, the latter being the most accurate.

The exclusion of big trees (DBH >45 cm) from the regression did not result in significant changes of the regression coefficients.

KEY WORDS: Amazon, biomass, Colombia, DBH, lowland rainforest, regression models.

INTRODUCTION

Biomass is regarded as an important parameter for the characterization of ecosystems since it reflects the ecosystem's capacity, during a certain timespan, in accumulating organic matter (Sarmiento 1984). In an undisturbed forest the accumulation is assumed to be maximal under the local environmental conditions (an equilibrium between production of new biomass and loss of living biomass due to mortality exists), and the biomass value can be used as a reference point. For instance, biomass values of mature rainforest plots have been used to calculate regeneration times after slash and burn agriculture, by extrapolation of biomass values of successional plots of different, known, ages (Saldarriaga et al. 1988). They are also necessary to quantify the nutrients stored in the vegetation part of the ecosystem (Jordan 1985), and for comparisons between different vegetation types, or between similar vegetation types in different localities.

In principle two methods are available for the determination of biomass. One method involves complete harvesting of plots and subsequent extrapolation to a hectare (Klinge & Herrera 1983, Klinge et al. 1975). The other method aims

to construct a functional relationship between tree weight and other tree dimensions such as stem diameter, height and wood density, by means of regression analysis (Jordan & Uhl 1978, Saldarriaga *et al.* 1988). The biomass of a plot is obtained by measuring the tree dimensions for all trees in the plot and calculating the weight of each tree from the calibrated function.

Different types of regression models and combinations of parameters have been used. Ogawa et al. (1965) used (DBH² × height) as an independent variable. Jordan & Uhl (1978) also used this model but in another model they included wood density, since a wide range of this parameter was present in their sample. Saldarriaga et al. (1988) constructed multiple regression models (with DBH, height and wood density as independent variables). Additionally, they observed a better fit when the regression analysis was performed separately for each of three DBH size ranges. Apparently, there is no single optimal regression model, and the selection of the best solution is not easy, as it involves choices between differently shaped functions, different transformations and selection of the independent variables to be used.

The goal of the present study was to provide a good calibration function for the estimation of above-ground tree biomass of mature 'terra firme' (never flooded) forest in the study area. Nine different regression models were applied on the data and evaluated for statistical correctness, accuracy of the estimate and practical usefulness. Additionally, the influence of bigger trees on the regression equation was examined by comparing the results of the calibration of the complete set with a calibration based on trees with diameters up to 45 cm only.

STUDY AREA

The area of study is located near Araracuara, Departamento Caquetá, Colombia, South America (0° 38′ S, 72° 22′ W) (Figure 1). The climate of the area can be classified as equatorial superhumid (A_f type sensu, Köppen 1936), a Walter diagram (Walter & Lieth 1960, Witte et al. 1988) of the climate is presented in Figure 2. The study site is situated c. 200 m above sea level on a lower, never flooded, terrace of the Caquetá river, which has its origin in the Andean mountain range. Total above-ground biomass of the site was estimated as 351 t ha⁻¹, estimates for the different compartments yielded 247 for the trunks, 71 for the branches, 20 for branchlets and 5 t ha⁻¹ for the leaves (Overman et al. 1990). Soils are classified as clayey typic Paleudults or ferric Acrisols (USDA and FAO classification, respectively, Duivenvoorden et al. 1988). The vegetation studied is mature rainforest, classified by the FAO as belonging to the group of ombrophilous tropical forest (Duivenvoorden et al. 1988).

METHODS

Owing to a very high tree species diversity, in combination with a low number of individual trees of each species per hectare in undisturbed rainforests

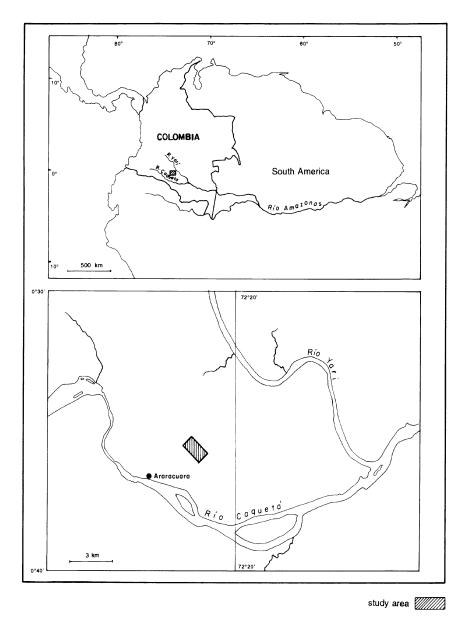


Figure 1. Location of the study near Ararcuara in Colombia

(Jordan & Uhl 1978, Whitmore *et al.* 1985), it was not practical to obtain sufficient observations to facilitate calibration for individual species, as is customary in temperate forests (Satoo & Madgwick 1982, Schmitt & Grigal 1981). Trees in the study site were therefore sampled irrespective of species.

To arrive at a dependable calibrated equation for biomass, which could serve as a basis for the accurate estimation of trees of all sizes present in the forest,

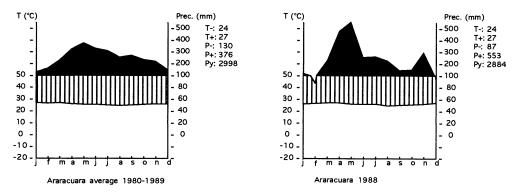


Figure 2. Walter diagrams showing the climate in Araracuara over five years and the weather during the study period (1988), indicating variability in precipitation per year. T-, T+: minimum and maximum monthly temperature (°C). P-, P+: minimum and maximum monthly precipitation (mm). Py: yearly precipitation (mm).

a more or less equal number of trees was selected randomly within every 10 cm DBH size class present in the forest. However, as the total number of trees per hectare in the study site was not equally distributed among the DBH size classes (there were many more trees with a small DBH), the sampling procedure cannot be regarded as strictly random. This type of sampling is called 'selected random', but it allows statistical analysis (Moore & Chapman 1986). A total number of 54 trees was sampled from an area of c. 2.5 ha (numbers sampled per 10 cm DBH class: class 1: 1, class 2: 11, class 3: 8, class 4: 8, class 5: 7, class 6: 5, class 7: 4, class 8: 4, class 9: 3, class 10: 3). Only one tree was sampled in the first class (0–10 cm DBH, with a DBH of 8.1 cm) as the precision of the available scale did not allow accurate measurements of the weights of smaller trees.

From each selected tree DBH was measured and, after felling, the length of the tree was determined. Each tree component (stem, branch, twig and leaf) was weighed separately with a hanging scale. Immediately after weighing, representative samples of each tree component were taken, in duplicate, for dry weight determination. For trees and branches with a diameter >30 cm, the weight was not determined by weighing but arrived at in the following way: the diameter was measured every metre and the volume of each metre length of log was calculated. Weight was then calculated by multiplying wood density by volume.

Since no appropriate portable scales were available in the field for weighing the fresh samples, they were wrapped in plastic bags to reduce evaporation and immediately weighed after returning from the field (c. 40 minute walk). After a period of air drying, the samples were oven dried at 105°C to constant weight. The total dry weight of leaves and of twigs per tree, and of the smaller branches and stems was calculated by multiplying the (mean) dry weight: fresh weight ratio of the samples by the fresh weight of the tree component. Dry weight of

stem and branches >30 cm diameter was calculated by multiplying the volume of the stem or branch by the respective wood density value.

Wood density for branch and stem samples (discs) was determined by averaging the wood density of the two discs of each component, wood density being calculated from the dry weight and volume of the sample discs. The total aboveground dry weight of a tree was calculated by summing the dry weight values of the different tree compartments.

To evaluate the regression models defined on the measured variables dry weight (DW), diameter at breast height (DBH), tree height (h) and wood density (d), three considerations are important: (1) the statistical correctness of the regression; (2) the accuracy of the obtained estimates has to be evaluated; and (3) the model must be of practical use. The significance of a regression can be tested in the usual ways, by F and T tests for significance and by checking residuals for adequacy of the model and validity of assumptions (Draper & Smith 1981).

To compare the accuracy of similar regression models, confidence limits can be calculated for its coefficients (Draper & Smith 1981). It is also possible to calculate an x% confidence interval for an individual observation (Glantz 1987). Disadvantages are, however, that for each value of the independent (X) variable, the confidence interval is different and has to be calculated separately. Moreover, this interval becomes relatively wide as the percentage of confidence increases towards 100%, and therefore loses its potential as a practical measure of accuracy in biomass studies on tropical rainforests.

Generally, the coefficient of determination (R^2) is used to evaluate the amount of variation explained by a regression, and is often used to select the best regression (Barney et al. 1978, Egunjobi 1976, Pastor et al. 1984, Rodriguez 1988, Santee & Monk 1981). R^2 however, gives large weights to observations with large magnitudes. Moreover the maximal attainable R^2 can be quite different between models (Draper & Smith 1981). Ogawa et al. (1965) and Saldarriaga et al. (1988) used an additional loss function, the cumulative percentage deviation (i.e. the ratio between the total estimated and observed weight of the sample trees), to select the best regression function. Overman (1989) observed that this ratio is unduly influenced by the accuracy in the estimation of big trees. In this study, in conjunction with R^2 , an additional loss function based on the absolute differences of individual trees is used, here referred to as the 'average of the absolute percentages deviation' (δB):

$$\delta \mathbf{B} = \frac{\sum_{n=1}^{n} \frac{|\hat{\mathbf{D}}\mathbf{W} - \mathbf{D}\mathbf{W}|}{\mathbf{D}\mathbf{W}} *100}{\mathbf{n}}$$
(1)

where DW is estimated, and DW is observed dry weight.

As it is based on absolute deviations this measure gives equal weight to observations with different magnitudes. Also, the accuracy of the estimates of

different models can be evaluated in terms of the original scale, which is intuitively appealing.

RESULTS

From a number of studies (Jordan & Uhl 1978, Ogawa et al. 1965, Pastor et al. 1984, Saldarriaga et al. 1988, Satoo & Madgwick 1982, Schmitt & Grigal 1981), it is known that biomass has a high correlation with DBH. In the present study the correlation between these parameters was also high (0.92, Table 1).

From a scatterplot showing the relation between DBH and DW (Figure 3a), it was clear however, that the relation was not simply linear but approaching the form:

$$DW = \alpha DBH^{\beta} + \varepsilon \tag{2}$$

This type of model is already widely reported for the relationship between biomass and DBH (Satoo & Madgwick 1982, Schmitt & Grigal 1981). The solution of the previous model ($\beta = 2.202 \pm 0.151$, Table 2) indicated that the value 2 for the exponent would be a reasonable choice. Transforming DBH to DBH² more or less removed the nonlinearity (Figure 3b) and a simpler, second order, linear model could be fitted:

$$DW = \alpha DBH^2 + \varepsilon \tag{3}$$

Both Figures 3a and 3b show an increase in variance with higher DBH values (heteroscedasticity). A transformation of the DW axis with the natural logarithm can alleviate this problem. To reobtain a linear relation, the same transformation was also needed for the DBH² scale (Figure 3c). The model became:

$$ln(DW) = constant + \alpha ln(DBH^2) + \epsilon$$
 (4)

To obtain a higher accuracy of the estimate, in other words to explain a larger part of the error term, more variables can be introduced into the regression

Table 1. Correlation coefficients between different tree parameters from 54 sample trees of mature 'terra firme' forest near Araracuara, Colombia.

	Dry weight (DW)	DBH	Tree height (h)	Wood density (d)
Dry weight	1			
DBH	0.92	1		
Tree height	0.73	0.83	1	
Wood density	0.42	0.29	0.29	1

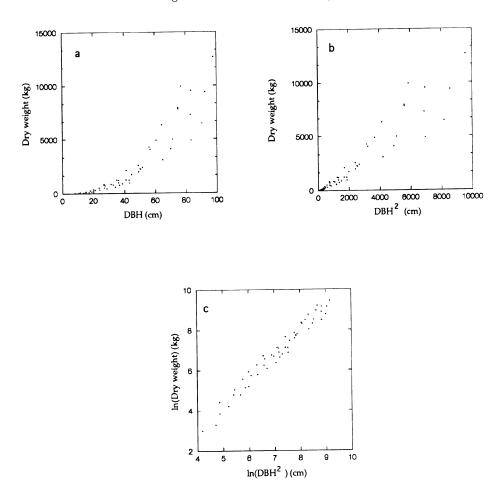


Figure 3. (a) Relation between DBH and dry weight, and (b) relation between DBH² and dry weight of sample trees from mature 'terra firme' forest near Araracuara, Colombia. (c) Relation between DBH² and dry weight of sample trees from mature 'terra firme' forest near Araracuara, Colombia after natural logarithm transformation of both abscissa and ordinate.

equation. One of the conditions of these multiple regression models is that the independent variables are not collinear. If collinearity exists there can be no unique solution to the regression problem and the model cannot be solved (Belsley *et al.* 1980). In the present study it was found that collinearity existed between most of the variables. As an indication, Table 1 already showed significant correlations between most of the variables. Only the correlations with wood density were low.

It is also possible to increase the variance in the independent variable by defining products between measured tree dimensions. More variability in the

independent variable can decrease the error term, leading to a more accurate prediction of biomass, without the technical problems of collinearity. The models that were eventually fitted and their results are presented in Table 2.

It is known that the least squares solution to a regression problem is sensitive to outliers (Draper & Smith 1981). Some outliers were detected in the present study as well, but deleting these observations did not result in significant changes of the coefficients.

All models had significant parameters (t test, P < 0.0001) and predicted the biomass reasonably well, indicated by the small standard error and high coefficients of determination (R^2). High R^2 values signify that the models are good impressions of how dry weight is related to the independent variables. δB , however, showed differences between the models regarding the accuracy of the estimates over the observation range. Regression models 1 and 2 produced higher percentages of deviation (R^2 0.90 and δB 39.4, respectively 0.81 and 62.8%, while deviations between 15–25% were found for the other models). The lowest δB (11.2% with R^2 0.99) was found for the multiplication model $DBH^2 \times height \times wood$ density (model 4).

To get an impression of the influence of high DBH values on the regression, in view of the relatively large amount of effort required to harvest the bigger

Table 2. Regression equations for estimation of above-ground biomass, using different models and combinations of independent variables. All regression equations are statistically significant (P < 0.0001), based on 54 sample trees from mature lowland 'terra firme' forest near Araracuara, Colombia. DW = aerial dry weight of the tree (kg), DBH = diameter at breast height; 1.30 m above ground level (cm); h = height of the tree (m); h = diameter at h = diameter and h = diameter at h = diameter at

No.	Regression model	Coefficient symbol	Coefficient value	Standard error	Width of 95% confidence interval	\mathbb{R}^2	δΒ* (%)
1	$DW = \alpha DBH^{\beta}$	α β	0.465 2.202	0.307 0.151	1.23 0.61	0.90	39.4
2	$DW = \alpha DBH^2$	α	1.120	0.040	0.16	0.94	62.8
3	$\ln(DW)=c+\alpha ln(DBH^2)$	$^{\mathrm{c}}_{\alpha}$	-1.966 1.242	$0.235 \\ 0.032$	0.94 0.13	0.97	25.6
4	$ln(DW) = c + \alpha ln(DBH^2 \times h \times d)$	$^{\mathrm{c}}_{lpha}$	-2.904 0.993	0.120 0.012	0.48 0.05	0.99	11.2
5	$\ln(\mathrm{D}W) = \mathrm{c} + \alpha \mathrm{ln}(\mathrm{D}BH^2 \times d)$	$^{\mathrm{c}}_{lpha}$	-0.906 1.177	0.125 0.018	0.50 0.07	0.99	14.8
6	$ln(DW) = c + \alpha ln(DBH^2 \times h)$	$^{\mathrm{c}}_{lpha}$	-3.843 1.035	0.259 0.025	1.05 0.10	0.97	24.3
7	$ln(DW) = c + \alpha ln(DBH^2) + \beta ln(d)$	c α β	-1.020 1.185 1.071	0.175 0.021 0.114	0.70 0.08 0.46	0.99	14.7

^{*} For explanation and calculation see text, Equation 1.

Table 3. Regression equations for estimation of above-ground biomass, using different models and combinations of independent variables. All regression equations are statistically significant (P < 0.0001), based on sample trees with DBH \leq 45 cm only (N = 33) from mature lowland 'terra firme' forest near Araracuara, Colombia. DW = aerial dry weight of the tree (kg), DBH = diameter at breast height; 1.30 m above ground level (cm); h = height of the tree (m); d = wood density (g cm⁻³).

No.	Regression model	Coefficient symbol	Coefficient value	Standard error	Width of 95% confidence interval	\mathbb{R}^2	δΒ* (%)
1	$DW = \alpha DBH^{\beta}$	α β	0.749 2.011	0.552 0.204	2.25 0.83	0.81	42.8
2	$DW = \alpha DBH^2$	α	0.780	0.039	0.16	0.93	43.5
3	$\ln(DW)=c+\alpha ln(DBH^2)$	$^{\mathrm{c}}_{\alpha}$	-2.059 1.256	0.393 0.061	1.60 0.25	0.93	27.5
4	$ln(DW) = c + \alpha ln(DBH^2 \times h \times d)$	$^{\mathrm{c}}_{lpha}$	-2.885 0.990	0.213 0.024	0.87 0.10	0.98	12.9
5	$ln(DW) = c + \alpha ln(DBH^2 \times d)$	$^{\mathrm{c}}_{lpha}$	-1.192 1.229	0.206 0.035	0.84 0.14	0.98	15.6
6	$\ln(DW) = c + \alpha \ln(DBH^2 \times h)$	$^{\mathrm{c}}_{lpha}$	-3.555 1.002	0.428 0.045	1.75 0.18	0.94	26.3
7	$ln(DW) = c + \alpha ln(DBH^2) + \beta ln(d)$	c α β	-1.322 1.239 1.106	0.256 0.037 0.148	1.04 0.15 0.60	0.98	15.0

^{*} For explanation and calculation see text, Equation 1.

trees in mature forests, the regression analysis was also performed on trees with DBH range up to 45 cm only (N = 33). The coefficients of determination appeared only slightly smaller and δB values increased a little (Table 3), compared with the corresponding values of the complete data set. The standard errors increased, but it might be assumed that sampling more smaller trees can compensate for this. The corresponding regression equations of the complete and the DBH \leq 45 cm data sets did not differ significantly (P < 0.05), which indicates that, at least in this study, bigger trees apparently did not have much influence on determining the coefficients of the regression equation.

DISCUSSION

Preliminary evaluation (Overman 1989, Overman et al. 1990) of the data of this study led to the conclusion that separate estimates for biomass of different tree compartments (leaves, twigs, branches) using DBH or different measures for crown volume as independent variable, did not yield statistically significant results. These studies also report the results of calibration in a 17-year-old successional forest. The regression equations for the successional and the mature forest could not be distinguished from each other statistically. Biomass estimates

per hectare for several lowland rainforest types in the study area were reported by Overman et al. (1990).

Many regression models could be designed to estimate the biomass. Few fulfil the considerations of statistical correctness, accurate estimations and practical usefulness. Multiple regression models involving DBH and height of the tree as independent variables suffered from collinearity and had to be rejected. Other models suffered from an increase in variance with increasing values of the independent variable (models 1 and 2 in Table 2). The low R² and high δB value for model 2 is believed to be also partly caused by the fact that an inadequate model was used. The square of DBH is only an approximation of the 'best' exponent value (i.e. 2,202, model 1 in Table 2). As a consequence, this model will not yield accurate estimations for all DBH classes. For models 3-7 the differences in R2 were small but the δB values clearly showed the influence of wood density on the accuracy of the estimate. The problem with this parameter is that it is very time consuming, not to mention destructive, to determine for every tree in a plot when estimating biomass on the basis of the calibrated function. Including the average wood density of the sample trees in the regression equation would merely signify adding a constant to the regression, while the increase in accuracy of models with wood density is caused by the fact that the wood density value of the individual tree is taken into account in the calculation of its biomass. Thus, models 4, 5 and 7 which include wood density had to be rejected for practical reasons. It seems worthwhile, however, to investigate quicker methods for determining wood density, for instance with samples taken by a tree corer, as wood density values between the lower and upper part of a stem do not appear to differ much (mean 0.041 g cm⁻³, Overman unpublished data). The remaining models 3 and 6 did not differ much in accuracy. Model 6, which included height of the tree, was preferred because it can overcome possible extreme variations in this parameter (thin long saplings or emergent trees).

Comparing the respective coefficients between Tables 2 and 3, these appeared very similar for the logarithmically transformed models. Apparently, big trees did not have a great influence on pinpointing the coefficients of the regression. This could be expected from the very linearly shaped data point distribution in Figure 3c. The 21 points on the right side of the diagram (representing trees with DBH >45 cm) are in line with the other points, so these will not alter the slope very much. A considerable time-saving in the field seems possible without losing too much accuracy, although more tests with other data are still necessary. Moreover, very high densities of small trees were observed in the mature forest near Araracuara. In 94 plots of 0.1 ha, Duivenvoorden & Lips (in press) report an average frequency of trees with a DBH >40 cm (in the population of trees with a DBH >1 cm) of 0.7%. Similar distributions in Amazon rainforest were reported by Jordan & Uhl (1978) and Saldarriaga *et al.* (1988). Jordan & Uhl found (calculated from Table 1, Jordan & Uhl 1978) that trees with DBH values <20 cm accounted for 36%, and trees with DBH values ≤45 cm

accounted for 85% of the biomass per hectare. Thus it is very important to estimate accurately the biomass of the smaller trees. A way of achieving this could be to construct regression equations based on smaller trees only, as appeared possible in the discussion above. The time-saving could be invested in sampling more smaller trees. As the number of samples increases, a more accurate regression equation would result, and at the same time an equation based on those trees that also make up the major part of the biomass per hectare.

ACKNOWLEDGEMENTS

The study forms part of the Tropenbos project in Colombia, South America. Fieldwork was supported by a grant of the Instituto Colombiano de Credito Educativo y Estudios Technicos en el Exterior (ICETEX). JPMO is indebted to J. F. Duivenvoorden for his generous help during the study and the early statistical elaboration of the data. We thank the Corporación Colombiana para la Amazonia-Araracuara, the Instituto Geográfico 'Agustín Codazzi' (IGAC), the Hugo de Vries Laboratory and the Tropenbos Foundation for the use of their facilities.

LITERATURE CITED

- BARNEY, R. J., VANCLEVE, K. & SCHLENTNER, R. 1978. Biomass distribution and crown characteristics in two Alaskan *Picea mariana* ecosystems. *Canadian Journal of Forest Research* 8:36–41.
- BELSLEY, D. A., KUH, E. & WELSH, R. E. 1980. Regression diagnostics. Identifying influential data and sources of collinearity. John Wiley & Sons Inc., New York. 292 pp.
- DRAPER, N. R. & SMITH, H. 1981. Applied regression analysis. 2nd edition. J. Wiley & Sons. 709 pp. DUIVENVOORDEN, J. F., LIPS, J. M., PALACIOS, P. A. & SALDARRIAGA, J. G. 1988. Levantamiento ecológico de parte de la cuenca del medio Caquetá en la Amazonia Colombiana. Colombia Amazonica 3(1):7–38.
- DUIVENVOORDEN, J. F. & LIPS, J. M. In press. Landscape ecology of the middle Caquetá basin. Explanatory notes to the maps. In Saldarriaga, J. & Van der Hammen, T. (eds). Studies on the Colombian Amazon Vol. 3. Programa Tropenbos-Colombia, Bogotá.
- EGUNJOBI, J. K. 1976. An evaluation of five methods for estimating biomass of an even-aged plantation of *Pinus caribea L. Oecologia Plantarum* 11(2):109-116.
- GLANTZ, S. A. 1987. Primer of biostatistics. 2nd edition. McGraw-Hill Inc., USA. 379 pp.
- JORDAN, C. F. 1985. Nutrient cycling in tropical forest ecosystems. Principles and their application in management and conservation. J. Wiley & Sons. 179 pp.
- JORDAN, C. F. & UHL, C. 1978. Biomass of a 'terra firme' forest of the Amazon Basin. Oecologia Plantarum 13(4):387–400.
- KLINGE, H. & HERRERA, R. 1983. Phytomass structure of natural plant communities on spodosols in Southern Venezuela: The tall Amazon Caatinga forest. *Vegetatio* 53:65–84.
- KLINGE, H., RODRIGUEZ, W. A., BRUNIG, E. & FITTKAU, E. J. 1975. Biomass and structure in a central Amazonian rain forest. Pp. 115–122 in Golley, F. B., Medina, E. (eds). *Tropical ecological systems*. Springer-Verlag, Berlin. 398 pp.
- KÖPPEN, W. 1936. Das geographische System der Klimaten. Pp. 1–44 in Köppen, W. & Geiger, R. (eds). *Handbuch der Klimatologie*. Band I, Part C, Berlin.
- MOORE, P. J. & CHAPMAN, S. B. (eds). 1986. *Methods in plant ecology*. Blackwell Scientific Publications. 536 pp.
- OGAWA, H., YODA, K., OGINO, K. & KIRA, T. 1965. Comparative ecological studies on three main types of forest vegetation in Thailand. II Plant biomass. *Nature and life in Southeast Asia* IV:49–80.
- OVERMAN, J. P. M. 1989. Quantitative estimators for aerial biomass determination of a mature and a successional forest in the Colombian Amazon. *Internal report no. 268. Hugo de Vries Laboratory, University of Amsterdam*, Amsterdam. 38 pp.

- OVERMAN, J. P. M., SALDARRIAGA, J. G. & DUIVENVOORDEN, J. F. 1990. Estimación de la biomasa ácrea en el bosque del medio Caquetá, Colombia. *Colombia Amazonica* 4(2):135–147.
- PASTOR, J., ABER, J. D. & MELILLO, J. M. 1984. Biomass prediction using generalized allometric regressions for some Northeast tree species. Forest Ecology and Management 7:265-274.
- RODRIGUEZ, L. V. A. 1988. Consideraciones sobre la biomassa, composición quimica y dinámica del bosque plúvial trópical de Colinas Bajas, Bajo Calima, Buenaventura, Colombia. *CONIF. Serie Documentacion No. 16.* 36 pp.
- SALDARRIAGA, J. G., WEST, D. C., THARP, M. L. & UHL, C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology* 76:938–958.
- SANTEE, W. R. & MONK, C. D. 1981. Stem diameter and dry weight relationships in *Tsuga canadensis* (L.) Carr. *Bulletin of the Torrey Botanical Club* 108(3):320-323.
- SARMIENTO, G. 1984. Los ecosistemas y la ecosfera. Editorial Blume, Barcelona. 272 pp.
- SATOO, T. & MADGWICK, H. A. I. 1982. Forest biomass. M. Nijhoff/W. Junk Publishers. The Hague. 152 pp.
- SCHMITT, M. D. C. & GRIGAL, D. F. 1981. Generalized biomass estimation equation for Betula papyrifera Marsh. Canadian Journal of Forest Research 11:837-840.
- WALTER, H. & LIETH, H. 1960. Klimadiagramm Weltatlas. VEB Gustav Fischer Verlag Jena.
- WHITMORE, T. C., PERALTA, R. & BROWN, K. 1985. Total species count in a Costa Rican tropical rain forest. *Journal of Tropical Ecology* 1(4):375-378.
- WITTE, H. J. L., WIJMSTRA, T. A. & YOUNG, R. 1988. Walter graph, a program for drawing Walter climatic diagrams. Hugo de Vries Technical note 15, University of Amsterdam, Amsterdam. 3 pp.

Accepted 19 September 1993