

The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates

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Abstract

The amount of carbon released to the atmosphere as a result of deforestation is determined, in part, by the amount of carbon held in the biomass of the forests converted to other uses. Uncertainty in forest biomass is responsible for much of the uncertainty in current estimates of the flux of carbon from land-use change. In the present contribution several estimates of forest biomass are compared for the Brazilian Amazon, based on spatial interpolations of direct measurements, relationships to climatic variables, and remote sensing data. Three questions were posed: First, do the methods yield similar estimates? Second, do they yield similar spatial patterns of distribution of biomass? And, third, what factors need most attention if we are to predict more accurately the distribution of forest biomass over large areas?

The answer to the first two questions is that estimates of biomass for Brazil's Amazonian forests (including dead and belowground biomass) vary by more than a factor of two, from a low of 39 PgC to a high of 93 PgC. Furthermore, the estimates disagree as to the regions of high and low biomass. The lack of agreement among estimates confirms the need for reliable determination of aboveground biomass over large areas. Potential methods include direct measurement of biomass through forest inventories with improved allometric regression equations, dynamic modelling of forest recovery following observed stand-replacing disturbances, and estimation of aboveground biomass from airborne or satellite-based instruments sensitive to the vertical structure plant canopies.

Keywords: Amazonia, biomass, carbon, deforestation, land-use change, spatial variability, tropical forests

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Introduction

With the use of satellite data to determine rates of deforestation and reforestation, the largest uncertainty in estimating fluxes of carbon from land-use change results from variation in estimates of forest biomass. Variation in estimates of biomass in the Brazilian Amazon, for example, was responsible for 60% of the variation in the estimated net carbon flux for the region (Houghton *et al.* 2000). Satellite data may eventually be developed to determine aboveground biomass directly, but neither

optical data nor radar data have yielded consistent results in forests with moderate to high biomass (Waring *et al.* 1995; Rignot *et al.* 1997; Nelson *et al.* 2000). Until new instruments are devised for determining reliable estimates of biomass for closed forests, biomass over large areas will have to be determined by alternative methods, for example, through field measurements, modelling, or a combination of both.

The purpose of this paper is to compare estimates of forest biomass over a large area, the Brazilian Amazon, where the area of forest is approximately 400×10^6 ha. Nonforests (for example, cerrado and water) were

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Table 1 Summary of biomass estimation methods

Method	Spatial resolution	Secondary forests	Potential or actual forest cover
Field measurements			
1 Interpolation of 44 independent measurements	5 km	avoided	potential
2 RADAMBRASIL (Brown & Lugo 1992)	1 km	some	potential
3 RADAMBRASIL (Fearnside 1997)	1 km	some	potential
Methods based on environmental gradients			
4 Brown	5 km	avoided	potential
5 Olson	1° × 1°	included	actual
Methods using remote sensing			
6 Potter	1° × 1°	some	actual
7 DeFries	1 km	some	actual

excluded from this analysis on the basis of maps. Estimates of absolute biomass and estimates of the spatial distribution of biomass were compared throughout Brazil's Amazonian forests.

Methods

Altogether, seven estimates of Brazilian Amazonian forest biomass were included in this comparison (Table 1). Three were based on ground measurements (forest surveys as well as destructive sampling of small areas); two were based on relationships between above-ground biomass and environmental parameters; and two were based, at least in part, on satellite data. Spatial resolutions of the original sources were retained when constructing maps of biomass. New maps generated herein had a resolution of 5-km.

Direct measurements of biomass and timber volumes in the field

Aboveground live biomass (AGLB). Measurements of biomass for 44 mature forests within or near the boundaries of the Brazilian Amazonian forest (Fig. 1) were assembled from the literature. The 44 sites were not obtained from 44 individual, published studies: some studies provided information for more than one site, and some sites were measured by more than one study (that is, the geographical coordinates were the same). The studies included, at one extreme, six forest surveys carried out by the FAO covering as much as 415 ha (Heinsdijk 1957, 1958a,b,c; Glerum 1960; Glerum & Smit 1962) and, at the other extreme, measurements on areas as small as 0.004 ha (Table 2). At 11 of the sites, including the six forest surveys, wood volumes, rather than biomass, were measured, and the data were converted to aboveground biomass using equations

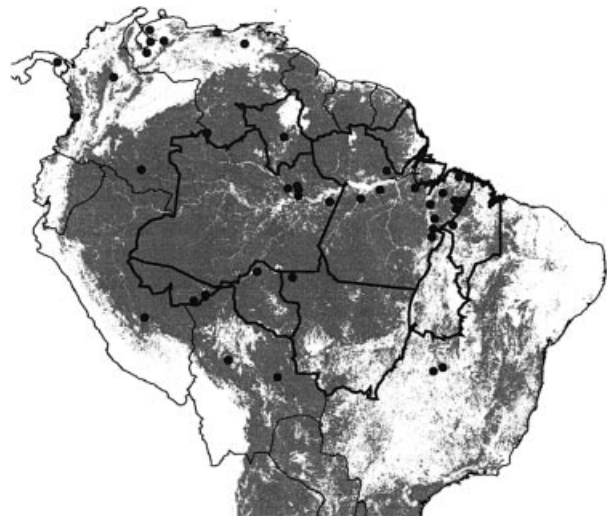


Fig. 1 Locations (black dots) of 44 measurements of living aboveground forest biomass in and around Amazonia. Grey areas represent forests with >40% tree cover (DeFries *et al.* 2000).

from Brown & Lugo (1992) (see next method). For each site a record was made of latitude and longitude, the vegetation type, aboveground live biomass (AGLB), size of plot, and area sampled (plot size times number of plots). Total aboveground biomass (TAGB) was also recorded, which includes standing and fallen dead material, along with belowground biomass (BGB), and basal area if these characteristics were reported. The minimum stem diameter measured varied among studies. No attempt was made to adjust the estimates for smaller stems, and thus some of the estimates may be low.

Components in addition to aboveground live biomass. Most studies reported AGLB, although in some cases it was difficult to tell whether the aboveground biomass

included dead material as well as live. Thirteen of the sites reported TAGB as well as AGLB, and in these 13 studies dead aboveground biomass averaged 9% of AGLB (range 2% – 17%) (Table 3). Six sites reported direct measurement of BGB (live and dead not generally distinguished), and from these sites BGB averaged 21% of AGLB (range 13% – 26%). The estimate is intermediate between means reported by Brown & Lugo (1992) (17%) and Cairns *et al.* (1997) (24%), and there is a suggestion that the percentage is inversely related to AGLB (or that belowground biomass is relatively constant over a broad range of aboveground biomass values). This finding contrasts with the study by Cairns *et al.* (1997) that reported a direct relationship between AGLB and BGB on the basis of 85 studies of forests from around the world. Many more than six of the 44 sites used herein had estimates of BGB, but the additional estimates were based on root/shoot ratios derived from the literature. For the percentages calculated here, only those sites where BGB was directly measured were used. Total biomass was converted to carbon assuming a carbon content of 50%.

Using these mean ratios, estimates of AGLB were increased by 9%, 21%, or 30% to account for dead biomass, belowground biomass, or both for those sites where either or both of the components were not measured directly. The full range found here (22% – 42% for individual sites) is smaller than the range reported for dead and belowground biomass on 23 forest plots in five life zones in Venezuela (20–58%) (Delaney *et al.* 1998).

Spatial extrapolation of site data. The geographical distribution of the sites is shown in Fig. 1. The initial approach was to overlay the 44 sites on a map of vegetation types. However, there are no vegetation maps for the region that distinguish subcategories within the category of moist tropical forests. Several maps were considered: the global vegetation map of Olson *et al.* (1983), a satellite-based map (Stone *et al.* 1994), and the IBGE map from Brazil (IBGE 1988). These maps distinguish agriculture, cerrado, open forest, and dense forest, but the latter (a single class) covers most of Amazonia. The exception is the RADAMBRASIL study (see below), which identified and mapped more than 100 classes of vegetation. However, the stem volumes are more variable within RADAMBRASIL classes than between them, suggesting that the classes are not useful for distinguishing biomass. As interpolating biomass on the basis of a vegetation map was unlikely to capture the diversity of cover types (let alone classes of biomass), an interpolation among all 44 sites was constructed using

the 'interpolate grid function' from ArcView®. The interpolation had a spatial resolution of 5 km. Nonforest areas were deleted from the map and not considered further.

Wood volumes from RADAMBRASIL converted to biomass with equations from Brown & Lugo (1992)

The RADAMBRASIL Project (DNPM 1973–83) made an inventory of stemwood volumes on thousands of 1-ha plots distributed over the Brazilian Amazon between 1973 and 1983, and produced a map of forest classes where each class was assigned an average stemwood volume. These wood volumes were converted to total aboveground biomass (TAGB) using two approaches. The first approach used the following equation (Brown & Lugo 1992):

$$\text{TAGB} = \text{Volume (m}^3 \text{ ha}^{-1}) \cdot \text{VEF} \cdot \text{WD} \cdot \text{BEF}, \quad (1)$$

where volumes were obtained from RADAMBRASIL, VEF (volume expansion factor to account for trees smaller than the minimum diameter measured) was 1.25 for dense forests and 1.5 for other-than-dense forests (trees with smaller diameters), WD was wood density (0.69 Mg m⁻³ as a weighted average for Amazonia) (Brown & Lugo 1992), and BEF (biomass expansion factor to account for biomass in addition to stemwood biomass) varied as a function of stemwood biomass (SB) as follows (Brown & Lugo 1992):

$$\text{for SB} < 190 \text{ Mg ha}^{-1}, \text{ BEF} = e^{[3.213 - 0.506 \ln(\text{SB})]}$$

$$\text{for SB} > 190 \text{ Mg ha}^{-1}, \text{ BEF} = 1.74.$$

The variable BEF takes into account the observation that large trees have relatively more biomass in stems than small trees do. Stemwood biomass was determined from the product of volume, VEF and WD. As described above, the calculated aboveground biomass was increased by 9% to account for dead biomass and by an additional 21% to account for belowground biomass. The spatial resolution of the map thus generated was 1 km.

Wood volumes from RADAMBRASIL converted to biomass using data from Fearnside (1997)

The second approach for converting RADAMBRASIL stemwood volumes to biomass was Fearnside's (Fearnside 1997). His conversion yielded an Amazonia-wide estimate 60% higher than the estimate, above, based on equations from Brown & Lugo (1992). Fearnside assumed a belowground biomass that was 33.6% of aboveground biomass (rather than 21%) and increased aboveground biomass for components not included in FAO (1993) estimates as follows: + 5.3% for

Table 2 Location and characteristics of 44 sites in Amazonia where forest biomass has been measured

Reference	Country	Vegetation type	Latitude	Longitude	AGLB [Mg (dwt) ha ⁻¹]	Plot size (ha)	Area sampled (ha)
Sampled area > 5 ha							
Heinsdijk (1957)	Brazil	Terra firme forest	- 2.5	- 53.5	309	1	415
Heinsdijk (1958)	Brazil	Terra firme forest	- 3.5	- 57.5	254	1	252
Heinsdijk (1958)	Brazil	Terra firme forest	- 2.25	- 50.75	400	1	240
Heinsdijk (1958)	Brazil	Terra firme forest	- 2.5	- 48.5	337	1	200
Glerum & Smit (1962)	Brazil	Tropical forest	- 3.63	- 47.35	253	1	151
Glerum (1960)	Brazil	Terra firme forest	- 1.25	- 46.5	221	1	104
BOLFOR (1995)	Bolivia	Subhumid tropical forest	- 16.55	- 61.8	202	0.5	50
Kudrencky (1993); Annas (1996)	Bolivia	Tropical evergreen forest	- 15.217	- 66	166	0.5-1.0	26.15
Higuchi <i>et al.</i> (1994)	Brazil	Dense tropical moist forest	1.47	- 61.11	228	0.4	22.8
Higuchi <i>et al.</i> (1994)	Brazil	Dense tropical moist forest	- 5.23	- 49.10	185	0.4	22.8
Glerum & Smit 1962	Brazil	Evergreen seasonal forest	- 4.88	- 47.5	95	1	20
				mean	241		
				SE	26.8		
Sampled area < 5 ha and > 0.5 ha							
Jordan & Uhl (1978)	Venezuela	Tropical rainforest	1.9	- 67.1	336	0.5-1	> 1
Nepstad (1989)	Brazil	Terra firme (tropical moist forest)	- 2.983	- 47.517	264		5
Grimm & Fassbender (1981)	Venezuela	Montane forest	8.617	- 71.35	348	0.25	3.25
Salomao <i>et al.</i> (1996)	Brazil	Humid tropical forest	- 1.18	- 47.316	267	0.025	3
Overman <i>et al.</i> (1994)	Colombia	Lowland terra firme forest	- 0.633	- 72.367	343		2.5
Delaney <i>et al.</i> (1997)	Venezuela	Tropical moist transition to dry forest	9.5	- 70	296	0.25	2.25
Delaney <i>et al.</i> (1997)	Venezuela	Tropical lower montane moist forest	9.5	- 71	346	0.25	1.5
Faber-Langendoen & Gentry (1991)	Colombia	Rainforest	3.917	- 77.00	195		1.5
Uhl <i>et al.</i> (1988)	Brazil	Tropical forest	- 3.00	- 47.00	306	0.063	1.25
Brown <i>et al.</i> 1995	Brazil	Tropical moist forest	- 8.75	- 63.383	285		1
Delaney <i>et al.</i> (1997)	Venezuela	Tropical moist forest	9	- 64	358	0.25	1
Golley <i>et al.</i> (1975)	Panama	Tropical moist forest	8.5	- 78	269	0.25	1
Brown <i>et al.</i> 1992	Brazil	Open forest with bamboo	- 10.75	- 68.75	320		0.5
Delaney <i>et al.</i> (1997)	Venezuela	Tropical montane wet forest	10.5	- 71	314	0.25	0.5
Delaney <i>et al.</i> (1997)	Venezuela	Tropical very dry forest	10	- 66	140	0.25	0.5
Fölster <i>et al.</i> 1976	Colombia	Tropical seasonal evergreen forest	6.83	- 73.92	252	0.25	0.5
				mean	290		
				SE	17.2		
Sampled area < 0.5 ha							
Alves <i>et al.</i> (1997)	Brazil	Dense tropical forest	- 10.317	- 67.767	354	0.01	0.2
Carvalho Jr. (1995)	Brazil	Tropical rainforest	- 2.583	- 59.983	390	0.04	0.2
Klinge & Herrera (1978, 1983)	Venezuela	Evergreen lowland forest/caatinga	1.9	- 67.1	277	0.01	0.13
Klinge & Rodrigues (1973), Klinge & Herrera 1983)	Brazil	Terra firma tropical rainforest	- 3.1	- 60	406		0.215
Luckman <i>et al.</i> (1997)	Brazil	Tropical forest	- 3.212	- 55	284	0.05	0.1
McWilliam <i>et al.</i> (1993)	Brazil	Terra firme lowland rainforest	- 2.5	- 60.8	249	0.01	0.04

Table 2 (continued)

Reference	Country	Vegetation type	Latitude	Longitude	AGLB [Mg (dwt) ha ⁻¹]	Plot size (ha)	Area sampled (ha)
Russell (1983)	Brazil	Tropical rainforest	- 1.0	- 53.0 mean SE	413 339 27.8	0.033	0.073
Sample areas unknown							
Cardenas <i>et al.</i> (1982)	Brazil	Tropical forest	- 3.42	- 49.44	326		
ONERN (1990)	Peru	Subtropical & premontane tropical forests	- 11.77	- 72.93	124	0.2	
Fearnside <i>et al.</i> (1993)	Brazil	Lowland broadleaf dense forest	- 2.32	- 60.09	242		
Kauffman <i>et al.</i> (1995)	Brazil	Tropical evergreen & submontane forest	- 5.863	- 49.180	399		
Kauffman <i>et al.</i> (1995)	Brazil	Submontane open forest	- 9.2	- 60.5	299		
Kauffman <i>et al.</i> (1995)	Brazil	Tropical evergreen & submontane forest	- 4.5	- 49.0	268		
Saldarriaga <i>et al.</i> (1988)	Columbia & Venezuela	Tropical terra firma forest	1.933	- 67.05 mean SE	221 268 35.3	0.25	
Non-terra firme forests:							
De Paula <i>et al.</i> (1990)	Brazil	Gallery forest	- 15.45	- 47.57	144		1
De Paula <i>et al.</i> (1993)	Brazil	Gallery forest	- 15.45	- 47.57	127		1
Imanaencinas <i>et al.</i> (1995)	Brazil	Gallery forest	- 15.8	- 48.35 mean SE	132 135 6.1	0.1	1
All Sites				mean SE	271 12.8		

Table 3 Sites where total aboveground biomass (including live and dead) and belowground biomass were measured. Units are either Mg dry weight/ha or percentage

AGLB	TAGB	Dead biomass as % AGLB	Belowground biomass (BGB)	BGB as % AGLB	Reference
413.4	425.2	2.8	104	25.2	Russell (1983)
406.3			67	16.5	Klinge & Rodrigues (1973)
358	396.2	9.6			Delaney <i>et al.</i> (1997)
347.7	371.2	6.3	56.5	16.2	Grimm & Fassbender (1981)
346	395	12.4			Delaney <i>et al.</i> (1997)
343	351	2.3			Overman <i>et al.</i> (1994)
314	353.8	11.2			Delaney <i>et al.</i> (1997)
306.2	348	12.0			Uhl <i>et al.</i> (1988)
296	308	3.9			Delaney <i>et al.</i> (1997)
285	325	12.3			Brown <i>et al.</i> (1995)
267	320	16.6	68	25.5	Salomao <i>et al.</i> (1996)
264			35.4	13.4	Nepstad (1989)
221	247.3	11.9	58.2	26.3	Saldarriaga <i>et al.</i> (1988)
242.2	264.6	8.5	46	19.0	Fearnside <i>et al.</i> (1993)
140	155.2	9.8			Delaney <i>et al.</i> (1997)
Mean		9.1		20.5	
SD		4.2		5.2	
Coeff. variation		0.46		0.26	
Number of sites		13		7	

vines, + 0.2% for nontree components, + 12% for trees < 10 cm d.b.h., + 15.6% for form factor, + 3.6% for trees 30.0–31.8 cm d.b.h., – 6.6% for hollow trees, – 0.9% for bark, and + 2.4% for palms (Fearnside 1992; 2000). In addition, Fearnside (2000) added another 31% of AGLB to account for aboveground dead biomass (rather than the 9% found here). It was assumed here that the larger estimate for the entire region (from Fearnside 1997) applied to each cell. Thus, the spatial distribution of biomass was equivalent to the first estimate, but each cell was 60% higher.

Biomass from Olson et al. (1983)

A classic study by Olson *et al.* (1983) estimated total living biomass (above- and belowground) for 44 terrestrial ecosystems within seven broad groups [Carbon Dioxide Information and Analysis Center (CDIAC) website (<http://cdiac.ESD.ORNL.GOV/ftp/ndp017>)]. The distribution of ecosystems was determined from patterns of preagricultural vegetation, modern aerial surveys, and biomass measured at research sites. Olson's estimate in each cell was increased by 9% to account for dead biomass. Spatial resolution was 1° × 1°, coarser than most of the other sets of data considered in this analysis.

Biomass from S. Brown (unpubl. data)

Brown and colleagues have advanced a method for estimating potential biomass of tropical forest lands

(Brown *et al.* 1993; Iverson *et al.* 1994; Brown & Gaston 1995; Gaston *et al.* 1998). The method uses a rule-based model based on four scaled input layers: soil depth and texture, precipitation, elevation and slope, and a modified Weck's climatic index (an index that includes a measure of seasonality based on water availability and temperature). Each cell in one of these spatial layers ranges between 0 and 25, depending on the relationship between the environmental parameter and biomass, and the sum of the four layers determines an index of biomass (100% is maximum) (details of the scaling are given in Iverson *et al.* 1994). The method has been applied in tropical Asia (Brown *et al.* 1993; Iverson *et al.* 1994) and tropical Africa (Brown & Gaston 1995; Gaston *et al.* 1998). For this application to the Brazilian Amazon, the spatial resolution was 5 km.

The index of biomass was calibrated with data from the site measurements described above. Calibration requires finding an average maximum biomass against which to apply the index of each pixel. Three calibrations were used. The first was based on only 39 of the 44 of the sites because five sites fell outside of the Amazonian forest boundary on Brown's map. Each site where biomass was measured was compared with its index value on the map (0–100%), and a theoretical maximum biomass was calculated, assuming a linear relationship. This average maximum was used to convert the index value for each pixel to potential biomass. For example, if the measured biomass was 200 MgC ha⁻¹ at a site that corresponded to an index value of 75%, then the

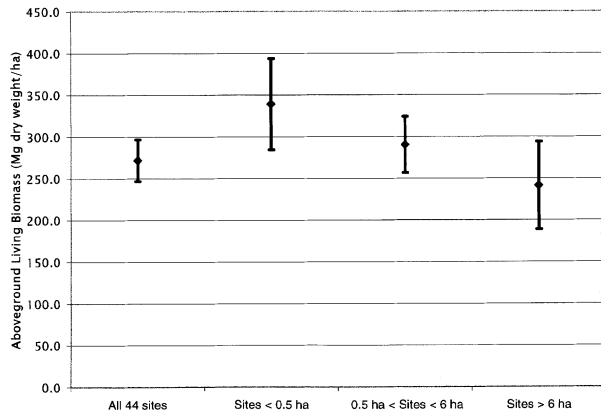


Fig. 2 Means ($\pm 1.96 \times SE$) of aboveground live biomass for sites grouped by area sampled

theoretical maximum biomass for that point was $(200/0.75 =) 267 \text{ MgC ha}^{-1}$. This calculated maximum does not represent expected or potential biomass. Rather, it provides a way of standardizing the 39 measurements to one average maximum. In this example, the application of the average maximum to the index for this location on the map would yield a potential biomass presumably close to 200 MgC ha^{-1} .

A second calibration was based on the six inventories of stemwood volume conducted by the FAO (1956–60) (Heinsdijk 1957, 1958a,b,c; Glerum 1960; Glerum & Smit 1962), each of which covered between 100 and 415 ha (Table 2). Stemwood volumes were converted to biomass, as described above (Brown & Lugo 1992). In this case, however, species-specific wood densities (from the surveys) were used unless the species was not identified in the inventory, in which case an average wood density (0.7369 Mg m^{-3}) (from the surveys) was employed. For this calibration six values were used to calculate a maximum biomass. Individual cells were then converted from the index to values of biomass, as above. The third calibration used data from the 16 sites where the area sampled was between 0.5 ha and 5 ha (Table 2).

Biomass from NASA-CASA (Potter 1999)

The NASA-CASA model has been used to simulate net primary production (NPP) and biomass in the Brazilian Amazon (Potter *et al.* 1998; Potter 1999). The spatial resolution is 1° latitude by 1° longitude. Biomass is determined as the difference between net primary production (NPP) and mortality (Potter 1999), where NPP is driven by the Normalized Difference Vegetation Index (NDVI) obtained from NOAA's Advanced Very High Resolution Radiometer (AVHRR) data, and mortality is estimated from the mean residence time of

carbon in standing woody material. Thus, biomass is an equilibrium value that is obtained by running the model for several centuries. Monthly NPP is decreased by departures of temperature from the temperature optimum for growth and by soil water deficits. Allocation of NPP to leaves, roots, and wood is based on ratios determined from the literature, and the proportion allocated to roots may be modified by soil fertility.

Percentage tree cover from satellite (DeFries *et al.* 2000)

The global map of percent tree cover recently developed by DeFries *et al.* (1999, 2000) is not an estimate of biomass or carbon. Nevertheless, the spatial distribution of tree cover has the potential to serve as a surrogate for the spatial distribution of biomass. In areas where herbaceous cover or bare soil is present, percentage tree cover should be positively correlated with biomass. Within forests with a high percentage of tree cover, however, biomass may vary as a function of tree height, tree architecture, wood density, and basal area, none of which is sensed with optical data, and thus variations in biomass at high percentage tree cover may be missed. Percentage tree cover was determined with a linear mixture model using metrics from NOAA's 1 km AVHRR data acquired in 1992–93 and processed under the guidance of the International Geosphere Biosphere Programme (Eidenshink & Faudeen 1994). Because of the difficulty of finding homogeneous end-members over areas as large as 1 km^2 , the mixture model was calibrated with LANDSAT MSS data from 156 scenes distributed globally (DeFries *et al.* 1999). Difficulties at very high and very low tree cover led to reported values that range between 10% and 80%, with 80% tree cover representing greater than or equal to 80% cover, and 10% representing tree cover equal to or less than 10%. The spatial resolution of the data was 1 km.

DeFries' map was calibrated with the map interpolated from the 44 sites (above). Sixty percent of DeFries' pixels had a tree cover of $>80\%$. The biomass values from the interpolated map were used for these pixels because the sites for that interpolation were in undisturbed forests. The mean of these pixels was used to calculate the biomass values for the rest of DeFries' pixels, assuming that the range of 10–80% in DeFries' map corresponded, linearly, to a range 0–X, where X was the mean of pixels where tree cover was $>80\%$.

The seven methods are summarized in Table 1.

Spatial distribution of Amazonian biomass

The present study not only compared the estimates of total forest biomass but also investigated the relative

Table 4 Estimates of the total carbon in biomass and mean biomass of tropical moist forests in the Brazilian Amazon

	Total carbon in biomass (PgC)	Mean biomass (MgC ha ⁻¹)	Mean biomass of deforested areas	
			(MgC ha ⁻¹)	(rel. to mean biomass for all Amazonian forests)
1 Independent measurements	76.5	192	131	0.68
2 RADAMBRASIL (Brown <i>et al.</i> 1992)	62.5	156	150	0.96
3 RADAMBRASIL (Fearnside 1997)	93.1	232	223	0.96
4 Brown (calibrated with 39 of 44 points)	73.0	183	176	0.96
Brown (calibrated with forest surveys)	78.0*	196*	244*	1.25
Brown (calibrated with areas >0.5 ha)	78.8*	197*	247*	1.25
5 Olson	38.9	100	110	1.10
6 Potter	78.2	196	149	0.76
7 DeFries	69.2	178	154	0.87
Mean	70	177	156	
SE	8	17	15	

*These estimates not included in the means and SE.

distribution of high-, medium-, and low-biomass forests generated by each approach. This comparison was to determine whether the approaches were consistent in showing forests with the highest biomass to be in the centre of the Amazon, for example, or in the northwestern region. Each estimate was standardized so that biomass classes were divided into high, medium, and low relative to each study. Each of the three classes was represented by approximately a third of the pixels.

Results

Plot data

Components of biomass. As presented in the methods section, dead biomass averaged 9% of aboveground live biomass (AGLB) (range 2–17%) (Table 3), and belowground biomass (BGB) averaged 21% of AGLB (range 13% – 26%). Thus AGLB accounts for approximately 70% of total biomass.

Variation related to area sampled. AGLB of Amazonian forests varied from 95 to 413 Mg (dwt) ha⁻¹ (48–206 MgC ha⁻¹) in the 41 terra firme locations where it was measured (Table 2). Including dead and belowground components yielded a mean (unweighted by area) of 271 Mg (dwt) ha⁻¹ (136 MgC ha⁻¹). The areas sampled varied from 0.04 ha to 415 ha. Three of the 44 sites were in non terra firme forests, and seven of the terra firme sites did not report the area sampled. The remaining 34 terra firme sites were divided into three groups, depending on the area sampled (< 0.5 ha, between 0.5 and 5 ha, > 5 ha). The area sampled was determined by plot size times number of plots. There was a tendency for smaller sampled areas to yield

larger estimates of biomass, as noted previously (Brown & Lugo 1992), but the tendency was not significant (Fig. 2).

Total Amazonian biomass

Estimates of the total amount of carbon (0.5 × biomass) in the biomass of forests in the Brazilian Amazon (including dead material as well as live, and below-ground biomass, but not including soil) ranged over more than a factor of two, from 39 to 93 PgC (Table 4). The mean (± SE) of seven estimates (taking the 39-site calibration of Brown) was 70 (± 7) PgC. Over the 400 × 10⁶ ha of Amazonian forest, the average biomass in the region was 177 (± 17) MgC ha⁻¹.

The highest estimate (93.1 PgC) was Fearnside's (1997); the lowest estimate was based on the work of Olson *et al.* (1983) (38.9 PgC, increased by 9% to include dead biomass). Not surprisingly, the estimates from Brown's model (73.0–78.8 PgC) were close to the estimate based on the 44 points (76.5 PgC), for Brown's indices were calibrated with subsamples of those same points.

The estimates from Brown's approach varied little when different sites were used to calibrate the index. When 39 sites were used, the total biomass for the Brazilian Amazon was 73.0 PgC. When only the six FAO forest inventories were used, the total biomass was 78.0 PgC; if the plots >0.5 and <5 ha were used, the estimate was 78.8 PgC. The differences are small, but they are in the opposite direction of what would be expected from the means of the three different groups (Fig. 2). The difference suggests that the spatial distribution of sites used for calibration is also important in determining the mapped biomass. As noted above, the biomass determined from forest surveys was not significantly different

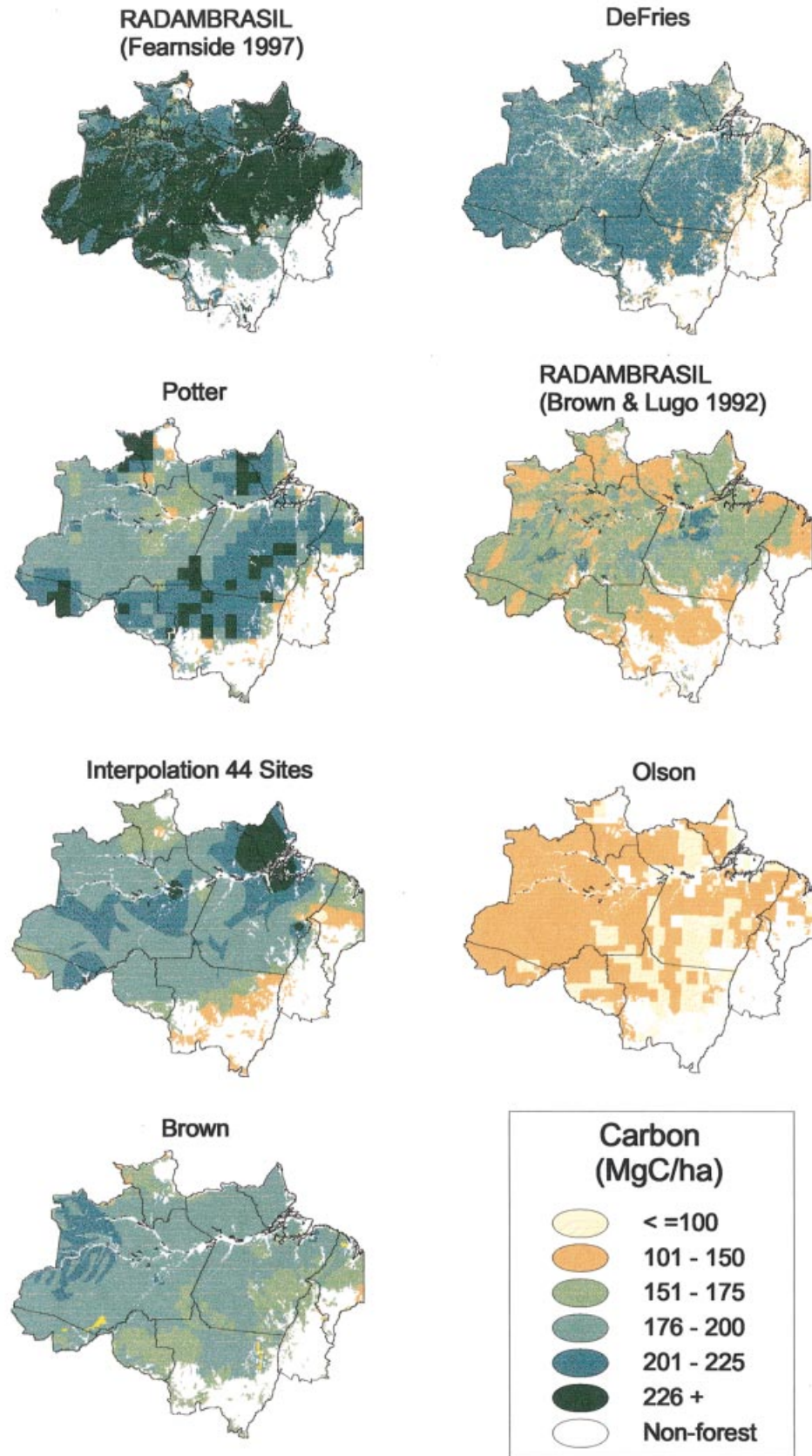


Fig. 3 Seven estimates of the storage of carbon in forest biomass

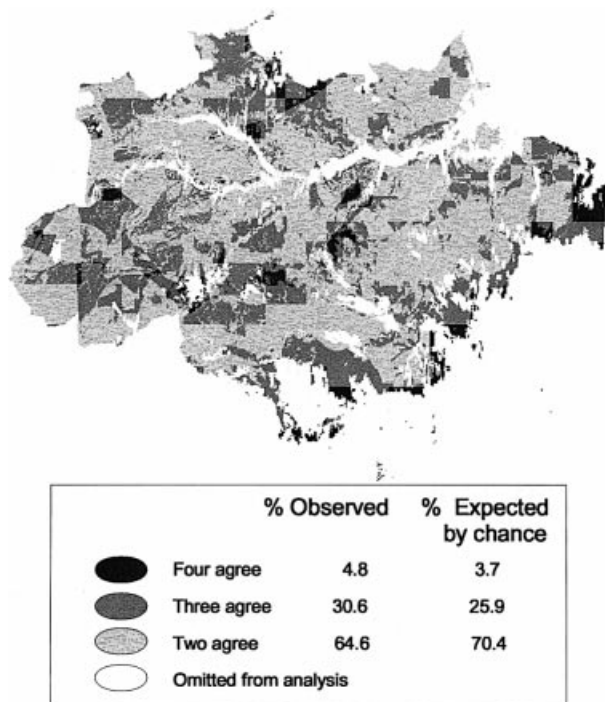


Fig. 4 Areas in the Brazilian Amazon where estimates of high, low or intermediate biomass agree among analyses

from the biomass determined from destructive sampling on small plots.

Spatial distribution of Amazonian biomass

The distribution of biomass in the Brazilian Amazon, according to different estimates, is shown in Fig. 3. The low estimate of Olson *et al.* (1983) stands out, as does the high estimate attributed to Fearnside (1997). Despite similar estimates of total biomass for the five other maps, their distributions of biomass show little agreement. For example, the location of forests with high biomass runs E–W through central Amazonia in the ‘interpolation of 44 sites’ and in the RADAMBRASIL maps, is in the north-west in Brown’s map, and is largely in the south in Potter’s map. The maps by Brown and Potter are almost the reverses of each other with respect to the placement of high- and low-biomass forests. The distribution of biomass in DeFries’ map is a function of the openness of the canopy. At least some of the variation results from human disturbance of the landscape.

As described in the methods, each map was divided into three classes of approximately equal area: high-, medium-, and low-biomass forests. Four of these maps were overlaid and examined for broad agreement on the spatial distribution of biomass. One of the maps based on the RADAMBRASIL survey was excluded because the

spatial distribution (although not the absolute biomass) of the two estimates was identical. The maps of Olson *et al.* (1983) and DeFries *et al.* 2000) were also excluded because biomass could not be divided into three equal-area classes. Olson *et al.* provide only two classes, and, according to DeFries *et al.* 60% of the basin has > 80% tree cover. For Brown’s analysis, index values were used, rather than the estimate of biomass calibrated with field measurements. For the four maps compared, estimates of the total carbon in biomass range from 62.5 to 78.2 PgC. This range is more than three times smaller than the range for all seven estimates (22%, as opposed to 77%, of the mean) (Table 3).

The spatial comparison shows that all four maps agree over less than 5% of the Brazilian Amazon (Fig. 4). By chance, a three-sided ‘coin’ (high, medium, or low) tossed four times will yield the same side in about 3.7% of the trials, so the observed agreement is only slightly better than random. Three maps agree in 30.6% of the Amazon, again slightly better than expected by chance (25.9%). Two maps agree in 64.6% of the region, compared with a 70.4% agreement by chance. Thus, despite reasonable agreement in total carbon storage among these four estimates, estimates of the spatial distribution of this storage show little agreement.

Discussion

Implications

One of the arguments for acquiring spatially detailed data to calculate sources and sinks of carbon is that the areas affected by land-use change may not be representative of the average biomass for the region. There may be systematic differences between the ecosystems present and the ecosystems actually cleared. If so, calculated fluxes of carbon based on larger-area averages would be biased.

This argument was tested by comparing the overall mean forest biomass with the mean biomass of forests that had been deforested. Deforested pixels (including areas identified as secondary forests) were obtained from a 1986 Landsat-based map of deforestation (Houghton *et al.* 2000). Most of the studies showed the biomass of deforested forests to have been systematically lower than the mean biomass of Amazonian forests. Exceptions included Olson’s estimate and those calibrations of Brain’s index that were based on large sampled areas. The mean was 12% lower, and the range was from 32% lower (interpolation of 44 sites) to 25% higher (Table 4). The argument that greater geographical detail will increase the accuracy of flux estimates obviously depends on how well biomass is known. For the forests

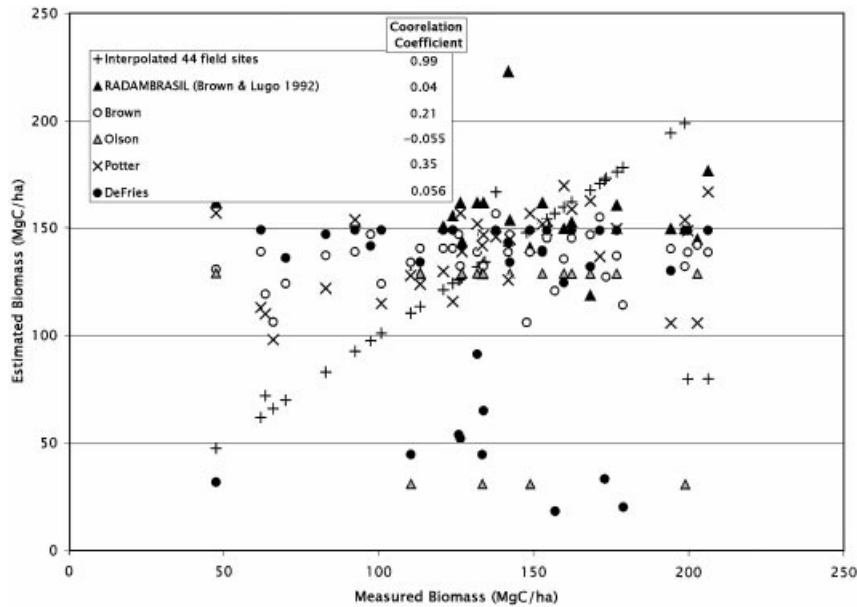


Fig. 5 Correspondence between ground measurements of biomass and mapped estimates

of the Brazilian Amazon spatial variations in biomass are too uncertain at present for accurate calculations of flux.

Similarities and dissimilarities of approaches

Some of the differences among estimates may result from differences between actual and potential biomass. This distinction has two overlapping components: first, distinguishing secondary from primary (undisturbed) forests, and, second, distinguishing forests from non-forests (for example, agricultural lands). Secondary forests were largely ignored in Brown's estimate and the interpolation based on 44 sites. The 44 sites were generally limited to mature, or primary, forests (to the extent that such a designation is possible in the field), although the volume data from forest inventories may have included secondary forests (Brown & Lugo 1992). It is likely that the RADAMBRASIL survey also included some secondary forests, for the intent of the survey was to characterize the forests in existence rather than potential forests. Because the two estimates based on the RADAMBRASIL study account for a large part of the range in estimates, the difference attributable to different treatments of secondary forests in these approaches must be minor. Nevertheless, the RADAMBRASIL study, Brown's estimate, and the estimate based on 44 sites, may have overestimated current biomass in the region because of their avoidance of secondary forests. The two studies based on remote sensing and Olson's estimate, on the other hand, explicitly account for secondary and degraded

forests, although Olson's approach may have overestimated their importance in the Amazon. Olson *et al.* (1983) used one estimate of biomass to apply to tropical moist forests worldwide, yet logging and other forms of use have historically been less in Amazonia than in the old world tropics.

The extent to which nonforested lands were considered in the approaches also accounts for some of the variability. Clearings or openings within forested regions were generally not recognized in the ground-based approaches (the 44 sites and RADAMBRASIL) or in Brown's maps of potential biomass. On the other hand, the maps of DeFries, Olson, and Potter did account for cleared areas, although only Olson's estimate of biomass is qualitatively consistent with this accounting.

Although optical data (the AVHRR data used in DeFries' and Potter's approaches) may not be useful for distinguishing between different classes of biomass within intact, closed forests, they do distinguish openings and clearings in the forest. According to DeFries' map of tree cover, 40% of the Amazonian forest is open or disturbed to some extent. By comparison, the area classified as deforested using LandsatTM data (30 m resolution) accounted for approximately 14% of the region (Houghton *et al.* 2000). Calibrating DeFries' map with the map interpolated from 44 sites yields a total biomass of 69 PgC, 10% less than the estimate based on 44 sites. The estimate of 10% is crude but gives an indication of the difference between potential and actual forest biomass (including cleared and open forests) for the region.

Accuracy

With the exception of Olson's map (which has only two categories of biomass) and DeFries' map of percentage forest cover, neither of which appears useful for estimating variations in biomass within closed forests, it is not possible to assess which of the methods included in this analysis is the most accurate. If it is assumed that the 44 ground measurements reflect biomass accurately in their respective locations, then each map can be evaluated on how well it corresponds to these measurements. The answer is: not very well. The map based on a spatial interpolation of the 44 points showed, not surprisingly, the best agreement, with a correlation coefficient of 0.99 (Fig. 5). The correlation coefficients for the other estimates, based on pairwise comparison with the ground studies, ranged between 0.05 and 0.35. The correlation is poor. However, the lack of correlation does not necessarily invalidate the estimates because only six of the 44 ground points are of a spatial scale (> 100 ha) appropriate for comparison with map pixels. Most of the ground measurements were made on areas of less than 1 ha, while the estimates obtained from modelling, satellite, or interpolations were for areas no less than 1 km² and, in Olson's and Potter's cases, for areas as large as 1° × 1°. The small test sites are not a fair test of the accuracy of estimates that are spatially much more coarse.

Which (if any) of the seven estimates of biomass in Fig. 3 best reflects the true distribution of biomass? It is suggested that neither Olson's estimate nor those based on AVHRR (Potter's and DeFries') are sensitive to spatial variations in the biomass of closed forests. However, determining which of the remaining four estimates presented here is best will have to await a comparison with data not available for the present analysis or with data from a future measurement campaign with widely distributed sites.

Next steps

If the accuracy of large-area estimates of biomass is to be improved, what are the most critical limitations? Are more plots needed? Larger plots? Repeated measurements of the same plots? More measurements of below-ground biomass or dead biomass? Better ways of extrapolating from plots to large areas? Several recommendations are suggested by the results of this analysis.

First, a major fraction of the uncertainty of Amazonian forest biomass results from incomplete measurements at single plots; that is, from the amount of carbon held in components other than living aboveground biomass of trees greater than some arbitrary minimum. In addition to dead biomass and belowground biomass, uncertainties result from the amount of carbon held in small trees,

hollow trees, lianas, and other nontree vegetation, as well as from the density of wood for individual species (Brown & Lugo 1992; Fearnside 1992; 2000). Additional field measurements would help to resolve these uncertainties only if they include additional components as a part of the measurements, and only if they are based on replicated plots of a sufficient size, distributed in a sufficiently unbiased design.

In addition, the biomass of trees is often not measured directly but, instead, based on measurements of diameter and allometric regression equations. The present suite of regression equations is relatively small and, despite recent work in Amazonia (Araújo *et al.* 1999; Nelson *et al.* 1999), includes few trees with large diameters — the trees that have a marked influence on the shape and error of the regression. Clearly more data from destructively harvested large diameter trees are needed. Allometric regression equations also need to be developed for estimating root biomass, which is exceedingly difficult and impractical to measure directly over large areas.

Additional, isolated field measurements are unlikely to add to our understanding of the spatial patterns of biomass in Amazonia, however. For a better understanding of the spatial patterns a systematic assessment of variation at fine spatial scales is needed — 10s to 100s of metres if the spatial information on biomass is to match the spatial information on deforestation. From the coarse resolutions evaluated in this study, it is not clear that the variation in biomass within a forest stand is less than the variation across the entire Amazon basin. In Fig. 5, the low variation in biomass within each map (*y*-axis) relative to its variation in ground points (*x*-axis) suggests that most of the variability is at scales smaller than the resolution of map pixels. Attempts herein to use kriging to extrapolate the 44 site measurements across the region were unsuccessful because the variation in biomass was as large between closely spaced plots as it was between more distant plots. Kriging is useful in interpolating points in space, (i) when some of the points are close enough in space to include fine-scale variability and (ii) when the fine-scale variability is less than coarse-scale variability. The fine-scale variability in forests is large and probably related to time since last tree fall or to microscale variations in soil properties or hydrology (Laurance *et al.* 1999). The distribution of samples used herein did not include fine-scale data, but such data may be available from limited inventories (Brown *et al.* 2000; Clark *et al.* unpubl. data; Higuchi *et al.* unpubl. data; Uhl *et al.* unpubl. data). They might also exist in the form of measurements of basal area and canopy heights over larger regions of Amazonia. An analysis of such data might help define the appropriate sample size, distribution, and density needed for a large-scale inventory of biomass (Brown *et al.* 1995). As shown above, there is a

slight negative correlation (of questionable significance) between area sampled and reported biomass. The correlation does not explain the differences between estimates compared here, however (Table 4 or, e.g., Brown & Lugo 1992 vs. Fearnside 1992).

Third, there is a need for understanding not only the patterns of biomass distribution over large regions, but also changes in biomass. All of the approaches compared in this analysis treat biomass as a static, rather than a dynamic, property of ecosystems. In fact, biomass is continually changing as a result of disturbances and recovery, and perhaps as of result of regional and global changes in climate, atmospheric concentrations of CO₂, or other factors. Even if biomass were directly measured today, in most places it would be different a year from now because of either natural or human-induced disturbances. A more accurate conception of biomass is to consider its dynamic nature. The need for direct measurements of change in tropical regions is critical for understanding the global carbon cycle, because estimates of the source/sink are not as well constrained for the tropics as they are in temperate and boreal regions. Inversion analyses based on atmospheric measurements and models do not have CO₂ sampling stations near tropical forests and, furthermore, atmospheric transport over tropical regions is poorly understood. Similarly, the forest inventories routinely carried out in most northern mid-latitude nations (Birdsey & Heath 1995; Nabuurs *et al.* 1997; Shvidenko & Nilsson 1998; Kurz & Apps 1999) are lacking in tropical forests.

Both intensive and extensive measurements of biomass are appropriate. Intensive measurements should include repeated monitoring at permanent plots. How old are 'mature' forests? When were they last disturbed? How long do they accumulate carbon? At what rates? What are the rates of tree mortality and how variable are they? Extensive studies should be used to address broad spatial patterns of change. Possible methods include statistically designed ground measurements (forest surveys) and satellite-based measurements in combination with models. Natural disturbances at small spatial scales (for example, tree falls) are reasonably well documented. In contrast, natural disturbances at larger temporal and spatial scales are poorly understood. They might be studied in at least three ways.

Ground-based inventories. Continuous forest inventories, carried out routinely in the forests of most northern mid-latitude countries, provide a wealth of data on growth rates, mortality rates, and growing stocks that can be used to estimate biomass (e.g. Brown *et al.* 1999; Brown & Schroeder 1999; Caspersen *et al.* 2000), but they are expensive. They might be prohibitively expensive for the large area of the Amazon, although

there is much to be learned from repetitive sampling of a limited number of plots (Phillips *et al.* 1998). A combination of satellite and ground data is more efficient. For example, the percentage tree cover from satellite (DeFries *et al.* 2000), together with complementary data on tree density, basal area and height, would provide a good indicator of aboveground biomass, especially in closed-canopy forests.

Monitoring and modelling disturbance. Another approach would link remotely sensed disturbances with a dynamic ecosystem model. Biomass could be approximated by documenting disturbances in time and space and simulating recovery following disturbance. MODIS offers the opportunity to monitor disturbance of plant cover around the world at 1–2-day intervals, although monthly to seasonal coverage is likely to capture most disturbances. Spatially specific biomass could be calculated using ecosystem models that simulate the loss of biomass following disturbance and its accumulation during recovery. Such models are not trivial to develop, but they would provide a good alternative to existing static methods. The advantage of addressing dynamics is, of course, that it yields an estimate of change and thus spatially explicit sources and sinks of carbon.

More direct measurement of aboveground biomass with satellite. A more direct assessment of biomass and its changes might also be possible from airborne or satellite data. Optical and microwave (radar) data have not yet been successful in measuring forest biomass; they saturate with canopy closure or at relatively low levels of biomass, respectively (Waring *et al.* 1995; Rignot *et al.* 1997; Nelson *et al.* 2000). Different polarizations of synthetic aperture radar (SAR) have helped distinguish more structure in the canopy, but interpretations are difficult. Radar is sensitive to water content and branch architecture, neither of which is clearly related to biomass. Longer wavelength radars are not as likely to saturate even at high levels of biomass, but long-wave radars have been limited to airborne platforms. They have not been deployed in space.

A promising new approach is the use of lidar, which yields a measure of tree height (Magnussen & Boudewyn 1998) and is related to biomass (Means *et al.* 1999). Recent 3D models with lidar data suggest that the data are highly correlated with aboveground biomass in coniferous forests of northwestern USA (Lefsky *et al.* 1999a; Means *et al.* 1999) as well as in deciduous forests of eastern USA (Lefsky *et al.* 1999b). A NASA satellite equipped with a lidar designed to measure tree heights, biomass, and topography, the Vegetation Canopy Lidar

(VCL), was scheduled for launch in 2000, but as a consequence of funding and technical issues is currently expected to launch in 2002.

Given the Kyoto Protocol and the imminent need to determine sources and sinks of carbon resulting from land-use change (and, perhaps, from natural processes as well), methods that can determine biomass accurately, repeatedly, and inexpensively are desperately needed. If available, such methods would be used routinely by the world's nations.

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References

- Alves DS, Soares JV, Amaral S *et al.* (1997) Biomass of primary and secondary vegetation in Rondonia, Western Brazilian Amazon. *Global Change Biology*, **3**, 451–461.
- Annas RM (1996) *Structure of Two Forests of the Territorio Indigena Multiétnico with an Evaluation of Management Strategies*. Ciddendenbeni, Trinidad, Bolivia.
- Araújo TM, Higuchi N, Carvalho JA Jr (1999) Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Pará, Brazil. *Forest Ecology and Management*, **117**, 43–52.
- Birdsey RA, Heath LS (1995) Carbon changes in U.S. forests. In: *Productivity of America's Forests and Climate Change* (ed. Joyce LA), pp. 56–70. General Technical Report RM-GTR-271. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station Fort Collins, CO.
- BOLFOP (1995) *Projecto forestal de Lomerio – Plan de Manejo Forestal para la zona Norte*. Borrador 01/9/95.
- Brown IF, Nepstad DC, Luz LM, Alechandre AS (1992) Carbon storage and land use in extractive reserves, Acre, Brazil. *Environmental Conservation*, **19**, 307–315.
- Brown IF, Martinelli LA, Thomas WW, Moreira MZ, Ferreira CAC, Victoria RA (1995) Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. *Forest Ecology and Management*, **75**, 175–189.
- Brown S, Gaston G (1995) Use of forest inventories and geographic information systems to estimate biomass density of tropical forests: application to tropical Africa. *Environmental Monitoring and Assessment*, **38**, 157–168.
- Brown S, Lugo AE (1992) Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia*, **17**, 8–18.
- Brown SL, Schroeder PE (1999) Spatial patterns of aboveground production and mortality of woody biomass for eastern U.S. forests. *Ecological Applications*, **9**, 968–980.
- Brown S, Iverson LR, Prasad A, Liu D (1993) Geographical Distributions of Carbon in Biomass and Soils of Tropical Asian Forests. *Geocarto International*, **4**, 45–59.
- Brown S, Schroeder P, Kern JS (1999) Spatial distribution of biomass in forests of the eastern USA. *Forest Ecology and Management*, **123**, 81–90.
- Brown S, Burnham M, Delaney M, Vaca R, Powell M, Moreno A (2000) Issues and challenges for forest-based carbon-offset projects: a case study of the Noel Kempff Climate Action Project in Bolivia. *Mitigation and Adaptation Strategies for Climate Change*, **5**, 99–121.
- Cairns MA, Brown S, Helmer EH, Baumgardner GA (1997) Root biomass allocation in the world's upland forests. *Oecologia*, **111**, 1–11.
- Cardenas JDR, Kahn FL, Guillaumet JL (1982) Estimativa da fitomassa do reservatório da UHE de Tucuruí. In: *Projeto Tucuruí, Relatório Semestral January-Jun. 1982, 2: Limnologia, Macrófitas, Fitomassa, Degradação de Fitomassa, Doenças Endêmicas, Solos: Brazil, Ministério das Minas e Energia, Centrais Elétricas do Norte S.A. (ELETRONORTE) and Brazil, Instituto Nacional de Pesquisas da Amazônia (INPA)*, pp. 1–11. INPA, Manaus.
- Carvalho Jr, Ja Santos JM Santos MM (1995) A tropical rainforest clearing experiment by biomass burning in the Manaus region. *Atmospheric Environment*, **29**, 2301–2309.
- Caspersen JP, Pacala SW, Jenkins JC, Hurtt GC, Moorcroft PR, Birdsey RA (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science*, **290**, 1148–1151.
- De Paula J, Imaña Encinas J, Da Silva Pereira B (1993) Inventário de um hectare de mata ripária. *Pesquisa Agropecuária Brasileira*, **28**, 143–152.
- De Paula JE, Imaña Encinas J, De Mendonça RC, Leão DT (1990) Estudo Dendrométrico e Ecológico de Mata Ripária da Região Centro-Oeste. *Pesquisa Agropecuária Brasileira*, **25**, 43–55.
- DeFries RS, Townshend JRG, Hansen MC (1999) Continuous fields of vegetation characteristics at the global scale at 1-km resolution. *Journal of Geophysical Research*, **104**, 16,911–16,923.
- DeFries RS, Hansen MC, Townshend JRG, Janetos AC, Loveland TR (2000) A new global 1-km data set of percentage tree cover derived from remote sensing. *Global Change Biology*, **6**, 247–254.
- Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1997) The distribution of organic carbon in major components of forests located in five life zones of Venezuela. *Journal of Tropical Ecology*, **13**, 697–708.
- Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. *Biotropica*, **30**, 2–11.
- DNPM (1973–83) *Projeto RADAMBRASIL: Levantamento de Recursos Naturais*, Vols 1–23. Brazil, Ministério das Minas e Energia, Departamento Nacional de Produção Mineral (DNPM), Rio de Janeiro.
- Eidenshink JC, Faudeen JL (1994) The 1 km AVHRR global land data set: First stages in implementation. *International Journal of Remote Sensing*, **15**, 17 3443–17 3417 3462.
- Faber-Langendoen D, Gentry AH (1991) The structure and diversity of rain forests at Bajo Calima, Choco Region, Western Colombia. *Biotropica*, **23**, 2–11.
- FAO (1993) *Forest Resources Assessment 1990. Tropical Countries*. FAO Forestry Paper 112. FAO, Rome.
- Fearnside PM (1992) Forest biomass in Brazilian Amazonia:

- Comments on the estimate by Brown and Lugo. *Interciencia*, **17**, 19–27.
- Fearnside PM (1997) Greenhouse gases from deforestation in Brazilian Amazonia: net committed emissions. *Climatic Change*, **35**, 321–360.
- Fearnside PM (2000) Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Climatic Change*, **46**, 115–158.
- Fearnside PM, Filho NL, Fernandes PM (1993) Rainforest burning and the global carbon budget: Biomass, combustion efficiency and charcoal formation in the Brazilian Amazon. *Journal of Geophysical Research*, **98** (D9), 733–716.
- Fölster H, De Las Salas G, Khanna P (1976) A tropical evergreen forest site with perched water table, Magdalena Valley, Colombia. Biomass and bioelement inventory of primary and secondary vegetation. *Oecologia Plantarum*, **11**, 297–320.
- Gaston G, Brown S, Lorenzini M, Singh KD (1998) State and change in carbon pools in the forests of tropical Africa. *Global Change Biology*, **4**, 97–114.
- Glerum BB (1960) *Report to the Government of Brazil on a forest inventory in the Amazon Valley. Part 5: Region between Rio Caete and Rio Maracassume*. Expanded Technical Assistance Program. FAO, Rome.
- Glerum BB, Smit G (1962) *Report to the Government of Brazil on a combined forestry-soil survey along the road BR-14 from Sao Miguel do Guama to Imperatriz*. Expanded Technical Assistance Program. FAO, Rome.
- Golley FB, McGinnis JT, Clements RG, Child GI, Duever MJ (1975) *Mineral Cycling in a Tropical Moist Forest Ecosystem*. University of Georgia Press, Athens, GA.
- Grimm U, Fassbender HW (1981) Ciclos biodequímicos em un ecosistemas forestal de los Andes Occidentales de Venezuela. I. Inventario de las reservas organicas y minerales (N,P,K,Mg,Mn,Fe,Al,Na). *Turrialba*, **31**, 27–37.
- Heinsdijk D (1957) *Report to the Government of Brazil on a forest inventory in the Amazon Valley (Region between Rio Tapajos and Rio Xingu)*. Expanded Technical Assistance Program 57. FAO, Rome.
- Heinsdijk D (1958a) *Report to the Government of Brazil on a forest inventory in the Amazon Valley. Part 2: Region between Rio Xingu and Rio Tocantins*. Expanded Technical Assistance Program. FAO, Rome.
- Heinsdijk D (1958b) *Report to the Government of Brazil on a forest inventory in the Amazon Valley. Part 3: Region between Rio Tapajos and Rio Madeira*. Expanded Technical Assistance Program. FAO, Rome.
- Heinsdijk D (1958c) *Report to the Government of Brazil on a forest inventory in the Amazon Valley. Part 4: Region between Rio Tocantins and Rio Guama and Capin*. Expanded Technical Assistance Program. FAO, Rome.
- Higuchi N, Marden dos Santos J, Imanaga M (1994) Aboveground biomass estimate for Amazonian dense tropical moist forests. *Memorial Faculty of Agriculture, Kagoshima University*, **30**, 43–54.
- Houghton RA, Skole DL, Nobre CA, Hackler JL, Lawrence KT, Chomentowski WH (2000) Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. *Nature*, **403**, 301–304.
- IBGE (1988) *Mapa de Vegetacao do Brasil (as digitized at the U.S. Geological Survey's EROS Data Center, Sioux Falls, SD)*. Fundacao Instituto Brasileiro de Geografia e Estatistica/ Ministerio da Agricultura/ Instituto Brasileiro de Desenvolvimento Florestal. IBGE, Rio de Janeiro.
- Imanaencinas J, Depaula JE, Kleinn C (1995) Wood biomass of one gallery forest. *Pesquisa Agropecuaria Brasileira*, **30**, 421–427.
- Iverson LR, Brown S, Prasad A, Mitasova H, Gillespie AJR, Lugo AE (1994) Use of GIS for estimating potential and actual forest biomass for continental South and Southeast Asia. In: *Effects of Land Use Change on Atmospheric CO₂ Concentrations: South and Southeast Asia as a Case Study* (ed. Dale VH), pp. 67–116. Springer, New York.
- Jordan CF, Uhl C (1978) Biomass of 'terra firme' forest of the Amazon Basin. *Oecologia Plantarum*, **13**, 387–400.
- Kauffman JB, Cummings DL, Ward DE, Babbitt R (1995) Fire in the Brazilian Amazon: 1. biomass, nutrient pools, and losses in slashed primary forests. *Oecologia*, **104**, 397–409.
- Klinge H, Herrera R (1978) Biomass studies in Amazon caatinga forest in southern Venezuela. I. Standing crop of composite root mass in selected stands. *Tropical Ecology*, **19**, 93–110.
- Klinge H, Herrera R (1983) Phytomass structure of natural plant communities on spodosols in southern Venezuela: The tall Amazon Caatinga forest. *Vegetatio*, **53**, 65–84.
- Klinge H, Rodrigues WA (1973) Biomass estimation in a central Amazonian rain forest. *Acta Ciencias Venezuelana*, **24**, 225–237.
- Kudrencky J (1993) *Inventario Forestal San Jose de Cabitu. Ciddebeni (collection organization), Trinidad, Bolivia*.
- Kurz WA, Apps MJ (1999) A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications*, **9**, 526–547.
- Laurance WF, Fearnside PM, Laurance SG *et al.* (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management*, **118**, 127–138.
- Lefsky MA, Cohen WB, Acker SA, Parker GG, Spies TA, Harding D (1999a) Lidar remote sensing of the canopy structure and biophysical properties of Douglas-fir western hemlock forests. *Remote Sensing of Environment*, **70**, 339–361.
- Lefsky MA, Harding D, Cohen WB, Parker G, Shugart HH (1999b) Surface lidar remote sensing of basal area and biomass in deciduous forests of eastern Maryland, USA. *Remote Sensing of the Environment*, **67**, 83–98.
- Luckman A, Baker J, Kuplich TM, Yanasse CFC, Frery AC (1997) A Study of the Relationship between Radar Backscatter and Regenerating Tropical Forest Biomass for Spaceborne SAR Instruments. *Remote Sensing of the Environment*, **60**, 1–13.
- Magnussen S, Boudewyn P (1998) Derivations of stand heights from airborne laser scanner data with canopy-based quantile estimators. *Canadian Journal of Forest Research*, **28**, 1016–1031.
- McWilliam ALC, Roberts JM, Cabral OMR *et al.* (1993) Leaf area index and above-ground biomass of terra firme rain forest and adjacent clearings in Amazonia. *Functional Ecology*, **7**, 310–317.
- Means JE, Acker SA, Harding DJ *et al.* (1999) Use of large-footprint scanning airborne lidar to estimate forest stand characteristics in the western Cascades of Oregon. *Remote Sensing of the Environment*, **67**, 298–308.
- Nabuurs GJ, Paivinen R, Sikkema R, Mohren GMJ (1997) The

- role of European forests in the global carbon cycle – A review. *Biomass and Bioenergy*, **13**, 345–358.
- Nelson BW, Mesquita R, Pereira JLG, Souza SGA, Batista GT, Couto LB (1999) Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *Forest Ecology and Management*, **117**, 149–167.
- Nelson RF, Kimes DS, Salas WA, Routhier M (2000) Secondary forest age and tropical forest biomass estimation using thematic mapper imagery. *Bioscience*, **50**, 419–431.
- Nepstad DC (1989) Forest Regrowth on abandoned pastures in Eastern Amazonia: Limitations to tree seedling survival and growth. Doctoral Thesis, Yale University.
- Olson JS, Watts JA, Allison LJ (1983) *Carbon in Live Vegetation of Major World Ecosystems*. TR004. U.S. Department of Energy, Washington, DC.
- ONERN (1990) *Estudio semidetallado de suelos y forestales del curso Medio y Bajo Urubamba*. Oficina Nacional de Evaluación de Recursos Naturales (ONERN), Lima.
- Overman JPM, Witte HJL, Saldarriaga JG (1994) Evaluation of regression models for above-ground biomass determination in Amazon rainforest. *Journal of Tropical Ecology*, **10**, 207–218.
- Phillips OL, Malhi Y, Higuchi N *et al.* (1998) Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science*, **282**, 439–442.
- Potter CS (1999) Terrestrial biomass and the effects of deforestation on the global carbon cycle. *Bioscience*, **49**, 769–778.
- Potter CS, Davidson EA, Klooster SA, Nepstad DC, De Negreiros GH, Brooks V (1998) Regional application of an ecosystem production model for studies of biogeochemistry in Brazilian Amazonia. *Global Change Biology*, **4**, 315–333.
- Rignot E, Salas WA, Skole DL (1997) Mapping deforestation and secondary growth in Rondônia, Brazil, using imaging radar and thematic mapper data. *Remote Sensing of Environment*, **59**, 167–179.
- Russell CE (1983) Nutrient cycling and productivity of native and plantation forests at Jari Florestal, Para, Brazil. Doctoral thesis, University of Georgia. University Microfilms International, Ann Arbor, MI.
- Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence of forest succession in the Upper Rio Negro of Colombia and Venezuela. *Journal of Ecology*, **76**, 938–958.
- Salomão RP, Nepstad DC, Vieira IC (1996) Biomassa e estrutura de florestais tropicais e o efeito estufa. (Biomass and structure of tropical forests and the greenhouse effect). *Ciencia Hoje*, **21**, 38–47.
- Shvidenko A, Nilsson S (1998) Dynamics of forest resources of the former Soviet Union with respect to the carbon budget. In: *Carbon Mitigation Potentials in Forestry and Wood Industry* (eds Kohlmaier GH *et al.*), pp. 43–62. Springer, Berlin.
- Stone TA, Schlesinger P, Houghton RA, Woodwell GM (1994) A map of the vegetation of South America based on satellite imagery. *Photogrammetric Engineering and Remote Sensing*, **60**, 541–551.
- Uhl C, Buschbacher R, Serrão EAS (1988) Abandoned pastures in Eastern Amazônia, I: Patterns of plant succession. *Journal of Ecology*, **76**, 663–681.
- Waring RH, Way J, Hunt ER *et al.* (1995) Imaging radar for ecosystem studies. *Bioscience*, **45**, 715–723.