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Forest Ecology and Management 168 (2002) 311–321

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Total aboveground biomass in central Amazonian rainforests: a landscape-scale study

Henrique E.M. Nascimento^a, William F. Laurance^{a,b,*}

^a*Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA),
C.P. 478, Manaus AM 69011-970, Brazil*

^b*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama*

Received 16 May 2001

Abstract

Amazonian forests play a key role in the global carbon cycle, but there is much uncertainty about the quantity and distribution of carbon stored in these forests. We quantified total aboveground dry biomass (TAGB) in undisturbed central Amazonian rainforests, based on detailed estimates of all live and dead plant material within 20 1 ha plots spanning an extensive (ca. 1000 km²) study area. TAGB values in our study area were very high, averaging $397.7 \pm 30.0 \text{ Mg ha}^{-1}$. The most important component of aboveground biomass was large (≥ 10 cm diameter-at-breast-height (DBH)) trees, which comprised 81.9% of TAGB, followed by downed wood debris (7.0%), small trees, saplings, and seedlings (< 10 cm DBH; 5.3%), lianas (2.1%), litter (1.9%), snags (1.5%), and stemless palms (0.3%). Among large trees, aboveground biomass was greatest in intermediate-sized (20–50 cm DBH) stems (46.7% of TAGB), with very large (≥ 60 cm DBH) trees also containing substantial biomass (13.4% of TAGB). There were no significant correlations between large tree biomass and that of any other live or dead biomass component. An analysis based on the variability of our samples suggested that just 3–4 randomly positioned 1 ha plots would be sufficient to provide a reasonable estimate of mean TAGB in a landscape such as ours (with 95% confidence intervals being $< 10\%$ of the mean). This suggests that efforts to quantify Amazon forest biomass should be extensive rather than intensive; researchers should sample many geographically separate areas with a few plots each, rather than sampling a small number of areas more intensively.

Published by Elsevier Science B.V.

Keywords: Amazon basin; Biomass; Carbon cycle; Carbon storage; Global warming; Terra-firme forest; Tropical rainforest

1. Introduction

The rapid conversion of tropical forests is a major source of greenhouse gases such as carbon dioxide,

methane, and nitrous oxide, which are the principle causes of global warming (Houghton, 1991; Fearnside, 2000). Nowhere is deforestation occurring more rapidly than in Brazilian Amazonia, which contains about 40% of the world's remaining tropical rainforests (Laurance et al., 2001a). From 1995 to 1999, deforestation rates in the Brazilian Amazon averaged nearly 2 million hectares per year (INPE, 2000), not including extensive forest areas degraded by logging, ground fires, forest fragmentation, illegal

* Corresponding author. Present address: Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), C.P. 478, Manaus AM 69011-970, Brazil.
Tel.: +507-212-8252; fax: +507-212-8148.
E-mail addresses: laurancew@tivoli.si.edu, wfl@inpa.gov.br (W.F. Laurance).

gold-mining, and overhunting (Skole and Tucker, 1993; Laurance, 1998; Cochrane et al., 1999; Nepstad et al., 1999).

Despite the important role of Amazonian forests in the global carbon cycle (Fearnside, 1997a), data on biomass and carbon storage in the region are clearly inadequate (e.g. Brown et al., 1992a,b, 1995; Laurance et al., 1999). Biomass estimates for Amazonian forests have been the subject of considerable debate (e.g. Brown and Lugo, 1984, 1992; Fearnside, 1985, 1986, 1992) because of limited data, methodological differences among investigators, and small or incomplete measurements of biomass in some studies (cf. Houghton et al., in press). Current estimates of total carbon storage in Brazilian Amazonia vary by more than a factor of 2, from 39 to 93 Pg C, largely as a result of uncertainty in the quantity and spatial distribution of forest biomass (Houghton et al., in press). Houghton et al. (2000) concluded that 60% of the uncertainty in their estimates of annual carbon flux from Brazilian Amazonia resulted from varying estimates of forest biomass. Clearly, there is a need for additional measurements of biomass across large expanses of the Amazon basin.

In a recent study, Laurance et al. (1999) assessed the relationship between soil features and aboveground biomass of live trees for 65 1 ha plots arrayed across an extensive (ca. 1000 km²) central Amazonian landscape. Biomass estimates in this study were generated by measuring diameters of all large (≥ 10 cm diameter-at-breast-height (DBH)) trees and then using a correction factor to approximate biomass of small (< 10 cm DBH) trees. Here we provide a much more comprehensive estimate of aboveground biomass for the same study area, based on 20 randomly selected 1 ha plots in which biomass of all live and dead material (large trees, small trees, seedlings, palms, lianas, downed wood debris, snags, litter, aboveground root mat) was quantified. We also use an improved allometric model to estimate the biomass of large trees.

Our study had three goals: (1) To provide rigorous estimates of total aboveground dry biomass (TAGB) for intact forests in our study area; (2) To develop better correction factors for studies in which only large trees are measured; (3) To predict the number of 1 ha samples needed to reliably estimate aboveground biomass in these forests.

2. Methods

2.1. Study area and plots

The study area is a partially fragmented landscape in the central Amazon, 80 km N of Manaus, Brazil (2°30'S, 60°W) at 50–100 m elevation (Lovejoy et al., 1986). Rainforests in the area are terra-firme (not seasonally inundated). Rainfall ranges from 1900 to 3500 mm annually with a pronounced dry season from June to October. The forest canopy is 30–37 m tall, with emergents to 55 m. Species richness of trees is very high and can exceed 280 species (≥ 10 cm DBH) per hectare (de Oliveira and Mori, 1999).

The dominant soils in the study area are xanthic ferralsols, which are heavily weathered, acidic, and very poor in nutrients such as P, Ca and K (Chauvel et al., 1987). Similar nutrient-poor soils are prevalent throughout much of the Amazon basin (Richter and Babbar, 1991). Cation concentrations tend to be higher in more clayey soils, which are prevalent in flatter areas and ridgetops; these areas generally support greater tree biomass than do gullies and slopes, which have higher sand contents and lower cation concentrations (Laurance et al., 1999).

To conduct inventories of (TAGB), we sampled 20 1 ha plots located in large ($> 10^6$ ha) tracts of intact forest ($n = 18$ plots) and in the interior of a 100 ha forest fragment ($n = 2$ plots). The 20 plots were selected using stratified random sampling to ensure that they spanned the length and breadth of our 1000 km² study area and that pseudoreplication (i.e. having multiple plots in the same general area) was minimised. All plots were located in forest interiors (> 300 m from the nearest forest-pasture edge) to eliminate any influence of edge effects on forest biomass and dynamics (cf. Laurance et al., 1997, 1998a,b, 2000).

2.2. Large trees

For each plot, complete inventories of all large (≥ 10 cm DBH) trees were conducted from 1997 to 1999. Large (≥ 10 cm DBH) palms were included in these samples but are rare in our study plots ($< 1\%$ of stems, most of which are a single species [*Oenocarpus bacaba*]). Tree diameters were carefully measured (to the nearest 1 mm) using a DBH tape at 1.3 m height or

Table 1

Allometric formulas used to estimate aboveground dry biomass (kg ha^{-1}) for rainforest plants in this study, based on DBH or basal-area (BA) data^a

Plant group	Formula
Large (≥ 5 cm DBH) trees ^b	$\exp\{-0.370 + 0.333[\ln(\text{DBH})] + 0.933[\ln(\text{DBH})]^2 - 0.122[\ln(\text{DBH})]^3\}$
Small (1–5 cm DBH) primary trees ^c	$\exp[-1.7689 + 2.3770 \ln(\text{DBH})]$
Small (1–10 cm DBH) successional trees ^d	$\exp[2.4128 \ln(\text{DBH}) - 1.9968]$
Small (1–10 cm DBH) <i>Cecropia</i> trees ^d	$\exp[2.4257 \ln(\text{DBH}) - 2.5118]$
Small (1–10 cm DBH), stemmed palms ^e	$\{\exp[0.9285 \ln(\text{DBH}^2) + 5.7236]1.05001\}/10^3$
Lianas ^f	$\text{base}10[0.12 + 0.91 \log_{10}(\text{BA})]$

^a “exp” indicates that the natural logarithm ($e = 2.71828$) is raised to the power indicated in the formula (e.g. $\exp(0.35\text{DBH}) = e^{0.35\text{DBH}}$), whereas “base10” indicates that the base-10 logarithm is used (e.g. $\text{base}10(0.35\text{DBH}) = 10^{0.35\text{DBH}}$).

^b Chambers et al. (2001b).

^c This study.

^d Nelson et al. (1999).

^e Hughes (1997).

^f Putz (1983).

above any buttresses. DBH measurements were converted to estimates of aboveground dry biomass with an allometric model derived from 315 trees from local rainforests (Chambers et al., 2001b; Table 1). The trees used to derive this model ranged from 5 to 120 cm DBH and were destructively sampled at a site ca. 20 km southwest of our study area, in very similar lowland terra-firme forest. The allometric model of Chambers et al. (2001b) is a refinement of an earlier model by dos Santos (1996), which overestimates the biomass of large (≥ 60 cm DBH) trees while underestimating biomass of smaller trees.

2.3. Lianas

Aboveground dry biomass of lianas (woody vines) was estimated in the 20 plots from 1997 to 1999 (Laurance et al., 2001b). For each plot, diameters of all liana stems (≥ 2 cm DBH) were carefully measured at 1.3 m height with a DBH tape (to the nearest 0.1 mm), then converted to a biomass estimate using an allometric formula developed in an Amazonian rainforest in Venezuela (Putz, 1983; Table 1).

2.4. Small trees, palms, and small lianas

Data on small trees (including saplings and seedlings), palms, and small lianas were collected from 1999 to 2000 within a series of subsamples in each plot.

All data were converted to aboveground dry biomass estimates on a per-hectare basis.

The DBH of small trees and palms (DBH from 5.0 to 9.9 cm) were measured in 13 quadrats (20 m \times 20 m) per plot. To accomplish this each plot was divided into 25 quadrats, and every second quadrat was sampled (in a checker-board pattern) to ensure nearly uniform coverage of the plot. DBH data were converted to aboveground dry biomass estimates using the formulas of Chambers et al. (2001b) for primary-forest trees, Nelson et al. (1999) for successional trees, and Hughes (1997) for palms (Table 1). The models of Nelson et al. (1999) were developed using trees from our study area, while that of Hughes (1997) was for Mexican tropical rainforests.

DBH data for saplings (1.0–4.9 cm DBH), stemless palms, and small lianas (1.0–2.0 cm DBH) were recorded within 13 sub-quadrats (5 m \times 5 m) per plot. One sub-quadrat was nested within the southwest corner of each 20 m \times 20 m quadrat. Aboveground dry biomass estimates were generated using the formulas of Nelson et al. (1999) for successional-tree species and Putz (1983) for lianas. For primary-forest saplings, 40 individuals were randomly selected at six different sites in our study area, then cut at ground level and weighed. Samples of the trunk, branches, and leaves were removed, oven-dried, and reweighed, in order to estimate aboveground dry biomass for each individual. These data were used to derive an

allometric formula to predict biomass based on sapling DBH ($R^2 = 96.2\%$; Table 1). For abundant stemless palms (principally *Attalea* spp. and *Astrocaryum* spp.), leaves of individual plants were divided into three size-classes (0–2, 2–3 and >3 m height). The number of leaves in each size-class was counted and multiplied by an average leaf weight, derived by randomly sampling 10 leaves in each size-class that were oven-dried and weighed.

Seedling aboveground dry biomass was estimated by counting seedlings (>50 cm height but <1 cm DBH) within 13 samples (2 m × 2 m) per plot, with one sample located in the southwest corner of each sub-quadrat. Seedling counts were multiplied by average seedling weight, derived by randomly sampling 60 seedlings that were oven-dried and weighed.

2.5. Wood debris

Downed wood debris was non-destructively quantified in 1999–2000 using the planar-intersect method (Van Wagner, 1968; Brown, 1974). Fine (2.5–9.9 cm diameter) and coarse (≥ 10 cm diameter) wood debris fractions were estimated separately. Within each 20 m × 20 m quadrat, two 15 m long perpendicular transects were established (yielding 26 transects per plot). For each transect, fine debris was sampled along the first 5 m of the sample plane while coarse debris was sampled along the entire plane. All wood particles that intersected the planes were measured. Coarse debris was separated into sound and rotten classes, using criteria such as the condition of sapwood and heartwood (Delaney et al., 1998). Dry necromass was estimated with formulas in Brown (1974), using wood densities of 0.69 g cm⁻³ for sound coarse debris (mean wood density for Amazonian forests; Fearnside, 1997b), 0.34 g cm⁻³ for rotten coarse debris (Cummings, 1998) and 0.41 g cm⁻³ for fine debris (Cummings, 1998).

2.6. Snags

All plots were systematically surveyed on foot in 1999–2000 to identify trees that died but remained standing. Dry necromass was estimated using the formula of Chambers et al. (2001b), with values reduced by 10% to compensate for the loss of leaves, twigs and small branches (cf. Delaney et al., 1998). A

small proportion of snags (13%) had broken boles, and for these a taper function was used to estimate tree volume (volume = basal area × estimated bole height × 0.78; Graça et al., 1999), which was then multiplied by the mean density of sound wood (0.69 g cm⁻³) to yield a necromass estimate.

2.7. Litter standing crop

In each 20 m × 20 m quadrat, two 50 m × 50 cm samples (26 samples/plot) were removed to determine the biomass of litter (leaves, twigs, fruits) on the forest floor (this included fine live roots above the soil surface). These samples were located at the midpoint of the southern and western margins of each quadrat. Samples were collected during the 2001 wet season (January–March) and weighed in the field. A portion of each sample was then oven-dried, and the ratio of dry to wet litter weight was used to estimate litter dry mass.

2.8. Required sample size

We estimated the number of 1 ha samples needed to adequately assess TAGB in our landscape as a function of confidence-interval size, using the formula of Ott and Mendenhall (1990, p. 504): $N = (z^2 s^2)/E^2$, where z depends on the desired confidence interval (i.e. $z = 1.645$ for 90% confidence interval, 1.96 for 95% confidence interval, etc.), s^2 is the sample variance and E the tolerable error in Mg ha⁻¹. Required values for N were then plotted as a function of tolerable error.

3. Results

3.1. Total biomass

TAGB in the 20 plots ranged from 305 to 432 Mg ha⁻¹, with a mean of 397.7 ± 30.0 Mg ha⁻¹ (Table 2). When a data distribution was generated, TAGB values were skewed to the left (Fig. 1); most (85%) plots had values ranging from about 380–430 Mg ha⁻¹, but three plots had relatively low values (305–364 Mg ha⁻¹).

On average, large (≥ 10 cm DBH) trees comprised 81.9% of TAGB, followed by coarse downed wood

Table 2

Components of aboveground dry biomass for 20 1 ha plots in central Amazonian rainforest^a

Plot	Large trees	Small trees	Stemless palms	Lianas	Coarse debris	Fine debris	Snags	Litter	Total
1101	346.23	18.50	1.90	9.33	23.29	3.35	9.27	7.90	419.77
1102	255.28	24.02	1.48	6.10	28.74	2.74	12.57	7.72	338.64
1103	299.90	25.25	1.11	9.43	13.67	2.30	4.30	7.63	363.58
1113	359.60	21.85	2.23	4.63	30.14	2.91	1.60	6.73	429.69
1201.1	307.72	20.57	1.14	7.72	29.18	1.59	4.22	10.22	382.35
1201.2	335.72	25.28	1.02	9.41	18.79	2.72	6.80	6.06	405.80
1201.3	238.11	18.52	1.20	10.90	23.50	1.53	3.16	8.05	304.98
1301.1	327.20	19.67	1.37	6.69	33.06	4.47	1.95	7.20	401.60
1301.5	340.74	18.44	2.25	6.41	35.81	3.05	2.19	5.82	414.71
1301.7	329.58	25.47	1.39	8.05	36.15	3.47	6.09	7.16	417.34
1301.9	323.29	19.95	1.24	6.48	34.12	3.43	4.55	6.65	399.69
1501.1	348.29	18.78	1.81	7.94	14.13	3.19	8.58	7.07	409.78
1501.2	349.92	18.08	1.00	9.28	21.05	4.10	8.31	9.87	421.61
1501.3	334.37	19.45	0.85	9.04	25.53	3.26	8.18	8.73	409.41
2303.5	352.61	22.80	1.49	5.87	25.65	2.72	13.40	7.18	431.72
2303.6	352.36	22.32	1.12	5.75	11.91	3.00	7.33	8.93	412.74
3402.1	338.88	19.42	1.46	9.58	18.76	4.00	2.26	6.69	401.03
3402.3	317.11	21.42	0.32	9.07	31.30	3.05	10.81	5.93	399.01
3402.5	329.42	19.05	0.80	10.68	21.99	3.61	2.03	7.29	394.86
3402.7	323.89	23.28	0.43	13.67	19.44	2.61	5.29	6.92	395.25
Mean	325.51	21.11	1.28	8.30	24.81	3.05	6.14	7.49	397.68

^a Biomass estimates (Mg ha^{-1}) are shown for large (≥ 10 cm DBH) trees, small trees (including saplings and seedlings; < 10 cm DBH), stemless palms, lianas (≥ 1 cm DBH), coarse downed wood debris (≥ 10 cm diameter), fine downed wood debris (2.5–9.9 cm diameter), snags, and litter (leaves, fruits, flowers, fine aboveground roots).

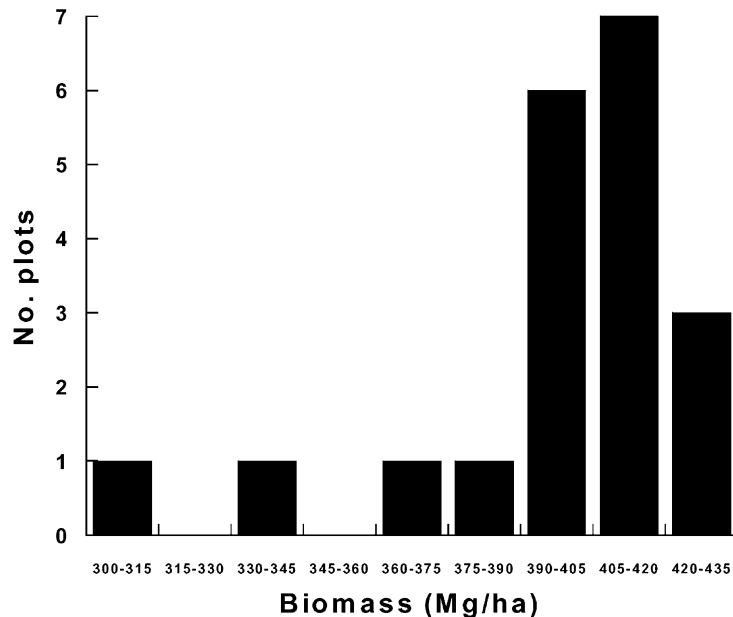


Fig. 1. Frequency distribution for TAGB in 20 1 ha plots in intact rainforests of the central Amazon.

Table 3

Aboveground biomass, number of stems, and percentage of TAGB for seven diameter-classes of large (≥ 10 cm DBH) trees in the central Amazon. Data shown are mean values (\pm S.D.) for 20 1 ha plots

Size-class (cm)	Biomass (Mg ha ⁻¹)	Stems (ha ⁻¹)	Percentage of TAGB
10–20	48.61 \pm 3.79	394.40 \pm 27.46	12.22
20.1–30	64.49 \pm 6.60	126.45 \pm 13.64	16.22
30.1–40	64.35 \pm 11.49	53.75 \pm 8.92	16.18
40.1–50	57.02 \pm 12.60	27.00 \pm 5.86	14.34
50.1–60	37.91 \pm 10.19	11.95 \pm 3.09	9.53
60.1–70	22.07 \pm 7.93	5.05 \pm 1.66	5.55
>70	31.05 \pm 12.76	4.70 \pm 2.00	7.81

debris (6.2%), small trees, saplings, and seedlings (5.3%), lianas (2.1%), litter (1.9%), snags (1.5%), fine downed wood debris (0.8%), and stemless palms (0.3%). Nearly nine-tenths of TAGB (89.6%) was live material, with the remainder comprised by wood debris, snags and litter (Table 2).

Among large trees, most of the aboveground biomass was concentrated in abundant, intermediate-sized (20–50 cm DBH) stems, which contained 46.7% of TAGB (Table 3). Although uncommon (averaging <10 stems ha⁻¹), very large canopy and emergent trees (≥ 60 cm DBH) contained 13.4% of TAGB, with the remainder (12.2%) in the smallest (10–20 cm DBH) size-class.

3.2. Correlations among biomass components

Surprisingly, there was no significant correlation between the biomass of large (≥ 10 cm DBH) trees and that of any other biomass component (small trees/seedlings, lianas, stemless palms, downed wood debris, snags, litter) ($r < 0.25$, $P > 0.30$ in all cases). There was also no significant relationship between large-tree biomass and all other live-plant biomass ($r = -0.24$), total necromass ($r = -0.06$), or all other live-plant biomass and necromass combined ($r = -0.16$) ($P > 0.30$ in all cases; Pearson correlations).

3.3. Estimating TAGB from large-tree biomass

Our results suggest that TAGB can be reliably estimated using measurements of large trees alone.

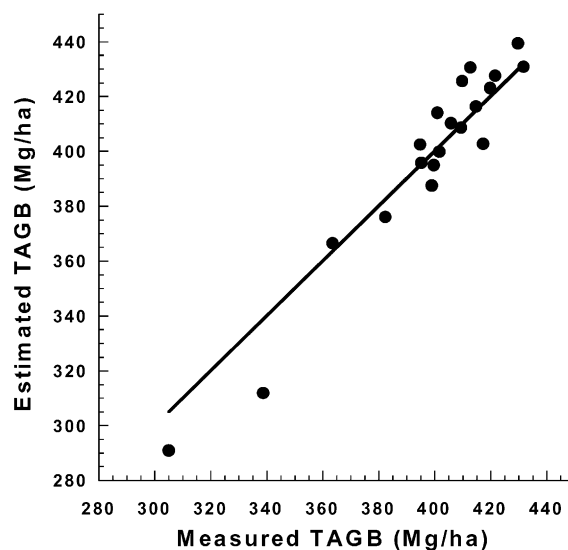


Fig. 2. Relationship between measured TAGB and estimated TAGB values (based on large-tree (≥ 10 cm DBH) biomass plus a 22.2% correction factor to account for the other biomass components). The line shows $Y = X$.

Large trees comprised over 80% of TAGB and, not surprisingly, there was a positive, linear relationship between large-tree biomass and TAGB (TAGB = $-67.7 + 0.981$ large-tree biomass; $R^2 = 94.3\%$, $P < 0.00001$; linear regression analysis). According to our data (Table 2), TAGB estimates can be derived by increasing large-tree biomass by a correction factor of 22.2% (6.5% for small trees, saplings, and seedlings; 3.0% for lianas and stemless palms; 12.7% for dead material). When we applied this correction, there was very good agreement between measured and estimated TAGB (Fig. 2). The average difference for our 20 plots was just 2.1% (range 0.1–7.9%).

3.4. Predicting adequate sample size

The analysis of tolerable error (Fig. 3) suggests that, for a landscape such as ours, three randomly positioned 1 ha plots would provide a reasonable estimate of mean TAGB if all components of aboveground biomass are directly measured. Ninety-five percent confidence intervals based on three plots would be ± 35 Mg, which represent errors of $<9\%$ in magnitude (i.e. because TAGB averaged nearly 400 Mg ha⁻¹), whereas errors for four plots would

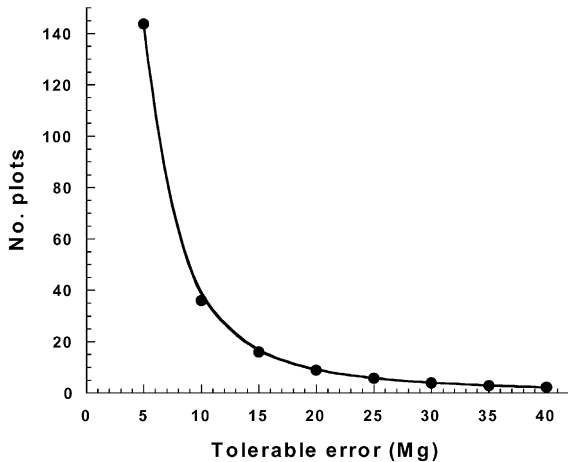


Fig. 3. Relationship between sample size (number of 1 ha plots) and tolerable error for estimating TAGB in central Amazonian rainforests. The curve was fitted by a smoothing function.

be ± 30 Mg (7.5% in magnitude). If TAGB is estimated by measuring large trees only, then four plots would be advisable to ensure that total sampling errors (7.5% tolerable error plus 2.1% average error from the correction factor) are $<10\%$.

The necessary sample sizes rise rapidly if higher levels of sample accuracy are needed (Fig. 3). For example, to achieve 95% confidence intervals of ± 20 Mg (ca. 5% error), nine plots would be needed. Likewise, 36 plots would be needed to achieve confidence intervals of ± 10 Mg, and 144 plots for intervals of ± 5 Mg.

4. Discussion

4.1. Total biomass

Our study provides the most comprehensive estimate presently available for TAGB in central Amazonian rainforests. A key conclusion is that biomass in these forests is very high, averaging nearly 400 Mg ha^{-1} . It is notable that this estimate was produced using an improved but relatively conservative allometric model (Chambers et al., 2001b) to estimate the biomass of large (≥ 10 cm DBH) trees. Our value is higher than most comparable estimates in other parts of the Amazon (e.g. Klinge and Rodriguez, 1973; Uhl and Jordan, 1984; Uhl et al., 1988; Brown

and Lugo, 1990, 1992; Brown et al., 1992a,b, 1995; Salomão et al., 1998), but clearly supports recent estimates of high biomass for central Amazonian forests (Fearnside, 1997a; Laurance et al., 1999).

Belowground biomass was not measured in this study but can be estimated from published works. In eight studies in the Neotropical and Caribbean regions reviewed by Houghton et al. (in press), belowground (root) biomass averaged 21.0% (range 13–34%) of aboveground biomass. Using this mean value, root biomass in our plots would be 84 Mg ha^{-1} on average. This estimate is reduced slightly if only studies in Amazonian terra-firme forests are considered (Klinge and Rodriguez, 1973; Jordan and Uhl, 1978; Saldarriaga et al., 1988; Nepstad, 1989); these averaged 17.5% (range 13.4–23.5%) of aboveground biomass. In this case, belowground biomass of roots would average 70 Mg ha^{-1} in our plots.

In addition to roots, Amazonian forests store large amounts of belowground carbon in the form of soil organic matter. Based on 1162 soil profiles throughout the Brazilian Amazon from the RADAMBRASIL project, Moraes et al. (1995) found that carbon density (excluding live roots) in the upper 1 m of soil averaged 103 Mg ha^{-1} . Remarkably, Davidson and Trumbore (1995) found an additional 200 Mg ha^{-1} of carbon in soil organic matter between 1 and 8 m depth in the eastern Amazon.

Collectively, these studies illustrate the high capacity of intact Amazonian forests for carbon storage. Assuming that 50% of biomass is carbon, aboveground carbon storage in our study area is nearly 200 Mg ha^{-1} , with perhaps another $35\text{--}40 \text{ Mg ha}^{-1}$ as belowground biomass and roughly 300 Mg ha^{-1} as soil organic matter. Forest conversion is unlikely to have major effects on deep soil organic matter, but it can dramatically reduce carbon storage aboveground and in the roots and upper soil layers (Kauffman et al., 1994, 1995; Fearnside, 1997a; Fearnside and Barbosa, 1998).

4.2. Components of aboveground biomass

In our 20 plots, large (≥ 10 cm DBH) trees comprised an average of 81.9% of TAGB, with the remainder divided between other live plants (7.7%) and dead material (10.4%). In tropical forests, large trees are inevitably the dominant component of aboveground

biomass. Indeed, in some forests up to a quarter of aboveground biomass is concentrated in the largest canopy and emergent trees (Clark and Clark, 1995), although in our study area nearly half of all biomass (46.7%) was in the intermediate-size-classes (20–50 cm DBH), with a lower proportion (13.4%) contained in the largest trees (≥ 60 cm DBH).

Understory plant biomass appears moderately low in central Amazonian forests. Although the forest understory is often quite dense (with many saplings and stemless palms), herbs, epiphytes, and climbing vines are less abundant than in many other neotropical forests (Guillaumet, 1987; Gentry, 1990). In our study area, for example aboveground biomass of lianas was lower, and comprised a smaller percentage of total forest biomass, than in other neotropical (Klinge and Rodriguez, 1974; Putz, 1983; Pérez-Salicrup, 1998), Asian (Ogawa et al., 1965; Kato et al., 1978), and African (Greenland and Kowai, 1960) forests. This low density of herbs, epiphytes, and lianas may result from extremely low soil fertility (Gentry and Emmons, 1987), and disturbance favouring lianas could also be limited by naturally low rates of tree mortality ($1.3 \pm 0.5\% \text{ yr}^{-1}$ over the past two decades) in our study area (Laurance et al., 2001b).

Estimates of standing stocks of wood debris are important for validating carbon cycling models (e.g. Chambers et al., 2000). In our study area, coarse wood debris (including snags) averaged $31.0 \pm 7.7 \text{ Mg ha}^{-1}$, which is higher than other estimates for dense forests of the central Amazon ($10.5\text{--}21.2 \text{ Mg ha}^{-1}$; Martius, 1997) but comparable to that in similar undisturbed forest about 20 km southwest of our study area ($29.7 \pm 12.2 \text{ Mg ha}^{-1}$; Summers, 1998). An empirical model incorporating long-term tree mortality and decomposition rate data predicts that standing stocks of biomass in coarse debris should be about 10% of that contained in large (≥ 10 cm DBH) trees (Chambers et al., 2001a). Based on our data, the Chambers model predicts that coarse debris should average 32.6 Mg ha^{-1} , which is very close to our observed mean of 31.0 Mg ha^{-1} .

It is interesting that we found no significant correlations between large-tree biomass and the other live and dead biomass components. One might expect, for example that large-tree biomass would be negatively correlated with liana biomass (cf. Laurance et al., 2001b) because lianas tend to suppress tree

growth and survival (Putz, 1984), or with wood debris and snags, because disturbed sites might have fewer large trees and more debris. The absence of such correlations might have resulted because tree mortality rates were generally low in our plots and because large-tree biomass did not span a particularly large range of values. If fragmented or logged forests were included in this study, tree mortality would have been much higher and correlations among various biomass components might well have become evident.

4.3. Developing correction factors

Our data suggest that TAGB of central Amazonian terra-firme forests can be effectively approximated by increasing biomass estimates for large (≥ 10 cm DBH) trees by 22.2%. Such correction factors have been used by many investigators (e.g. Brown and Lugo, 1984, 1992; Fearnside, 1992; Brown et al., 1995), as it is far easier to measure only large trees than all live and dead components of biomass. For our 20 plots, the mean difference between estimated and measured aboveground biomass was just 2.1% (Fig. 2).

Our correction factor incorporates aboveground mass estimates for all significant dead and live material aside from large trees. Estimates of dead material have varied considerably among studies, ranging from 2.3 to 16.6% of aboveground live biomass at 15 neotropical sites (Houghton et al., in press), although the overall mean (8.7%) did not differ greatly from that in this study (10.4%). As noted above, understory plant biomass is relatively low in central Amazonia; small trees (< 10 cm DBH), for example comprised 12% of large-tree biomass in the Rio Negro region of Venezuela (Jordan and Uhl, 1978) but only 6.5% in this study.

4.4. Sampling biomass in Amazonian forests

Our results suggest that, for a landscape such as ours, three randomly positioned plots will provide a reasonable degree of sample accuracy for estimating TAGB (Fig. 3). With just three plots, tolerable errors for the estimated mean (using 95% confidence intervals) were 35 Mg ha^{-1} , or under 9% in magnitude. If TAGB is estimated using large (≥ 10 cm DBH) trees only, then four plots would be advisable to limit overall sampling errors to ca. 10% in magnitude. This

result is fortunate, in the sense that a limited number of plots appears to provide a reasonably good estimate of average aboveground biomass at a landscape scale. This implies that efforts to quantify Amazon forest biomass should be extensive rather than intensive; researchers should sample a large number of geographically separate areas with a few plots each, rather than attempting to sample a small number of areas more intensively.

Our recommendation that 3–4 random samples will normally be sufficient for sampling Amazon forest biomass is based on the assumption that 1 ha plots will be used; for smaller plots, sample variances would undoubtedly be higher (Clark and Clark, 2000), especially for large trees (Brown et al., 1995), meaning that more plots would be needed. We also assume that biomass in other Amazonian landscapes is not more variable spatially than that in our study area. Although few comparable data are available (cf. Clark and Clark, 2000; for a study at a 600 ha scale in Costa Rica), we believe this assumption is reasonable except where forest disturbances, edaphic features, or climate (e.g. at forest-savanna ecotones) vary strongly across a particular study area. Finally, methodological differences among investigators will undoubtedly complicate efforts to quantify the spatial distribution of forest biomass (cf. Houghton et al., in press). Because most investigators work in a particular area, such differences will tend to overestimate among-site differences. Clearly, efforts to standardise biomass-estimation methods (e.g. Brown, 1997; Clark and Clark, 2000) will be just as important as expanding the geographic distribution of study sites across the Amazon basin.

4.5. Urgency of the problem

Amazon forests contain a very large stock of terrestrial carbon (Fearnside, 1997a; Houghton et al., in press) and are probably an important carbon sink (Grace et al., 1995; Phillips et al., 1998; Malhi et al., 2000; Chambers et al., 2001a). Thus, understanding the spatial distribution of biomass in these forests is an urgent priority. Our detailed survey indicates that, at least in the central Amazon, carbon storage in undisturbed forests is very high, suggesting that forest conversion is likely to be an even larger source of greenhouse gas emissions than previously anticipated.

This is important because plans are well underway to expand networks of highways, railroads, gas lines, and other major infrastructure projects in the Brazilian Amazon. By opening large expanses of the basin's remote interior to exploitative activities, these projects are predicted to sharply accelerate the pace of forest conversion and degradation (Carvalho et al., 2001; Laurance et al., 2001a). Agricultural practices in the Amazon are limited by very low soil fertility (Kauffman et al., 1994; Fearnside and Leal-Filho, 2001), and the economic value of intact forests for carbon storage, biodiversity conservation, and other natural ecosystem services may ultimately be far greater than that provided by forest conversion.

Acknowledgements

We thank Boone Kauffman for very helpful discussion and Jeff Chambers and two anonymous referees for comments on the manuscript. The NASA-LBA program, Mellon Foundation, National Institute for Amazonian Research (INPA), and Smithsonian Institution provided research support. This is publication number 356 in the BDFFP technical series.

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