Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama

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Summary

1 We estimated the dry, living, above-ground biomass (AGB) standing stock and its turnover in a 50-hectare forest plot located in moist tropical forest on Barro Colorado Island, Panama. The estimates were obtained using inventory data collected every 5 years from 1985 to 2000, including measurements of all trees ≥ 1 cm diameter.

2 Four different allometric regressions relating trunk diameter and height with AGB were compared. Based on the most consistent method, we estimated that the Barro Colorado forest holds 281 ± 20 Mg ha^{-1} (1 Mg = 10^3 kg) of AGB, lianas included. A third of the AGB is stored in trees larger than 70 cm in diameter.

3 Stand-level AGB increment (growth plus recruitment) was highest in the period 1985–90 (7.05 ± 0.32 Mg ha^{-1} year^{-1}, mean $\pm$ 95% confidence limits based on samples of multiple hectares) and smallest in the period 1990–95 (5.25 ± 0.26 Mg ha^{-1} year^{-1}), while AGB losses were similar during the three intervals (mean 5.43 ± 0.72 Mg ha^{-1} year^{-1}). This resulted in significant differences in AGB change (defined as increment minus loss) among census intervals; including branchfalls, the AGB of Barro Colorado Island increased in 1985–90 ($+0.82 \pm 0.84$ Mg ha^{-1} year^{-1}), decreased in 1990–95 (-0.69 ± 0.82 Mg ha^{-1} year^{-1}), and increased again in 1995–2000 ($+0.45 \pm 0.70$ Mg ha^{-1} year^{-1}). The 15-year average was $+0.20$ Mg ha^{-1} year^{-1}, but with a confidence interval that spanned zero (-0.68 to 0.63 Mg ha^{-1} year^{-1}).

4 Branchfalls and partial breakage of stems had a significant influence on the AGB changes. They contributed an average of 0.46 Mg ha^{-1} year^{-1} to the AGB loss. About 5% of AGB increment was due to trees less than 10 cm in diameter.

5 To test whether the AGB of tropical forests is increasing due to climate change, we propose that in each forest type, at least 10 hectares of forest be inventoried, and that measurements of the small classes (< 10 cm diameter) as well as large size classes be included. Biomass loss due to crown damage should also be estimated.

Key-words: above-ground biomass change, carbon cycle, dry living above-ground biomass, tropical rain forest

Journal of Ecology (2003) **91**, 240–252

Introduction

Tropical forests hold large stores of carbon and play a major role in the global carbon cycle (Dixon *et al.*

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1994; Phillips & Gentry 1994; Houghton *et al.* 2001). Their importance has attracted a great deal of experimental and theoretical attention (Malhi *et al.* 1999; Malhi & Grace 2000), and several recent advances have led to a variety of estimates of carbon stocks and fluxes (Malhi *et al.* 1998; Clark *et al.* 2001b; Gurney *et al.* 2002). Remotely sensed data have been used to estimate above-ground biomass (Dubayah & Drake 2000; Drake

et al. in press). Carbon fluxes have been estimated from *in situ* micrometeorological measures (Wofsy *et al.* 1993; Grace *et al.* 1995; Goulden *et al.* 1996; Malhi *et al.* 1998) and from inverse modelling of regional carbon fluxes (Rayner *et al.* 1999; Bousquet *et al.* 2000; Gurney *et al.* 2002). Despite these efforts, there remains much uncertainty about the role of tropical forests in the global carbon cycle (Prentice & Lloyd 1998; Malhi & Grace 2000; Gurney *et al.* 2002). In particular, it remains unclear whether old growth tropical forests represent a net sink of atmospheric carbon and how they will respond to future climate changes (Lloyd *et al.* 1995; Grace *et al.* 1995; Lloyd & Farquhar 1996; Körner 1998).

The traditional technique for estimating forest carbon stocks and fluxes is from forest inventories and allometric relationships between the above-ground biomass (AGB) of a tree and its trunk diameter (Brown *et al.* 1989; Brown 1997; Clark *et al.* 2001a). Potential changes in the other carbon pools of the ecosystem (litter, coarse woody debris, root biomass, soil organic matter) cannot be assessed with this technique. However, given that AGB represents a large fraction of total forest carbon stocks, this technique offers a practical and accurate way of evaluating current hypotheses concerning the carbon balance of tropical forests. For example, Phillips *et al.* (1998) used a data set of over 50 lowland forest inventories in Central and South America, to conclude that the stock of AGB is increasing in tropical forest ecosystems. However, there remain several issues concerning the interpretation of tropical forest inventories, including measurement error (Clark 2002), sampling error, and spatial variation (Keller *et al.* 2001). Keller *et al.* (2001) found that at least 25 quarter-hectare plots are required to estimate AGB of a given forest type to within 20% with 95% confidence. Yet, only 20 of the 50 Neotropical sites used in the study of Phillips *et al.* (1998), encompassing a large array of forest types, were larger than 1 ha, and only seven met Keller *et al.*'s (2001) minimum size requirement for a reliable AGB estimate.

Moreover, unlike standing stock, there is no quantitative estimate of the sampling effort required to obtain a reliable estimate of AGB change. As AGB change represents the difference of two imperfectly known quantities, it is reasonable to assume that estimates of AGB change may require considerably more sampling effort than estimates of AGB stocks. Thus, large-scale repeated surveys may be required to estimate AGB changes in a tropical forest.

The 50-hectare Forest Dynamics Plot on Barro Colorado Island (BCI) in Panama has been extensively studied since 1981 (Hubbell & Foster 1983). Careful and repeated measurements are available for all trees in the 50-ha plot, including smaller diameter classes (all trees ≥ 1 cm in diameter have been measured every 5 years). Here, we estimate the AGB of the Barro Colorado forest plot, with a special focus on spatial sampling error. We also appraise the magnitude of AGB changes (growth, recruitment, and loss), including smaller diameter classes, and consider how sample area affects these estimates.

Materials and methods

STUDY SITE AND DATA

The study was conducted in the moist lowland tropical forest on Barro Colorado Island (BCI), a research reserve of the Smithsonian Tropical Research Institute. Rainfall averaged 2637 ± 462 mm year^{-1} for the period 1929–2001, with a 4-month dry season between January and April (Condit *et al.* 2001). Mean humidity is 77.9%, and daily maximum and minimum temperatures are 30.81 °C and 23.42 °C (1971–2001 average). Further meteorological information about BCI is available at http://www.stri.org/tesp. The forest is partly deciduous, with about 10% of canopy leaves dropped at the peak of the dry season (Condit *et al.* 2001). The 50-ha plot was established in 1981 (Hubbell & Foster 1983, 1986; Condit 1995, 1998; Condit *et al.* 1995; Leigh 1999). All stems ≥ 1 cm in trunk diameter were mapped, measured and identified to species between 1981 and 1983 (taxonomy follows Croat 1978; D'Arcy 1987, or Condit *et al.* 1996, unless specified otherwise). The census was repeated in 1985 and every 5 years thereafter.

More than 200 000 individual trees of over 300 species have been recorded in each census. From 1985 forward, trunk diameter (henceforth referred to as diameter) was measured to the nearest millimetre at 1.30 m above ground or above buttresses. If a trunk was swollen at 1.30 m, the measurement was taken 20 mm lower (Condit 1995, p. 50). Points of measure (POM) were painted on buttressed stems during 1990–2000. In 1982, measurements were not always taken above buttresses, so we excluded the 1982 census from our analysis. Multi-stemmed, broken and re-sprouting trees were recorded and handled separately in growth analyses. Measurement problems were handled during each census by checking field sheets for consistency and by re-measuring problematic trees. A subsample of 1715 trees was re-measured to assess independently the quality of diameter data. About 96% of the data had a relative error of less than 10%. For a more detailed description of the field methodology, the reader is referred to Condit (1998).

ESTIMATE OF ABOVE-GROUND BIOMASS STOCK

We used four allometric regression equations to estimate AGB as a function of stem diameter, tree height and wood specific gravity, and different regressions for saplings and lianas.

Height

We have measured heights of 1414 trees of 83 species in the BCI plot using a Laser rangefinder (see O'Brien

et al. 1995 on part of this data set). Height was modelled as a function of diameter using an asymptotic allometric regression (Thomas 1996):

$$H = c(1 - \exp(-aD^b)) \qquad \text{eqn 1}$$

where c, a and b are species-specific parameters (see Table A1 in Supplementary Material). This model allows a height asymptote c; standard log-log regressions without the asymptote can considerably overestimate the size of large trees (Thomas 1996). For some species, however, the value of c does not correspond to a realistic height asymptote (e.g. 394 m for *Alchornea costaricensis*, see Table A1). In this situation, the asymptote in height is never reached, and equation 1 is equivalent to $H = caD^b$. For species lacking their own regression, an equation based on combined data from all species was used. Only one common species, *Gustavia superba* (Lecythidaceae), lacked its own regression.

Wood density

Wood specific gravity (oven-dry weight divided by green volume) is known for 123 species occurring in the BCI plot, mostly from the literature (Ovington & Olson 1970; van der Slooten *et al.* 1971; Chudnoff 1984; Wieman & Williamson 1989; Chichignoud *et al.* 1990; Lorenzi 1992; Malavassi 1992; Brown 1997; Fearnside 1997), but also from field work at BCI (H.C. Muller-Landau, unpublished results). For some species, only wood density at 12% moisture content was available; these were converted to wood specific gravity by multiplying by 0.8 (Brown 1997). All estimates of wood density are reported in Table A1. For the remaining species, we used the average of the mean density of these 123 species (0.54 g cm^{-3}). This average is lower than the mean reported by Brown (1997) for tropical America (0.60 g cm^{-3}, averaged over 470 species).

AGB estimation methods

We selected four AGB regression models from the literature (Brown *et al.* 1989; Chambers *et al.* 2001; Chave *et al.* 2001; Table 1). We examined how well each method predicted the results of the other methods using 200 subplots of 0.25 ha, and we selected the equation that had the highest mean correlation with the other three methods. These allometric models were constructed from samples of trees > 10 cm diameter. We therefore estimated the AGB of trees < 10 cm diameter using another model constructed from a sample of 66 trees < 10 cm harvested in the Los Tuxtlas region, Mexico (Hughes *et al.* 1999; Table 1). To account for the variation in wood specific gravity, we assumed that this equation was valid for species close to the mean wood specific gravity of the plot (0.54). For each tree < 10 cm, we then applied the regression of Hughes *et al.* (1999), then multiplied the obtained value by the tree's wood specific gravity divided by 0.54.

Liana AGB was estimated separately. An allometric equation was developed from two data sets to estimate the AGB of lianas: one for 17 individuals in Venezuela (Putz 1983) and one for 19 individuals in Brazil (Gerwing & Farias 2000). The allometric equation was $\ln(AGB) = 0.0499 + 2.053 \ln(D)$, where AGB is expressed in kg and the diameter in cm (S. J. DeWalt & J. Chave, unpublished data). We combined this information with a liana inventory in the BCI forest (Putz 1984) in which the diameter of all lianas above 1 cm was measured in 10 0.1 ha plots (40 × 25 m) near the 50-ha plot. We converted the liana diameters into AGB using the regression equation, and summed over the lianas to get a stand-level estimate of liana per ha.

To calculate the minimal sampling effort required to estimate the mean AGB, we quantified sampling error as follows. First, we computed sampling distributions by subsampling the data using subplots that ranged in size from 10 × 10 m (0.01 ha) to 100 × 100 m (1 ha). Then we computed the 2.5th percentile of the sampling distribution, which we denote as $AGB_{2.5}$, and the 97.5th percentile of the sampling distribution, which we denote as $AGB_{97.5}$. For subplots smaller than 1 ha, we computed the 95% confidence interval using the formula

$$CI95 = \frac{AGB_{97.5} - AGB_{2.5}}{\sqrt{N}} \qquad \text{eqn 2}$$

where N is the number of subplots. For 1 ha subplots, there are just 50 samples, so we were unable to obtain the 95% confidence intervals directly; instead we checked that the AGB distribution across subplots was Gaussian and used the formula $CI95 = 1.98 \times \sigma/\sqrt{N}$ to

Table 1 Regression equations used to estimate total above-ground biomass in the BCI forest. The first four were applied only to trees ≥ 10 cm diameter. D is the diameter measured at 1.30 above ground, below irregularities, or above buttresses (in cm). ρ is the oven-dry wood specific gravity (in g cm^{-3}). ρ_{av} is the mean wood specific gravity of the plot (0.54 g cm^{-3}). H is total tree height (in m) and AGB is the above ground biomass (in kg tree^{-1})

Method	Regression equation	Sample size	Minimal d.b.h.	Location	Reference
1	$AGB = \exp[-2.00 + 2.42 \ln(D)]$	378	10 cm	Pantropical	Chave *et al.* (2001)
2	$AGB = \exp[-0.37 + 0.333 \ln(D) + 0.933 \ln(D)^2 - 0.122 \ln(D)^3]$	316	5 cm	Brazil	Chambers *et al.* (2001)
3	$AGB = \exp[-3.114 + 0.972 \ln(D^2 H)]$	168	5 cm	Pantropical	Brown *et al.* (1989)
4	$AGB = \exp[-2.409 + 0.952 \ln(\rho D^2 H)]$	94	10 cm	Pantropical	Brown *et al.* (1989)
Saplings	$AGB = \rho/\rho_{av} \exp[-1.839 + 2.116 \ln(D)]$	66	1 cm	SE Mexico	Hughes *et al.* (1999)

estimate the confidence interval, where σ is the standard error. In addition, we computed the spatial auto-correlation among plots for the various estimated quantities (Legendre & Legendre 1983, p. 349).

Habitat variation in above-ground biomass

We examined variation in AGB across diameter classes and habitats. We used the habitat classification of Harms *et al.* (2001), who assigned each 20×20 m sub-plot of the 50-ha plot into one of seven possible categories: young forest (48 plots, forest cleared 150 years ago), riparian forest (32 plots, referred to as 'stream'), swamps (30 plots), forest on slopes (284), on the low plateau (620), and on the high plateau (170).

BIOMASS CHANGES

Above-ground biomass change, denoted ΔAGB, is due to growth *G*, plus recruitment *R*, minus loss *M*. More precisely, *G* can be defined as the annual increment of AGB due to the growth of trees that were alive during two successive censuses, *M* as the annual loss of AGB due to the mortality of trees that died by the second interval, and *R* as the annual ingrowth of AGB due to recruitment into the minimal diameter class between the first and second censuses. Clark *et al.* (2001a) refer to AGB increment as the sum of AGB growth plus recruitment.

Denoting the above ground biomass of tree *i* at time *t* by $AGB_i(t)$ and defining its increment between census time *t* and census time $t + \Delta t$ as

$$\Delta AGB_i(t) = AGB_i(t + \Delta t) - AGB_i(t) \qquad \text{eqn 3}$$

The total biomass is $AGB = \sum_i AGB_i(t)$, and the total increment is, in $Mg\ ha^{-1}\ y^{-1}$

$$G = \sum_i \frac{\Delta AGB_i(t)}{\Delta t} \qquad \text{eqn 4}$$

where the sum is taken over all the surviving trees in the census plot. The precise interval of measurement between two censuses, Δt, may vary among trees.

By convention, AGB loss is defined by

$$M = \frac{1}{T} \sum_{i \in EM} AGB_i(t) \qquad \text{eqn 5}$$

where *EM* is the subset of trees alive at time t_i and dead at the next census, and *T* is the mean census period (5 years). Clark *et al.* (2001a) define AGB recruitment *R* as given by equations 3 and 4, where AGB at time *t* is the AGB of a minimum-sized tree, and AGB at time $t + \Delta t$ is that of the recruited tree. The alternative hypothesis is to assume that the AGB of the tree before it recruited was zero (Y. Malhi *et al.*, unpublished results). When the minimal tree diameter is 1 cm, we tested that both assumptions yield almost undistinguishable results.

Using discrete time steps leads to a slight underestimate of AGB increment and loss because trees that die between two censuses grow some biomass before they die (Delaney *et al.* 1998). Trees that die between censuses survive, on average, half of the census period Δt. During this period, they grow a fraction $(G + R)/AGB$ of biomass above ground, thus the additional growth term is roughly $(G + R)/AGB \times M \times (T/2)$. If $G + R = M = 5$ Mg ha^{-1} year^{-1}, $T = 5$ year, and AGB = 300 Mg ha^{-1} this additional term would be about 0.2 Mg^{-1} ha^{-1} year. However, AGB losses should also be inflated by a term of the same magnitude. Thus, the estimates of AGB change are unaffected.

To reduce measurement error in calculating fluxes, problematic records were checked individually. There were 788 trees (0.3% of the total sample, 2.7 m² ha^{-1}) with anomalous diameter increases (> 35 mm year^{-1}) or decreases (< 5 mm year^{-1}) between two censuses. The diameter measurement in each of four censuses, 1985–2000, were checked in all 788 cases, and most had one obviously outlying diameter record. We used the three other measurements to replace the egregious one with an interpolated value. After these changes, we were left with five anomalous measurements, large changes where we could not easily detect the error. We excluded these five from estimates of AGB growth and loss (this is equivalent to setting the growth of these trees to zero). In addition, for 5071 cases (out of 591 099) where the point-of-measure of stem diameter changed between censuses, we assumed a zero change: these trees (*c*. 10% of the stand basal area) were excluded from AGB flux estimates. We also tested the importance of these excluded trees in the estimate of AGB change by assuming that these trees had had an average growth in diameter.

Major trunk or crown loss above the POM was noted in the field in 1985 for all trees, and in 1990–2000 for trees ≥ 10 cm diameter. In 2002, we checked a random sample of 191 of the trees marked as damaged in 2000. For each, we estimated the height at which the trunk broke and the amount of crown lost, compared the broken height to the predicted height from regression, and assumed that trunk biomass was reduced by the fraction of height lost. We further assumed that crown biomass was reduced by the amount of crown that we estimated to be missing. If crown AGB is 25% of total AGB (Malhi *et al.* 1999; J. Chave, unpublished results), we can convert these figures to a crude estimate of the percentage AGB lost to the break. The mean percentage lost per tree was multiplied by the number of trees recorded with a new break above the POM in each census period. For trees < 10 cm diameter, we had to assume that the percentage AGB loss per tree was the same as it was in the sample of trees > 10 cm diameter we checked in 2002, as no damaged smaller trees were checked.

All trees recorded as broken below the POM, but which survived and sprouted a new stem, were noted in each census (Condit 1998). Here, we treat these cases

as mortality and then recruitment in the AGB flux estimates.

Results

ABOVE-GROUND BIOMASS STOCK

Estimate of above-ground biomass stock

The four equations yielded comparable but statistically different estimates of AGB (Table 2). The variation among the methods was 26% of the mean estimate. Method 4 had the highest correlation with other methods, and method 2 the lowest (Table 3). Using method 4, the mean estimated AGB of trees above 1 cm diameter was 274 Mg ha^{-1}. The mean basal area was 31 m^2 ha^{-1}. Hereafter, we report only the results obtained by method 4.

Table 2 Above-ground tree biomass in the 50-ha plot at BCI, using the first four regression methods described in Table 1. Liana and sapling AGB is excluded

	Mean AGB (Mg ha^{-1})				
Method	1985	1990	1995	2000	Average
1	261	269	263	267	265
2	308	317	314	317	314
3	296	302	296	299	298
4	272	277	273	275	274

Table 3 Matrix of correlations among the four regression methods, based on subplots of 1/4 hectare. The last line shows the average of the cross-correlations for each method. The most representative regression is the one with highest mean r^2, i.e. method 4

r^2	1	2	3	4
1	1	0.617	0.822	0.742
2	*	1	0.559	0.657
3	*	*	1	0.849
4	*	*	*	1
Mean r^2	0.729	0.613	0.765	0.806

The five species holding the largest proportion of AGB were *Trichilia tuberculata* (22.0 Mg ha^{-1}), *Quararibea astrolepsis* (19.3 Mg ha^{-1}), *Alseis blackiana* (11.2 Mg ha^{-1}), *Ceiba pentandra* (10.7 Mg ha^{-1}) and *Prioria copaifera* (10.1 Mg ha^{-1}). See Table A2 in Supplementary Material for a full list of AGB per species. We estimated that the plot has 7.7 Mg ha^{-1} of liana AGB. This is close to the values given in DeWalt *et al.* (2000) for two transects in the old-growth forests of BCI (6.46 and 4.33 Mg ha^{-1}). Including lianas, the mean AGB stock in the BCI forest was 281 Mg ha^{-1}. The main tree census does include palms, but they contributed only a small fraction of the AGB (1.5 Mg ha^{-1}, i.e. about 0.5%).
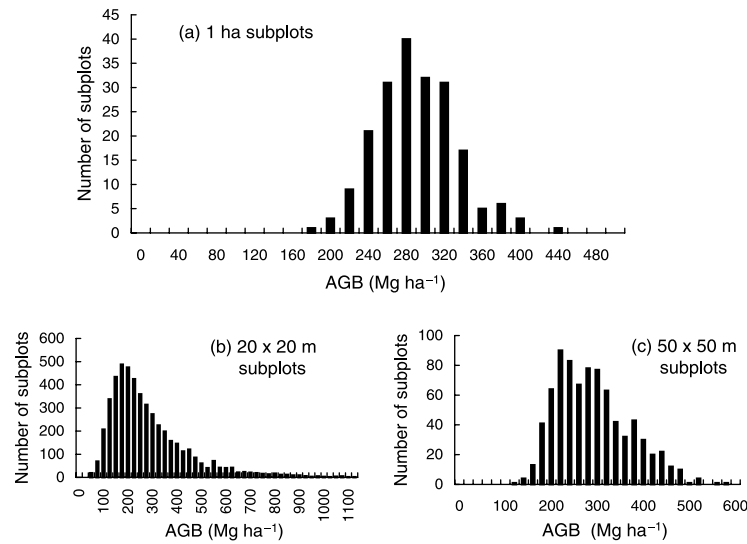
Variation in AGB with diameter class

Less than 1% of the total AGB was in stems < 5 cm diameter, and less than 5% in stems < 10 cm diameter (Table 4). The class contributing most to the AGB was 30–40 cm diameter. About 50% of the AGB was in stems < 50 cm diameter and 90% in stems < 130 cm (only 72 trees were > 130 cm). Trees commonly defined as large, that is above 70 cm in diameter (Clark & Clark 1996), numbered 521 overall and carried 32% of the AGB (Table 4).

Variation in AGB across the plot

Variation in AGB within the 50-ha plot was high (Fig. 1). Among 0.25-ha plots, the mean standard deviation was 128 Mg ha^{-1}, and the 95% confidence interval on the mean AGB was around 20 Mg ha^{-1}. For small subplot sizes, the distribution of AGB estimates was strongly skewed to the left, but as subplot size increased, the sampling distribution was more symmetric (Fig. 1). The confidence interval on the AGB estimate did not depend strongly on the size of the subplot (Table 5). AGB was not spatially autocorrelated in any year at any subplot size (*t*-test $r^2 < 0.001$).

The 95% confidence interval for 200 subplots of 0.25 ha was 20.1 Mg ha^{-1}, or ± 3% of the mean (Table 5).

Table 4 Cumulative frequency distribution for total AGB in the 50-ha plot for diameter classes (mean of four censuses)

Diameter class (cm)	Number of stems per d.b.h. class	AGB per d.b.h. class (Mg ha^{-1})	Biomass (% total)	Cumulative biomass (% total)
1–5	175 580	4.67	1.70	100.00
5–10	29 016	6.91	2.52	98.30
10–20	13 319	28.92	10.57	95.78
20–30	3 635	30.49	11.14	85.21
30–40	1 787	32.85	12.01	74.06
40–50	954	30.85	11.28	62.06
50–60	556	27.44	10.03	50.78
60–70	324	22.95	8.39	40.75
70–80	175	17.16	6.27	32.36
80–100	179	25.30	9.25	26.09
100–125	84	17.23	6.30	16.84
125–150	33	9.25	3.38	10.54
150–200	24	12.49	4.57	7.16
200–250	9	7.08	2.59	2.59

Fig. 1 Above-ground biomass in subplots of the BCI permanent sample plot. (a) number of 1-ha subplots per AGB class in the 50-ha plot. (b) 20 × 20 m subplots, 50 × 50 m subplots.

Table 5 Error analysis for mean AGB. The two-sided 95% confidence interval was estimated using subplots that varied both in area and number (see equation 2)

Subplot size	Number of subplots	CI95	95% CI (in Mg ha⁻¹) from one 1-ha plot	Minimal number of subplots* (Mg ha⁻¹)
10 × 10	5000	17.4	123	481
10 × 20	2500	18.7	132	279
20 × 20	1250	20.0	142	160
20 × 50	500	21.4	151	73
50 × 50	200	20.1	142	26
50 × 100	100	22.4	158	16
100 × 100	50	23.5	166	9

*Minimal number of subplots required to know the mean biomass with 20% error (±10%) within the 95% confidence interval.

Table 6 Mean and 95% confidence limits of total AGB (in Mg/ha) in various habitat types of the 50 ha plot at BCI. Habitats after the classification of Harms *et al.* (2001)

Forest type	Number of subplots	Mean number of trees > 1 cm	Mean basal area (m² ha⁻¹)	1985	1990	1995	2000	Mean
Young forest	48	4690	27.15	207.2 ± 14.5	215.0 ± 15.0	214.8 ± 15.4	218.7 ± 14.1	213.9 ± 14.7
Stream	32	4130	26.09	194.4 ± 20.0	219.7 ± 23.2	230.7 ± 23.0	232.3 ± 24.7	219.3 ± 22.7
Mixed	66	4303	28.06	258.3 ± 32.3	257.8 ± 23.8	255.9 ± 22.2	261.8 ± 21.5	258.6 ± 24.6
Low plateau	620	4704	30.00	267.3 ± 7.9	270.1 ± 8.0	263.0 ± 6.9	268.5 ± 7.7	267.2 ± 7.6
High plateau	170	4289	31.74	265.9 ± 13.1	279.7 ± 15.1	274.7 ± 13.7	276.1 ± 14.3	274.1 ± 14.0
Swamp	30	2580	33.24	277.0 ± 32.3	302.2 ± 35.2	310.2 ± 37.5	314.3 ± 37.4	301.0 ± 35.5
Slope	284	4501	34.91	307.3 ± 14.4	304.1 ± 12.0	303.3 ± 12.6	301.2 ± 11.5	304.0 ± 12.6
Mean	1250	4514	31.11	271.8 ± 11.0	275.8 ± 10.7	271.9 ± 10.8	274.9 ± 10.8	273.6 ± 10.8

If the total area sampled were 1 ha, the 95% confidence interval would have been 142 Mg ha⁻¹. Following this route, it is easy to show that a minimum of 26 such subplots would be needed to estimate the AGB within ± 10% of the mean.

Variation of above-ground biomass with habitat

The section of young forest held between 207 and 219 Mg ha⁻¹, significantly less than the overall average

AGB of 274 Mg ha⁻¹ (Table 6). Mean basal area was also lower than in the rest of the forest, at 27.1 m² ha⁻¹. The AGB of the young forest did not change significantly over 15 years.

Riparian forests also had a significantly lower AGB than average (219 ± 23 Mg ha⁻¹), and a lower mean basal area (26.1 m² ha⁻¹, Table 6). At the other extreme, forests on slopes had a significantly higher AGB than the average (304 ± 13 Mg ha⁻¹, $P < 0.05$), a high basal area (34.9 m² ha⁻¹), but average tree density, suggesting

Table 7 AGB changes (in Mg ha^{-1} year^{-1}) in the 50-ha plot of BCI for three census intervals. Mean growth, loss and recruitment for all trees over 1 cm diameter and over 10 cm diameter, and 95% confidence limits calculated across the 1250 20 × 20 m subplots. AGB change is growth plus recruitment minus loss

	1985–90		1990 –1995		1995 –2000	
	Trees > 1 cm	Trees > 10 cm	Trees > 1 cm	Trees > 10 cm	Trees > 1 cm	Trees > 10 cm
Growth	6.47 (6.31,6.85)	5.26 (5.12,5.64)	5.04 (4.92,5.28)	4.39 (4.28,4.62)	5.81 (5.68,6.06)	5.05 (4.92, 5.28)
Recruitment	0.58 (0.54,0.89)	0.74 (0.67,1.05)	0.21 (0.20,0.30)	0.38 (0.33,0.53)	0.11 (0.11,0.18)	0.24 (0.21,0.34)
Loss	5.60 (0.45,6.40)	5.50 (5.35,6.30)	5.34 (5.19,6.24)	5.18 (5.03,6.06)	5.34 (5.19,6.23)	5.22 (5.07, 6.12)
Loss in crown damage	0.62	0.64	0.61	0.64	0.13	0.24
Change	0.82 (−0.09,1.38)	0.08 (−0.77,0.60)	−0.69 (−1.59,−0.34)	−1.19 (−2.05,−0.78)	0.45 (−0.39,0.81)	−0.06 (−0.16,0.29)

Table 8 AGB increment (growth plus recruitment), AGB loss (excluding branchfalls), and change across diameter classes. All the quantities are in Mg ha^{-1} year^{-1}

	1985–90			1990–1995			1995–2000		
Diameter	Increment	Loss	Change	Increment	Loss	Change	Increment	Loss	Change
1–5	1.10	0.09	1.01	0.49	0.17	0.33	0.44	0.15	0.30
5–10	0.66	0.12	0.54	0.55	0.14	0.41	0.50	0.17	0.33
10–20	1.04	0.55	0.49	0.98	0.55	0.43	1.01	0.65	0.36
20–30	0.86	0.56	0.30	0.89	0.54	0.35	0.95	0.64	0.31
30–40	0.83	0.74	0.09	0.64	0.62	0.02	0.82	0.64	0.18
40–50	0.77	0.78	−0.01	0.46	0.62	−0.16	0.61	0.61	0.00
50–60	0.61	0.75	−0.14	0.38	0.63	−0.25	0.48	0.48	0.00
60–70	0.46	0.43	0.03	0.22	0.49	−0.27	0.31	0.46	−0.15
70–80	0.32	0.38	−0.06	0.15	0.39	−0.24	0.22	0.24	−0.02
80–100	0.25	0.39	−0.14	0.17	0.45	−0.28	0.26	0.56	−0.30
100–125	0.10	0.44	−0.34	0.14	0.36	−0.22	0.18	0.47	−0.29
125–150	0.01	0.05	−0.04	0.03	0.00	0.03	0.06	0.06	0.00
150–200	0.04	0.08	−0.04	0.09	0.17	−0.08	0.05	0.07	−0.02
200–250	0.00	0.24	−0.24	0.06	0.21	−0.15	0.03	0.14	−0.11

that this habitat holds more large trees than the rest of the forest. The swamp had a typical AGB of 301 ± 35 Mg ha^{-1} but this figure increased from 277 to 314 Mg ha^{-1} between 1985 and 2000.

ABOVE-GROUND BIOMASS CHANGE

AGB changes

During the three census intervals, AGB growth varied between 5.04 Mg ha^{-1} year^{-1} and 6.47 Mg ha^{-1} year^{-1}. AGB loss was more consistent, between 5.34 and 5.60 Mg ha^{-1} year^{-1} (Table 7). These figures exclude the growth and loss missed in dead trees, which we estimated at 0.2 Mg ha^{-1} year^{-1}. AGB recruitment was much larger during 1985–90 (0.58 Mg ha^{-1} year^{-1}) than during the subsequent intervals (< 0.21 Mg ha^{-1} year^{-1}).

Trees with major crown damage lost, on average, 42% of their AGB. This leads to an estimate of 0.62, 0.61, and 0.13 Mg/ha/year AGB loss due to crown damage in the three census intervals.

AGB change was positive during 1985–90, but this increase was not quite significantly different from zero (Table 7). During the 1990–95 interval, AGB change was significantly negative. Finally, during the 1995–2000 interval, AGB change was positive but not

significantly so. The 15-year average AGB change was +0.20 Mg ha^{-1} year^{-1} (95% CL [−0.68, 0.63]).

These estimates assume a zero growth in trees measured at different points of measure. Under the alternative assumption of a mean growth rate for these trees, they grew 0.63, 0.56 and 0.12 Mg ha^{-1} year^{-1} in the three census intervals.

As most of the available censuses are based on trees above 10 cm diameter (e.g. Phillips *et al*. 1998), we recalculated these fluxes excluding trees less than 10 cm diameter. This yielded different results (Table 7): the 15-year average of AGB change was almost significantly negative (−0.39 Mg ha^{-1} year^{-1}, 95% CL [−1.00, 0.04]).

Estimate of AGB change by diameter class

AGB increment was a steadily decreasing function of diameter, from a maximum of around 1 Mg ha^{-1} year^{-1} in 1–10 cm and 10–20 cm trees (Table 8, Fig. 2). Most of the AGB increment was in the diameter class 1–25 cm and as much as 20% was in the 1–10 cm class. AGB loss was more evenly distributed, with a median in 30–50 cm trees (Fig. 2). AGB change was positive in the 1–30 cm diameter class but negative in the 40–110 cm class. For larger diameter classes, changes were not significantly different from zero.
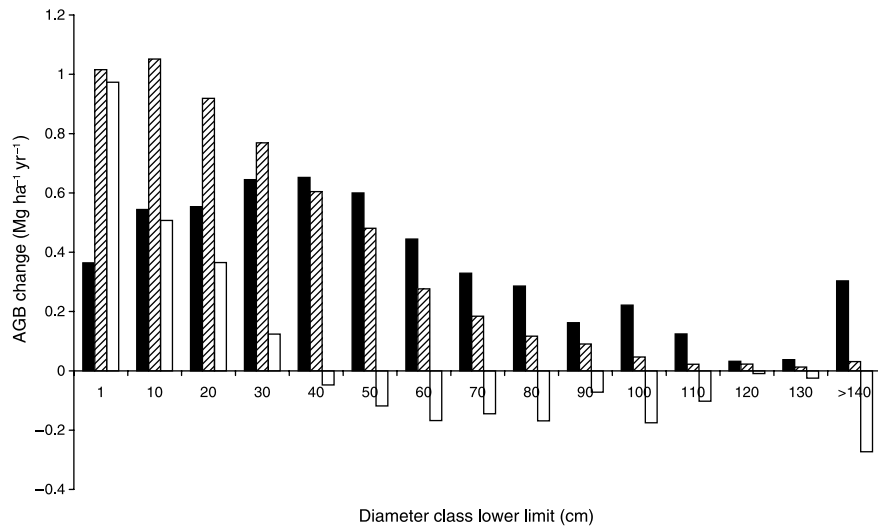
Fig. 2 Changes in AGB by diameter class. Black, net loss; shaded, net growth; white, net change. In the first diameter class (1–10 cm), AGB change includes ingrowth (net recruitment) of newly measured saplings. The last diameter class includes all trees more than 140 cm diameter. Curves were averaged over the period 1985–2000.

Variation in AGB change across the plot

Using 95% confidence intervals, we calculated the minimum area that should be sampled to estimate AGB growth or mortality within ± 10% of their means (see equation 2). Averaging over the three 5-year periods, we found that a plot of at least 9 ha would be required to estimate the AGB increment, and 40 ha the AGB loss. Finally, we used 95% confidence intervals to compute how much area should be sampled to test whether the observed increase in AGB was significant: the mean AGB change over 15 years was + 0.21 Mg ha^{-1} year^{-1} with a 95% confidence of –0.68 to 0.63 Mg ha^{-1} year^{-1}. As we found no spatial autocorrelation in AGB growth or mortality across subplots ($r^2 < 0.001$ in all cases), we might assume that the BCI plot is representative of the surrounding forest; if so, a significant trend would be detected if at least 60 ha had been censused.

Variation in turnover across forest types

We did not find a correlation between AGB stock and AGB change across 20×20 m subplots ($r^2 < 0.05$). However, AGB change varied among forest types. The highest AGB increase was in the swamp (+2.69 Mg ha^{-1} year^{-1}), followed by streamsides (+2.28 Mg ha^{-1} year^{-1}) and secondary forest (+1.28 Mg ha^{-1} year^{-1}). During the period 1985–90, swamp and riparian forests had the highest increase, above 4 Mg ha^{-1} year^{-1}, twice the amount observed in drier habitats. During the period 1990–95 only the wetter habitats (swamp and riparian forests) had significant increase in AGB (over 2 Mg ha^{-1} year^{-1}). Between 1985 and 2000, four of the seven habitats had a significant positive change in AGB ($P < 0.05$), driven mostly by the increase during the period 1985–90.

Discussion

ACCURACY OF THE ESTIMATES

The estimated above-ground biomass at BCI, 281 Mg ha^{-1} with lianas, is within the range of values obtained by harvest experiments, which vary from 200 to 500 Mg ha^{-1} (Brown 1997; Clark *et al.* 2001b). We found that large trees (> 70 cm diameter) held about a third of the biomass, compared with 14% to 30% at La Selva, Costa-Rica (Clark & Clark 2000). Reliable biomass estimates for large trees are therefore important, and errors associated with large stems can lead to substantial estimation errors.

With a sample of 50 ha, confidence in the estimated AGB was ± 20 Mg ha^{-1}, or less than 10% of the estimated AGB. But sampling error was high; single hectares of the 50 ha plot varied in AGB from as low as 170 Mg to over 400 Mg, and a single, 1-ha plot would have provided very little information about the biomass of the surrounding forest. Sampling error as we define it here has two fundamentally different sources. One is caused by the fact that sample sizes are not infinite and that there are errors in measurement. This is sampling error in the narrow sense: multiple estimates from a homogeneous population will not be identical. The second source is spatial variation in AGB, not due to error but due to the fact that different parts of the forest are really different. However, as we found minimal spatial autocorrelation in AGB estimates, spatial variation should be similar to strict sampling error. Regardless, both are relevant to studies of tropical forest AGB: together they determine the quality of the estimate of a forest's carbon stock.

Regressions used for estimating biomass are an additional source of error (Ketterings *et al.* 2001). The four methods we used resulted in AGB estimates varying

from 267 to 346 Mg ha^{-1}, an error of ± 10%, comparable with sampling error across 50 ha. An obvious shortcoming of most regression methods is that all species from these highly diverse forests are lumped together, ignoring differences in architecture (King 1991), carbon allocation (Poorter 2001), and the number of hollow trees (Fearnside 1996). We partially overcame this problem by developing individual height regressions for most of the common tree species, and by including information on wood specific gravity when available. Ideally, we might like to have one carefully tested regression method for each species, but it seems unlikely this will ever be achieved in a diverse rain forest, especially in protected areas where harvest experiments are impossible. We have presented a consistent set of results, using the same regression method, and we are therefore confident that even though the estimates presented here might be biased, at least the trends between censuses should not be.

Variation of AGB across forest types explained little of the variance in our AGB estimates. Sections of young forest are dominated by different species than pristine sections (Condit *et al*. 1995), and they held significantly less AGB. Riparian forests also held less AGB on a per-hectare basis, but both represent a small part of the forest. Thus, most spatial variation was not associated with topographic variation.

Our error analysis provides guidelines for designing optimal sampling strategies. We confirm the result of Keller *et al*. (2001) that 6 ha or more of forest inventory is needed to predict, with 95% confidence, the above-ground biomass of a forest within ± 10% of its mean. Samples of a one hectare have extremely low confidence for AGB stock, let alone turnover.

ACCURACY OF AGB CHANGE AND NPP

AGB growth varied substantially among census intervals. The largest growth rate was observed in the 1985–90 period, with much lower growth thereafter (Condit *et al*. 1999). High growth may have been related to the dramatic 1982–83 El Niño drought, which substantially elevated forest growth and mortality (Condit *et al*. 1992, 1995, 1999); however, we cannot suggest why growth would remain high several years after the El Niño.

Our estimates of ABG change, and the conclusions we draw from them, differ from those of Phillips *et al*. (1998). Based on a stand-level allometry between basal area and AGB developed for a forest near Manaus, central Amazonia, they computed an increase of 0.55 Mg ha^{-1} year^{-1} in AGB between 1985 and 1990 in the 50-ha plot of BCI. Based on the same minimal diameter cut-off (10 cm) and for the same period, we calculate an AGB increase of +0.08 Mg ha^{-1} year^{-1}. This value clearly differs from the prediction of Phillips *et al*. (1998). In addition, the AGB change over 15 years (1985–2000) is only –0.39 Mg ha^{-1} year^{-1} based on trees over 10 cm diameter and +0.20 Mg ha^{-1} year^{-1}

based on trees over 1 cm diameter, neither being significantly different from zero. Our conclusion is in large part driven by our accounting of AGB loss due to trees that broke but did not die between two censuses. Trunk and crown damage caused a loss of 0.46 Mg ha^{-1} year^{-1}, and this offsets the significant AGB increase that would have been indicated by diameter growth alone.

The comparison between the results from the full census and from trees ≥ 10 cm also shows a great discrepancy, mainly because about 20% of the AGB growth is in trees < 10 cm. Thus including only trees ≥ 10 cm in the study leads to a systematic and serious underestimation of the AGB increment. This point has been overlooked in previous studies (e.g. Clark *et al*. 2001a,b) and deserves careful scrutiny.

In the above estimates, we assumed that trees with problems of point-of-measure had a zero growth in AGB. We also tested the alternative hypothesis that these trees had a mean growth rate; this resulted in an average increase of 0.63, 0.56 and 0.12 Mg ha^{-1} year^{-1} in the three census intervals (0.44 Mg ha^{-1} year^{-1} over the 15-year period). Under these assumptions the AGB changes during the three periods would be +1.45 Mg ha^{-1} year^{-1} (significant increase), –0.13 Mg ha^{-1} year^{-1} (not significant), 0.57 Mg ha^{-1} year^{-1} (not significant). The 15-year average AGB change would be +0.64 Mg ha^{-1} year^{-1} (not significant: 95% CL [–0.25, 1.06]). Thus, although our conclusions for the periods 1985–90 and 1990–95 would be altered, the 15-year trend would not.

Given our estimate of AGB change, we cannot reject the null hypothesis that the above-ground portion of the BCI forest is in carbon balance with the atmosphere. Indeed, the measured increases were restricted to the period with high growth (1985–90), and did not continue after 1990. These results bring into question the hypothesis that tropical forests are a net carbon sink, and point to the need for field censuses that are carefully designed to test this hypothesis.

In a comprehensive review, Clark *et al*. (2001a, p. 358) recommend that a careful measurement of trees above 10 cm diameter should suffice to get an accurate measurement of AGB increment. This can be tested with our data. Excluding trees less than 10 cm diameter of the sample implies a reduction of about 5% in the measurement of the AGB increment. This observation has important implications for the response of an ecosystem to increased levels of CO_2. Indeed, small trees may respond faster to CO_2 changes than large trees, as suggested by direct experiment (Würth *et al*. 1998), in which case observed increases in atmospheric CO_2 might be most easily observed in smaller diameter classes. Unfortunately, very few studies have looked at the long-term dynamics of saplings in rain forest understory.

Increase in AGB was greater in wet or partially inundated habitats (swamps, riparian forest) than in well-drained habitats. This tendency is clear during the 1990–95 period, when all the non-wet habitats lost

AGB while AGB increased in the wet habitats. Yet, climate did not change between the 1985–90 and the 1990–95 periods, so climate does not seem to explain this change.

A PRELIMINARY CARBON BUDGET

Our results can be combined with previously published data to provide a first carbon budget for the BCI forest. Litterfall (leaves, fruits and fine woody debris) averages 11.2 Mg ha^{-1} year^{-1}, excluding losses to herbivory (Leigh & Windsor 1982 and S.J. Wright, personal communication, cited in Leigh 1999). An additional 0.3 Mg ha^{-1} year^{-1} is lost to vertebrate herbivores (Wright *et al.* 1994) and about 0.5 Mg ha^{-1} year^{-1} to insects (Leigh & Windsor 1982; Leigh 1999). Coarse wood litterfall due to tree damage may represent an additional 0.46 Mg ha^{-1} year^{-1} as reported in the present study, or as much as 1 Mg ha^{-1} year^{-1}, as in some Amazonian forests (Delaney *et al.* 1998; Chambers *et al.* 2001). Thus, above-ground NPP is estimated at 18 Mg ha^{-1} year^{-1} for the BCI forest. For comparison, a similar estimate at the Pasoh forest reserve, peninsular Malaysia (Condit *et al.* 1999), yields a figure close to 20 Mg ha^{-1} year^{-1}, or about 1000 gC m^{-2} year^{-1} (Kira 1978; for a compendium of published studies see Clark *et al.* 2001b). A study in a tropical forest near Manaus, Brazil, reports a lower above-ground NPP of about 14 Mg ha^{-1} year^{-1}, or 700 gC m^{-2} year^{-1}, excluding herbivory and coarse litterfall (Malhi *et al.* 1999). Dry biomass units are converted into carbon units by assuming 0.5 g of dry matter per g of C (Leigh & Windsor 1982).

The total amount of atmospheric carbon fixed during the photosynthetic reaction (gross primary productivity) was estimated at 55 Mg ha^{-1} year^{-1} for the BCI forest (2750 gC m^{-2} year^{-1}) from a global GPP model (Ruimy *et al.* 1995). This figure is comparable with estimates from micrometeorological experiments in Rondônia (Lloyd *et al.* 1995) and near Manaus, Brazil (Malhi *et al.* 1999), but much lower than those of simple photosynthesis models (Kira 1978; Leigh 1999). In addition, Kursar (1989) measured soil respiration in the BCI forest and found that the soil released 1625 gC m^{-2} year^{-1}. Therefore, an equivalent of 32.5 Mg ha^{-1} year^{-1} (in dry biomass units) is released into the atmosphere by the processes of below-ground autotrophic respiration and heterotrophic respiration. A similar value of 33 Mg ha^{-1} year^{-1} (1650 gC m^{-2} year^{-1}), was reported for the Manaus forest by Malhi *et al.* (1999). Finally, Cavelier *et al.* (1999) report values on fine root productivity for irrigated and non-irrigated experimental sites, suggesting a rate of root detritus production of about 8.8 Mg ha^{-1} year^{-1}, vs. 12.6 Mg ha^{-1} year^{-1} reported by Malhi *et al.* (1999).

Overall, the BCI-Manaus comparison shows surprisingly similar figures of above-ground NPP, soil respiration and root detritus production. Unlike Malhi *et al.* (1999), however, we would be tempted to assume that the forest is in carbon balance, and not use the net total uptake estimated by eddy-covariance methods to estimate the carbon budget as they did. Indeed, there is strong evidence that tower-based micrometeorological techniques do not fully measure night-time release of CO_2, and hence substantially overestimate net CO_2 uptake (Malhi & Grace 2000). This would imply a lower below-ground activity than reported in Malhi *et al.* (1999). In any case, it is important to stress that we do not have a great confidence on the quality of these estimates, yet we hope this comparison will motivate future work on these issues.

Conclusions

In a recent synthesis, Malhi & Grace (2000) suggest that the terrestrial tropics may be absorbing 2 Pg C year^{-1}, equivalent to 1.1 Mg ha^{-1} year^{-1} of carbon, or 2 Mg ha^{-1} year^{-1} of dry matter, of which 2.4 Pg C year^{-1} is offset by deforestation. As evidence for such a large uptake, they cite inverse modelling studies (Rayner *et al.* 1998; Bousquet *et al.* 2000), but other more recent inverse modelling results (Gurney *et al.* 2002) suggest that the tropical uptake is considerably smaller and still poorly resolved. The estimated tropical flux of +1.2 Pg C year^{-1} (Gurney *et al.* 2002), minus the CO_2 emissions due to tropical deforestation of 2.4 Pg C year^{-1} (Malhi & Grace 2000), lead to a sink of less than 1.2 Pg C year^{-1}, 40% less than the value of 2 Pg C year^{-1} suggested by Malhi & Grace (2000). Moreover, the uncertainty on the flux estimated by inverse modelling is very large, over 1 Pg C year^{-1} (Gurney *et al.* 2002).

Here, we have addressed another line of evidence in favour of a tropical sink of atmospheric carbon: the evidence of an AGB sink from forest inventories (Phillips *et al.* 1998). Even if half of Malhi & Grace's (2000) purported sink of 2 Pg C year^{-1} is attributable to soil carbon, we are left with an AGB change of about 1 Mg ha^{-1} year^{-1} of dry matter. Our 15-year average estimate for the 50-ha forest plot of BCI is +0.21 Mg ha^{-1} year^{-1} with a 95% confidence interval of [–0.68, 0.63] in Mg ha^{-1} year^{-1}, with all of the increase occurring between 1985 and 1990. Our results do not exclude the possibility that tropical forests are a net carbon sink, especially because the below-ground carbon cycle remains poorly known, but they do not support a sink of 1 Mg ha^{-1} year^{-1}. More important, they show that the sampling uncertainty (not to mention the measurement uncertainty) is much greater than the size of the sink itself. Thus, we cannot reject the hypothesis that the above-ground portion of the BCI forest is in carbon balance with the atmosphere. The calculation of confidence intervals for the changes in AGB is a crucial point for testing hypotheses of atmospheric carbon sequestration by tropical forests, as is the assessment of temporal fluctuation in productivity driven by short-term climatic variation.

Acknowledgements

Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC757/JEC757sm.htm:

Table A1 Specific gravity (g cm^{-3}) of species present in the BCI 50-ha plot.

Table A2 AGB (in Mg ha^{-1}) for each of the 317 species occurring in the 50-ha permanent plot of BCI between 1985 and 2000.

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