

Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability

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ABSTRACT. Biomass content and turnover rate were estimated for a lowland wet rain forest in French Guiana. A regression model relating the biomass of a tree to its dbh (diameter at breast height) was deduced from previously published data. A power-law allometric relationship of the form $AGTB = aD^b$ was used to estimate the tree biomass, AGTB (Mg ha^{-1}), from its dbh D (cm). Using direct measurements of tree biomass in the literature, the best-fit allometric exponent $b = 2.42$ ($SD = 0.02$) was found. The logarithm of the coefficient a was normally distributed with an average of -2.00 ($SD = 0.27$). This method was applied to two permanent research stations of the lowland tropical rain forest of French Guiana: the Nouragues and Piste de Saint-Elie. At the Nouragues, the biomass was estimated from trees 10 cm in diameter on two plots covering a total surface area of 22 ha and yielded an average biomass of 309 Mg ha^{-1} ($\pm 32 \text{ Mg ha}^{-1}$, 95% confidence interval). Spatial variability was also addressed at the Nouragues by estimating the biomass of trees ≥ 30 cm dbh over a total surface area of 82 ha. For the wet tropical forest vegetation type, an average of 284 Mg ha^{-1} was obtained (spatial variability $\pm 55 \text{ Mg ha}^{-1}$). Biomass turnover was evaluated at Piste de Saint-Elie from two transects (0.78 and 1 ha) on which all trees ≥ 5 cm in diameter were recorded and mapped twice in 10 y. Transect 1 showed a slight increase in biomass, from 245 to 260 Mg ha^{-1} (338 to 345 Mg ha^{-1} for transect 2), corresponding to a net increase of $1.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ($0.7 \text{ Mg ha}^{-1} \text{ y}^{-1}$), and the biomass ingrowth was $3.2 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ($2.8 \text{ Mg ha}^{-1} \text{ y}^{-1}$). These figures are discussed in the light of the natural recruitment dynamics of tropical forests.

KEY WORDS: allometric laws, biomass estimation, error propagation, French Guiana, wet tropical forests

INTRODUCTION

Biomass is an important parameter for characterizing a forest ecosystem. The efficiency of carbon storage in organic matter reflects the quality of environmental conditions: climate, soil structure and nutrient availability. A precise

knowledge of the biomass is crucial for harvesting assessments (Vanclay 1995) and, at a much larger scale, for the study of greenhouse warming scenarios (Houghton *et al.* 2000, Shukla *et al.* 1990). Atmospheric carbon uptake by the vegetation is believed to play a major role in the global climate changes of the century to come (Fan *et al.* 1998, Phillips *et al.* 1998). An estimated 37% (428 Pg = $428 \cdot 10^{15}$ g) of the world's living terrestrial carbon pool (1146 Pg) is stored in tropical forests (Dixon *et al.* 1994), more than half of which is in the neotropics (53%).

Although the need is great, little is known about inter-site and temporal variability of forest biomass in tropical zones, compared to the large amount of information available in temperate regions (see Brown 1997 for a recent review). Previous studies on biomass estimates for tropical forests range between 148 and 669 Mg ha⁻¹ (1 Mg ha⁻¹ = 106 g ha⁻¹), the latter from Kira (1971). Direct assessment of the aboveground biomass is strenuous; all trees must be felled and weighed in a small sample area, in order to parameterize a regression method. Moreover, direct biomass estimates are generally based upon small sample units, typically less than 100 trees \geq 10 cm dbh, that is, less than 1/5 ha. Large trees (\geq 70 cm dbh) have an overwhelming weight in the average biomass content of a forest and they may be under or over-represented in small sampling units. Therefore, even direct biomass estimates should be interpreted with caution. In the absence of any such data, the use of functional relationships between surrogate variables, such as the dbh, and the biomass, is the most natural way to proceed, provided the error on such estimates is systematically investigated (I. F. Brown *et al.* 1995).

In the present paper, we propose an estimation method for the biomass of a lowland tropical rainforest in French Guiana. We give a new argument based on theoretical considerations, to justify the power-law allometric relationship between biomass and dbh. A careful analysis of previously published data on tree biomass in similar forest types provides an estimation of the error on the coefficients of the regression model. This method is then applied to two permanent plots in French Guiana: the Nouragues Research Station (100 km inland) and the Piste de Saint-Elie Research Station (coastal rain forest). Finally, we discuss the reliability of our estimates, and the influence of soil on the spatial variation of the biomass.

STUDY AREA

French Guiana

French Guiana, an overseas French territory, lies between 2°10' and 5°45'N and 51°40' and 54°30'W in northeastern South America. Of the region, 97% is covered by lowland wet tropical forest (Figure 1). A phytogeographic description of the region is found in Lindeman & Moolenaar (1959) and Lindeman & Mori (1989). Annual rainfall is between 1650 and 4000 mm⁻¹, with a decreasing gradient from the coastal area to the southern tip of the country. A pronounced

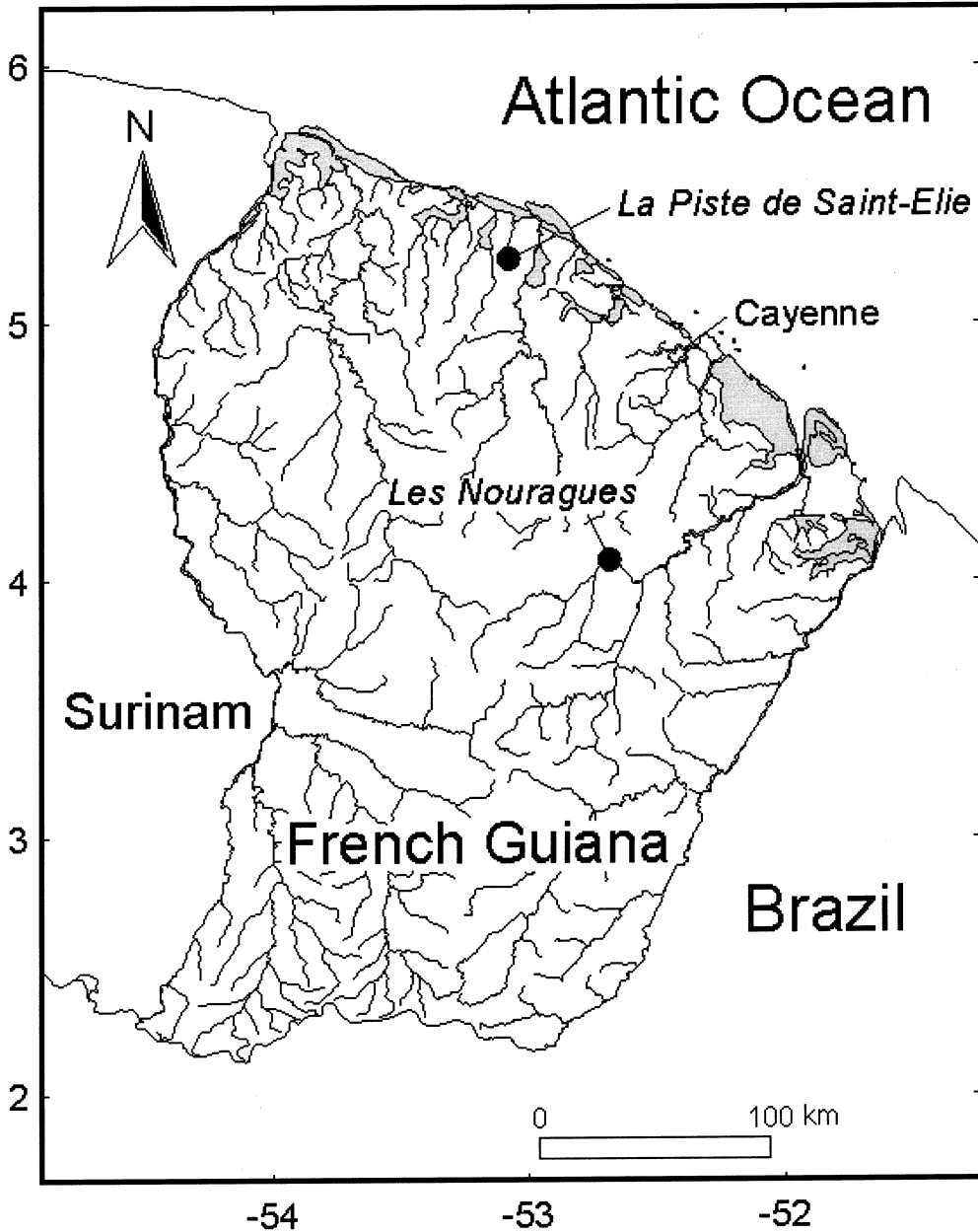


Figure 1. Location of the field stations Les Nouragues and La Piste de Saint-Elie in French Guiana, South America. The grey regions along the coast give the locations of the coastal savannas. The rest of the country is covered by the tropical rain forest (lines show the river courses).

dry season of 2 mo is recorded from September to November and a short dry season in March, both related to the displacement of the inter-tropical convergence zone (ITCZ).

The average temperature is 25.8 °C with an annual amplitude of 2 °C and

daily amplitudes of 7 °C in the rainy season (10 °C during the dry season). Geology is typical of the Guiana Shield with a central pediplain and sparse rugged mountains of Precambrian metamorphic and granitic rocks. The altitude is less than 500 m above sea level.

The Nouragues

The Nouragues Research Station is located 10 km north of the Arataye river, 4°50'N and 52°42'W (Poncy *et al.* 1998). This research station was created in 1987, near to a granite hill (inselberg). Annual rainfall is 2757 mm y⁻¹ (from 1989 to 1998) with around 70 mm mo⁻¹ in September and November and more than 300 mm mo⁻¹ in January and from April to June. Rock savanna is found on the inselberg (Larpin 1993), while the surrounding forest is a typical lowland wet tropical rain forest (Poncy *et al.* 1998).

The permanent plot extends over 82 ha of undisturbed old-growth forest, separated into two geologically different areas (Figure 2). Analysis of the spatial patterns of ground-level light intensity has been discussed by L. Cournac and coworkers (unpubl. data). A first plot of 70 ha ('grand plateau', hereafter

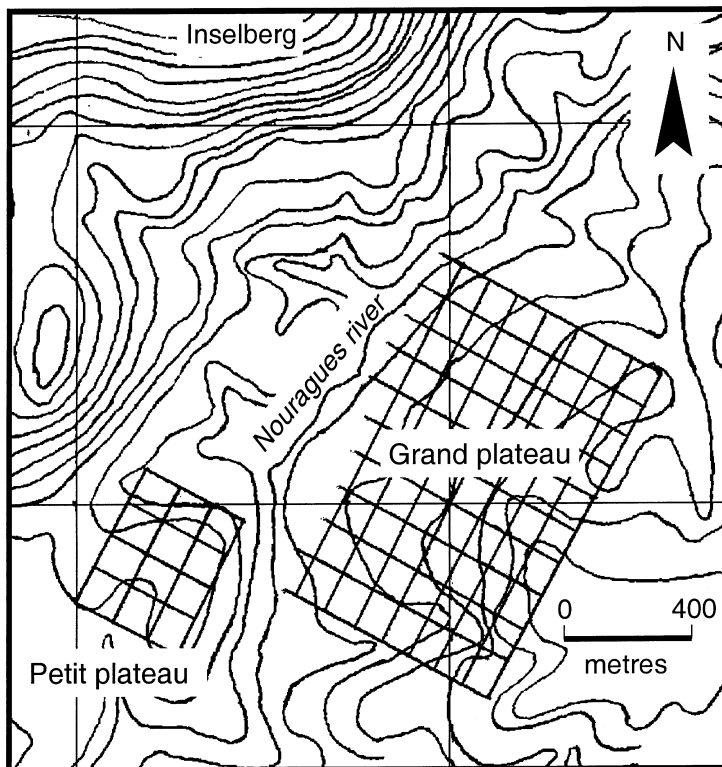


Figure 2. The permanent plots of the Nouragues. Elevation lines are drawn at 20 m intervals (maximal elevation: 411 m at the top of the inselberg). A large sampling plot (70 ha), called 'grand plateau' (GP) has been established east of the Nouragues river, and a smaller plot was located west of the river ('petit plateau' or PP, 12 ha in size).

referred to as GP) is on metamorphic bed-rock of the Paramaca series, covered with clayey soil. A second plot of size 12 ha ('petit plateau', or PP) is on granitic and crystalline bed-rocks covered with sandy clayey soil.

GP has all trees ≥ 30 cm dbh tagged, mapped, measured and identified. This information was also recorded in one strip of 1000-m \times 100-m (10 ha) for all trees ≥ 10 cm dbh. PP has all 6441 trees ≥ 10 cm dbh mapped, measured and identified. Buttressed trees were measured 50 cm above buttresses following the standard procedure discussed in Sheil (1995) and Condit (1998). The frequency distributions are given for both plots in Table 1.

The southernmost part of GP is largely dominated by lianas, which results in a dense layer of vegetation, and a low density of tree stems. This liana forest is considered as being a different forest type, and therefore we did not include it in our biomass estimate of the wet rain forest.

The floristic inventory is very rich, with over 1200 species of angiosperms, dominated by Orchidaceae, Mimosaceae and Rubiaceae (AUBLET database for the Nouragues area; Poncy *et al.* 1998). Over 145 tree species were identified in the permanent plots. Concerning trees above 30 cm dbh, the dominant families are Caesalpiniaceae (20.1%), Lecythidaceae (12.9%), Mimosaceae (10.1%) and Sapotaceae (9.25%). The diversity index (number of species per ha for trees ≥ 10 cm dbh) ranges between 160 and 260 species ha⁻¹.

Piste de Saint-Elie

The research station of Piste de Saint-Elie (5°30'N, 53°00'W) is located 16 km south of Sinnamary and has been much studied since 1976 (Lescure *et al.* 1983, Lescure & Boulet 1985, Pélissier & Riéra 1993, Puig *et al.* 1990, Roggy *et al.* 1999). Annual rainfall is slightly above 3000 mm y⁻¹. The monthly rainfall pattern is more variable than in the Nouragues. The forest mostly grows on a mantle of schist covered by a sandy clayey soil (Lescure & Boulet 1985). The floristic composition differs slightly from that at the Nouragues, the dominant families being Lecythidaceae (28%), Caesalpiniaceae (22%) and Chrysobalana-ceae (12%), for trees ≥ 20 cm dbh (Pélissier & Riéra 1993). The diversity index is between 160 and 180 species ha⁻¹.

Table 1. Frequency distribution in class of dbh (interval size: 10 cm) at the Nouragues Research Station, for the two plots where all trees ≥ 10 cm dbh were measured (a 10-ha strip in the 'grand plateau' GP, and the 12-ha 'petit plateau' PP, see Figure 2). The third line gives the frequency distribution for all 9892 trees ≥ 30 cm dbh recorded over the entire 82-ha plot (PP+GP).

	Dbh (cm)							
	10–19	20–29	30–39	40–49	50–59	60–69	70–79	
PP (12 ha)	3767	1280	603	315	178	111	64	
GP (10 ha)	3215	1015	442	245	106	76	43	
82 ha	—	—	7194	2973	1413	807	442	
	80–89	90–99	100–109	110–119	120–129	130–139	≥ 140	Total
PP (12 ha)	38	17	14	6	6	4	9	6440
GP (10 ha)	25	20	10	8	9	6	4	5295
82 ha	272	140	93	50	42	21	42	9892

The plots analysed in the course of the present investigation are the same as those described in Pélissier & Riéra (1993). All trees ≥ 5 cm dbh were tagged, mapped, measured and identified to the species both in 1981 and 1991 (Pélissier & Riéra 1993). Transect 1 is a strip of 20-m \times 360-m (0.78 ha) with 919 trees in 1981, and 916 in 1991. Transect 2 has a size of 20-m \times 500-m (1 ha) and had 1168 trees in 1981 (1160 in 1991).

METHODS

Allometric relationship between biomass and dbh

In almost all studies, both in temperate (Bunce 1968, Rapp *et al.* 1999, Whitaker & Woodwell 1968) and in tropical areas (Araújo *et al.* 1999, Brown 1997, Edwards & Grubb 1977, Laurance *et al.* 1997, Lescure *et al.* 1983, Overman *et al.* 1994, Ovington & Olson 1970), a strong correlation was found between AGTB, the aboveground dry biomass of a tree (organic matter content) and its dbh D with a linear regression coefficient greater than $r^2 = 0.97$. The best-fit regression including only the dbh is

$$\ln(\text{AGTB}) = \alpha + b \ln(D) \quad (1)$$

AGTB is measured in kg and D is in cm. For the sake of simplicity we use the notation $\alpha = \ln(a)$ throughout this paper. We also distinguish between the biomass for one tree (AGTB) and the tree aboveground biomass of a sampled area (B). The coefficients α and b given in the literature are presented in Table 2 (for a related discussion, see Alves *et al.* 1997, Araújo *et al.* 1999, Overman *et al.* 1994). In most cases, the tree height H is not a good estimator of the aboveground biomass. This observation should not be surprising in view of the high variability of tree architectures in the tropical zone (Hallé *et al.* 1978). For monopodial architectures and accurate height estimates, the best estimator for AGTB is $D^2 H$, as expected from a simple scaling argument. In contrast, for tropical forests, the height of the largest trees is often estimated within a range of 5–10 m. Moreover, the use of a three-parameter regression, including the height, leads almost systematically to a higher correlation coefficient r than the two-parameter regression (Eqn 1), even if the additional variable H is poorly measured. Therefore, we follow previous discussions (Lescure *et al.* 1983, Overman *et al.* 1994) and we retain D only.

Measurements in temperate forests (Bunce 1968, Rapp *et al.* 1999) and in tropical forests (see below and Table 2) suggest that the power-law regression (4) is consistent with physiological constraints imposed to trees. A recent study by West *et al.* (1997) (see also Enquist *et al.* 1998) on the metabolic rates of living organisms shows that tree-like structures of the respiratory and blood vessels networks implies that the metabolic rate should scale as $\text{AGTB}^{3/4}$. This relationship, referred to as Kleiber's law was shown to fit experimental results over a 26-fold range in the logarithm of the biomass (from one mammalian cell to an elephant). The allometric relationship between the variables of the

Table 2. Coefficients for the allometric relationship $\ln(\text{AGTB}) = \alpha + b \ln(D)$ for 11 published datasets. Only trees ≥ 10 cm dbh were selected, except for study 1. Although these data were collected in very different forests, a striking similarity is observed both for the exponent b and the constant α (r is the linear correlation coefficient). Small trees strongly affect the allometric coefficients, as evidenced in study site 1, where trees were sampled from 1 cm dbh upwards.

Study	α	b	r	Number of trees	Location	Reference
1	-2.88	2.72	0.97	1412*	French Guiana	Lescure <i>et al.</i> (1983)
2	-1.97	2.48	0.96	54	Colombia	Overman <i>et al.</i> (1994)
3	-2.00	2.55	—	319+	Manaus, Brazil	Higuchi <i>et al.</i> (1998)
4	-2.55	2.65	0.97	127	Para, Brazil	Araújo <i>et al.</i> (1999)†
5	-2.41	2.41	0.95	15	Puerto Rico	Ovington & Olson (1970)
6	-2.00	2.36	0.96	39	New Guinea	Edwards & Grubb (1977)
7	-1.81	2.32	0.98	92	Costa Rica	Brown (1997)§
8	-2.43	2.57	0.96	30	Brazil	Brown (1997)§
9	-2.26	2.66	0.97	15	Para, Brazil	Brown (1997)§
10	-2.26	2.60	0.98	38	Indonesia	Brown (1997)§
11	-2.39	2.56	0.99	22	Cambodia	Brown (1997)§

* only 418 trees ≥ 5 cm dbh; † estimated; + trees ≥ 5 cm dbh.

§ from published and unpublished databases, see Brown (1997).

model also relates the basal diameter D of the tree structure (aorta for the blood system, trunk for a tree) to the biomass AGTB through $\text{AGTB} \sim D^{8/3}$. The reader is referred to Enquist *et al.* (1998) for further details on this theory. The slight but systematic departure from the theoretical 8/3 exponent observed in Table 2 may reflect other physiological constraints on trees.

Derivation of the allometric equation

We used published datasets providing the biomass AGTB and the dbh D of felled and weighed trees, to obtain the best estimate of α and b in Eqn (1). These datasets are numbered 4 to 11 in Table 2 (most of them gathered in Brown 1997), and they correspond to 378 trees ≥ 10 cm dbh.

For all eleven datasets reported in Table 2 a best-fit of the form of Eqn (1) was available. These results and the corresponding estimates of α and b are reported in Table 2 for each separate study. Eqn (1) provides an excellent linear correlation coefficient in all cases, and the b exponent ranges from 2.32 to 2.72.

In Figure 3, the biomass of each tree from studies 4 to 11 was plotted against its dbh. This represents 378 trees ≥ 10 cm dbh overall, with 135 ≥ 30 cm dbh, and 32 large trees (≥ 70 cm dbh). No pattern seems to emerge if both quantities are plotted using linear axes (left panel of Figure 3). However, a log-log plot (right panel) clearly shows that all the points are around a line with a well-defined slope, $b = 2.42$, and a best-fit constant $\alpha = -2.00$ ($r^2 = 0.97$), an observation consistent with Eqn (1).

It was assumed that the variability in this best-fit equation does not affect the parameter b but only α . This assumption is motivated by the observation that 97% of the datapoints in Figure 3 fall in a strip of height 0.78 (dashed lines in Figure 3). Tree-to-tree variability was estimated by computing α for each tree, from the formula $\alpha = \ln(\text{AGTB}) - b \ln(D)$. This random variable has

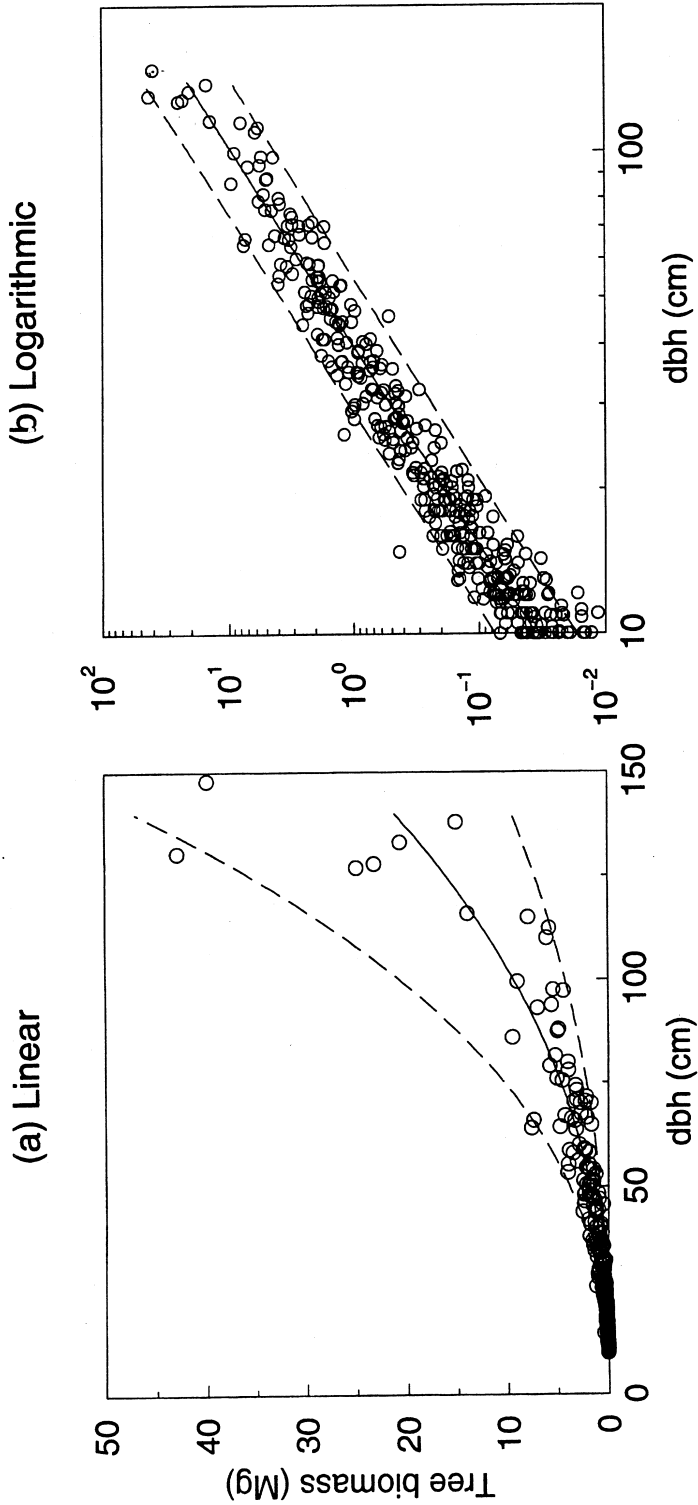


Figure 3. Aboveground biomass (Mg ha^{-1}) versus dbh (cm) for 378 trees weighed and found in the literature (Table 2) plotted with (a) linear scales, and (b) logarithmic scales. In (b), the fitted line for the power regression (Eqn 1, see text) is shown. Dashed lines indicate the strip of height 0.78 used to propagate the errors at the stand level (see text, section *Error propagation*).

a mean -2.00 and a unimodal distribution. Moreover, a χ^2 -test on the distribution shows that it is normally distributed (histogram with 19 classes, $\chi^2 = 6.38$, $P < 0.01$). The standard deviation on α is $\Delta\alpha = 0.27$. Therefore, our best fit yields

$$\ln(\text{AGTB}) = -2.00 \pm 0.27 + 2.42 \ln(D) \quad (2)$$

For example, the average estimated biomass for a tree of dbh 30 cm is $\text{AGTB} = 508$ kg, the lower bound is $\text{AGTB}_{\min} = 344$ kg (-32%) and the upper bound is $\text{AGTB}_{\max} = 750$ kg ($+47\%$).

It should be emphasized that datasets 4–11 span a large range in tropical rainforest types, from moist forests (rainfall less than 3000 mm y^{-1} and more than 1500 mm y^{-1}) to wet forests (rainfall more than 3000 mm y^{-1}). However, Overman *et al.* (1994) have predicted very close estimates ($\alpha = -1.97$, $\Delta\alpha = 0.235$ and $b = 2.48$) on the basis of their dataset of 54 trees (terra firme forest with 3000 mm y^{-1} rainfall), which we have not included in the present relationship.

Our approach contrasts with previous work (Brown 1997) which attempted to find a locally derived best-fit equation in order to compute the biomass, and which yielded very different allometric forms for different forest types. To test the variability of the regression with forest types, we have selected trees ≥ 10 cm dbh. A direct power-law fit of the data yields: for wet plots (rainfall ≥ 3000 mm y^{-1}) $b_{\text{wet}} = 2.41$, $\alpha_{\text{wet}} = -2.14$, $\Delta\alpha_{\text{wet}} = 0.33$, ($n = 146$, $r^2 = 0.98$) and, for moist plots (rainfall < 3000 mm y^{-1}) $b_{\text{moist}} = 2.54$, $\alpha_{\text{moist}} = -2.19$, $\Delta\alpha_{\text{moist}} = 0.37$ ($n = 105$, $r^2 = 0.98$). Our choice ($b = 2.42$, $\alpha = -2.00$, $\Delta\alpha = 0.27$) results in an over-estimation for the wet plots (ratio observed biomass over predicted biomass, ρ , is $\rho = 0.8$, $\text{SD} = 0.25$) and an under-estimation for the moist plots ($\rho = 1.2$, $\text{SD} = 0.51$). For the purpose of the present study, the rainfall pattern around 3000 mm y^{-1} in French Guiana justifies our choice.

Error propagation

A simple method to propagate the errors from the tree-scale estimate to the plot-scale estimate is presented. Throughout this study, we took sampling units of 1 ha in area.

The biomass was estimated for Q different replicates of each 1-ha sampling unit, by assuming that the error on the logarithm of the biomass estimate of one tree, $\ln(\text{AGTB})$ was normally distributed, with a variance $\Delta\alpha$, as discussed above. Then, the tree biomasses are summed over all the trees yielding a biomass estimate B_q for the replicate $q \in \{1, \dots, Q\}$ of the sampling unit (1 ha). The average estimated biomass and the SD are therefore $B = (1/Q) \sum_{q=1}^Q B_q$, and $(\Delta B)^2 = (1/Q) \sum_{q=1}^Q (B_q - B)^2$. For the present study, we took $Q = 1000$ in all cases. Assuming that the B_q are normally distributed, the 95% confidence interval on B is given by $B \pm 1.96\Delta B$. In fact, the hypothesis of independence on the B_q variables is not strictly valid and the actual distribution slightly departs from

a Gaussian (I. F. Brown *et al.* 1995). Nevertheless, the normal distribution provides a reasonable estimate of the confidence interval.

Small trees and belowground biomass

Trees less than 10 cm dbh contribute little to the total aboveground biomass. Nevertheless, this leads to a systematic underestimate of B , about 2% of the total biomass (Lescure *et al.* 1983).

The root biomass can be indirectly estimated using the ratio of root-to-shoot (R/S) biomass found in the literature, e.g. 0.19 (Jackson *et al.* 1996) or 0.24, SD = 0.14 (Cairns *et al.* 1997). The total soil organic matter (roots plus soil carbon) represents almost half of the total carbon content in tropical evergreen forests of South America (Dixon *et al.* 1994).

RESULTS

Biomass estimates at the Nouragues

To estimate the average biomass at the Nouragues research station, we used the two subplots on which all trees were measured from 10 cm dbh and above (the 10-ha strip in the GP, plus the 12-ha PP, see Study Area and Figure 2). The biomasses corresponding to trees $\geq 10, 30$ and 70 cm dbh, were evaluated and the errors were propagated. The statistical confidence interval (at 95%) was recorded, together with the maximal and the minimal values reached during the pseudo-replication (Table 3).

For trees ≥ 10 cm dbh, the average stem number N is slightly greater than 500, and the basal area around 32 m² ha⁻¹. The average biomass is 301 Mg ha⁻¹ in the GP plot, and 317 Mg ha⁻¹ in the PP. The error due to biomass estimate at the tree level yields an uncertainty of ± 32 Mg ha⁻¹ (95% CI) so the two subplots do not support a significantly different amount of biomass.

The overall biomass estimates were found to be 301 ± 32 Mg ha⁻¹ in the 10-ha strip of the GP, and 317 ± 32 Mg ha⁻¹ in the 12-ha PP. This difference is not statistically significant (χ^2 -test, $P > 0.05$). However, the largest biomass

Table 3. Biomass estimates for the 22 ha on which all trees above 10 cm dbh were recorded (one 10-ha subplot of the GP and the entire 12-ha PP). N_{av} is the average number of stems per ha in the various dbh classes, A_{av} is the average basal area per ha (for each tree, $A = \pi D^2/4$, where D is the dbh) in m² ha⁻¹, and B_{av} is the average biomass in Mg ha⁻¹. The error on B_{av} gives the 95% CI, while B_{min} and B_{max} give respectively the smallest and the largest biomass found among the hectares of the two subplots.

		N_{av}	A_{av}	B_{av}	B_{min}	B_{max}
GP plots (n = 10)						
Trees	≥ 10 cm dbh	522	31.1	301 \pm 32	230 \pm 21	416 \pm 38
	≥ 30	99	21.5	237 \pm 32	158 \pm 21	356 \pm 38
	≥ 70	12	8.9	118 \pm 30	67 \pm 21	242 \pm 37
PP plots (n = 12)						
Trees	≥ 10 cm dbh	534	33.7	317 \pm 32	250 \pm 24	394 \pm 46
	≥ 30	114	23.9	254 \pm 32	192 \pm 24	327 \pm 45
	≥ 70	13	8.9	114 \pm 29	69 \pm 22	178 \pm 44

content for a 1-ha sampling unit was found to be $416 \pm 38 \text{ Mg ha}^{-1}$, while the smallest biomass content was $230 \pm 21 \text{ Mg ha}^{-1}$, a significant difference ($P < 0.01$). This suggests that above a size of several hectares, the statistical variations are averaged out. The root biomass was roughly estimated to $75 \pm 45 \text{ Mg ha}^{-1}$ for our study sites, consistent with the 42 Mg ha^{-1} measured at Piste de Saint-Elie (Lescure *et al.* 1983).

Only 19% (respectively 21%) of the trees are $\geq 30 \text{ cm}$ in the GP (respectively PP) but they contribute to 69% (respectively 71%) of the basal area and as much as 79% (respectively 81%) of the aboveground biomass. The influence of large trees in estimating the average biomass of an area is even more pronounced when we consider trees $\geq 70 \text{ cm dbh}$. Only 12 to 13 large trees ha^{-1} are found (about 2.5% of the trees) but they contribute to 39% of the biomass in the GP (36% in the PP). Therefore, the critical size of the sampling area can be related to the number of large trees in the sample. As a rule of thumb, an area with more than 100 large trees ($\geq 70 \text{ cm dbh}$ in rain forests) gives a statistically averaged biomass estimate.

For comparison, we have used the allometric equations developed in Lescure *et al.* (1983), which was used recently (Roggy *et al.* 1999). The average biomass computed with this method yields 428 Mg ha^{-1} in the PP plot, a 36% increase compared with the result of the present work. Likewise, the quadratic equation proposed in Brown (1997): $\text{AGTB} = 21.30 - 6.95 D + 0.74 D^2$ yielded 242 Mg ha^{-1} also for the PP plot, that is a 23% decrease. The fact that the latter regression equation underestimates the biomass has already been discussed by Clark & Clark (2000).

Spatial variability of the biomass estimate for the Nouragues

Trees $\geq 30 \text{ cm dbh}$ contribute to $80 \pm 4\%$ (SD) of the biomass in the 22 ha sampled to 10 cm in dbh. Thus biomass estimates from trees $\geq 30 \text{ cm dbh}$ is strongly correlated with the estimates using all trees $\geq 10 \text{ cm dbh}$. This relationship offered the possibility to compute the biomass for the entire 82-ha permanent plot. The hectare-by-hectare estimates are highly variable, and range from 28 to 423 Mg ha^{-1} , as shown in Figure 4.

The histogram of these 82 values (Figure 5) shows that the 9 ha corresponding to the liana forest (southern tip of the GP) support much less biomass than the rest of the plot (less than 100 Mg ha^{-1}). On the other hand, two units have more than 400 Mg ha^{-1} . When the 9 ha of the liana forest are discarded, the average biomass estimate is 284 Mg ha^{-1} . However, the standard deviation is as much as 55 Mg ha^{-1} ($n = 71$). This is to be compared with the 95% confidence interval resulting from the allometric regression (typically 30 Mg ha^{-1}). The spatial variability signalled by a broad histogram in Figure 5 cannot be an artefact of our allometric equation. Therefore, estimating the biomass from only one hectare would have yielded a typical error of $\pm 20\%$ on the result, due to the sampling error for large trees.

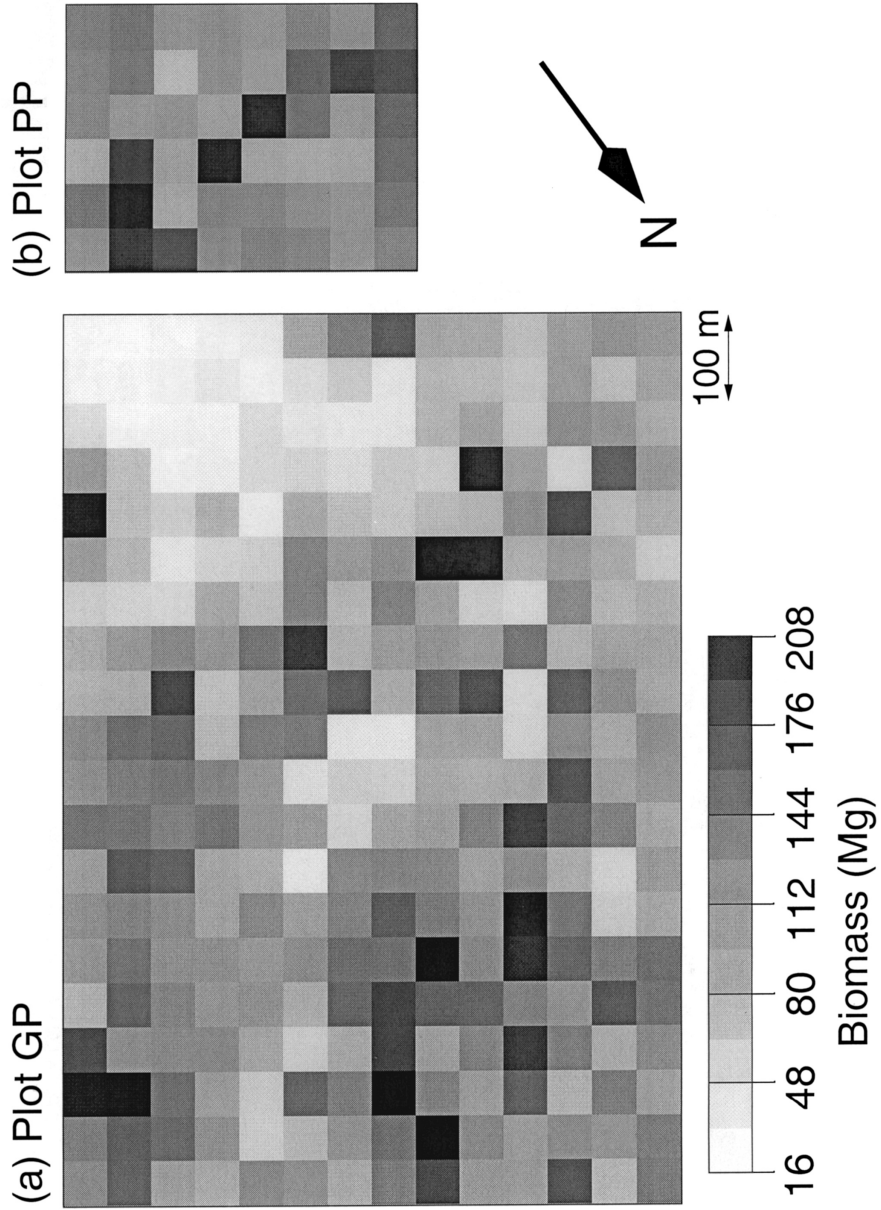


Figure 4. Spatial variability of the biomass for 82 ha at the Nouragues station for (a) grand plateau (plot GP) and (b) petit plateau (plot PP). The spatial distribution is shown with a resolution of 50-m \times 50-m. Black quadrats correspond to high biomass ($\geq 400 \text{ Mg ha}^{-1}$) while white ones correspond to low biomass ($< 200 \text{ Mg ha}^{-1}$).

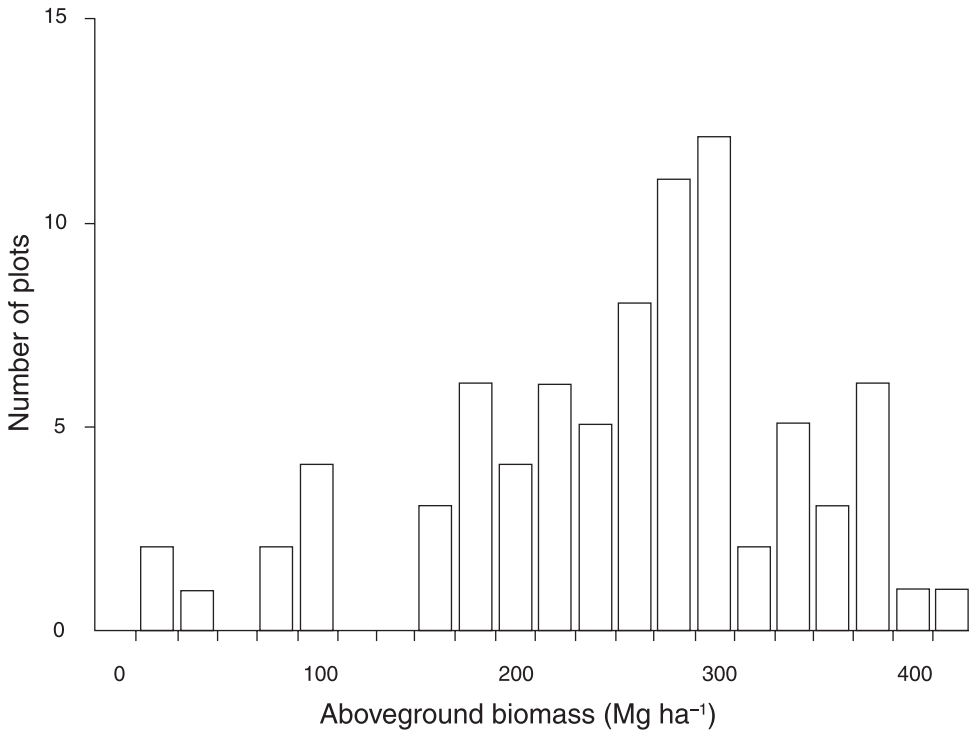


Figure 5. Histogram of aboveground biomass of trees in the 82 1-ha sampling units of the Nouragues Research Station. The frequency distribution shows two distinct patterns: nine sampling units show a biomass $< 100 \text{ Mg ha}^{-1}$, and correspond to a part of the plot dominated by lianas (cf. Fig. 4, upper left part of the GP plot). From 150 Mg ha^{-1} and above (i.e. excluding the nine units dominated by the liana forest), the average of the distribution is 284 Mg ha^{-1} ($\text{SD} = 55 \text{ Mg ha}^{-1}$).

Variation of the biomass in time at Piste de Saint-Elie

To evaluate the change in biomass over time, we analysed two transects of Piste de Saint-Elie, on which all trees $\geq 5 \text{ cm dbh}$ were measured first in 1981 and then again in 1991. No such data were available at the Nouragues research station. The trees were tagged so we knew which trees were recruits and which ones had died during the 10-y span. Therefore, the trees' net primary production NPP (uptake of carbon by trees present at both censuses) and the net ecosystem production NEP (uptake of carbon by trees from photosynthesis minus losses through death) could be estimated.

Trees between 5 cm and 10 cm dbh represent 2 to 4% of the total biomass (Lescure *et al.* 1983), and the fraction of biomass contained in trees $\geq 30 \text{ cm dbh}$ is slightly lower than in the Nouragues. The changes in biomass are similar for all dbh classes, although the fluctuations in stem numbers are not as regular.

In transect 1, the estimated biomass rose from 314 Mg ha^{-1} in 1981 to 333 Mg ha^{-1} in 1991, thus gaining 6.1% ($\text{NEP} = 1.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$, 95% CI: 0.2 Mg

Table 4. Average stem number per ha N_{av} , average basal area A_{av} in $\text{m}^2 \text{ha}^{-1}$, and average biomass estimate B_{av} in Mg ha^{-1} (with 95% CI) for two transects at Piste de Saint-Elie, both in 1981 and 1991. All trees ≥ 5 cm were measured. The data obtained for Transect 1 are given per ha.

Population	Transect 1 (0.78 ha)			Transect 2 (1 ha)		
	N_{av}	A_{av}	B_{av}	N_{av}	A_{av}	B_{av}
1981	1178	35.8	314 ± 32	1168	37.9	338 ± 27
1991	1174	37.8	333 ± 29	1160	38.6	345 ± 27
Deaths	96	1.80	14.0 ± 4	113	2.62	22.3 ± 6.0
Recruits	92	0.28	1.1 ± 0.1	105	0.29	1.2 ± 0.1
Net change	-0.4%	+6.9%	+6.1%	-0.1%	+1.8%	+1.9%

$\text{ha}^{-1} \text{y}^{-1}$). The net loss due to mortality was $1.4 \text{ Mg ha}^{-1} \text{y}^{-1}$, and the increase due to recruits was $0.11 \text{ Mg ha}^{-1} \text{y}^{-1}$. The biomass accumulation in trees present both in 1981 and in 1991 was $\text{NPP} = 3.2 \text{ Mg ha}^{-1} \text{y}^{-1}$. This significant increase both in NPP and NEP was mainly due to the disturbance dynamics (the closure of a treefall gap during this period).

In transect 2, the biomass increased from 338 to 345 Mg ha^{-1} that is $+1.9\%$ ($\text{NEP} = 0.7 \text{ Mg ha}^{-1} \text{y}^{-1}$, 95% CI: $0.2 \text{ Mg ha}^{-1} \text{y}^{-1}$). The NPP was $2.8 \text{ Mg ha}^{-1} \text{y}^{-1}$, the gain due to recruits of $0.12 \text{ Mg ha}^{-1} \text{y}^{-1}$, and the loss $2.2 \text{ Mg ha}^{-1} \text{y}^{-1}$ (mortality). Therefore, the biomass turnover rate (NPP) was around $3 \text{ Mg ha}^{-1} \text{y}^{-1}$ at the Piste de Saint-Elie research station during this period.

DISCUSSION

Reliability of biomass estimates

The aboveground biomass estimates rely on several assumptions, and those should not be understated. First, the coefficient α is estimated at -2.00 ± 0.27 (SD) while the exponent b is assumed constant ($b = 2.42$). This result comes from a relatively large number of trees, yet from heterogeneous sources (Table 2). It would be extremely useful to obtain more reliable data. However, Figure 3 and statistical tests indicate that the allometric Eqn (1) is a better regression equation than a quadratic equation (Brown 1997). So far, no study has addressed the issue of the intrinsic error induced by the use of a regression equation, though several papers have attempted to find the best-fit regression (Araújo *et al.* 1999, Lescure *et al.* 1983, Overman *et al.* 1994) with quite inconclusive results. The main problem with these regression equations is that their reliability degrades as the diameter increases, resulting in a strong discrepancy in the estimates for large trees. The power-law equation suggested in Lescure *et al.* (1983) yielded a 39% over-estimate of total biomass compared with our estimate, while Brown's (1997) quadratic equation yielded a 23% underestimate.

The range of variation in the parameters is intrinsically large and the estimation of this range is far more important than the precise estimation of the average value. Overall, a Monte-Carlo sampling has shown that our average estimate had an error of $\pm 30 \text{ Mg ha}^{-1}$ around the mean (95% CI), which means an error of

about $\pm 10\%$. This error is related to the variability of plant functional types, and could only be reduced using other surrogate variables, such as wood density, plant form geometry, or bole height. More importantly, this assumes that the regression model was constructed from a large tree sample, which is not strictly valid. For example, a sample twice as big in size (e.g. 800 trees) may lead to significant changes in the allometric equation. This caution should be borne in mind when attempting to estimate the carbon pools over large spatial scales (Dixon *et al.* 1994). Most regression models to date are parameterized with a very small number of large trees (≥ 70 cm dbh). For example, Higuchi *et al.* (1998) have used a dataset with five large trees. We have used 32 measurements for large trees in the present work, which is still too few.

Finally, although the biomass of lianas is generally believed to be small (Putz 1983), in disturbed areas such as liana forests small trees and lianas contribute more to the total biomass. Therefore we have certainly underestimated the error in the nine plots of the liana forest.

Influence of soil and fine-resolution variability

The influence of soil characteristics on the uptake capacity of organic matter has been long debated. Recent studies in the neotropics (Laurance *et al.* 1999, Roggy *et al.* 1999) found that nutrient content of the soil significantly affected the carbon storage capacity of a forest. At the Nouragues, the two subplots PP and GP are on different soils. Excluding the liana forest, we found no clear evidence of a correlation between soil and aboveground biomass. It seems that small fluctuations in soil nutrient content mainly affect floristic characteristics (Newbery & Proctor 1984), although they were recently claimed to account for as much as a third of the observed biomass variability (Laurance *et al.* 1999) in a large-scale experiment of the Brazilian lowland rain forest. The most relevant cause of spatial variability in biomass is related to water retention and drainage capacity. Indeed a clear correlation has been found between well-drained soils and large trees in various forests (Condit *et al.* 1995, Lescure & Boulet 1985). We are unable to confirm this particular point since both subplots PP and GP have very similar drainage.

Our results show the significant spatial variability of biomass at a fine-scale resolution. This is a clear illustration of the disturbance-driven, mosaic-like patterns in an old-growth forest, which have been observed for a long time (the sylvigenetic cycle of Aubréville 1938, Hallé *et al.* 1978, Riéra 1995). Hence, the first cause of spatial variability of biomass seems to be related to disturbances rather than deterministic factors (edaphic variability). This hypothesis was confirmed in our study at Piste de Saint-Elie, where the variability in biomass was shown to be correlated to canopy gap openings. Analysis of our results at the Nouragues shows that an estimate based only on a 1-ha sampling unit would have led to an error far greater than the error resulting from the use of an allometric regression. This means that the choice of site position and its size can be crucial for estimating the biomass content of a given forest, especially

for quantifying the forest carbon pools in tropical areas as was done in Phillips *et al.* (1998) or in Houghton *et al.* (2000).

Temporal variability in biomass

Values found in the literature suggest a biomass accumulation (NPP) of 2–4 Mg ha⁻¹ y⁻¹ (Brown & Lugo 1990, Lugo & Brown 1992) and significantly more for secondary forests (Alves *et al.* 1997, Lugo & Brown 1992). Our result is consistent with this estimate (3.2 Mg ha⁻¹ y⁻¹, and 2.8 Mg ha⁻¹ y⁻¹). The ingrowth rate (NEP) was 1.9 Mg ha⁻¹ y⁻¹ (transect 1) and 0.7 Mg ha⁻¹ y⁻¹ (transect 2), consistent with the figures proposed by Phillips *et al.* (1998) in Amazonia (0.97 ± 0.58 Mg ha⁻¹, $n = 40$). However, the increase in transect 1 was largely due to the local disturbance dynamics. Though, the small sample size has certainly led to a strong bias in our estimate. In transect 1, one tree ≥ 70 cm dbh (out of nine trees) died during the 10 y resulting in a net loss of 0.4 Mg ha⁻¹ y⁻¹ alone. In transect 2, one large tree out of 10 died (-0.6 Mg ha⁻¹ y⁻¹).

Increasing turnover rate certainly allows the ecosystem to store more carbon (Phillips & Gentry 1994, Phillips *et al.* 1998). However, the current estimates lack reliable error bars and therefore deciding whether increasing the atmospheric CO₂ concentration does increase significantly the carbon sequestration in rain forests is still a matter of debate (Condit 1997, Houghton *et al.* 2000, Nepstad *et al.* 1999, Sheil 1996).

CONCLUSIONS

In the Nouragues, where no previous biomass study was available, we found an average of 309 ± 32 Mg ha⁻¹ over 22 ha. Using the entire 82-ha permanent sampling plot this estimate dropped to 284 Mg ha⁻¹, with a spatial variability of ± 55 Mg ha⁻¹ (SD) and extreme values of 28 and 432 Mg ha⁻¹. The complementary study at Piste de Saint Elie gave estimated biomass figures of 314 and 338 Mg ha⁻¹ (in 1981) and 333 and 345 Mg ha⁻¹ (in 1991) comparable with the values obtained at the Nouragues and with previous direct measurements (Lescure *et al.* 1983).

This study suggests that the neotropical forests have carbon storage properties that would deserve further scrutiny. The most important improvement over the present study would be to test the estimates of the regression equations with a larger dataset, especially in the large diametric classes, and to assess their sensitivity to environmental factors.

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