

BIOMASS VARIABILITY IN TROPICAL AMERICAN LOWLAND RAINFORESTS

VARIABILIDAD DE LA BIOMASA EN SELVAS TROPICALES AMERICANAS DE BAJA ALTITUD

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ABSTRACT

Tropical forest accumulates one of the largest biomasses among terrestrial ecosystems, however its precise amount and patterns of spatial variation are still imperfectly known. We discuss these issues on the basis of available data on the most widespread type of tropical American lowland rainforest (*terra firme* forest), considering the estimates of live tree aboveground biomass (LTAB) and total aboveground biomass (TAGB), in old-growth stands in different regions, and suggest probable sources of their broad variation. Methodological shortcomings arising from sampling design and intensity, size of sample unit, and allometric equations used to calculate biomass from field data are firstly considered. TAGB estimates based on 0.25 to one hectare plots ranged throughout the region from 160 to 435 Mg ha⁻¹, while estimates of LTAB range from 167 to 419 Mg ha⁻¹. With smaller plots, the range extends from 115 to 864 Mg ha⁻¹. Structural differences concerning biomass distribution among two other life-forms: palms and woody lianas, and its allocation among plant structures, also show broad variation, contributing to the richness and variety of rainforest types. Amounts and patterns of vertical variability of root biomass are still much less known, and the scarcity of field data makes difficult to disclose either general patterns or determining factors. The available data suggest that belowground biomass reaches at least about 20% of the aboveground counterpart. Distribution of fine roots illustrates the contrasted patterns and show how they are exploiting different soil horizons. Conclusions stress the large variability in structural features among tropical American lowland rainforests. Apart from variation due to methodological procedures, there are real differences in biomass among old-growth forest types, which are evident at all spatial scales, from the single plot to the whole area of this biome.

Key words: aboveground biomass, tree biomass, Amazonia, forest structure, root biomass

RESUMEN

Las selvas de baja altitud presentan una de las mayores biomásas entre los ecosistemas continentales, sin embargo la cantidad precisa y sus escalas y patrones de variación espacial permanecen aun imperfectamente conocidos. Discutimos estos puntos en base a los datos disponibles para bosques maduros en América tropical (bosques de *terra firme*), considerando tanto estimados de biomasa aérea de árboles vivos (LTAB) como de biomasa aérea total (TAGB), así como algunos datos de biomasa subterránea en diferentes regiones. En primer lugar tomamos en cuenta las limitaciones metodológicas que surgen del diseño y la intensidad de muestreo, del tamaño de la unidad de muestreo, y de las ecuaciones alométricas que se utilizan para calcular la biomasa a partir de los datos de campo. Los estimados conocidos indican que la LTAB en parcelas de 0,25 a una hectárea cubren un rango de 167 a 419 Mg ha⁻¹, los de TAGB de 160 a 435 Mg ha⁻¹, mientras que con parcelas menores los valores extremos son 115 y 864 Mg ha⁻¹. La contribución a la biomasa aérea de palmas y lianas, también muestra grandes diferencias entre sitios. Igualmente, la representación de árboles pequeños, medianos y grandes en el total de la biomasa aérea, difiere ampliamente a lo largo de estas selvas. La distribución de la biomasa aérea entre diferentes estructuras contribuye asimismo a la riqueza y variedad de estos ecosistemas. Las cantidades y los patrones de variación vertical de la biomasa radical son aun menos conocidos, de modo que con los pocos datos disponibles se dificulta incluso señalar tendencias generales. Estos datos indican

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que la biomasa subterránea alcanza alrededor del 20% de la biomasa aérea. Las conclusiones enfatizan la gran variabilidad en características estructurales de las selvas americanas. Aparte de la variación debida a diferentes procedimientos metodológicos, existe una variación real en biomasa entre selvas maduras, evidente a diferentes escalas espaciales, desde la parcela hasta el conjunto del bioma. Se destaca la idea de que la variación es parte esencial de la estructura del sistema y que precisamente a través del análisis de la misma se podrán conocer mejor los determinantes ecológicos y la dinámica de las selvas tropicales.

Palabras clave: biomasa aérea, biomasa arbórea, Amazonia, estructura del bosque, biomasa radical

INTRODUCTION

The quantification of basic structural and functional features of tropical rainforests steadily improved during the last two decades. Up to the 1980s, carbon stocks, gains and losses, had been studied in a few sites (for general overviews see UNESCO 1978, Golley 1983), but afterwards the interest in biomass, its distribution in above- and belowground structures, and other forest aspects relevant for furthering the knowledge on carbon dynamics and nutrient cycling, proceeded rather rapidly although unevenly from a bio-geographical viewpoint. In the Amazonian – Guianan humid forests the knowledge on carbon stocks is advancing at increasing rates, surely because the huge area these ecosystems occupy, the high rates of deforestation during the last decades, and the ecological risks implied in the degradation of primary forests or in their conversion to croplands and pastures. Among the undesirable consequences of deforestation outstands the efflux of CO₂ from the vegetation and soil sinks to the atmosphere and its effects on global warming. The knowledge on structural aspects, carbon stocks and productive processes in other tropical American lowland humid forests, progressed much more slowly. Apart from two well known protected areas: Barro Colorado Island in Panamá and La Selva in Costa Rica, these ecosystem aspects have been scarcely dealt with in the Brazilian Atlantic rainforests, the Chocó forests in Colombia, or the Central American formations from Nicaragua to southern México.

Since many large forest formations are rapidly disappearing due to land use intensification and increased population and socio-economic pressures, such studies are urgently needed (Sarmiento 2000). Thus in the case of the Brazilian Mata Atlântica, from more than one million km² of its original area, less than 5 % still remained at the beginning of the 21st century (Dean 1995, SOS Mata Atlântica 1999). Furthermore, the numerous isolated fragments existing today, surrounded by pastures

and croplands, within a densely populated area, have been heavily degraded by logging, firewood production and other extractive activities (Agarez 2001). The fate of the Amazonian forests at the long run does not seem to be very promising either. Although their large extension precludes their short-term disappearance, in the other countries of the Amazonian Basin, with the outstanding exception of Venezuela, a fragmented landscape starts to be dominant, where the former continuity of the forest cover has vanished and the small forest fragments become increasingly degraded (Laurance and Bierregaard 1997, Laurance 1998).

Despite the steady progress in the knowledge of tropical American rainforests, a large majority of the studies in the last years considered them in the context of the global carbon cycle. In consequence, they dealt with those aspects more closely related to CO₂ emissions, like tree aboveground biomass in primary and secondary systems, the fate after burning of the carbon accumulated in the different forest structures, as well as the dynamics of carbon in the soil (Cerri *et al.* 1991, 2000, Fearnside *et al.* 1993, Kauffman *et al.* 1988, 1995, Graça *et al.* 1999). But an approach focused on the structure and functioning of the forest ecosystem has, at the most, been subsidiary to those primary interests. Our objectives in this review are more akin to this last context, therefore we will consider biomass amount and distribution as basic features of forest ecosystems, and we will give more emphasis to the diversity of estimates than to the search for representative averages.

We start discussing the effects of methodological procedures and habitat heterogeneity on the estimates of various carbon pools, to follow with an overview of the data on forest above and below-ground biomass. Based on the analysis and comparison of the available information we point out the high structural variability among old-growth tropical rain forests, showing a three-fold variation in tree, and total above- and below-ground biomass, as well as in

the relative contribution of other life forms. We review data on above and below-ground forest biomass, and when opportune we refer to structural data from which biomass estimates are obtained. The relevant literature on these issues in neotropical forests is already impressive. In order to make ecologically meaningful comparisons among regions, sites and plots, we have restricted ourselves to just one type of tropical lowland rainforest, the so-called *terra firme* forests in Brazilian Amazonia, the most widespread and best known tropical American humid forest ecosystem. By *terra firme* forest we refer to an evergreen forest ecosystem on fairly well drained upland soils, mostly ultisols and oxisols, less often andosols, without significant periods of either soil water deficiency or excess. Therefore in this review we do not take into account other extensive rainforest types, such as the Amazonian *caatingas* on white sands, the littoral *restingas* and mangroves, the *varzeas*, *igapós*, and related flood plain systems, as well as the montane and semideciduous formations (Prance 1985). However, within *terra firme* forests, different types have been recognized, like dense, open, ecotone, palm and bamboo forests, which correspond to the climatic, geomorphic and soil variability inherent to a so widespread ecosystem type.

METHODOLOGICAL SHORTCOMINGS

To start with, we want to discuss the influence of methodological procedures on the estimation of biomass amount, considering firstly what is it measured?, and secondly, how is it measured? including the equations most generally used to estimate the different fractions of the forest total biomass. The basic field measurements to quantify above-ground forest mass are stem diameter at breast height (DBH) and total height of every tree, palm, and woody liana in a sample plot. Data from forest plots generally refer to trees over a minimum size or stem diameter, being a DBH ≥ 10 cm the lower limit most frequently taken in ecological studies, while a DBH ≥ 30 -35 cm, is generally used in forestry inventories. Thus, the smaller trees, saplings and seedlings, not always enter into these estimates, and palms and lianas are never taken into account in wood inventories. Other life forms widely occurring in tropical forests, like vascular epiphytes, stem-less palms, tree-ferns, bamboo and other large tree-like monocots, shrubs and herbs, requiring different sampling procedures and

equations, have been neglected in most studies. The same may be said about standing dead trees which have barely been taken into account. Consequently, rather few quantifications of total aboveground mass (TAGB) are currently available.

The situation is still more complicated with estimates of total below-ground biomass (TBGB). Most often estimates just refer to its most active, and more easy to estimate fraction, fine roots (variously defined as being ≥ 10 to ≥ 2 mm in diameter). Few estimates of the more passive coarse roots have been published, and still less for taproots, despite the fact they accumulate the largest proportion of carbon allocated to below-ground plant parts. Measurements of fine root biomass are generally limited to the uppermost soil layers where they are most abundant, while roots below one meter depth are normally ignored. Furthermore, most estimates do not distinguish live from dead roots, and consequently below-ground biomass really appears as a mixture of fractions which includes active, young roots, senescent roots, and dead but still little decomposed plant material.

Wood density may be another source of error since values averaging many species have to be used, and frequently they have been obtained in forests of an entirely different tree composition. For old-growth forests wood densities around 0.65 - 0.70 g cm⁻³ are generally used (Fearnside 1997, Muller-Landau 2004), but it has been shown that wood density have meaningful patterns of regional variation, being significantly higher in eastern and central than in western Amazonia (Baker *et al.* 2004). Being wood density dependent on tree composition this fact points out another interesting relationships between forest structure and floristic diversity. Finally, if biomass estimates are to be converted into carbon stocks, a 50% C content for the whole biomass may be an acceptable average. However, wood have a mean carbon content of 45 to 48 %, other plant structures, particularly the metabolically more active organs, like fine roots, young leaves, and flowers, do have smaller C contents, of about 40 to 45 %, while palm stems and leaves average 41 to 46 % carbon (Graça *et al.* 1999). Then, to get more accurate estimates of carbon content each fraction of the total biomass has to be taken into account.

Direct harvest is the most straightforward way to measure tree weight. However, it is far from being a practical procedure and it has been applied just to quite small plots (Klinge *et al.* 1975,

Fearnside *et al.* 1999, Graça *et al.* 1999). Therefore, some indirect methods based on more easily measured tree and plot characteristics are usually used to get estimates with a variable degree of accuracy. The biomass of a tree depends on its basal area, height, wood density and crown shape. These structural parameters, together with the density of trees and the tree-size distribution in forest plots, allow the estimation of wood volume and total tree biomass using allometric formulae. In principle, these formulae obtained from measurements of a few trees and statistical correlations among various combinations of stem diameter, tree height, density, wood volume and biomass, are just valid for a given species in a precise habitat, but due to the amazing diversity of tree species in tropical forests, all them are considered together, and very often plot to plot differences among forest ecosystems in tree architecture are also ignored.

Different equations obviously result in divergent estimates. Thus, by applying to the same field data from an eastern Amazonian forest plot, 14 formulae developed for typical vegetation of the Amazon region, a fresh-weight range from 85 to 709 Mg ha⁻¹ was obtained, while harvesting and weighting all trees with DBH ≥ 10 cm (127 trees in a 0.2-ha plot), gave a total weight of 170 Mg ha⁻¹ (Araujo *et al.* 1999). It is interesting to remark that among the 14 equations, just five gave an acceptable estimate of the real amount, only one of these five considered tree height, and none was obtained from *in situ* data. The selection of an equation always implies a certain bias given that it resulted from the destructive sampling of a few trees, being thereafter applied to a whole forest stand (Overman *et al.* 1994, Araujo *et al.* 1999, Nelson *et al.* 1999, Clark and Clark 2000, Chambers *et al.* 2001). Among other differences, the various equations give different weight to the largest trees, making estimates heavily dependent on their number (Clark and Clark 1995, Chambers *et al.* 1998). Thus, a tree 138 cm DBH, the largest destructively measured in the study, weighted 30,060 kg, whereas according to 14 different equations, the weight of such a tree ranged from 20,985 to 134,468 kg (Araujo *et al.* 1999). In Rondonia where 474 trees ≥ 10 cm DBH were measured in one 1-ha plot, the 15 largest trees accumulated 142 Mg ha⁻¹, half the total LTAB, and the three largest individuals accumulated 23% of the plot LTAB (Brown *et al.* 1995). Five equations, all based exclusively on

DBH, give wide differences in tree weight, particularly in the case of very large trees (Figure 1). It may be realized therefore that large trees play a key role in the amount of rainforest biomass and how the logging of a few commercially valuable trees leads to dramatic decreases.

Basal area (m²/m²), a frequently calculated parameter in forest inventories, is certainly related to above-ground biomass, as may be realized from the fact that above-ground biomass is calculated out of the same data source basal area is: the DBH of all individual trees in the stand. However, their relationship is uncertain since it is impossible to disclose, from basal area figures, to what extent they depend the most on size-class distribution or on tree density. On the other hand, above-ground biomass has been shown to heavily depend on size-class frequency, while its relation with tree-density is remarkable weaker (see, for instance, Table 1) Therefore, applying allometric equations to all individual-tree diameters (height and wood density may also be used as descriptors) to later sum-up the results, seems to be the unavoidable way to go. In addition, there is a close relationship between LTAB and wood volume. For commercial purposes the latter commonly appears in forest inventories and, regarded as a constant proportion of the former, may be used as a LTAB predictor. However, which the exact proportion wood amounts in a forest stand depends very much on forest architecture and wood density. In consequence, the relationship between LTAB and wood volume renders very idiosyncratic formulas (see, for instance, Table 5 on proportion of stem weight in different rainforests).

Three sources of data may be used in biomass studies. Firstly, large forest inventories directed to get estimates of the actual amount of wood in extensive forest tracts. Usually these inventories give for each commercial tree (DBH ≥ 30 to 35 cm), its species, DBH and height. A second source of field data are small plots, in the order of 0.1 ha to a few hectares, inventoried with different scientific aims, such as studies on forest diversity, structure, functioning and dynamics. Often, besides the mass of live trees (LTAB), other components of the forest vegetation are also taken into account in these plots. Finally, a third kind of methodology combines field data with remote sense information, in order to scale up from small, intensively studied plots, to landscapes and whole regions. Although highly promising, most of these remote sense

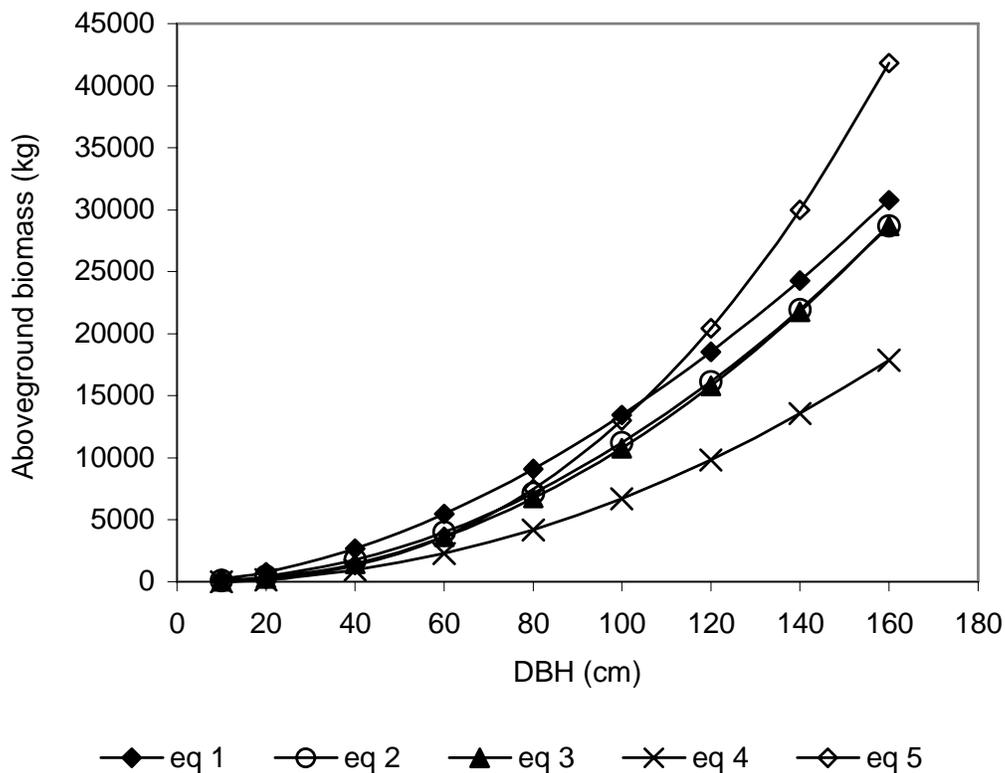


Figure 1. Aboveground tree biomass (B , kg), as a function of DBH (cm), according to five different allometric formulae which have been used in estimates of Amazonian forests biomass. 1) $B = 4.06 (\text{DBH})^{1.76}$ (Araujo *et al.* 1999); 2) $B = 1.12 (\text{DBH})^2$ (Overman *et al.* 1994); 3) $B = 38.49 - 11.79 \text{DBH} + 1.193 (\text{DBH})^2$ (Brown *et al.* 1989); 4) $B = 21.297 - 6.953 \text{DBH} + 0.74 (\text{DBH})^2$ (Brown *et al.* 1989); 5) $\ln B = -1.966 + 1.242 \ln (\text{DBH})^2$ (Overman *et al.* 1994). Formulae taking only into account DBH were considered in this comparison.

methods still are at an experimental stage (Nelson *et al.* 2000, Boyd *et al.* 1999, Steiniger 2000, Foody *et al.* 2001, 2003, Santos *et al.* 2003, Hirata *et al.* 2005).

Small plots have sharp limitations in representativeness, depending on their size, number, and location. Plot size and numbers usually result from a compromise between effort and tolerable errors, while plot location is often subjectively biased. The “majestic-forest bias”, consisting in the selection of the “best” forest stands, does not seem to be uncommon (Phillips *et al.* 2002a). The dependence of estimates on sampling design has been clearly shown in La Selva, Costa Rica (Clark and Clark 2000). Three different data sets from the same 573-ha old-growth forest were used to obtain the forest biomass applying in the three cases

the same equation. One set came from 1170 circular 0.01-ha plots, regularly distributed throughout the area at the corners of a 20 x 20 m grid. The second set came from three subjectively sited plots of 4, 4, and 4.4 ha. The third from 18 0.5-ha plots subjectively located in order to sample the existing soil variation. Mean aboveground tree biomass amounted to 182.9 ± 8.4 , 160.5 ± 4.2 , and $186.1 \pm 6.6 \text{ Mg ha}^{-1}$, respectively (Table 1). That is, estimates differed by 16 % among the three data sets. Sampling design, together with the size and form of each sampling unit (the sampled areas were roughly similar) surely accounts for these differences. When the basic data have been taken with different sampling designs and converted into biomass using different equations, results will be hardly comparable.

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Plot size also has a decisive weight in the resulting estimates. Very small plots, below 0.1 ha or so, result in widely divergent estimates within the same apparently homogeneous forest stand, mainly due to the heterogeneity in forest biomass produced by gap dynamics that lead to small patches with divergent biomass accumulation. As plot size increases these differences tend to disappear since the estimates averages the biomass of small patches.

Quantifications of below-ground biomass are heavily influenced by sampling procedures (auger or pits), sampling design and intensity, the separation of roots from the soil (washing and sieving), as well as by the decision on when to sample (Böhm 1979, Aber *et al.* 1985, Lauenroth 2000). Normally root data obtained with augers are not at all comparable to data obtained from soil pits. Methodological shortcomings become still more important in the case of coarse roots, because of the large spatial heterogeneity of this stock and the more rudimentary methodologies at hand.

Total stocks

Above-ground biomass

TAGB represents the largest organic carbon pool in mature tropical forest ecosystems, followed by the soil C pool, and then by the C stock in the belowground biomass. Despite its importance, TAGB continues to be one poorly quantified stock.

This is firstly due to the inherent methodological difficulties in quantifying the large and heterogeneous biomass of species-rich forests; secondly because of its wide variability within and between forest communities; and thirdly, due to the dramatic changes in biomass induced by gap dynamics and by successions after natural or human-induced disturbances.

At the scale of the whole Brazilian Amazonia data sets from forest inventories were used to provide biomass figures, mainly for purposes of greenhouse calculations. The large number of plots over areas of thousands of ha, seemed to be more representative at this regional scale than scattered small plots from which more detailed measurements are generally obtained. The mean LTAB of trees ≥ 10 cm DBH, in dense forests, was estimated in 298 Mg ha⁻¹, using a FAO data set, and in 227 ± 24 Mg ha⁻¹, using a RADAMBRASIL data set (Brown and Lugo 1992). In order to obtain a mean value for TAGB of all Amazonian forests, through the application of different adjustments, a figure of 290 Mg ha⁻¹ was obtained as a best estimate of the average aboveground biomass, live plus dead, of trees, woody lianas and palms, in dense *terra firme* forests (Fearnside 1992). More recently, a thorough review of forest biomass amounts concluded that estimates of the carbon sink in Brazilian Amazonian forests vary by more than a factor of two, and that they even disagree as to which are the regions of

Table 1. Estimates (mean \pm standard error, SD: standard deviation) of number of trees ≥ 10 cm dbh (N) and LTAB, in a 573-ha stand of old-growth forest, at La Selva, Costa Rica. Estimates were obtained by three different data sets, applying the same equation: $B \text{ (kg)} = 21.297 - 6.953 D + 0.74 D^2$. Data from Clark and Clark 2000.

Plot size (ha)	Number of		Area			
	plots	sampled	N	N	LTAB	LTAB
		(ha)	(Stems ha ⁻¹)	(SD)	(Mg ha ⁻¹)	(SD)
4, 4, 4.4	3	12.4	462 \pm 47	81	182.9 \pm 8.4	14.5
0.5	18	9	504 \pm 22	93	160.5 \pm 6.6	28
0.01	1170	11.7	448 \pm 6	205	186 \pm 6.6	225.7

high and low biomass (Houghton *et al.* 2001). In any case, all these means make sense in the context of the global carbon cycle and the greenhouse effect, as broad regional figures, but they do not say much about the structure and carbon stocks of any forest stand in particular.

Field measures of forest structure in small plots and the application of allometric formulae to estimate biomass in neotropical rainforests, steadily multiplied from the 1980s. Most of these data comes from the Brazilian Amazonia., and a few from some other sites in Colombia, Venezuela, Perú, French Guiana, Panamá and Costa Rica. Selected estimates of LTAB, either of trees over 10 cm DBH, or of all live trees, based on inventories of small plots, illustrate about the broad range of forest biomass which has been reported, from 167 to 419 Mg ha⁻¹. Estimates of TAGB in turn, extend from 160 to 435 Mg ha⁻¹ (Table 2). In this dataset we have only take into account biomass estimates of old-growth forest stands, since obviously logged stands or succession stages reach lesser amounts.

Surveys of many plots over rather extensive areas covering heterogeneous landscapes, or of many quite small plots within a given stand, also gave a wide spectrum of estimates, from 115 to 864 Mg.ha⁻¹ (Table 3). The most comprehensive estimates of TAGB and its components in Central Amazonia were obtained by sampling random plots of undisturbed, dense primary *terra firme* forest over an area of 100,000 ha, on oxisols (Laurance *et al.* 1999, Nascimento and Laurance 2002). In the first study, the biomass of live trees ≥ 10 cm DBH, was estimated in 65 1-ha plots, adding to these amounts an additional 12 % to account for the smaller trees (following Jordan and Uhl 1978). LTAB of all trees ranged from 231 to 492 Mg ha⁻¹, with a mean and standard error of 356 ± 47.0 Mg ha⁻¹ (Table 3). In the second paper, 20 of the 65 1-ha plots were used in a more detailed estimate of TAGB, now considering all life forms and the dead material too (Nascimento and Laurance 2002). TAGB ranged from 305 to 432 Mg ha⁻¹, with a mean of 398 ± 30 Mg ha⁻¹ (Table 3). The most comprehensive data on TAGB in Rondonia (south western Brazilian Amazonia) were obtained from 20 0.79-ha sites, which included dense, open and ecotone, undisturbed *terra firme* forests, on different land forms and soil types (Cummings *et al.* 2002). The mean amounted to 341 ± 14 Mg ha⁻¹, with a range from 287 to 534 Mg ha⁻¹ (Table 3) Although TAGB did not significantly differ among

the three types of forest, the aboveground biomass of trees over 10 cm DBH was significantly different in close (307 ± 33 Mg ha⁻¹) and in open forests (238 ± 8 Mg ha⁻¹).

In eastern Amazonia (Pará), LATB in mature forests, including woody lianas, reached 314 Mg ha⁻¹, of which 43 Mg ha⁻¹ (14 %) was lianas (Gerwing and Lopes Farias 2000). In the Tapajoz National Forest (Pará), estimates of woody biomass in thirteen 0.25-ha plots ranged from 241 to 864 Mg ha⁻¹ with a mean of 419 Mg ha⁻¹ (Williams *et al.* 2002) (Table 3). This is the widest range reported for a given area in the whole Amazon region, and it seems to be due both to the small size of the sampling plots and to a real landscape heterogeneity, with a large variation in soil features among sites and plots.

In the Vaupés Department, one of the less known areas of the Colombian Amazonia, TAGB and LTAB were estimated in three 1-ha plots, on very poor oxisols (Ballesteros 1996) In two of them, rather low figures were obtained (167-173 Mg ha⁻¹), but in the third one TAGB amounted to 260 Mg.ha⁻¹ (Table 2). In the Venezuelan Amazonia, the mean of four plots gave a LTAB of 234 Mg ha⁻¹, with a range from 212 to 246 Mg ha⁻¹ (Table 2).

Outside Amazonia, in 22 1-ha plots of mature, apparently homogeneous upland forest at the Les Nouragues Station, French Guiana, LTAB (trees ≥ 10 cm DBH) gave a mean of 309 ± 32 Mg ha⁻¹ (95% confidence interval, Chave *et al.* 2001). In 50 ha of old-growth rainforest in Barro Colorado Island, Panamá, TAGB (trees ≥ 1 cm DBH plus woody lianas) gave a mean of 281 ± 20 Mg ha⁻¹ (Chave *et al.* 2003), Finally, at La Selva Station, Costa Rica, we already mentioned the wide divergence in TAGB estimates by using different methods (Table 1). All these data show the extension of biomass variability in rather small rainforest stands that appear as homogeneous under physiognomic and floristic criteria.

All these data strongly suggest that beyond the effect of field procedures and allometric formulae, there undoubtedly are real biomass differences among tropical American rainforest sites. In any particular area, and using similar procedures, large differences among plots do appear, with means showing wide confidence intervals. LATB shows a seven-fold amplitude throughout the Americas (Tables 2 and 3). Structural differences, including biomass amounts, have been evidenced at least at five spatial scales.

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Table 2. Estimates of total aboveground biomass (TAGB, live trees + palms + lianas) or live tree aboveground biomass (LTAB), in old-growth tropical American lowland (*terra firme*) rainforests.

Reference	Country, State or site	TAGB (Mg ha ⁻¹)	Plot size (ha)	Area sampl. (ha)
Clark & Clark 2000	Costa Rica, La Selva	160 ± 4.2	0.5	9
		182.9 ± 8.4	4	12.4
		186.1	0.01	11.7
Higuchi <i>et al.</i> 1994	Brazil, Pará	185.3 ± 6.6	0.4	22
	Brazil, Roraima	227.9 ± 6.4	0.4	22
Ballesteros 1996	Colombia, Vaupés	174	1	1
		178	1	1
		268	1	1
Faber-Langendoen & Gentry 1991	Colombia, Chocó	195	1.5	1.5
DeWalt & Chave 2004	Panamá, Barro Colorado	214.4 ± 46.4	0.05	0.3
	Costa Rica, La Selva	234.0 ± 60.9	0.05	0.3
McWilliam <i>et al.</i> 1993	Brazil, Amazonas	265*	0.04	0.04
Fearnside <i>et al.</i> 1999	Brazil, Pará	262.5*	0.006	0.216
DeWalt & Chave 2004	Brazil, Amazonas	269.2 ± 45.5	0.05	0.3
Chave <i>et al.</i> 2003	Panamá, Barro Colorado	281 ± 20	0.25	50
Kauffman <i>et al.</i> 1995	Brazil, Rondonia	260 ± 20		a few ha
		337 ± 36		a few ha
	Brazil, Pará	277 ± 36		
		413 ± 71		
Keller <i>et al.</i> 2001	Brazil, Pará	309	100	392
Graça <i>et al.</i> 1999	Brazil, Rondonia	311 ± 49*	0.006	0.072
Hughes <i>et al.</i> 2001	Brazil, Rondonia	311		1.5
Gerwin & Lopes 2000	Brazil, Pará	314		
Salamao <i>et al.</i> 1996	Brazil, Pará	320	3	3
Uhl <i>et al.</i> 1988	Brazil, Pará	348	0.063	1.25
Overman <i>et al.</i> 1990	Colombia, Caquetá	351		2.5
Kauffman <i>et al.</i> 1995	Brazil, Rondonia	361		a few ha
Klinge <i>et al.</i> 1975	Brazil, Amazonas	380		0.215
Nascimento & Laurance 2002	Brazil, Amazonas	397.7 ± 30	1	20

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Continuación Tabla 2.

Reference	Country, State or site	LTAB (Mg ha ⁻¹)	Plot size (ha)	Area sampl. (ha)
DeWalt & Chave 2004	Perú, Manu National Park	392.1 ± 96.9	0.05	0.3
Guild <i>et al.</i> 1998	Brazil, Rondonia	399 ± 45		1.5
Kauffman <i>et al.</i> 1995	Brazil, Pará	435		a few ha
Ballesteros 1996	Colombia, Vaupés	167	1	1
		173	1	1
		260	1	1
Saldarriaga <i>et al.</i> 1988	Venezuela, Amazonas	234 ± 22	0.03	0.36
Cochrane <i>et al.</i> 1999	Brazil, Pará	242		
Nascimento & Laurance 2002	Brazil, Amazonas	325.7 ± 24.6	1	20
Chave <i>et al.</i> 2001	French Guiana, St Elie	333 ± 29	0.78	0.78
		345 ± 27	1	1
Cummings <i>et al.</i> 2002	Brazil, Rondonia, open for. ecotone forest dense forest	312.8 ± 6.7	0.79	6.32
		350.2 ± 26.2	0.79	5.53
		376.6 ± 33.4	0.79	3.16
Keller <i>et al.</i> 2001	Brazil, Pará	264	100	392
Nepstad 1989	Brazil, Pará	264		5
Salamao <i>et al.</i> 1996	Brazil, Pará	266	3	3
Gerwin & Lopes 2000	Brazil, Pará	271		
Brown <i>et al.</i> 1995	Brazil, Rondonia, open for.	285	1	1
Uhl <i>et al.</i> 1988	Brazil, Pará	306	0.063	1.25
Chave <i>et al.</i> 2001	French Guiana, Nouragues	309 ± 32	1	22
Chambers <i>et al.</i> 2003	Brazil, Amazonas	324.1 ± 17	1	21
Brown <i>et al.</i> 1992	Brazil, Acre	320	0.5	0.5
Lescure <i>et al.</i> 1983	French Guiana, St Elie	323		
Jordan & Uhl 1978	Venezuela, Amazonas	335	0.5 - 1	1
Laurance <i>et al.</i> 1999	Brazil, Amazonas	356 ± 47	1	65
Delaney <i>et al.</i> 1997	Venezuela, Bolívar	398	0.25	1
Alves <i>et al.</i> 1997	Brazil, Rondonia	409	0.01	0.2
Williams <i>et al.</i> 2002	Brazil, Pará, Tapajoz N.F.	419	0.25	16.25

* destructive sampling

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Table 3. Aboveground biomass estimates in tropical American lowland rainforests. Estimates from several plots in the same region. Minimum–mean–maximum in Mg ha⁻¹.

Reference	Country, State	Biomass	Plot size (ha)	Plot number
Higuchi <i>et al.</i> 1994	Brazil, Pará	115-186-636	0.4	57
	Brazil, Pará	241-419-864	0.25	13
Laurance <i>et al.</i> 1999	Brazil, Amazonas	231-356-492	1	65
Chambers <i>et al.</i> 2001	Brazil, Amazonas	232-324-391	1	21
Higuchi <i>et al.</i> 1994	Brazil, Roraima	185-228-643	0.4	57
Chave <i>et al.</i> 2001	French Guiana,	230-301-416	1	10
	French Guiana,	250-317-394	1	12
Cummings <i>et al.</i> 2002	Brazil, Roraima	287-341-534	0.79	20
Nascimento & Laurance 2002	Brazil, Amazonas	305-398-432	1	20
Chave <i>et al.</i> 2003	Panamá, Barro Colorado	180-274-340	0.25	200
Clark & Clark 2000	Costa Rica, La Selva	149-160-167	0.5	18
Total range		115-864	0.25 to 1	493

Firstly, at the single-plot scale. Thus in one hectare of Amazonian forest in Rondonia, the alive aboveground biomass estimated in 40 sampling units of 250 m², ranged from less than 100 to more than 1000 Mg ha⁻¹ (Brown *et al.* 1995). Secondly, at the landscape scale, in the order of a few hundred of ha and comprising different habitats, like in the case of La Selva, Costa Rica (see Table 1). Third, at the regional scale, of thousands of km² (Laurance *et al.* 1999, Nascimento and Laurance 2002, Cummings *et al.* 2002, Williams *et al.* 2002) and fourth at the level of a formation, such as the Amazonian *terra firme* rainforest, at these two scales environmental heterogeneity must be playing a most important role (Laurance *et al.* 1999). And finally at the largest scale embracing the whole evergreen, lowland rainforest area, from Costa Rica and Panamá to Perú and Central Brazil, where other

factors besides the actual environment have to be considered, related to paleogeography and biogeographical history. Just restricting our attention to means leads to ignore large differences which could be due to habitat conditions, natural dynamics, environmental history or stochastic reasons, hiding what seems to be a most general fact, the large structural heterogeneity of these ecosystems at all spatial scales.

The biomass share of different life-forms

The share of the total forest biomass of different life-forms provides some insight on forest structure, though unfortunately it has only been quantified in a few sites and just for two peculiar forms in tropical forests: palms and woody lianas. The contribution of woody lianas has been poorly

estimated because of the paucity of field data to obtain allometric equations. The diversity, abundance, and biomass of woody lianas widely vary across Tropical American rainforests, ranging from less than 1% to 13.7 % of the forest aboveground biomass (Table 4). Woody lianas seem to attain a maximum diversity and abundance in young secondary forests, but their basal area and biomass remain constant across stand ages from 20-40 year-old stands to mature forests (Dewalt *et al.* 2000). In western Amazonia, large lianas are becoming increasingly dominant during the last 20 years of the twentieth century (Phillips *et al.* 2002 b). Liana abundance greatly increases in forest within 100 m of the edge of fragments but liana aboveground biomass increases only slightly (Laurance *et al.* 2001). Anyway, despite their usually small biomass as compared with trees, the share of liana leaves in the total leaf biomass of a rainforest is so important that they may be responsible for up to 40% of leaf productivity (Schnitzer and Bongers 2002, Phillips *et al.* 2002 b).

Palms also largely vary in abundance, diversity and biomass across neotropical rainforests (Table 4), from only 0.3 % of the live aboveground biomass in Central Amazonia (Klinge *et al.* 1975) up to 11 % in the ecotone forest in Rondonia (Cummings *et al.* 2002). We must notice however, that in spite

of their relatively low biomass, palms significantly contribute to total leaf biomass and LAI, since the allocation to leaves in palms (around 15% in central Amazonia, Klinge 1973 b) is much higher than in trees of similar height,

Epiphytes may be conspicuous components of tropical forests, but their biomass has rarely been estimated, except in some montane forests where this life-form reaches its largest diversity and weight. Thus, In a moist subtropical forest in Taiwan, epiphytes, mostly ferns and bryophytes, reached 3.36 Mg ha⁻¹, less than 2% of the TAGB, but their ecological role is evidenced by their contribution to total leaf biomass (Hsu *et al.* 2002).

Variability in tree size distribution among old-growth tropical forests

Striking differences may be seen when comparing tree size distribution in rainforest types (Figure 2). In the eight forests represented in Figure 2, small trees (1-10 cm DBH) contribute from 3 % to 6% of the total tree biomass, differing from the estimated 12 % found by Jordan and Uhl, 1978, and later used by Laurance *et al.* 1999. The contribution of the 10-30 cm DBH class size also varies across the different forests from 16% to 33 % of the total aboveground tree biomass, that of the 30-70 cm DBH class varies from 31 % to 52%

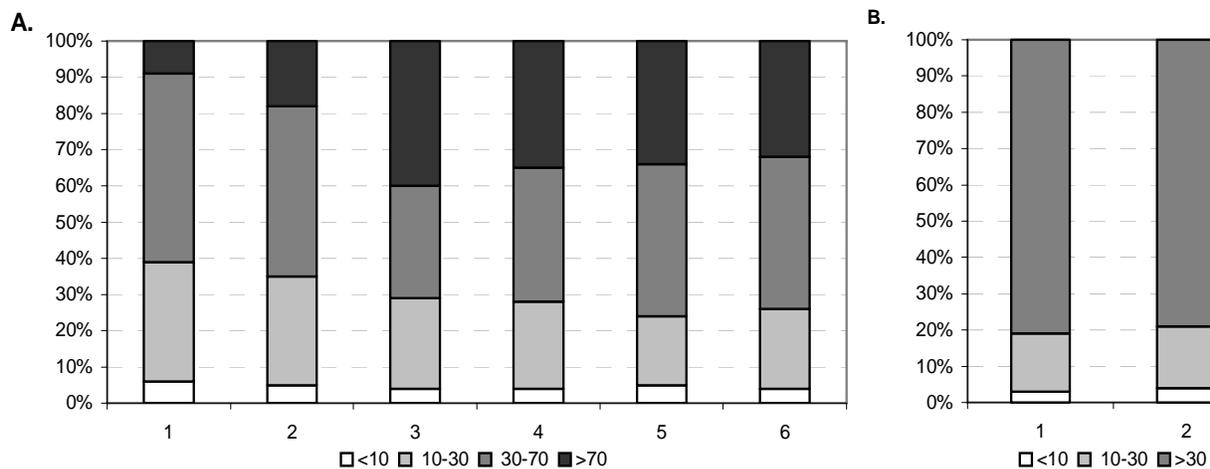


Figure 2. Per cent of LTAB shared by different tree size classes (DBH cm), in selected neotropical rainforests. A.1. Central Amazonia, Brazil (Nascimento and Laurance 2002); 2., 3. and 4. Rondonia, Brazil, open, ecotone and dense forests, respectively (Cummings *et al.* 2002); 5. Les Nouragues, French Guiana (Chave *et al.* 2001); 6. Barro Colorado, Panamá (Chave *et al.* 2003). B.1. Cocha Cashu, Perú; 2. La Selva, Costa Rica. 1-2 (DeWalt and Chave 2004).

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Table 4. Aboveground biomass of woody lianas (Mg ha^{-1}) and its share of forest aboveground biomass (%), in some tropical American rainforests.

Reference	Country, State	Biomass	Share %
Cummings <i>et al.</i> 2002	Brazil, Rondonia	0.5	0.2
DeWalt & Chave 2004	Costa Rica, La Selva	8.0 ± 8.0	3.4
Nascimento & Laurance 2002	Brazil, Amazonas	8.3*	2.1
DeWalt & Chave 2004	Brazil, Amazonas	11.9 ± 6.2	4.4
	Perú, Manu National Park	15.0 ± 10.6	3.8
Putz 1983	Venezuela, Amazonas	15.7	4.5
DeWalt & Chave 2004	Panamá, Barro Colorado	17.2 ± 5.3	8.0
Gerwin & Lopes F. 2000	Brazil, Pará	43	13.7

* Range in 20 1-ha plots: $4.63 - 13.67 \text{ Mg ha}^{-1}$

in five forests, and the largest trees contribute from 9% to 40% in the same five forests. We may notice therefore, that even considering mature forests, the share of different tree size classes in the total tree biomass may significantly differ from site to site and across regions.

Variability in biomass allocation among forest types

A sharp contrast also appears when comparing tree carbon allocation in different sites and regions. Thus, the distribution of biomass among boles and branches are totally different in three Amazon regions (Table 5), suggesting deep architectural contrasts among these forest communities. When biomass allocation in all tree species in one plot were analysed, large differences did appear. Thus in eastern Amazonia, the proportion of above-ground tree weight allocated to crowns ranged from 7 % to 86 % in 127 individuals ($\text{DBH} \geq 10 \text{ cm}$) of 50 tree species (Araujo *et al.* 1999), suggesting that carbon allocation at the ecosystem level sharply depends on floristic composition having therefore a large variability at the landscape scale. But in any case, most of the TAGB is wood, since besides boles

and branches of live and dead trees, the downed wood debris are also quantitatively important, reaching from 5 % to 10 % of the TAGB (Kauffman *et al.* 1988, 1995, Cummings *et al.* 2002). Data from other Amazonian forests confirm the absolute preponderance of wood. In various sites in Pará, the carbon allocated to wood amounted to 95 % of the TAGB carbon (Kauffman *et al.* 1995, Fearnside *et al.* 1999).

The proportion of the aboveground biomass allocated to leaves decreases with tree size, from about 8 % in small trees to about 2% in the largest ones (Brown *et al.* 1995), while it remains more or less constant with forest age across secondary succession. Leaf area index (LAI) behaves similarly, attaining 5 to 6 in mature forests (Saldarriaga *et al.* 1988, McWilliam *et al.* 1993). The relative decrease in leaf biomass with tree size seems to be a general fact in trees (Kozłowski *et al.* 1991). However, it is worth of notice how in mature tropical rain forests, the assimilatory biomass of canopy trees scarcely represents 2 % to 5 % of the total biomass, and a smaller proportion of the forest TAGB. This biomass provides the organic carbon necessary to build and maintain the remaining plant structures. In all other life forms

the ratio between the mass of assimilatory organs and the rest of the plant is substantially higher.

Below-ground biomass

Stocks and vertical distribution

Plant carbon allocated to underground structures and the share of roots of the total rainforest biomass are two poorly quantified properties. According to an overall review, the average root biomass of nine tropical evergreen forests, six of which in tropical America, was 49 Mg ha⁻¹, with a mean root/shoot ratio of 0.19 (Jackson *et al.* 1996). Applying this ratio to the amounts of TAGB previously discussed, the total belowground biomass (TBGB) in neotropical lowland rainforests, would range from about 40 to 80 Mg ha⁻¹.

Either the total root biomass or a fraction of it, have been quantified in a few tropical American rainforests (Table 6). Their broad variability is clearly evident (36 to 68 Mg ha⁻¹). This variability surely arises from the use of different field sampling procedures, the sampling to different depths, and a real variability among rainforest ecosystems. The amount of coarse roots is almost unknown. By excavating the root systems of 379 trees and 51 palms a broad root fresh weight of about 50 Mg ha⁻¹, was estimated, that is over 30 Mg ha⁻¹ dry weight, but this figure surely represents an underestimate of root matter since tap roots were not excavated (Klinge 1973 b). In the upper Río Negro, Venezuela, total root biomass (0-70 cm) of a *terra firme* forest amounted to 39 Mg ha⁻¹, 33 Mg ha⁻¹ (85 %) in the

0-30 cm soil layer, of which 13 Mg ha⁻¹ (33 % of the total root biomass), in the organic and A₁ (10 cm) horizons (Saldarriaga 1994).

The relationship between height of trees and the ratio of below-ground to above-ground biomass decreases exponentially, with low trees having a ratio around 0.4, decreasing in the highest trees to 0.05 (Klinge 1973 b). Therefore, we may attend that mature forests, having a high canopy, would allocate a smaller proportion of their carbon to below-ground structures.

Apparently, about 70 % of the underground biomass in tropical forests occurs in the uppermost 30 cm of the soil (Jackson *et al.* 1996). However, in most studies deeper layers have not been taken into account. There is some debate about the amount of carbon stored in deep roots in Amazonian forests, since fine roots were found to a depth of 18 m. Thus, fine root distribution in three sites in Pará, showed a fine root biomass from 1 to 6 m depth, of 2 to 3 Mg ha⁻¹ (Nepstad *et al.* 1994), pointing out how a non negligible proportion, from 10 % to 15% of the active below-ground biomass, occurs deep in the soil. Obviously, the amount of coarse roots in these deep layers, though it has not been quantified, must also be important.

Fine root mass and production have been related to soil characteristics (Gower 1987, Cavelier 1992, Silver *et al.* 2002). Carbon, nitrogen and CEC were significantly correlated with the vertical distribution of fine roots in a lowland rainforest in Panamá, while total nitrogen explained most of the variation in root biomass (Cavelier 1992). This high correlation open the possibility of predicting fine

Table 5. Per cent of the LTAB allocated to different tree structures, obtained by destructively sampled trees, in three Amazonian rainforests. 1: Eight trees, Rondonia, Brazil; 2: 315 trees, Central Amazonia, Brazil; 3: 126 trees, Rio Negro region, Amazonas, Venezuela.

Reference	Fine		Coarse	
	Leaves	branches	branches	Stem
1. Brown <i>et al.</i> 1995	4	7	14	74
2. Higuchi <i>et al.</i> 1998	1	11	30	58
3. Saldarriaga <i>et al.</i> 1988	5	11	34	50

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Table 6. Total root biomass (Mg ha⁻¹) and fine root biomass (g m⁻²), in selected tropical American lowland rainforests.

Total roots			
Reference	Country, State or site	Depth (cm)	Root biomass
Klinge 1973	Brazil, Amazonas	107	40*
Lescure <i>et al.</i> 1983	French Guiana, St Elie		42
Russell 1983	Brazil, Pará		60
Saldarriaga <i>et al.</i> 1988	Venezuela, Amazonas	70	39**
Nepstad <i>et al.</i> 1994	Brazil, Pará		35
Salamao <i>et al.</i> 1996	Brazil, Pará		68
Delaney <i>et al.</i> 1997	Venezuela, Bolívar	100	57
Silver <i>et al.</i> 2000	Brazil Pará	100	36-55***
Fine roots, less than 10 mm			
Klinge 1973	Brazil, Amazonas	107	843
Saldarriaga <i>et al.</i> 1988	Venezuela, Amazonas	10	740
	Venezuela, Amazonas	70	1760
Kindel 2001	Brazil, ES, Sooretama	12	705
	Brazil, ES, Linhares		559
Garay, unpublished	French Guina, Nouragues		548
	Brazil, ES, Linhares	15	750

* Less than 40 mm ** Less than 50 mm *** Sandy soil and clayed soil

root distribution from soil data. Soil texture seems to be one of the factors more closely related to fine root amount. Root carbon (0-100 cm) was significantly higher in sandy soils than in clay soils (21 ± 7 vs 11 ± 2 Mg C ha⁻¹), in the Tapajoz National Forest, Pará (Silver *et al.* 2000). Fine root biomass to 40 cm depth, was about 6 Mg ha⁻¹ in sandy soils and about 3.7 Mg ha⁻¹ in clay soils, confirming the greater root development on the more dystrophic, sandy soils, though in this case water retention capacity may also play a role. Most records of high fine root amounts come from

spodosols, oxisols, and ultisols, suggesting the higher development of fine roots in acid soils, where Al and Fe play key roles in soil chemistry and evolution (Vogt *et al.* 1996).

When live and dead fine roots have been distinguished and quantified, their respective proportions show great spatial and temporal variations. Partly because the inherent difficulties in distinguishing live, senescent, and dead roots, but also because the seasonal dynamics of fine roots is not yet clear. Only 20% of the fine root stock was alive in south eastern Venezuelan

rainforests, 80 % being necromass (Priess *et al.* 1999). This fact was explained by the slow decomposition of nutrient-poor fine roots. In Pará, in six plots along a gradient of soil texture, live fine roots were just an small proportion of total fine root biomass, less than 10% in all sites (Silver *et al.* 2000). In this case the root C:N (60 to 70 in sandy soils) and C:P (1,900 to 6,500) were quite low, suggesting a very poor substrate for decomposers and therefore a long turnover time for the fine root necromass.

Given the methodological shortcomings in measuring roots in forests, a search to estimates based on existing vegetation or environmental data was pursued (Vogt *et al.* 1996, Cairns *et al.* 1997). Considering all types of forests, aboveground biomass, age and latitude appear as the three most important predictors, explaining together 84% of the variation of root biomass between forest ecosystems (Cairns *et al.* 1997). This conclusion is not surprising, since it confirms that the two major factors related to root biomass in tropical forests are the aboveground biomass and the succession stage.

In summary, total root weight, fine and coarse, live and dead, represents a significant part of the total vegetation biomass in old-growth rainforests. Surely, available data underestimate total below-ground biomass, not just because they ignore roots in deep soil, but also because coarse roots, particularly tap roots, have rarely been considered in these estimates. Fine roots probably share at least 20%, and sometimes 50 %, of TBGB, with a sharp concentration in the topsoil, but they seem to extend far beyond the uppermost soil layers. With the few data available, it seems almost impossible to predict the variation in belowground biomass among communities, habitats, or regions.

CONCLUSIONS

The question about which may be the best estimate of above- and belowground rainforest biomass is only relevant when referring to averages useful to evaluate carbon stocks and emissions to the atmosphere during deforestation, mainly directed to feed global carbon cycle or climate change models (Brown and Lugo 1992, Fearnside 1992, Houghton *et al.* 2001). From an ecological viewpoint, much more interesting that means is to emphasize rainforest structural diversity, clearly

expressed in the wide range of above- and below-ground biomass estimates. Various factors seem to be responsible for a so large variability. Four types of uncertainties associated with estimates of biomass stocks have been set for: error in tree measurements, error due to the choice of an allometric model, sampling uncertainty related to the size of the study plot, and representativeness of small plots across the entire forest landscape (Chave *et al.* 2004). These authors stress the role of the allometric model as the most important source of error, we have already shown how different equations result in quite different estimates even for the same field data (Figure 1). But certainly plot size and sampling design decisively in the possibility of extrapolate the estimates to whole forest stands or landscapes. Data from too small plots (less than 0.5 ha) give very rough approximations to the forest stand biomass (see for instance the wide range of biomass estimates in Williams *et al.* 2002, Table 3). From a strictly statistical viewpoint some kind of randomization in plot location has to be used to estimate errors, which is not the case when just one continuous plot has been inventoried, or when the precise location of plots depends on predetermined criteria, like sampling “good” or “pristine” forests. Furthermore, the structural and life-form components of the total biomass (live trees, other life-forms, standing dead and downed wood) must be sampled differently and therefore their variability is not fully comparable.

But differences among estimates do not solely depend on methodological procedures, as shown by data obtained using the same field methods and the same equation (Brown *et al.* 1995). Thus, open, dense, and ecotone *terra firme* forests, in Rondonia, show significant differences in tree biomass (Cummings *et al.* 2002). Our first conclusion therefore is, that mature rainforest ecosystems, at least in tropical America, show large structural heterogeneity expressed at any scale of analysis, from single plots within a given landscape, to the region, or to the whole geographical area of this biome. Variability in structural features and functional diversity seem to be key ecological features of these tropical ecosystems. Either referring to aboveground tree biomass, to the relative contribution of other life forms, to carbon allocation among plant structures, or to the amount and distribution of root systems, variation is always the rule and similarity among stands, the exception. And this is the case even disregarding the huge

differences shown by secondary stages during forest regrowth.

At least three groups of factors may determine structural heterogeneity in old-growth rainforests. First, gap dynamics, responsible for intricate mosaics of forest patches with contrasting structural features (see for instance Gerwing and Lopes 2000, Bugman 2001). Second, habitat heterogeneity, often expressed as a particularly fine grain of spatial variability in soil conditions, mainly concerning water availability and nutrient stocks (see for instance Korning *et al.* 1994, Duivenvoorden 1995, Lips and Duivenvoorden 1996, IGAC 1996, Botschek *et al.* 1996). And third, regional diversification, mainly determined in the lowland tropics by rainfall patterns and probably also by past Quaternary events (Ab'Saher 1982, van der Hammen 1992, Mayle *et al.* 2004).

Our review refers to the old-growth, upland, *terra firme* forest, on acid, highly weathered, nutrient-poor ultisols and oxisols, or to andosols in volcanic areas, like Central America. LTAB estimates in Amazonia ranged from 232 to 492 Mg ha⁻¹, that is a two-fold difference in 60 1-ha plots (Laurance *et al.* 2002). The range of biomass in the same forest type in Rondonia was equally wide, 298 to 533 Mg ha⁻¹ (Cummings *et al.* 2002). Root biomass in this kind of ecosystem reaches about 20% of the total biomass, half of it is fine root biomass, highly concentrated in the topsoil, but extending to more than six meters in depth (Nepstad 1994). Trees contribute from 80 % to 90 % of total biomass in mature tropical American rainforests, being the contribution of the largest trees particularly significant. The total aboveground biomass of two life forms may attain significant amounts: palms and woody lianas, while the biomass of epiphytes in lowland rainforests is almost unknown.

Data on belowground biomass are troublesomely deficient. most figures surely are underestimates. Its minor but most active fraction, fine roots, concentrated in the uppermost soil layers, is better known than coarse roots. Both may attain great depths, and this hidden component certainly constitutes one of the largest gaps in knowledge.

Given that aboveground, belowground, and total rainforest biomass, are so highly variable amounts, depending heavily on the spatial scale to be considered, and given that these features are sharply determined by the ecosystem dynamics, it

may be asked if these structural parameters have any usefulness as functional descriptors. Furthermore, annual increments in tree biomass have been reported in long-term monitoring plots both in Amazonian and Guianan forests (Phillips *et al.* 1998, Chave *et al.* 2001, Baker *et al.* 2004), even in steady state systems like old-growth tropical forests are supposed to be, rendering transitory any estimation. In 59 Amazonian sites the LTAB of trees ≥ 10 cm DBH has increased by 1.22 ± 0.43 Mg ha⁻¹ yr⁻¹ (Baker *et al.* 2004). The question is that biomass certainly represents a dynamic ecosystem property, continuously changing. Precisely by its dynamic nature, when the patterns of variability, both spatial and temporal, at all scales of analysis, would be adequately assessed, it would represent one valuable indicator of the ecosystem functioning.

As a last issue, we would like to present a concise list of relevant questions which may guide research priorities on biomass stocks and allocation, aimed to furthering our understanding on the ecology of rainforest ecosystems.

- How reliable are biomass estimates obtained by applying current methodologies?
- How this reliability varies according to the different components of rainforest biomass?
- Which are the possible errors and uncertainties that render unreliable many biomass estimates?
- How large is biomass variability within a single, apparently homogeneous forest stand?
- What kind of factors promotes biomass variability?
- At which spatial scales operate the different determinants of biomass variation?
- Which are the ecological processes behind spatial and temporal variability?

Though even propose preliminary responses to these questions lay far beyond the objective of this review, we find useful to provide at least this short inventory of some key unresolved matters.

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