Article:
Baker, T.R., Phillips, O.L., Malhi, Y. et al. (15 more authors) (2004) Increasing biomass in Amazonian forest plots. Philosophical Transactions Of The Royal Society Of London Series B - Biological Sciences, 359 (1443). pp. 353-365. ISSN 1471-2970

doi: 10.1098/rstb.2003.1422

THE ROYAL SOCIETY

Published online 11 February 2004

Increasing biomass in Amazonian forest plots

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A previous study by Phillips *et al.* of changes in the biomass of permanent sample plots in Amazonian forests was used to infer the presence of a regional carbon sink. However, these results generated a vigorous debate about sampling and methodological issues. Therefore we present a new analysis of biomass change in old-growth Amazonian forest plots using updated inventory data. We find that across 59 sites, the above-ground dry biomass in trees that are more than 10 cm in diameter (AGB) has increased since plot establishment by 1.22 ± 0.43 Mg per hectare per year ($ha^{-1}\,yr^{-1}$, where $1\ ha = 10^4\ m^2$), or 0.98 ± 0.38 Mg $ha^{-1}\,yr^{-1}$ if individual plot values are weighted by the number of hectare years of monitoring. This significant increase is neither confounded by spatial or temporal variation in wood specific gravity, nor dependent on the allometric equation used to estimate AGB. The conclusion is also robust to uncertainty about diameter measurements for problematic trees: for 34 plots in western Amazon forests a significant increase in AGB is found even with a conservative assumption of zero growth for all trees where diameter measurements were made using optical methods and/or growth rates needed to be estimated following fieldwork. Overall, our results suggest a slightly greater rate of net stand-level change than was reported by Phillips *et al.* Considering the spatial and temporal scale of sampling and associated studies showing increases in forest growth and stem turnover, the results presented here suggest that the total biomass of these plots has on average increased and that there has been a regional-scale carbon sink in old-growth Amazonian forests during the previous two decades.

Keywords: Amazonia; biomass; carbon; permanent plot; tropical forests

1. INTRODUCTION

Quantifying changes over time in the carbon storage of Amazonian forests is extremely important for understanding current and future trends in the global carbon cycle (Prentice *et al.* 2001). Variation occurs over a range of time-scales and monitoring these patterns remains a considerable challenge. Over short time-scales, at a number of Amazonian sites, measurements of carbon dioxide fluxes between the forest and atmosphere have been made by eddy covariance systems to estimate forest carbon balance (Grace *et al.* 1995; Malhi *et al.* 1998), but it is difficult to extend these measurements over many years or many sites. Inversion models, which combine data on the concentrations of carbon dioxide, oxygen and their isotopes

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One contribution of 17 to a Theme Issue 'Tropical forests and global atmospheric change'.

with atmospheric circulation models to predict patterns of carbon dioxide sources and sinks, can be used on large scales (Gurney *et al.* 2002), but are poorly constrained in tropical regions. By contrast, repeated measurements of permanent sample plots can potentially provide direct estimates of changes in tropical forest biomass with the requisite spatial and temporal coverage from a wide variety of sites.

The potential value of using long-term data from tropical forest plots for studying changes in biomass was highlighted by a study of 68 pantropical sites (Phillips *et al.* 1998). Over the period 1975–1996, in 40 sites across Amazonia, total AGB increased by 0.97 ± 0.58 Mg ha^{-1} yr^{-1}, which is equivalent to 0.88 ± 0.53 Mg ha^{-1} yr^{-1} for trees that are 10 cm or more in diameter. This value was used to estimate a total carbon sink across Amazonia of 0.44 ± 0.26 Gt C yr^{-1}. However, the result generated a vigorous debate about the methodology that should be used to estimate changes in forest biomass from permanent plot measurements. For example, it was suggested that it could be explained by a potential sampling bias towards successional forest on floodplain sites or by poor tree-measurement techniques (Clark 2002; but see also Phillips *et al.* 2002*a*). In addition, the problems inherent in including small plot sizes, where the AGB is not normally distributed, and the potential importance of changes in the carbon stocks of other compartments, such as coarse woody debris, have also been noted (Chave *et al.* 2003, 2004; Rice *et al.* 2004).

The method of AGB estimation used by Phillips *et al.* (1998), on a stand-level basis using plot basal area values is also open to criticism. It is well known that the large number of published biomass equations can give substantial variation in stand-level AGB estimates (Araújo *et al.* 1999; Chambers *et al.* 2001; Baker *et al.* 2004). However, it is not known whether the observed patterns of net biomass *change* are sensitive to the equation used to estimate AGB. In addition, the method of Phillips *et al.* (1998) does not explicitly account for spatial or temporal variation in tree size-frequency distributions or variation in wood specific gravity. As mean tree size and wood specific gravity vary at a regional scale across the Amazon basin (Malhi *et al.* 2002; Baker *et al.* 2004), estimates of AGB change across all sites should ideally include these factors. Also, given the substantial changes over time in Amazon forest dynamics (Phillips & Gentry 1994; Phillips *et al.* 2004; Lewis *et al.* 2004), estimates of AGB change need to incorporate any potential changes in forest structure or functional composition.

A re-examination of pan-Amazonian forest plot data is therefore needed to directly address these issues and provide improved estimates of AGB change. Using old-growth forest plot data, we ask the following questions.

(i) Do the patterns of AGB change depend on the allometric equation used to calculate biomass?
(ii) Are the patterns of change sensitive to spatial or temporal variation in tree size-frequency distributions or wood specific gravity?
(iii) Is there any consistent regional-scale change in AGB?
(iv) Are conclusions about the direction of change influenced by uncertainty concerning problematic tree records?

2. MATERIAL AND METHODS

Inventory data were used from 59 forest sites from across the range of local and regional environmental gradients that occur in Amazonia, including *terra firme* forest on both clay-rich and white-sand substrates, and seasonally flooded forest (figure 1, table 1). All sites examined were in lowland forest (less than 500 m a.m.s.l.) consisting of an apparently mature forest with natural gap-phase dynamics and a canopy dominated by non-pioneer species. None of the plots is believed to have experienced any recent, major, direct human impact. The individual plots range in size from 0.4 to 9.0 ha (median 1.0, mean 1.3 ha), and in total encompass 78.9 ha of forest (table 1). Initial measurement dates vary from 1979 to 1998, and census intervals from 4.0 to 21.7 years (median 10.2, mean 10.9 years; table 1). Overall, the results are based on measurements of 54 364 stems that were 10 cm or more in diameter, and a total sampling effort of 863.8 hectare years. For all plots, family and generic taxonomy has been standardized following the procedures described in Baker *et al.* (2004). Wood specific gravity data are derived from a variety of publications. These sources and the approach used to match specific gravity data to tree records are also described in Baker *et al.* (2004).

Compared with the 40 Amazonian sites included in Phillips *et al.* (1998), the total number has increased by 19 in this study. Thirty-one sites have been retained and extended by including more recent census data, and 28 new sites have been added. However, nine sites have been omitted where AGB change was previously calculated from published stand-level data and where we do not have tree diameter data and taxonomic information.

To make comparisons of rates of AGB change between different landforms, we distinguish two groups of sites, separating 12 plots on old, recent or contemporary floodplains, from forests growing on older surfaces (table 1). This categorization is somewhat subjective, and the 'floodplain' forests in particular comprise sites growing under a wide range of edaphic conditions. Three of the plots (LSL-01, LSL-02 and TIP-03) are flooded annually and one plot (JAS-05) is likely to have been occasionally flooded in the recent past. However, the other eight plots (all CUS, TAM-01, 02, 04 and 06) have been *terra firme* forest for hundreds or thousands of years, and therefore represent the 'Holocene floodplain'. Fluvial geomorphological features and carbon dating suggest that the youngest of the Holocene floodplain sites, TAM-04, must be at least 900 years old (Phillips *et al.* 2002*a*).

The substrates underlying all of the other plots are thought to have been deposited prior to the Holocene. Within these forests, we distinguish sites in western and eastern Amazonia to compare regional patterns of AGB change (table 1, figure 1).

In each plot, all trees greater than or equal to 10 cm in diameter at 1.3 m (= dbh) have been measured during each census, with a consistent effort in all plots for all censuses to measure buttressed trees above the top of the buttress. Increasing steps are being made to standardize all aspects of tree measurements across all sites: the most recent measurements of the 34 western Amazon plots, from Peru, Bolivia and Ecuador, have been undertaken by an overlapping group of researchers during 1998–2002, using standard measurement protocols that have been progressively refined (Phillips & Baker 2002). Since 2000, this fieldwork has formed part of the RAINFOR project (Malhi *et al.* 2002). For buttressed trees, for example, current procedures involve measuring tree diameter 50 cm above the top of the buttress, using ladders if necessary, marking the point of measurement with paint and recording its height.

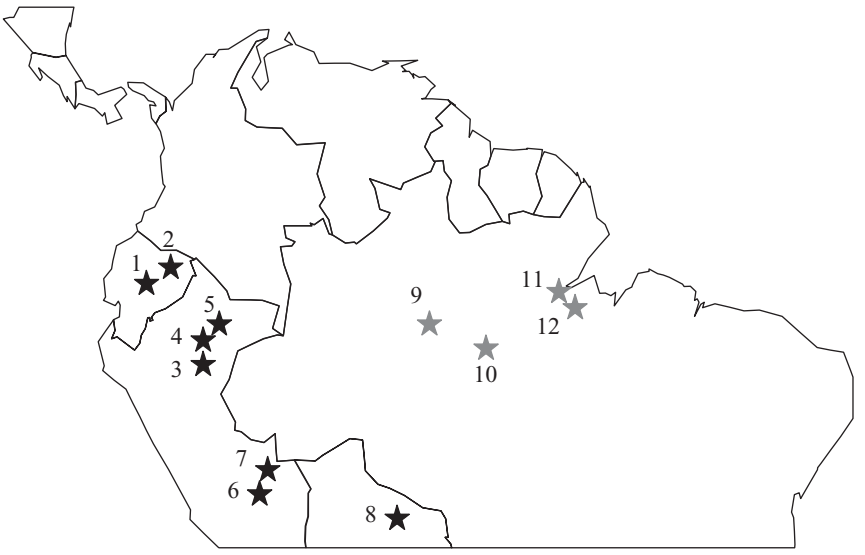

Figure 1. Location of forest sites in western (black symbols) and eastern (grey symbols) Amazonia. 1, Jatun Sacha; 2, Bogi, Tiputini; 3, Allpahuayo; 4, Yanamono; 5, Sucusari; 6, Tambopata; 7, Cusco Amazonico; 8, Huanchaca, Las Londras, Chore, Cerro Pelao, Los Fierros; 9, BDFFP, BIONTE, Jacaranda; 10, Tapajos; 11, Jari; 12, Caxiuana.

Even with careful field procedures, some difficulties will always arise in reconciling new plot data with previous measurements. With the large dataset presented here, compiled from such a diversity of sources and sites, dealing with these problems is particularly important, and as a result of the recent western Amazon fieldwork standard procedures were developed to deal with problematic tree records. In the first instance, identifying erroneous records is difficult, because the potential range of growth rates varies with tree size, species and the census interval. As a guide, plot data were screened for growth rates that exceed or fall below certain limits (less than or equal to -0.2 cm yr^{-1} or greater than or equal to 4 cm yr^{-1}, following Sheil (1995)), but final decisions on any alterations to the original data were made on a tree-by-tree basis. Obvious typographical errors or unusual measurement values in an otherwise steady sequence were corrected by linear interpolation. In some cases, however, the most recent diameter measurement was implausibly less than previous values, occasionally by up to 10 cm. This pattern was probably caused by a lower point of measurement in previous censuses, owing to uncertainty in locating the top of the buttress. For these trees, prior growth was estimated using the median growth rate of the appropriately (10–20 cm, 20–40 cm, or more than 40 cm) sized class.

These tree records, where the diameter data have been altered following fieldwork, clearly introduce uncertainty into estimates of AGB change. Another source of uncertainty is the use of optical methods (digital camera or Relaskop) to measure the diameter of some trees in some plots. Optical methods tend to underestimate tree diameter, and although we have included a theoretical correction factor (see Phillips & Baker 2002) to account for inevitable parallax effects, it is clear that these methods are less precise than using a tape-measure as they cannot integrate irregularities in bole shape. Therefore, using the 34 western Amazon plots, we evaluate the impact of these trees on conclusions concerning the direction or magnitude of AGB change. This was achieved by comparing AGB change using the whole dataset with values when these records are excluded. Removing records makes the conservative assumption that no excluded stem grew during the census interval.

Stand above-ground biomass (kg dry weight ha^{-1}) for all trees that are 10 cm or more dbh (AGB), including palms, was calculated using a variety of allometric equations as follows:

$$\mathrm{AGB} = \sum_{1}^{n} \exp[0.33(\ln D_i) + 0.933(\ln D_i)^2 - 0.122(\ln D_i)^3 - 0.37], \quad (2.1)$$

$$\mathrm{AGB} = \sum_{1}^{n} \frac{\rho_i}{0.67} \{\exp[0.33(\ln D_i) + 0.933(\ln D_i)^2 - 0.122(\ln D_i)^3 - 0.37]\}, \quad (2.2)$$

$$\mathrm{AGB} = \sum_{1}^{n} \exp[2.42(\ln D_i) - 2.00], \quad (2.3)$$

$$\mathrm{AGB} = \sum_{1}^{n} \frac{\rho_i}{0.58} \{\exp[2.42(\ln D_i) - 2.00]\}, \quad (2.4)$$

$$\mathrm{AGB} = 0.6 \times [66.92 + (16.85 \times \mathrm{BA})], \quad (2.5)$$

where D_i and ρ_i are, respectively, the diameter and wood density of tree i, n is the number of stems per plot, and BA is the plot basal area, calculated as

$$\mathrm{BA} = \sum_{1}^{n} \pi (D_i/2)^2.$$

The different AGB equations reflect different underlying datasets of tree mass data, the inclusion of exclusion of variation in wood specific gravity, and tree-by-tree and stand-level approaches to calculating biomass. Equation (2.1) was obtained from data for 315 trees, harvested in five 0.04 ha (20 m $\times$ 20 m) plots, as part of the BIONTE project, near Manaus, Brazil (Chambers *et al.* 2001). Equation (2.2) is a modified version, incorporating a simple multiplication factor to account for variation in wood specific gravity between species (Baker *et al.* 2004). Equation (2.3) was derived from an independent set of tree diameter and mass data of 378 trees (Chave *et al.* 2001), and equation (2.4) is the same relationship, but including wood specific gravity (Baker *et al.* 2004). By contrast, equation (2.5) is based on the same tree

Table 1. Site descriptions, location and biomass data for 59 forest plots in Amazonia.
(AGB values were calculated using equation (2.2) (Baker *et al.* 2004). Plot data are the best available to the lead author at the time of final analyses, but are subject to future revision as a result of additional censuses and continued error checking. Abbreviations: lat., latitude; long., longitude; dec, decimal.)

name	code	country	region	lat. (dec)	long. (dec)	principal investigator(s)	institution	forest type	plot size (ha)	initial census date	final census date	census interval (years)	AGB (Mg ha^{-1}) start	AGB (Mg ha^{-1}) end	AGB change (Mg ha^{-1} yr^{-1})
Allpahuayo A, clay-rich soils[a]	ALP-11	Peru	west	−3.95	−73.43	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	0.44	1990.87	2001.03	10.15	272.35	269.51	−0.28
Allpahuayo A, sandy soils[a]	ALP-12	Peru	west	−3.95	−73.43	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	0.40	1990.87	2001.03	10.15	267.98	266.46	−0.15
Allpahuayo B, sandy soils[a]	ALP-21	Peru	west	−3.95	−73.43	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	0.48	1990.87	2001.04	10.16	285.33	287.61	0.22
Allpahuayo B, clay-rich soils[a]	ALP-22	Peru	west	−3.95	−73.43	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	0.44	1990.87	2001.04	10.16	226.71	241.02	1.41
BDFFP, 2303 Faz. Dimona 4,5[b]	BDF-01	Brazil	east	−2.40	−60.00	W. Laurance	Smithsonian	*terra firme*	2.00	1985.29	1997.71	12.42	376.48	378.67	0.18
BDFFP, 1101 Gaviao	BDF-03	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	1.00	1981.12	1999.29	18.17	330.13	338.90	0.48
BDFFP, 1102 Gaviao	BDF-04	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	1.00	1981.12	1999.29	18.17	325.80	250.68	−4.13
BDFFP, 1103 Gaviao	BDF-05	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	1.00	1981.21	1999.29	18.08	288.74	304.29	0.86
BDFFP, 1201 Gaviao[b]	BDF-06	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	3.00	1981.29	1999.29	18.00	289.83	295.04	0.29
BDFFP, 1109 Gaviao	BDF-08	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	1.00	1981.62	1999.46	17.83	329.49	318.90	−0.59
BDFFP, 1301 Florestal	BDF-10	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	1.00	1983.46	1997.12	13.67	316.23	326.88	0.78
BDFFP, 1301 Florestal 2[b]	BDF-11	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	3.00	1983.46	1997.12	13.67	334.82	354.72	1.46
BDFFP, 1301 Florestal 3[b]	BDF-12	Brazil	east	−2.40	−59.90	W. Laurance	Smithsonian	*terra firme*	2.00	1983.46	1997.12	13.67	332.42	348.98	1.21
BDFFP, 3402 Cabo Frio	BDF-13	Brazil	east	−2.40	−60.00	W. Laurance	Smithsonian	*terra firme*	9.00	1985.86	1998.87	13.02	321.97	342.19	1.55
BDFFP, 3304 Porto Alegre[b]	BDF-14	Brazil	east	−2.40	−60.00	W. Laurance	Smithsonian	*terra firme*	2.00	1984.21	1998.37	14.17	368.40	356.11	−0.87
Bionte 1	BNT-01	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	1.00	1986.50	1999.20	12.70	332.21	370.45	3.01
Bionte 2	BNT-02	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	1.00	1986.50	1999.20	12.70	350.03	389.57	3.11
Bionte 4	BNT-04	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	1.00	1986.50	1999.20	12.70	318.98	331.91	1.02
Bionte T4 B2 SB1	BNT-05	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	1.00	1986.50	1993.50	7.00	306.99	324.03	2.43
Bionte T4 B1 SB3	BNT-06	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	1.00	1986.50	1993.50	7.00	376.03	363.59	−1.78
Bionte T4 B1 SB4	BNT-07	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	1.00	1986.50	1993.50	7.00	349.44	358.61	1.31
Bogi 1 (PA)	BOG-01	Ecuador	west	−0.70	−76.48	N. Pitman, A. DiFiore	Duke University, NYU	*terra firme*	1.00	1996.29	2002.13	5.83	262.71	289.42	4.58

(*Continued*.)

Table 1. (*Continued.*)

name	code	country	region	lat. (dec)	long. (dec)	principal investigator(s)	institution	forest type	plot size (ha)	initial census date	final census date	census interval (years)	AGB (Mg ha^{-1}) start	AGB (Mg ha^{-1}) end	AGB change (Mg ha^{-1} yr^{-1})
Bogi 2 (PB)	BOG-02	Ecuador	west	−0.70	−76.47	N. Pitman, A. DiFiore	Duke University, NYU	*terra firme*	1.00	1996.29	2002.13	5.83	211.43	221.98	1.81
Caxiuana 1	CAX-01	Brazil	east	−1.70	−51.53	S. Almeida	Museu Goeldi	*terra firme*	1.00	1994.50	2002.88	8.38	369.60	378.73	1.09
Caxiuana 2	CAX-02	Brazil	east	−1.70	−51.53	S. Almeida	Museu Goeldi	*terra firme*	1.00	1995.50	2003.21	7.71	367.48	364.62	−0.37
Chore 1	CHO-01	Bolivia	west	−14.35	−61.16	T. Killeen	Museo Noel Kempff	*terra firme*	1.00	1996.50	2001.44	4.94	117.52	124.82	1.49
Cerro Pelao 1	CRP-01	Bolivia	west	−14.54	−61.48	T. Killeen	Museo Noel Kempff	*terra firme*	1.00	1994.21	2001.45	7.25	212.54	213.66	0.15
Cerro Pelao 2	CRP-02	Bolivia	west	−14.53	−61.48	T. Killeen	Museo Noel Kempff	*terra firme*	1.00	1994.27	2001.46	7.19	220.84	233.83	1.81
Cuzco Amazonico, CUZAM1E	CUZ-01	Peru	west	−12.50	−68.95	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	1.00	1989.39	1998.77	9.38	252.19	283.34	3.32
Cuzco Amazonico, CUZAM1U	CUZ-02	Peru	west	−12.50	−68.95	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	1.00	1989.42	1998.77	9.35	216.95	248.66	3.39
Cuzco Amazonico, CUZAM2E	CUZ-03	Peru	west	−12.49	−69.11	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	1.00	1989.40	1998.77	9.37	217.50	250.26	3.50
Cuzco Amazonico, CUZAM2U	CUZ-04	Peru	west	−12.49	−69.11	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	1.00	1989.44	1998.78	9.34	269.52	289.19	2.11
Huanchaca Dos, plot 1	HCC-21	Bolivia	west	−14.56	−60.75	L. Arroyo	Museo Noel Kempff	*terra firme*	1.00	1996.52	2001.43	4.91	245.28	249.19	0.80
Huanchaca Dos, plot 2	HCC-22	Bolivia	west	−14.57	−60.74	L. Arroyo	Museo Noel Kempff	*terra firme*	1.00	1996.54	2001.43	4.89	263.77	270.88	1.45
Jacaranda, plots 1–5	JAC-01	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	5.00	1996.50	2002.50	6.00	319.46	315.88	−0.60
Jacaranda, plots 6–10	JAC-02	Brazil	east	−2.38	−60.10	N. Higuchi	INPA	*terra firme*	5.00	1996.50	2002.50	6.00	315.41	311.52	−0.65
Jatun Sacha 2	JAS-02	Ecuador	west	−1.07	−77.60	D. Neill	Herbario Nacional	*terra firme*	1.00	1987.63	2002.04	14.42	248.81	247.96	−0.06
Jatun Sacha 3	JAS-03	Ecuador	west	−1.07	−77.67	D. Neill	Herbario Nacional	*terra firme*	1.00	1988.88	2002.04	13.17	231.88	262.78	2.35
Jatun Sacha 4	JAS-04	Ecuador	west	−1.07	−77.67	D. Neill	Herbario Nacional	*terra firme*	0.92	1994.50	2002.04	7.54	282.69	318.58	4.79
Jatun Sacha 5	JAS-05	Ecuador	west	−1.07	−77.67	D. Neill	Herbario Nacional	*terra firme*, floodplain	1.00	1989.38	2002.04	12.67	268.10	286.83	1.48
Jari 1[c]	JRI-01	Brazil	east	−1.00	−52.05	N. Silva	CIFOR, EMBRAPA	*terra firme*	1.00	1985.50	1996.00	10.50	392.50	387.09	−0.51

(*Continued.*)

Table 1. (*Continued.*)

name	code	country	region	lat. (dec)	long. (dec)	principal investigator(s)	institution	forest type	plot size (ha)	initial census date	final census date	census interval (years)	AGB (Mg ha^{-1}) start	AGB (Mg ha^{-1}) end	AGB change (Mg ha^{-1} yr^{-1})
Los Fierros Bosque I	LFB-01	Bolivia	west	−14.61	−60.87	T. Killeen	Museo Noel Kempff	*terra firme*	1.00	1993.62	2001.40	7.78	221.59	239.95	2.36
Los Fierros Bosque II	LFB-02	Bolivia	west	−14.60	−60.85	T. Killeen	Museo Noel Kempff	*terra firme*	1.00	1993.65	2001.40	7.76	271.17	284.99	1.78
Las Londras, plot 1	LSL-01	Bolivia	west	−14.40	−61.13	L. Arroyo	Museo Noel Kempff	seasonally flooded	1.00	1996.53	2001.48	4.95	164.82	173.32	1.72
Las Londras, plot 2	LSL-02	Bolivia	west	−14.40	−61.13	L. Arroyo	Museo Noel Kempff	seasonally flooded	1.00	1996.53	2001.48	4.95	176.84	203.55	5.39
Sucusari A	SUC-01	Peru	west	−3.23	−72.90	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	1.00	1992.13	2001.06	8.93	285.61	278.52	−0.79
Sucusari B	SUC-02	Peru	west	−3.23	−72.90	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	1.00	1992.13	2001.07	8.93	298.08	287.49	−1.18
Tambopata plot 0	TAM-01	Peru	west	−12.85	−69.28	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	1.00	1983.78	2000.59	16.81	250.49	260.01	0.57
Tambopata plot 1	TAM-02	Peru	west	−12.83	−69.28	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	1.00	1979.87	2000.58	20.71	241.64	260.07	0.89
Tambopata plot 2 clay	TAM-04	Peru	west	−12.83	−69.28	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	0.42	1983.79	1998.75	14.96	268.33	288.62	1.36
Tambopata plot 3	TAM-05	Peru	west	−12.83	−69.28	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	1.00	1983.70	2000.56	16.86	243.37	266.21	1.35
Tambopata plot 4	TAM-06	Peru	west	−12.83	−69.30	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*, floodplain	0.96	1983.71	2000.55	16.84	233.51	281.95	2.88
Tambopata plot 6	TAM-07	Peru	west	−12.83	−69.27	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	1.00	1983.76	1998.73	14.97	250.82	257.26	0.43
Tapajos, RP014, 1–4[d]	TAP-01	Brazil	east	−3.31	−54.94	N. Silva	CIFOR, EMBRAPA	*terra firme*	1.00	1983.50	1995.50	12.00	262.17	296.14	2.83
Tapajos, RP014, 5–8[d]	TAP-02	Brazil	east	−3.31	−54.94	N. Silva	CIFOR, EMBRAPA	*terra firme*	1.00	1983.50	1995.50	12.00	332.04	373.82	3.48
Tapajos, RP014, 9–12[d]	TAP-03	Brazil	east	−3.31	−54.94	N. Silva	CIFOR, EMBRAPA	*terra firme*	1.00	1983.5	1995.50	12.00	346.21	377.28	2.59
Tiputini 2	TIP-02	Ecuador	west	−0.63	−76.14	N Pitman	Duke University	*terra firme*	0.80	1997.71	2002.13	4.42	257.12	260.84	0.84
Tiputini 3	TIP-03	Ecuador	west	−0.64	−76.15	N. Pitman	Duke University	seasonally flooded	1.00	1998.13	2002.13	4.00	250.07	255.15	1.27
Yanamono A	YAN-01	Peru	west	−3.43	−72.85	O. Phillips, R. Vasquez	Leeds, Proy. Flora del Peru	*terra firme*	1.00	1983.46	2001.05	17.59	290.11	299.20	0.52

[a] Allpahuayo A and B contain two distinctive soil types that are treated separately in these analyses.
[b] These sites comprise non-contiguous 1 ha plots separated by less than 200 m.
[c] Twenty-five 10 m × 10 m subplots, within each of four nearby 1 ha plots.
[d] Twelve 0.25 ha plots laid out in a randomized fashion over an area of 300 m × 1200 m; treated as 3 × 1 ha units.

harvest data as equations (2.1) and (2.2), but calculates AGB on a stand, rather than tree-by-tree, basis, using the relationship between basal area and fresh above-ground biomass of trees more than 5 cm in diameter for the five 0.04 ha subplots (Phillips *et al.* 1998).

We focus on testing whether there have been concerted within-site changes in AGB since plot establishment, by calculating AGB change between the first and last census for each plot. Errors are expressed as 95% confidence limits of the mean. Here, units of dry mass are used for AGB and AGB change. However, AGB values can also be expressed in terms of carbon by assuming a carbon content of 50% (Houghton *et al.* 2001), so carbon change metrics can be calculated simply by dividing the reported values by 2.

To determine whether there have been concerted changes in the AGB of Amazonian plots, it is important to consider whether our approach for assessing the significance of the overall trend is statistically robust. Three issues are relevant: the distribution of AGB change, the statistical independence of the plots and any systematic variation in the sampling error. The first issue is not a concern here—rates of AGB change are normally distributed over the time-scale of this study (figure 2). This pattern shows that we have avoided the potential problems associated with small plot sizes (e.g. 0.2 ha or less), where distributions of AGB and AGB change are skewed because of large trees (Chave *et al.* 2003, 2004). The other issues, however, are more complex. Variation in tropical forest climates, soils, productivity, species richness and composition has a spatial component at multiple scales (ter Steege *et al.* 2003; Tuomisto *et al.* 2003; Malhi & Wright 2004) so there is no spatial scale at which plots are truly independent. For this study a key question is whether structural and dynamic data from plots within individual Amazon landscapes (e.g. plots with the same code in table 1), separated on a scale of a few hundred metres to a few kilometres, should be combined. The evidence from central America suggests that spatial autocorrelation in tropical forest structure is not important at these scales: forest structure is very heterogeneous at landscape scales (e.g. Clark *et al.* 1998), and AGB is not spatially autocorrelated at any scale across contiguous 1 ha plots within a 50 ha plot in Panama (Chave *et al.* 2003). In this study we therefore treat each plot as an independent datum.

Sampling error concerns the reliability of the estimate of AGB change from an individual plot. Variation in sampling error is therefore determined by plot size, the length of the census interval and also any variation in errors made during plot measurements, derived from the tree diameter measurements or uncertainty about trees on plot boundaries, etc. (Chave *et al.* 2003, 2004). Such measurement errors themselves also vary with plot size and/or the length of the monitoring period: tree-level measurement errors will average out at expanding spatial and temporal scales, and over multiple censuses, since previous errors can be corrected. If the sampling errors are confounded with the variable of interest, in this case the magnitude of AGB change, significance tests may prove unreliable (Gurevitch & Hedges 1999). In this study, it is therefore important to note that there are no significant correlations between AGB change and plot size, census interval length or the product of these two factors, the number of 'hectare years' of monitoring. However, as well as showing unweighted AGB change results, we also generate a set of values in which AGB change estimates are weighted by the number of 'hectare years' of monitoring, to attempt to account for unequal sampling errors. Equally, this approach is an imperfect solution as sampling error may not be a simple linear function of the

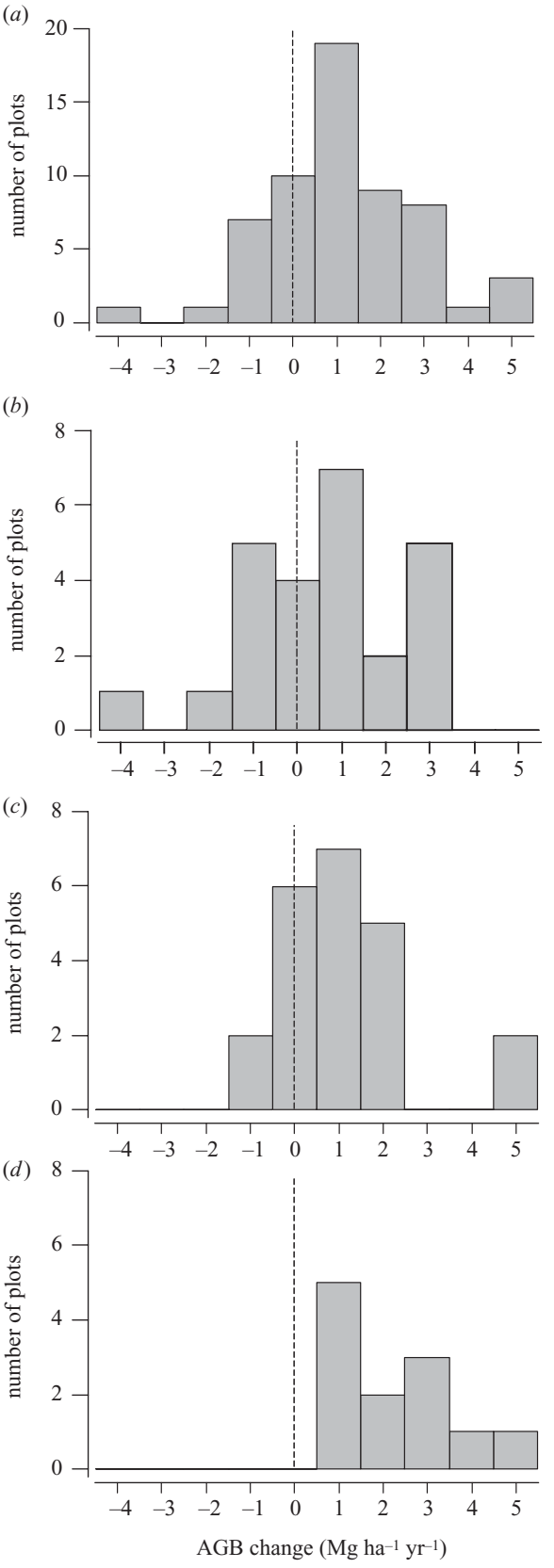

Figure 2. Frequency distribution of rates of change in above-ground biomass for trees ⩾ 10 cm dbh (AGB) for (*a*) all 59 plots, mean change ±95% CI 1.22 ± 0.43 Mg ha^{-1} yr^{-1}, (*b*) pre-Holocene central and eastern Amazon forests, mean change ±95% CI 0.73 ± 0.68 Mg ha^{-1} yr^{-1}, (*c*) pre-Holocene western Amazon forests, mean change ±95% CI 1.17 ± 0.62 Mg ha^{-1} yr^{-1}, and (*d*) Holocene floodplain and contemporary floodplain plots, mean change ±95% CI 2.32 ± 0.79 Mg ha^{-1} yr^{-1}. AGB change calculated using equation (2.2).

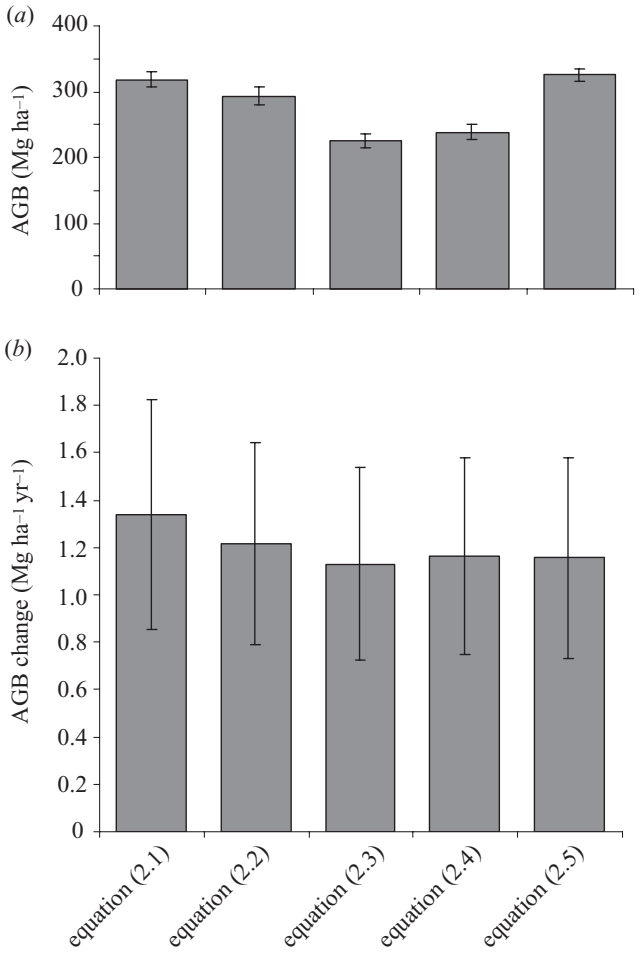

Figure 3. Estimates of (*a*) mean AGB and (*b*) mean AGB change based on five different allometric equations for calculating biomass with inventory data. Error bars are 95% confidence limits of the mean values.

monitoring effort, and other factors, such as plot shape and the number of censuses, may also be important. Overall, it is important to note that the unweighted mean is an unbiased estimate of the overall trend (Gurevitch & Hedges 1999). The weighted and unweighted estimates therefore simply provide different metrics, defined in different ways, for examining among-site change.

3. RESULTS

AGB estimates using stand-level and tree-by-tree approaches based on the same underlying tree mass data give very similar estimates across the plot network (318.3 ± 11.7 and 325.5 ± 10.2 Mg ha^{-1}, respectively; figure 3; equations (2.1) and (2.5)). However, when variation in wood specific gravity is incorporated into the same tree-by-tree equation, the among-plot AGB estimate drops slightly (figure 3; equation (2.2)). This pattern is owing to the lower specific gravity values of western Amazon forests compared with the central Amazon site where the original biomass equation was developed. AGB estimates derived using equations based on the compilation of tree mass data by Chave *et al.* (2001) are substantially lower (225.3 ± 10.3 and 239.0 ± 12.6 Mg ha^{-1}, respectively; figure 3; equations (2.3) and (2.4)). However, despite these significant differences between AGB estimates, estimates of *change* derived using different allometric equations are remarkably similar (figure 3). For all the subsequent results we use equation (2.2) to estimate AGB, as this equation was developed solely using Amazonian tree mass data and adjusts for the regional-scale variation in stand-level wood specific gravity.

Across all plots, AGB change is normally distributed (Kolmogorov–Smirnov test, $D = 0.08$, n.s.). AGB has increased since plot establishment by 1.22 ± 0.43 Mg ha^{-1} yr^{-1} or $0.50 \pm 0.17\%$ yr^{-1} (unweighted average, figure 2*a*) or 0.98 ± 0.38 Mg ha^{-1} yr^{-1} (weighted by hectare years of monitoring). The lower value using the weighted average largely reflects the fact that the three plots with the highest rates of AGB change (BOG-01, JAS-04 and LSL-01) have been monitored for comparatively short periods (4.9–6.9 years).

AGB change is significantly positive in both non-floodplain and floodplain sites, and floodplain plots have higher rates of increase than non-floodplain sites (2.32 ± 0.79 Mg ha^{-1} yr^{-1} unweighted and 2.08 ± 0.74 Mg ha^{-1} yr^{-1} weighted ($n = 12$, figure 2*d*), compared with 0.93 ± 0.46 Mg ha^{-1} yr^{-1} unweighted and 0.80 ± 0.42 Mg ha^{-1} yr^{-1} weighted ($n = 47$)). The patterns of AGB change are also broadly spatially consistent. Increases have occurred in non-floodplain forests in both eastern (figure 2*b*) and western (figure 2c) Amazonia, although the rate of change is only marginally significant when the central and eastern Amazonia plots are considered alone (central and eastern Amazon ($n = 25$), 0.73 ± 0.68 Mg ha^{-1} yr^{-1} unweighted, 0.70 ± 0.58 Mg ha^{-1} yr^{-1} weighted; western Amazonia ($n = 22$), 1.17 ± 0.62 Mg ha^{-1} yr^{-1} unweighted and 1.08 ± 0.59 Mg ha^{-1} yr^{-1} weighted). The tendency for higher absolute rates of AGB change in western Amazon forests is not significant (*t*-test, $p = 0.36$). Owing to the lower overall AGB in western Amazon forests, regional differences in the relative rates of change are greater than the differences in absolute rates (based on unweighted estimates, central and eastern Amazon, $0.23 \pm 0.21\%$ yr^{-1}; western Amazon, $0.51 \pm 0.25\%$ yr^{-1}), but the regional difference is again not significant (*t*-test, $p = 0.10$).

Overall, basal area change represents a very good measure of AGB change within Amazonian forest plots (figure 4; $\Delta\text{AGB} = 9.57(\Delta\text{BA}) + 0.12$, $r^2 = 0.89$, $p < 0.001$). In a multiple regression analysis, change in stand-level wood specific gravity was included as an additional term, but was not individually significant and did not lead to any improvement in predictions of AGB change.

Excluding records of trees measured using optical methods and individuals where growth rates have been estimated following fieldwork does not alter the significance of the direction of AGB change. Of the total western Amazonian dataset of 24 229 trees, 322 trees have been measured with a Relaskop or digital camera and diameter measurements for a partly overlapping set of 492 trees were interpolated or otherwise re-estimated following fieldwork. The total number of trees in at least one of these categories is 609 (2.5% of all stems). If we apply the conservative assumption that all 609 individuals have zero growth over the measurement period, then the AGB change estimate declines by *ca.* 30% in both floodplain and non-floodplain sites (floodplain: from 2.32 ± 0.79 Mg ha^{-1} yr^{-1} to 1.70 ± 0.83 Mg ha^{-1} yr^{-1} (unweighted) and 2.08 ± 0.74 Mg ha^{-1} yr^{-1} to 1.46 ± 0.75 Mg ha^{-1} yr^{-1} (weighted); non-floodplain: 1.17 ± 0.62 Mg ha^{-1} yr^{-1} to 0.79 ± 0.61

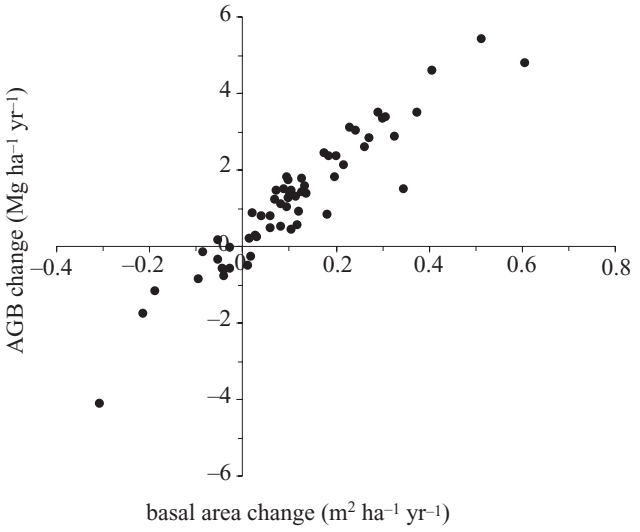

Figure 4. The relationship between basal area change and AGB change.

Mg ha^{-1} yr^{-1} (unweighted) and 1.08 ± 0.59 Mg ha^{-1} yr^{-1} to 0.68 ± 0.59 Mg ha^{-1} yr^{-1} (weighted)). These trees have a disproportionate impact on the stand-level estimates because the most difficult trees to measure tend to be the largest individuals. However, although these factors introduce uncertainty in the magnitude of change, for the western Amazon plots, AGB change remains significantly positive, even when these trees are excluded.

4. DISCUSSION

The re-analysis of Amazonian forest plot data presented here supports the original findings of Phillips *et al.* (1998). This study demonstrates that since plot establishment, AGB has increased by 1.21 ± 0.43 Mg ha^{-1} yr^{-1} (unweighted) or 0.98 ± 0.38 Mg ha^{-1} yr^{-1} (weighted by monitoring effort). These values are higher than the comparable unweighted result for stems that were 10 cm or more in diameter obtained in the original study (0.88 ± 0.52 Mg ha^{-1} yr^{-1}). Here, we have also shown that this pattern is neither confounded by spatial or temporal variation in wood specific gravity, nor dependent on the allometric equation used to estimate AGB. Moreover, the AGB of the western Amazon forests has increased even when the most difficult-to-measure trees are discounted.

It is noteworthy that the stand-level approach used by Phillips *et al.* (1998) to estimate biomass from inventory data is comparable with tree-by-tree methods, as the stand- and tree-level equations based on the same underlying tree mass data (equations (2.1) and (2.5), figure 3) give extremely similar results. This similarity is because the basal area of individual trees is roughly linearly related to tree biomass up to relatively large sizes (80–90 cm bole diameter). Even though at the very largest sizes, tree basal area overestimates tree biomass (Chave *et al.* 2004), at the stand level the linear correlation between basal area and AGB holds (Baker *et al.* 2004). Therefore, within our plots, AGB can be estimated directly from stand-level basal area regardless of how that basal area is distributed between stems of different sizes. Equally, any changes in the distribution of basal area between trees of different sizes did not affect the relationship between basal area change and AGB change. As a result of these patterns, stand-level basal area change provides a very good estimate of stand-level AGB change (figure 4).

A limitation of the method of AGB estimation used by Phillips *et al.* (1998) is that it did not account for wood specific gravity, which varies both between forests and, potentially, over time. For example, stand-level wood specific gravity is lower in western than eastern Amazon forests and causes significant regional-scale variation in AGB (Baker *et al.* 2004). In addition, reported increases in the rate of forest dynamics (Phillips & Gentry 1994; Lewis *et al.* 2004; Phillips *et al.* 2004) might be expected to favour faster-growing species with lower wood specific gravity values. Overall, AGB estimates are slightly lower when specific gravity is included (equation (2.2) compared with equation (2.1); figure 3). This is because the underlying tree mass–diameter relationships were developed in central Amazon forests, where stands have relatively high wood specific gravity values compared with most plots in western Amazonia (Baker *et al.* 2004). However, AGB change estimates are only weakly affected by the equation used (figure 3). Spatial variation in wood specific gravity therefore does not confound previously reported increases in AGB. In addition, the close correlation between basal area and AGB change (figure 4), shows that the changes in AGB have been caused by an overall structural change in these plots, and suggests that any compositional shifts between tree species with differing wood specific gravity have not significantly affected stand-level AGB estimates.

A recent study of AGB change in a 50 ha plot in Panama by Chave *et al.* (2003) estimated the component of AGB lost to stem breakages and concluded that this factor could have an important effect on the overall pattern of AGB change. We did not estimate stem damage but this does not mean that there is an extra biomass loss term missing from our approach. Our estimates of the initial and final AGB assume that the degree of stem damage in our plots matches that of the destructively harvested populations that underlie the allometric models and, more importantly, that the proportion of stand-level damage does not change over time. Thus, our approach assumes that damaged trees die and are replaced by other individuals that themselves gradually accumulate damage. Under these assumptions, no extra terms need to be included in the calculation of AGB change.

Uncertainty about some diameter measurements does not influence the significance of the direction of AGB change in western Amazonia. As AGB change remained significantly positive even when problematic tree records were deleted, we can have a high degree of confidence in the overall result. However, it is clear that improving techniques for measuring trees will increase the precision of the estimates. Problems always arise in the interpretation of recensus data from forest plots, and techniques are routinely applied to remove tree records that show excessive growth or shrinkage (Condit *et al.* 1995; Chave *et al.* 2003), or to replace them with values that are likely to be more representative, such as the mean species-level growth rates (Rice *et al.* 2004). The differences between removing and estimating the growth of these trees can be substantial. For example, Chave *et al.* (2003) showed that for a 50 ha plot in semi-evergreen forest in Panama, AGB change estimated from 1985 to 2000 was greater by 0.44 Mg ha^{-1} yr^{-1} when

mean stand-level growth rates were used to estimate the growth of trees where the point of measurement had been altered between censuses, as compared with the approach of simply removing these records. In this case, the difference is equivalent to almost 50% of the mean rate of AGB increase in the Amazonian plots. When the interest is primarily in determining mean or median species-level parameters, deleting a small number of records is unlikely to have a large effect on the reported trends. However, simply removing records involves making the assumption that these trees did not grow and therefore introduces a downward bias to stand-level growth estimates. This problem is increased by the fact that these individuals also tend to be larger, often buttressed trees that make a greater relative contribution to overall stand-level productivity as a result of their size.

Estimating the growth of these trees is obviously a more satisfactory option for obtaining unbiased estimates of AGB change. How should this be done? Despite the importance of 'problem tree' records to calculations of stand-level parameters, there is no consensus on whether mean or median, species- or stand-level growth rates should be used for estimating the growth rates of problematic trees. We suggest that as diameter increment distributions are strongly skewed, median growth rates within an appropriately sized class will provide the best estimate. In addition, although species-level estimates may be possible for some common species, stand-level values will always be required for rarer species and may be the clearest and most robust method to apply to all stems. Of course, the best way to avoid these uncertainties is to ensure high-quality field measurements. However, although the quality of forest plot data may continue to improve over time, problematic records can never be fully eliminated. Analyses of stand-level parameters should ideally present results including and excluding any altered records, so that the effect of these procedures can be evaluated.

Overall, AGB change ranges from -4.14 to 5.40 Mg $ha^{-1}\,yr^{-1}$, with a mean value of 1.22 ± 0.43 Mg $ha^{-1}\,yr^{-1}$ (figure 2). What processes may have determined this distribution? Some of the variability between plots is doubtless caused by variability in the natural disturbance regime. For example, the greatest decrease in AGB occurs in BDF-04 where 145.4 Mg was lost between censuses in 1987 and 1991, owing to mortality caused by flooding. Equally, some of the plots with high rates of AGB increase may be recovering from mortality events prior to plot establishment. None of the plots is, however, obviously strongly successional. The Bolivian plots with low AGB values, for example, are located in forest types that are typically less massive than other Amazon forests. The plot with the lowest AGB, CHO-01, comprises evergreen liana forest, representing substantial areas of the southern fringe of Amazonia, possibly as a result of fire or an interaction between poor soils and seasonal drought (Killeen 1998).

Determining why most plots show moderate increases in AGB is difficult when changes in AGB are considered alone, as we have done here, without examining simultaneous changes in growth and mortality rates. In particular, it is not possible to distinguish with certainty whether increases are driven by widespread recovery from a previous disturbance, or by an overall increase in forest productivity. In Amazonia, mega El Niño events (Meggers 1994) provide one mechanism that potentially could drive a broad-scale increase in AGB owing to succession, as it is well known that El Niño events cause increased tree mortality (Condit *et al.* 1995; Nakagawa *et al.* 2000; Laurance *et al.* 2001). However, the increase in AGB reported here has occurred despite two of the most severe El Niños on record occurring during the monitoring period (Malhi & Wright 2004), suggesting that El Niño events may not necessarily dominate tropical forest dynamics over decadal time-scales (Williamson *et al.* 2000). In addition, it is difficult to reconcile the spatial variability of El Niño intensity across Amazonia (Malhi & Wright 2004) with the spatial consistency in the patterns of AGB change.

While successional processes may not explain the overall trend, could they explain the significantly higher rates of increase in AGB of the floodplain plots? Succession obviously dominates patterns of biomass accumulation on young Amazonian floodplains where forest establishes and develops on aggrading river sediments (Salo *et al.* 1986). Whether it continues to influence patterns of biomass change in the plots studied here depends on the age of the stands, and the time taken by successional forest to reach biomass values equivalent to old-growth forest. Although both factors are difficult to quantify, current understanding suggests that the ages of the forests are far greater than the persistence of successional effects on biomass accumulation. For example, although data are sparse, studies of forest recovery following complete human clearance for agriculture suggest that biomass approaches old-growth values after 100 years (Guariguata & Ostertag 2001). By contrast, geomorphological features and carbon dating suggest that the Holocene floodplain sites in southern Peru are at least 900 years old (Phillips *et al.* 2002*a*). It is also noteworthy that the AGB and stand-level wood specific gravity of the floodplain plots suggest that they are structurally no different from plots on older land surfaces (floodplain versus non-floodplain sites for western Amazon plots: AGB 256.7 ± 20.4 versus 257.8 ± 16.3 Mg ha^{-1}, wood specific gravity (stems basis) 0.61 ± 0.03 versus 0.62 ± 0.02 g cm^{-3}). Given these patterns, it is difficult to attribute a significant role for primary succession in the dynamics of these forests.

An alternative explanation for the observed increase in AGB is that stand-level growth rates have increased. Compelling evidence for an increase in Amazonian forest productivity has emerged from combined analyses of stem and basal area dynamics of an overlapping set of plots. These indicate (Lewis *et al.* 2004) that increases in stem recruitment, stem mortality and total stem density, and stand growth rates, basal area mortality and total basal area, have on average all occurred, with stem recruitment gains generally leading stem mortality gains (Phillips *et al.* 2004). It is argued that these patterns are incompatible with forest succession, but are most plausibly driven by an enhancement of stand-level growth rates (Lewis *et al.* 2004). In this context, the higher rates of AGB change in floodplain forests may be associated with the potential for greater increases in growth on the more fertile soils that are typically found in these sites. However, such an explanation, among such a heterogeneous group of post-Pleistocene substrates, remains tentative.

An important question for the overall carbon balance of these plots is whether the increase in the biomass of the

trees 10 cm or more in dbh might be offset by changes in the biomass of other compartments (e.g. small trees, lianas, CWD, fine litter or soil carbon). Trees that are less than 10 cm dbh and lianas comprise only *ca*. 5% and 2%, respectively, of the total above-ground biomass, including necromass, in a central Amazonian forest (Nascimento & Laurance 2002). However, small trees can have a significant influence on calculations of stand-level patterns of biomass change (Chave *et al.* 2003). In this context, the increasing recruitment rates in Amazonian forest plots (Phillips *et al.* 2004) and the increases in the abundance of large lianas (Phillips *et al.* 2002*b*), suggest that the biomass of both of these compartments is increasing.

Changes in the stocks of CWD, fine litter and soil carbon are broadly controlled by inputs from living above-ground biomass. Therefore, the question of whether changes in their biomass can alter the overall trend in forest carbon balance determined from trees that are 10 cm or more in dbh depends on their rate of turnover and the time-scale of the study. In short-term studies (e.g. 2 years; Rice *et al.* 2004), pools and fluxes of CWD may be partly independent of simultaneous changes in the biomass of larger trees, and be substantially controlled by mortality events prior to the measurement period. However, over longer time-scales, stocks of CWD must be closer to equilibrium with inputs from mortality. The turnover rate of CWD is *ca*. 7–10 years (Chambers *et al.* 2000), similar to the median length of plot monitoring (10.2 years) in this study. Although a fraction of the CWD will derive from mortality prior to monitoring, this component will have much less impact on the ecosystem carbon balance than in short-term studies. In fact, increasing rates of mortality (Lewis *et al.* 2004; Phillips *et al.* 2004), suggest that stocks of CWD will have increased substantially in our plots.

Fine litter has a short turnover time (Clark *et al.* 2002), so fine litter carbon should reflect decadal trends in AGB and productivity. By contrast, soil carbon is very heterogeneous, and deep-soil carbon turns over at time-scales substantially longer than the scale of this study (Trumbore 2000). Changes in this pool may still therefore be responding to events that occurred prior to the establishment of these plots. Overall, longer-term monitoring of these plots and specific studies of other components of the total biomass of these forests are required to examine changes in total biomass. However, since trees that are 10 cm or more in diameter represent a large fraction of total above-ground biomass, this study has a relatively long temporal period, and there has been a concurrent acceleration in forest dynamics, we suggest that changes in carbon of other compartments are unlikely to counteract the increase in trees that are 10 cm or more in diameter. The likelihood is that the increase in total carbon storage has been greater than the increase in carbon stored in trees that are 10 cm or more in diameter.

If the carbon pool stored in these Amazonian forest plots has increased, can its rate of increase be extrapolated to a regional scale? A key issue is whether biomass loss from relatively rare but high-intensity disturbance events that occur beyond the scale of current sampling may offset any increase in the biomass of other regions. Major disturbance events occur in tropical forest as a result of, for example, fire, windstorms and landslides (Whitmore & Burslem 1998), but obtaining data on their frequency, distribution and magnitude to quantify their importance for regional-scale patterns of carbon cycling is extremely difficult. In the context of the Amazon, analysis of satellite images has, however, provided some quantitative data on the frequency of destructive blowdown events owing to storms (Nelson *et al.* 1994). Where such events are most concentrated, return times are estimated at 5000 years (Nelson *et al.* 1994). However, this type of disturbance would have to be much more frequent to substantially alter the observed mean increase in carbon storage. For instance, if the current mean rate of AGB change persists for a total monitoring effort of 5000 hectare years, this would equate to a total accumulation of 6100 Mg. If all the biomass were then destroyed by a severe storm in one 1 ha plot with a mean AGB of 300 Mg ha^{-1}, then the total biomass accumulation would decline by 5% and the estimated mean rate of increase in AGB would fall from 1.22 to 1.16 Mg ha^{-1} yr^{-1}. This is clearly a crude simplification, but it shows that the rarity of such events in Amazonian forests means that their effects on regional-scale carbon cycling will be small (Nelson *et al.* 1994).

This study demonstrates a significant increase in the carbon of forest plots across Amazonia, and an important challenge is to integrate these trends in old-growth forest into regional-scale models of carbon flux. Equally, future trends in the carbon storage of these plots remains uncertain, and careful monitoring of Amazonian forest plots remains a high priority, particularly in the face of predicted regional drying (Cox *et al.* 2000), which may enhance tree mortality and reduce growth rates. In addition, biotic feedbacks may ultimately limit biomass accumulation (Phillips *et al.* 2002*b*), and given the recent acceleration in forest dynamics (Lewis *et al.* 2004; Phillips *et al.* 2004), potential changes in tree composition may also have important implications for carbon cycling and biodiversity within these forests.

Development of the RAINFOR network, 2000–2002, was funded by the European Union Fifth Framework Programme, as part of CARBONSINK, part of the European contribution to the Large Scale Biosphere–Atmosphere Experiment in Amazonia (L.B.A.). RAINFOR field campaigns were funded by the National Geographic Society (Peru 2001), CARBONSINK-LBA (Bolivia 2001) and the Max-Planck-Institut für Biogeochemie (Peru & Bolivia 2001; Ecuador 2002; Brazil 2003). The authors gratefully acknowledge the support and funding of numerous organizations who have contributed to the establishment and maintenance of individual sites: in Bolivia (T.J.K., L.A.), US National Science Foundation, the Nature Conservancy–Mellon Foundation (Ecosystem Function Program), FONAMA (Fondo Mundial del Medio Ambiente) and USAID through the Missouri Botanical Garden; in Brazil (S.A.) Conselho Nacional de Desenvolvimento Cientifico e Tecnológico (CNPq), Museu Goeldi, Estação Científica Ferreira Penna; (S.G.L., W.F.L.) Andrew W. Mellon Foundation, NASA-LBA Program, Conservation, Food and Health Foundation, MacArthur Foundation; (J.N.M.S.) Jari Celulose SA, EMBRAPA/Jari; in Ecuador (D.N.) Liz Claiborne and Art Ortenberg Foundation, National Geographic Society, Fundación Jatun Sacha; (N.P., A.D.) Estación Científica Yasuni de la Pontificia Universidad Católica del Ecuador, Estación de Biodiversidad Tiputini; in Peru (O.P., R.V.) Natural Environment Research Council, National Geographic Society, National Science Foundation, WWF-US/Garden Club of America, Conservation International, MacArthur Foundation, Andrew W. Mellon Foundation, ACEER, Albergue Cuzco Amazonico,

Explorama Tours S.A., Explorers Inn, IIAP, INRENA, UNAP and UNSAAC. T.R.B. gratefully acknowledges financial support from the Max Planck Institut für Biogeochemie.

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GLOSSARY

AGB: above-ground dry biomass in trees of more than 10 cm in diameter
CWD: coarse woody debris
dbh: diameter at breast height