



ELSEVIER

Forest Ecology and Management 5793 (2001) 1–11

 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 (STRI) Unit 0948, APO AA 34002, Apartado 2072, Balboa, 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. © 2001 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 gold-mining, and overhunting (Skole and Tucker, 44

* 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.: +55-92-642-1148; fax: +55-92-642-2050.

E-mail addresses: laurancew@tivoli.si.edu, wfl@inpa.gov.br (W.F. Laurance).

45 1993; Laurance, 1998; Cochrane et al., 1999; Nepstad
46 et al., 1999).

47 Despite the important role of Amazonian forests
48 in the global carbon cycle (Fearnside, 1997a), data
49 on biomass and carbon storage in the region are
50 clearly inadequate (e.g. Brown et al., 1992a,b, 1995;
51 Laurance et al., 1999). Biomass estimates for Ama-
52 zonian forests have been the subject of considerable
53 debate (e.g. Brown and Lugo, 1984, 1992; Fearnside,
54 1985, 1986, 1992) because of limited data, metho-
55 dological differences among investigators, and small
56 or incomplete measurements of biomass in some
57 studies (cf. Houghton et al., in press). Current esti-
58 mates of total carbon storage in Brazilian Amazonia
59 vary by more than a factor of 2, from 39 to 93 Pg C,
60 largely as a result of uncertainty in the quantity and
61 spatial distribution of forest biomass (Houghton
62 et al., in press). Houghton et al. (2000) concluded
63 that 60% of the uncertainty in their estimates of
64 annual carbon flux from Brazilian Amazonia
65 resulted from varying estimates of forest biomass.
66 Clearly, there is a need for additional measurements
67 of biomass across large expanses of the Amazon
68 basin.

69 In a recent study, Laurance et al. (1999) assessed the
70 relationship between soil features and aboveground
71 biomass of live trees for 65 1 ha plots arrayed across
72 an extensive (ca. 1000 km²) central Amazonian land-
73 scape. Biomass estimates in this study were generated
74 by measuring diameters of all large (≥ 10 cm di-
75 ameter-at-breast-height (DBH)) trees and then using
76 a correction factor to approximate biomass of small
77 (< 10 cm DBH) trees. Here we provide a much more
78 comprehensive estimate of aboveground biomass for
79 the same study area, based on 20 randomly selected
80 1 ha plots in which biomass of all live and dead
81 material (large trees, small trees, seedlings, palms,
82 lianas, downed wood debris, snags, litter, aboveground
83 root mat) was quantified. We also use an improved
84 allometric model to estimate the biomass of large
85 trees.

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

2. Methods

2.1. Study area and plots

95 The study area is a partially fragmented landscape
96 in the central Amazon, 80 km N of Manaus, Brazil
97 (2°30'S, 60°W) at 50–100 m elevation (Lovejoy et al.,
98 1986). Rainforests in the area are terra-firme (not
99 seasonally inundated). Rainfall ranges from 1900 to
100 3500 mm annually with a pronounced dry season from
101 June to October. The forest canopy is 30–37 m tall,
102 with emergents to 55 m. Species richness of trees is
103 very high and can exceed 280 species (≥ 10 cm DBH)
104 per hectare (de Oliveira and Mori, 1999).

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

116 To conduct inventories of (TAGB), we sampled 20
117 1 ha plots located in large ($> 10^6$ ha) tracts of intact
118 forest ($n = 18$ plots) and in the interior of a 100 ha
119 forest fragment ($n = 2$ plots). The 20 plots were
120 selected using stratified random sampling to ensure
121 that they spanned the length and breadth of our
122 1000 km² study area and that pseudoreplication (i.e.
123 having multiple plots in the same general area) was
124 minimised. All plots were located in forest interiors
125 (> 300 m from the nearest forest-pasture edge) to
126 eliminate any influence of edge effects on forest
127 biomass and dynamics (cf. Laurance et al., 1997,
128 1998a,b, 2000).

2.2. Large trees

130 For each plot, complete inventories of all large
131 (≥ 10 cm DBH) trees were conducted from 1997 to
132 1999. Large (≥ 10 cm DBH) palms were included in
133 these samples but are rare in our study plots ($< 1\%$ of
134 stems, most of which are a single species [*Oenocarpus*
135 *bacaba*]). Tree diameters were carefully measured (to
136 the nearest 1 mm) using a DBH tape at 1.3 m height or

93

94

95

96

97

98

99

100

101

102

103

104

105

106

107

108

109

110

111

112

113

114

115

116

117

118

119

120

121

122

123

124

125

126

127

128

129

130

131

132

133

134

135

136

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).

137 above any buttresses. DBH measurements were con- 162
 138 verted to estimates of aboveground dry biomass with 163
 139 an allometric model derived from 315 trees from local 164
 140 rainforests (Chambers et al., 2001b; Table 1). The 165
 141 trees used to derive this model ranged from 5 to 166
 142 120 cm DBH and were destructively sampled at a site 167
 143 ca. 20 km southwest of our study area, in very similar 168
 144 lowland terra-firme forest. The allometric model of 169
 145 Chambers et al. (2001b) is a refinement of an earlier 170
 146 model by dos Santos (1996), which overestimates the 171
 147 biomass of large (≥ 60 cm DBH) trees while under- 172
 148 estimating biomass of smaller trees. 173

149 2.3. Lianas 174

150 Aboveground dry biomass of lianas (woody vines) 175
 151 was estimated in the 20 plots from 1997 to 1999 176
 152 (Laurance et al., 2001b). For each plot, diameters of 177
 153 all liana stems (≥ 2 cm DBH) were carefully measured 178
 154 at 1.3 m height with a DBH tape (to the nearest 179
 155 0.1 mm), then converted to a biomass estimate using 180
 156 an allometric formula developed in an Amazonian 181
 157 rainforest in Venezuela (Putz, 1983; Table 1). 182

158 2.4. Small trees, palms, and small lianas 183

159 Data on small trees (including saplings and seed- 184
 160 lings), palms, and small lianas were collected from 185
 161 1999 to 2000 within a series of subsamples in each 186

162 plot. All data were converted to aboveground dry 163
 164 biomass estimates on a per-hectare basis. 165

166 The DBH of small trees and palms (DBH from 5.0 167
 168 to 9.9 cm) were measured in 13 quadrats 169
 170 (20 m \times 20 m) per plot. To accomplish this each plot 171
 172 was divided into 25 quadrats, and every second quad- 173
 174 rat was sampled (in a checker-board pattern) to ensure 174
 175 nearly uniform coverage of the plot. DBH data were 175
 176 converted to aboveground dry biomass estimates using 176
 177 the formulas of Chambers et al. (2001b) for primary- 177
 178 forest trees, Nelson et al. (1999) for successional trees, 178
 179 and Hughes (1997) for palms (Table 1). The models of 179
 180 Nelson et al. (1999) were developed using trees from 180
 181 our study area, while that of Hughes (1997) was for 181
 182 Mexican tropical rainforests. 182

183 DBH data for saplings (1.0–4.9 cm DBH), stemless 183
 184 palms, and small lianas (1.0–2.0 cm DBH) were 184
 185 recorded within 13 sub-quadrats (5 m \times 5 m) per plot. 185
 186 One sub-quadrat was nested within the southwest 186
 187 corner of each 20 m \times 20 m quadrat. Aboveground 187
 188 dry biomass estimates were generated using the for- 188
 189 mulas of Nelson et al. (1999) for successional-tree 189
 190 species and Putz (1983) for lianas. For primary-forest 190
 191 saplings, 40 individuals were randomly selected at six 191
 192 different sites in our study area, then cut at ground 192
 193 level and weighed. Samples of the trunk, branches, 193
 194 and leaves were removed, oven-dried, and reweighed, 194
 195 in order to estimate aboveground dry biomass for each 195
 196 individual. These data were used to derive an allo- 196

metric 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 $397.7 \pm 30.0 \text{ Mg ha}^{-1}$ (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

235

236

237

238

239

240

241

242

243

244

245

246

247

248

249

250

251

252

253

254

255

256

257

258

259

260

261

262

263

264

265

266

267

268

269

270

271

272

273

274

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).

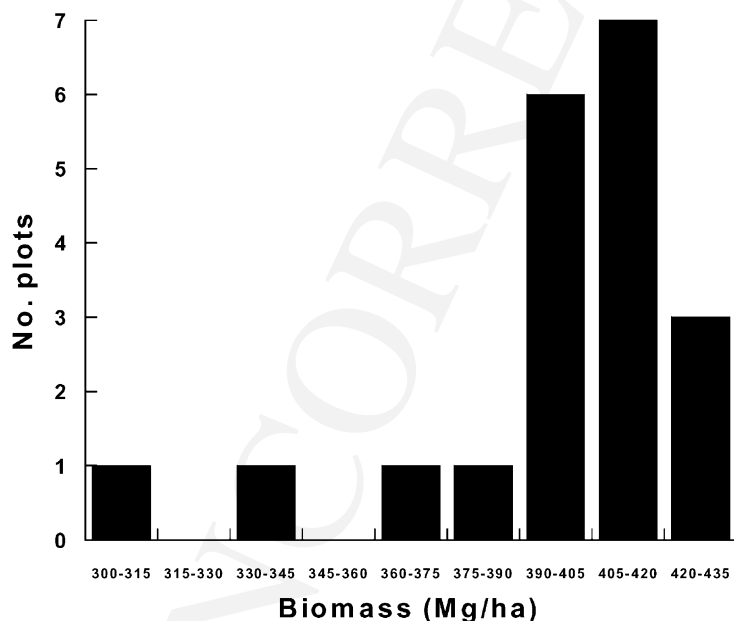


Fig. 1. Frequency distribution for TAGB in 20 1 ha plots in intact rainforests of the central Amazon.

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

275 debris (6.2%), small trees, saplings, and seedlings
 276 (5.3%), lianas (2.1%), litter (1.9%), snags (1.5%), fine
 277 downed wood debris (0.8%), and stemless palms
 278 (0.3%). Nearly nine-tenths of TAGB (89.6%) was live
 279 material, with the remainder comprised by wood
 280 debris, snags and litter (Table 2).

281 Among large trees, most of the aboveground bio-
 282 mass was concentrated in abundant, intermediate-
 283 sized (20–50 cm DBH) stems, which contained
 284 46.7% of TAGB (Table 3). Although uncommon
 285 (averaging < 10 stems ha⁻¹), very large canopy and
 286 emergent trees (≥ 60 cm DBH) contained 13.4% of
 287 TAGB, with the remainder (12.2%) in the smallest
 288 (10–20 cm DBH) size-class.

289 3.2. Correlations among biomass components

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

301 3.3. Estimating TAGB from large-tree biomass

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

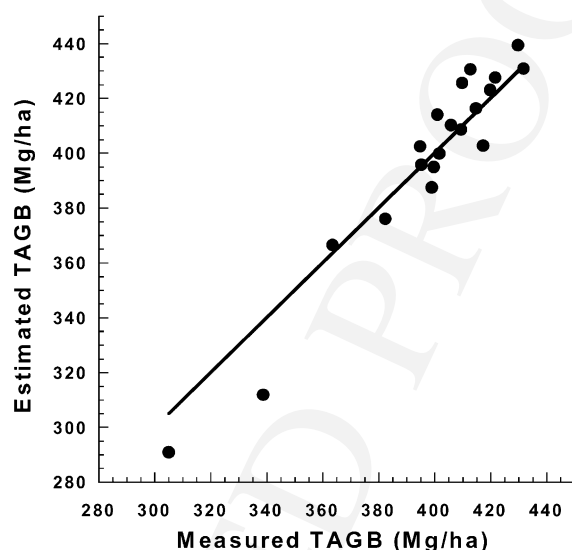


Fig. 2. Relationship between measured TAGB and estimated TAGB values (based on large-tree (> 10 cm DBH) biomass plus a 22.2% correction factor to account for the other biomass components). The line shows $Y = X$.

304 Large trees comprised over 80% of TAGB and, not
 305 surprisingly, there was a positive, linear relationship
 306 between large-tree biomass and TAGB (TAGB =
 307 $-67.7 + 0.981$ large-tree biomass; $R^2 = 94.3\%$,
 308 $P < 0.00001$; linear regression analysis). According
 309 to our data (Table 2), TAGB estimates can be derived
 310 by increasing large-tree biomass by a correction factor
 311 of 22.2% (6.5% for small trees, saplings, and seed-
 312 lings; 3.0% for lianas and stemless palms; 12.7% for
 313 dead material). When we applied this correction, there
 314 was very good agreement between measured and
 315 estimated TAGB (Fig. 2). The average difference
 316 for our 20 plots was just 2.1% (range 0.1–7.9%).

317 3.4. Predicting adequate sample size

318 The analysis of tolerable error (Fig. 3) suggests that,
 319 for a landscape such as ours, three randomly posi-
 320 tioned 1 ha plots would provide a reasonable estimate
 321 of mean TAGB if all components of aboveground
 322 biomass are directly measured. Ninety-five percent
 323 confidence intervals based on three plots would be
 324 ± 35 Mg, which represent errors of $< 9\%$ in magnitude
 325 (i.e. because TAGB averaged nearly 400 Mg ha⁻¹),
 326 whereas errors for four plots would be ± 30 Mg (7.5%

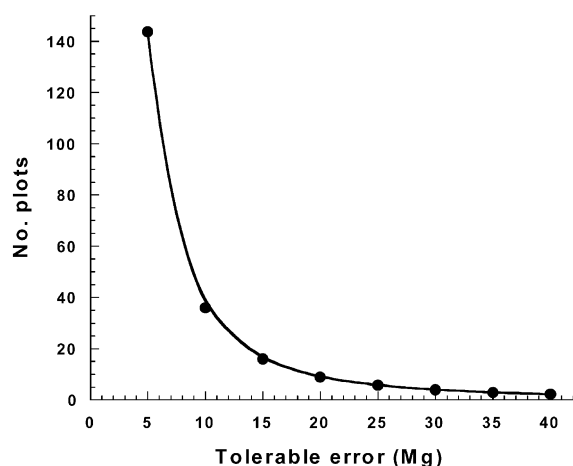


Fig. 3. Relationship between sample size (number of 1 ha plots) and tolerable error for estimating TAGB in central Amazonian rainforests. The curve was fitted by a smoothing function.

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

398 biomass. Indeed, in some forests up to a quarter of
 399 aboveground biomass is concentrated in the largest
 400 canopy and emergent trees (Clark and Clark, 1995),
 401 although in our study area nearly half of all biomass
 402 (46.7%) was in the intermediate-size-classes (20–
 403 50 cm DBH), with a lower proportion (13.4%) con-
 404 tained in the largest trees (>60 cm DBH).

405 Understory plant biomass appears moderately low
 406 in central Amazonian forests. Although the forest
 407 understory is often quite dense (with many saplings
 408 and stemless palms), herbs, epiphytes, and climbing
 409 vines are less abundant than in many other neotropical
 410 forests (Guillaumet, 1987; Gentry, 1990). In our study
 411 area, e.g. aboveground biomass of lianas was lower,
 412 and comprised a smaller percentage of total forest
 413 biomass, than in other neotropical (Klinge and Rodri-
 414 guez, 1974; Putz, 1983; Pérez-Salicrup, 1998), Asian
 415 (Ogawa et al., 1965; Kato et al., 1978), and African
 416 (Greenland and Kowai, 1960) forests. This low density
 417 of herbs, epiphytes, and lianas may result from extre-
 418 mely low soil fertility (Gentry and Emmons, 1987),
 419 and disturbance favouring lianas could also be limited
 420 by naturally low rates of tree mortality ($1.3 \pm$
 421 $0.5\% \text{ yr}^{-1}$ over the past two decades) in our study
 422 area (Laurance et al., 2001b).

423 Estimates of standing stocks of wood debris are
 424 important for validating carbon cycling models (e.g.
 425 Chambers et al., 2000). In our study area, coarse wood
 426 debris (including snags) averaged $31.0 \pm 7.7 \text{ Mg ha}^{-1}$,
 427 which is higher than other estimates for dense forests
 428 of the central Amazon ($10.5\text{--}21.2 \text{ Mg ha}^{-1}$; Martius,
 429 1997) but comparable to that in similar undisturbed
 430 forest about 20 km southwest of our study area
 431 ($29.7 \pm 12.2 \text{ Mg ha}^{-1}$; Summers, 1998). An empirical
 432 model incorporating long-term tree mortality and
 433 decomposition rate data predicts that standing stocks
 434 of biomass in coarse debris should be about 10% of
 435 that contained in large (≥ 10 cm DBH) trees (Cham-
 436 bers et al., 2001a). Based on our data, the Chambers
 437 model predicts that coarse debris should average
 438 32.6 Mg ha^{-1} , which is very close to our observed
 439 mean of 31.0 Mg ha^{-1} .

440 It is interesting that we found no significant correla-
 441 tions between large-tree biomass and the other live and
 442 dead biomass components. One might expect, e.g. that
 443 large-tree biomass would be negatively correlated
 444 with liana biomass (cf. Laurance et al., 2001b)
 445 because lianas tend to suppress tree growth and sur-

446 vival (Putz, 1984), or with wood debris and snags,
 447 because disturbed sites might have fewer large trees
 448 and more debris. The absence of such correlations
 449 might have resulted because tree mortality rates were
 450 generally low in our plots and because large-tree
 451 biomass did not span a particularly large range of
 452 values. If fragmented or logged forests were included
 453 in this study, tree mortality would have been much
 454 higher and correlations among various biomass com-
 455 ponents might well have become evident.

4.3. Developing correction factors 456

457 Our data suggest that TAGB of central Amazonian
 458 terra-firme forests can be effectively approximated by
 459 increasing biomass estimates for large (≥ 10 cm DBH)
 460 trees by 22.2%. Such correction factors have been
 461 used by many investigators (e.g. Brown and Lugo,
 462 1984, 1992; Fearnside, 1992; Brown et al., 1995), as it
 463 is far easier to measure only large trees than all live
 464 and dead components of biomass. For our 20 plots, the
 465 mean difference between estimated and measured
 466 aboveground biomass was just 2.1% (Fig. 2).

467 Our correction factor incorporates aboveground
 468 mass estimates for all significant dead and live material
 469 aside from large trees. Estimates of dead material
 470 have varied considerably among studies, ranging from
 471 2.3 to 16.6% of aboveground live biomass at 15
 472 neotropical sites (Houghton et al., in press), although
 473 the overall mean (8.7%) did not differ greatly from
 474 that in this study (10.4%). As noted above, understory
 475 plant biomass is relatively low in central Amazonia;
 476 small trees (<10 cm DBH), e.g. comprised 12% of
 477 large-tree biomass in the Rio Negro region of Vene-
 478 zuela (Jordan and Uhl, 1978) but only 6.5% in this
 479 study.

4.4. Sampling biomass in Amazonian forests 480

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

490 result is fortunate, in the sense that a limited number of
 491 plots appears to provide a reasonably good estimate of
 492 average aboveground biomass at a landscape scale.
 493 This implies that efforts to quantify Amazon forest
 494 biomass should be extensive rather than intensive;
 495 researchers should sample a large number of geogra-
 496 phically separate areas with a few plots each, rather
 497 than attempting to sample a small number of areas
 498 more intensively.

499 Our recommendation that 3–4 random samples will
 500 normally be sufficient for sampling Amazon forest
 501 biomass is based on the assumption that 1 ha plots will
 502 be used; for smaller plots, sample variances would
 503 undoubtedly be higher (Clark and Clark, 2000), espe-
 504 cially for large trees (Brown et al., 1995), meaning that
 505 more plots would be needed. We also assume that
 506 biomass in other Amazonian landscapes is not more
 507 variable spatially than that in our study area. Although
 508 few comparable data are available (cf. Clark and
 509 Clark, 2000; for a study at a 600 ha scale in Costa
 510 Rica), we believe this assumption is reasonable except
 511 where forest disturbances, edaphic features, or climate
 512 (e.g. at forest-savanna ecotones) vary strongly across a
 513 particular study area. Finally, methodological differ-
 514 ences among investigators will undoubtedly compli-
 515 cate efforts to quantify the spatial distribution of forest
 516 biomass (cf. Houghton et al., in press). Because most
 517 investigators work in a particular area, such differ-
 518 ences will tend to overestimate among-site differ-
 519 ences. Clearly, efforts to standardise biomass-
 520 estimation methods (e.g. Brown, 1997; Clark and
 521 Clark, 2000) will be just as important as expanding
 522 the geographic distribution of study sites across the
 523 Amazon basin.

524 4.5. Urgency of the problem

525 Amazon forests contain a very large stock of ter-
 526 restrial carbon (Fearnside, 1997a; Houghton et al., in
 527 press) and are probably an important carbon sink
 528 (Grace et al., 1995; Phillips et al., 1998; Malhi
 529 et al., 2000; Chambers et al., 2001a). Thus, under-
 530 standing the spatial distribution of biomass in these
 531 forests is an urgent priority. Our detailed survey
 532 indicates that, at least in the central Amazon, carbon
 533 storage in undisturbed forests is very high, suggesting
 534 that forest conversion is likely to be an even larger
 535 source of greenhouse gas emissions than previously

536 anticipated. This is important because plans are well
 537 underway to expand networks of highways, railroads,
 538 gas lines, and other major infrastructure projects in the
 539 Brazilian Amazon. By opening large expanses of the
 540 basin's remote interior to exploitative activities, these
 541 projects are predicted to sharply accelerate the pace of
 542 forest conversion and degradation (Carvalho et al.,
 543 2001; Laurance et al., 2001a). Agricultural practices
 544 in the Amazon are limited by very low soil fertility
 545 (Kauffman et al., 1994; Fearnside and Leal-Filho,
 546 2001), and the economic value of intact forests for
 547 carbon storage, biodiversity conservation, and other
 548 natural ecosystem services may ultimately be far
 549 greater than that provided by forest conversion.

Acknowledgements

550 We thank Boone Kauffman for very helpful discus-
 551 sion and Jeff Chambers and two anonymous referees
 552 for comments on the manuscript. The NASA-LBA
 553 program, Mellon Foundation, National Institute for
 554 Amazonian Research (INPA), and Smithsonian Insti-
 555 tution provided research support. This is publication
 556 number in the BDFFP technical series.
 557

References

- 559 Brown, J.K., 1974. Handbook for Inventorying Downed Woody
 560 Material. USDA Forest Service, Ogden, UT, 25 pp.
 561 Brown, S., 1997. Estimating Biomass and Biomass Change of
 562 Tropical Forests: A Primer. Forestry Paper 134, FAO, Rome.
 563 Brown, S., Lugo, A.E., 1984. Biomass of tropical forests: a new
 564 estimate based on forest volumes. *Science* 223, 1290–1293.
 565 Brown, S., Lugo, A.E., 1990. Biomass estimates for Brazil's
 566 Amazonian moist forests. In: Forest'90: Annals of the First
 567 International Symposium on Environmental Studies on Tropi-
 568 cal Rain Forests, Manaus, Brazil, pp. 46–52.
 569 Brown, S., Lugo, A.E., 1992. Aboveground biomass estimates for
 570 tropical moist forests of the Brazilian Amazon. *Interciencia* 17,
 571 8–18.
 572 Brown, S., Lugo, A.E., Iverson, L.R., 1992a. Processes and lands
 573 for sequestering carbon in the tropical forest landscape. *Water*
 574 *Air Soil Pollut.* 64, 139–155.
 575 Brown, I.F., Nepstad, D.C., Pires, O., Luz, L.M., Alechandre,
 576 A.S., 1992b. Carbon storage and land-use in extractive reserves,
 577 Acre, Brazil. *Environ. Conserv.* 19, 307–315.
 578 Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z.,
 579 Ferreira, C.A., Victoria, R.A., 1995. Uncertainty in the biomass
 580 of Amazonian forests: an example from Rondônia, Brazil.
 581 *Forest Ecol. Mgmt.* 75, 175–189.

- 582 Carvalho, G., Barros, A.C., Moutinho, P., Nepstad, D.C., 2001.
583 Sensitive development could protect the Amazon instead of
584 destroying it. *Nature* 409, 131.
- 585 Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L.V., Melack,
586 J.M., 2000. Decomposition and carbon cycling of dead trees in
587 tropical forests of the central Amazon. *Oecologia* 122, 380–
588 388.
- 589 Chambers, J.Q., Higuchi, N., Tribuzy, E.S., Trumbore, S.E., 2001a.
590 Carbon sink for a century. *Nature* 410, 429.
- 591 Chambers, J.Q., dos Santos, J., Ribeiro, R.J., Higuchi, N., 2001b.
592 Tree damage, allometric relationships, and above-ground net
593 primary production in central Amazon forest. *Forest Ecol.*
594 *Mgmt.*, in press.
- 595 Chauvel, A., Lucas, Y., Boulet, R., 1987. On the genesis of the soil
596 mantle of the region of Manaus, Central Amazonia, Brazil.
597 *Experientia* 43, 234–240.
- 598 Clark, D.B., Clark, D.A., 1995. Abundance, growth and mortality
599 of very large trees in neotropical lowland rain forest. *Forest*
600 *Ecol. Mgmt.* 80, 235–244.
- 601 Clark, D.B., Clark, D.A., 2000. Landscape-scale variation in forest
602 structure and biomass in a tropical rain forest. *Forest Ecol.*
603 *Mgmt.* 137, 185–198.
- 604 Cochrane, M.A., Alencar, A., Schulze, M.D., Souza, C.M.,
605 Nepstad, D.C., Lefebvre, P., Davidson, E., 1999. Positive
606 feedbacks in the fire dynamics of closed canopy tropical
607 forests. *Science* 284, 1832–1835.
- 608 Cummings, D.L., 1998. Total aboveground biomass and structure
609 of tropical forest delineated by Projeto RABAMBRASIL in
610 northern Rondônia, Brazil. M.Sc. Thesis. Oregon State
611 University, Corvallis, OR.
- 612 Davidson, E.A., Trumbore, S.E., 1995. Gas diffusivity and the
613 production of CO₂ in deep soils of the eastern Amazon. *Tellus*
614 *B* 47, 550–565.
- 615 Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., Quintero,
616 N.B., 1998. The quantity and turnover of dead wood in
617 permanent forest plots in six life zones of Venezuela.
618 *Biotropica* 30, 2–11.
- 619 de Oliveira, A.A., Mori, S.A., 1999. A central Amazonian terra
620 firme forest. I. High tree species richness on poor soils.
621 *Biodivers. Conserv.* 8, 1219–1244.
- 622 dos Santos, J., 1996. Análise de modelos de regressão para estimar
623 a fitomassa de floresta tropical úmida de terra-firme da
624 Amazônia Brasileira. Ph.D. Thesis. Universidade Federal de
625 Viçosa, Viçosa, Minas Gerais, Brazil.
- 626 Fearnside, P.M., 1985. Brazil's Amazon forest and the global
627 carbon problem. *Interciencia* 10, 179–186.
- 628 Fearnside, P.M., 1986. Brazil's Amazon forest and the global
629 carbon problem: reply to Lugo and Brown. *Interciencia* 11, 58–
630 64.
- 631 Fearnside, P.M., 1992. Forest biomass in Brazilian Amazonia:
632 comments on the estimate by Brown and Lugo. *Interciencia* 17,
633 19–27.
- 634 Fearnside, P.M., 1997a. Greenhouse gases from deforestation in
635 Brazilian Amazonia: net committed emissions. *Climatic*
636 *Change* 35, 321–360.
- 637 Fearnside, P.M., 1997b. Wood density for estimating forest biomass
638 in Brazilian Amazonia. *Forest Ecol. Mgmt.* 90, 59–87.
- Fearnside, P.M., 2000. Global warming and tropical land-use
639 change: greenhouse gas emissions from biomass burning,
640 decomposition and soils in forest conversion, shifting cultivation
641 and secondary vegetation. *Climatic Change* 46, 115–
642 158.
- Fearnside, P.M., Barbosa, R.I., 1998. Soil carbon changes from
643 conversion of forest to pasture in Brazilian Amazonia. *Forest*
644 *Ecol. Mgmt.* 108, 147–166.
- Fearnside, P.M., Leal-Filho, N., 2001. Soil and development in
645 Amazonia: lessons from the biological dynamics of forest
646 fragments project. In: Bierregaard, R.O., Gascon, C., Lovejoy,
647 T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: The*
648 *Ecology and Conservation of a Fragmented Forest*. Yale
649 University Press, New Haven, CT, in press.
- Gentry, A.H., 1990. Floristic similarities and differences between
650 southern central America and upper and central Amazonia. In:
651 Gentry, A.H. (Ed.), *Four Neotropical Rainforests*. Yale
652 University Press, New Haven, CT, pp. 141–157.
- Gentry, A.H., Emmons, L.H., 1987. Geographic variation in
653 fertility and composition of the understory of neotropical
654 forests. *Biotropica* 19, 216–227.
- Graça, P.M.L.A., Fearnside, P.M., Cerri, C.C., 1999. Burning of
655 Amazonian forest in Ariquemes, Rondônia, Brazil: biomass,
656 charcoal formation and burning efficiency. *Forest Ecol. Mgmt.*
657 120, 179–191.
- Grace, J., Lloyd, J., McIntyre, J., Miranda, A., Meir, P., Miranda,
658 H., Nobre, C., Moncrieff, J., Massheder, J., Malhi, Y., Wright,
659 I., Gash, J., 1995. Carbon dioxide uptake by an undisturbed
660 tropical rain forest in southwest Amazonia, 1992 to 1993.
661 *Science* 270, 778–780.
- Greenland, D.J., Kowai, J.M.L., 1960. Nutrient content of the moist
662 tropical forest of Ghana. *Plant Soil* 12, 154–174.
- Guillaumet, J.-L., 1987. Some structural and floristic aspects of the
663 forest. *Experientia* 43, 241–251.
- Houghton, R.A., 1991. Tropical deforestation and atmospheric
664 carbon dioxide. *Climatic Change* 19, 99–118.
- Houghton, R.A., Skole, D.L., Nobre, C.A., Hackler, J.L.,
665 Lawrence, K.T., Chomentowski, W.H., 2000. Annual fluxes
666 of carbon from deforestation and regrowth in the Brazilian
667 Amazon. *Nature* 403, 301–304.
- Houghton, R.A., Lawrence, K.T., Hackler, J.L., Brown, S., in press.
668 The spatial distribution of forest biomass in the Brazilian
669 Amazon: a comparison of estimates. *Glob. Change Biol.*
670 681
- Hughes, R.F., 1997. Effects of deforestation and land use on
671 biomass, carbon and nutrient pools in the Los Tuxtlas region,
672 Mexico. Ph.D. Dissertation. Oregon State University, Corvallis,
673 OR.
- INPE, 2000. Deforestation estimates in the Brazilian Amazon.
674 Instituto Nacional de Pesquisas Espaciais, São José dos
675 Campos, Brazil.
- Jordan, C., Uhl, C., 1978. Biomass of a terra firme forest of the
676 Amazon Basin. *Oecologia Plantarum* 13, 387–400.
- Kato, R., Tadaki, Y., Ogawa, H., 1978. Plant biomass and growth
677 increment studies in Pasoh Forest. *Malaysian Nature J.* 30,
678 211–224.
- Kauffman, J.B., Sanford, R.L., Cummings, D.L., Salcedo, I.H.,
679 Sampaio, E.V.S.B., 1994. Biomass and nutrient dynamics
680 691

- 696 associated with slash fires in neotropical dry forests. *Ecology*
697 74, 140–151.
- 698 Kauffman, J.B., Cummings, D.L., Ward, D.E., Babbit, R., 1995.
699 Fire in the Brazilian Amazon. I. Biomass, nutrient pools, and
700 losses in slashed primary forests. *Oecologia* 104, 397–408.
- 701 Klinge, H., Rodriguez, W., 1973. Biomass estimation in central
702 Amazonian rain forest. *Acta Cient. Venez.* 24, 225–237.
- 703 Klinge, H., Rodriguez, W., 1974. Phytomass estimation in a central
704 Amazonian rain forest. In: *Proceedings of the IUFRO Congress*
705 *on Forest Biomass Studies*, Vol. 15, Rome.
- 706 Laurance, W.F., 1998. A crisis in the making: responses of
707 Amazonian forests to land use and climate change. *Trends*
708 *Ecol. Evol.* 13, 411–415.
- 709 Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de Merona,
710 J.M., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in
711 Amazonian forest fragments. *Science* 278, 1117–1118.
- 712 Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., Laurance,
713 S.G., 1998a. Rain forest fragmentation and the dynamics of
714 Amazonian tree communities. *Ecology* 69, 2032–2040.
- 715 Laurance, W.F., Laurance, S.G., Delamonica, P., 1998b. Tropical
716 forest fragmentation and greenhouse gas emissions. *Forest*
717 *Ecol. Mgmt.* 110, 173–180.
- 718 Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P.,
719 Lovejoy, T.E., Rankin-de Merona, J.M., Chambers, J.Q.,
720 Gascon, C., 1999. Relationship between soils and Amazon
721 forest biomass: a landscape-scale study. *Forest Ecol. Mgmt.*
722 118, 127–138.
- 723 Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos,
724 H.L., Lovejoy, T.E., 2000. Rainforest fragmentation kills big
725 trees. *Nature* 404, 836.
- 726 Laurance, W.F., Cochrane, M.A., Bergen, S., Fearnside, P.M.,
727 Delamonica, P., Barber, C., D'Angelo, S., Fernandes, T., 2001a.
728 The future of the Brazilian Amazon. *Science* 291, 438–439.
- 729 Laurance, W.F., Perez-Salicrup, D., Delamonica, P., Fearnside, P.M.,
730 D'Angelo, S., Jerozolinski, A., Pohl, L., Lovejoy, T.E., 2001b.
731 Rain forest fragmentation and the structure of Amazonian liana
732 communities. *Ecology* 82, 105–116.
- 733 Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R.,
734 Quintela, C.E., Harper, L.H., Brown, K.S., Powell, A.H.,
735 Powell, G.V.N., Schubart, H.O.R., Hays, M.B., 1986. Edge and
736 other effects of isolation on Amazon forest fragments. In:
737 Soulé, M.E. (Ed.), *Conservation Biology: The Science of*
738 *Scarcity and Diversity*. Sinauer, Sunderland, MA, pp. 257–285.
- 739 Malhi, Y., Nobre, A.D., Grace, J., Kruijt, B., Pereira, M., Culf, A.,
740 Scott, S., 2000. Carbon dioxide transfer over a central
741 Amazonian rain forest. *J. Geophys. Res.* 57, 34534–34547.
- 742 Martius, C., 1997. Decomposition of wood. In: Junk, W.J. (Ed.),
743 *Decomposition of Wood*. Springer, New York, pp. 267–276.
- 744 Moraes, J.L., Cerri, C.C., Mellilo, J., Kicklighter, D., Neill, C.,
745 Skole, D., Stuedler, P., 1995. Soil carbon stocks of the Brazilian
746 Amazon basin. *Soil Sci. Soc. Am. J.* 59, 244–247.
- 747 Nelson, B.W., Mesquita, R., Pereira, J.L.G., Souza, S.G.A., Batista,
748 G.T., Couto, L.B., 1999. Allometric regressions for improved
749 estimates of secondary forest biomass in the central Amazon.
750 *Forest Ecol. Mgmt.* 117, 149–167.
- 751 Nepstad, D.C., 1989. Forest regrowth on abandoned pastures in
752 eastern Amazonia: limitations to tree seedling survival and
753 growth. Ph.D. Thesis. Yale University Press, New Haven, CT.
- 754 Nepstad, D.C., Verissimo, A., Alencar, A., Nobre, C., Lima, E.,
755 Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza,
756 E., Cochrane, M., Brooks, V., 1999. Large-scale impoverish-
757 ment of Amazonian forests by logging and fire. *Nature* 398,
758 505–508.
- 759 Ogawa, K., Yoda, K., Ogino, K., Kira, T., 1965. Comparative
760 ecological studies on three main types of forest vegetation in
761 Thailand. II. Plant biomass. *Nature Life Southeast Asia* 4, 49–
762 80.
- 763 Ott, L., Mendenhall, W., 1990. *Understanding Statistics*, 5th
764 Edition, PWS-Kent Publishing, Boston, MA.
- 765 Pérez-Salicrup, D.R., 1998. Effects of liana cutting on trees and
766 tree seedlings in a tropical forest in Bolivia. Ph.D. Thesis.
767 University of Missouri, St. Louis, MO.
- 768 Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.,
769 Vasquez, R., Laurance, S.G., Ferreira, L., Stern, M., Brown, S.,
770 Grace, J., 1998. Changes in the carbon balance of tropical
771 forests: evidence from long-term plots. *Science* 282, 439–442.
- 772 Putz, F.E., 1983. Liana biomass and leaf area of a terra firme forest
773 in the Rio Negro Basin, Venezuela. *Biotropica* 15, 185–189.
- 774 Putz, F.E., 1984. The natural history of lianas on Barro Colorado
775 Island, Panama. *Ecology* 65, 1713–1724.
- 776 Richter, D.D., Babbar, L.I., 1991. Soil diversity in the tropics. *Adv.*
777 *Ecol. Res.* 21, 315–389.
- 778 Saldarriaga, J.G., West, D.C., Tharp, M.L., Uhl, C., 1988. Long-
779 term chronosequence of forest succession in the Upper Rio
780 Negro of Colombia and Venezuela. *J. Ecol.* 76, 938–958.
- 781 Salomão, R.P., Nepstad, D.C., Vieira, I.C., 1998. Biomassa e
782 estoque de carbono de florestas tropicais primarias e secundarias.
783 In: Gascon, C., Moutinho, P. (Eds.), *Floresta Amazônica: Dinamica,*
784 *Regeneração e Manejo*. National Institute for
785 Amazonian Research (INPA), Manaus, Brazil, pp. 99–119.
- 786 Skole, D., Tucker, C.J., 1993. Tropical deforestation and habitat
787 fragmentation in the Amazon: satellite data from 1978 to 1988.
788 *Science* 260, 1905–1910.
- 789 Summers, P.M., 1998. Estoque, decomposição, e nutrientes da
790 liteira grossa em floresta de terra-firme, na Amazônia central.
791 M.Sc. Thesis, National Institute for Amazonian Research
792 (INPA), Manaus, Brazil.
- 793 Uhl, C., Jordan, C.F., 1984. Vegetation and nutrient dynamics
794 during five years of succession following forest cutting and
795 burning in the Rio Negro Region of Amazonia. *Ecology* 65,
796 1976–1990.
- 797 Uhl, C., Buschbacher, R., Serrao, E.A.S., 1988. Abandoned
798 pastures in eastern Amazonia. I. Patterns of plant succession.
799 *J. Ecol.* 76, 633–681.
- 800 Van Wagner, C.E., 1968. The line-intersect method in forest fuel
801 sampling. *Forest Sci.* 14, 20–26.