Changes in Amazonian Forest Biomass, Dynamics, and Composition, 1980–2002

Oliver L. Phillips,[1] Niro Higuchi,[2] Simone Vieira,[3] Timothy R. Baker,[1]
Kuo-Jung Chao,[1] and Simon L. Lewis[1]

Long-term, on-the-ground monitoring of forest plots distributed across Amazonia provides a powerful means to quantify stocks and fluxes of biomass and biodiversity. Here we examine the evidence for concerted changes in the structure, dynamics, and functional composition of old-growth Amazonian forests over recent decades. Mature forests have, as a whole, gained biomass and undergone accelerated growth and dynamics, but questions remain as to the long-term persistence of these changes. Because forest growth on average exceeds mortality, intact Amazonian forests have been functioning as a carbon sink. We estimate a net biomass increase in trees ≥10 cm diameter of 0.62 ± 0.23 t C ha^{-1} a^{-1} through the late twentieth century. If representative of the wider forest landscape, this translates into a sink in South American old-growth forest of at least 0.49 ± 0.18 Pg C a^{-1}. If other biomass and necromass components also increased proportionally, the estimated South American old-growth forest sink is 0.79 ± 0.29 Pg C a^{-1}, before allowing for possible gains in soil carbon. If tropical forests elsewhere are behaving similarly, the old-growth biomass forest sink would be 1.60 ± 0.58 Pg C a^{-1}. This bottom-up estimate of the carbon balance of tropical forests is preliminary, pending syntheses of detailed biometric studies across the other tropical continents. There is also some evidence for recent changes in the functional composition (biodiversity) of Amazonian forest, but the evidence is less comprehensive than that for changes in structure and dynamics. The most likely driver(s) of changes are recent increases in the supply of resources such as atmospheric carbon dioxide, which would increase net primary productivity, increasing tree growth and recruitment, and, in turn, mortality. In the future the growth response of remaining undisturbed Amazonian forests is likely to saturate, and there is a risk of these ecosystems transitioning from sink to source driven by higher respiration (temperature), higher mortality (drought), or compositional change (functional shifts toward lighter-wooded plants). Even a modest switch from carbon sink to source for Amazonian forests would impact global climate, biodiversity, and human welfare, while the documented acceleration of tree growth and mortality may already be affecting the interactions of thousands of plant and millions of animal species.

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[1] Earth and Biosphere Institute, School of Geography, University of Leeds, Leeds, UK.

[2] Laboratório de Silvicultura Tropical, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

[3] Laboratório de Ecologia Isotópica, USP, CENA, Piracicaba, Brazil.

1. INTRODUCTION

Given the scale of the anthropogenic experiment with the atmosphere-biosphere system, it is self-evident that all ecosystems on Earth are now affected by human activities. Processes such as deforestation are physically obvious, but others, such as hunting and surface fires, although subtler, still affect biodiversity in insidious ways [cf. *Lewis et al.*, 2004a; *Malhi and Phillips*, 2004]. Anthropogenic atmospheric change will become more significant during this century, as carbon dioxide concentrations reach levels unprecedented for at least 20 million years [e.g., *Retallack*, 2001] and climates move beyond Quaternary envelopes [*Meehl et al.*, 2007]. Moreover, the rate of change in these basic ecological drivers is without precedent in the evolutionary span of most species on Earth today. This is the Anthropocene [*Crutzen*, 2002]: we live in epoch-making times.

Changes in tropical forests matter for three reasons. First, tropical forests play an important role in the global carbon cycle and, hence, affect the rate of climate change, as ~40% of terrestrial vegetation carbon stocks lie within tropical forests [*Malhi and Grace*, 2000]. Second, as tropical forests are home to at least half of all Earth's species, changes here have large impacts on global biodiversity and the cultures, societies, and economies that are bound to that biodiversity [*Groombridge and Jenkins*, 2003]. Finally, as different plant species vary in their ability to store and process carbon, climate and biodiversity changes are linked by feedback mechanisms [e.g., *Cox et al*., 2000; *Lewis*, 2006].

2. A NETWORKED APPROACH

Biodiversity change as a consequence of recent climate change is now widely documented in better-studied temperate areas [e.g., *Parmesan and Yohe*, 2003]. However, documentation in the tropics is much sparser and often focused on a few well-known locations; while this brings benefits, it is also risky. Inevitably, site-centric science is skewed, since peculiar features of that site, such as anthropogenic isolation, unusual soil conditions, cyclones, or fires, can all color interpretations. In most fields, such as climate change, it would be obvious folly to infer the presence or absence of global effects from records at one or two sites, but in ecological science, attempts are often made to scale from one or two local case studies to the regional and global.

To avoid the pitfalls of the single-site approach, since 2000, we and others have tried to develop a standardized, international, long-term network of permanent plots in mature forests across Amazonia, by drawing together the existing efforts of local botanists and foresters, often working hitherto largely in isolation, and extending the site network when possible to fill spatial and environmental gaps. This network of Amazonian-forest researchers, known as "Red Amazónica de Inventarios Forestales" (RAINFOR or Amazon Forest-Inventory Network, http://www.geog.leeds.ac.uk/projects/rainfor/), now represents the long-term ecological monitoring efforts of 35 institutions worldwide including from all Amazonian countries except Suriname. Here we synthesize recent results from the network to assess how Amazonian forests are changing on average. Where appropriate, we also discuss results from additional, individual sites where these may shed further light on the processes involved.

3. METHODOLOGY

For these analyses, we define a monitoring plot as an area of old-growth forest where all trees ≥10 cm diameter at breast height (dbh, measured at 1.3 m height or above any buttress or other deformity) are tracked individually over time. All trees are marked with a unique number, measured, mapped, and identified. Periodically (generally every 5 years), the plot is revisited, and all surviving trees are re-measured, dead trees are noted, and trees recruited to 10 cm dbh are uniquely numbered, measured, mapped, and identified. This allows calculation of (1) the cross-sectional area that tree trunks occupy (basal area), which can be used with allometric equations to estimate tree biomass [*Higuchi et al*., 1998; *Baker et al.*, 2004a; *Chave et al.*, 2005]; (2) tree growth (the sum of all basal-area increments for surviving and newly recruited stems over a census interval); (3) the total number of stems present; (4) stem recruitment (number of stems added to a plot over time); and (5) mortality (either the number or basal area of stems lost from a plot over time). We present results from 50 to 91 plots, depending upon selection criteria for different analyses (most critically, the number of census intervals from a plot and whether only stem-count data or the full tree-by-tree data set is available). More plots are used to assess stem-density change than biomass change because full tree-by-tree data are required to calculate biomass (using the methods of *Baker et al.* [2004a]), whereas stem-change data can often be obtained from published studies.

The plots span the Amazonian forests of northern South America (Figure 1), including Bolivia, Brazil, Ecuador, French Guiana, Peru, and Venezuela, from the driest to the wettest and the least to the most fertile Amazonian forests. Most are 1 ha in size and comprise ~600 trees of ≥10 cm dbh, but the smallest is 0.25 ha and the largest 9 ha. Many plots have been monitored for more than a decade, although they range in age from 2 to 25 years. The earliest plot inventory was in 1971, the latest in 2007. Here we analyze in full results of censuses completed up to 2002. Details of the exact plot locations, inventory and monitoring methods, and

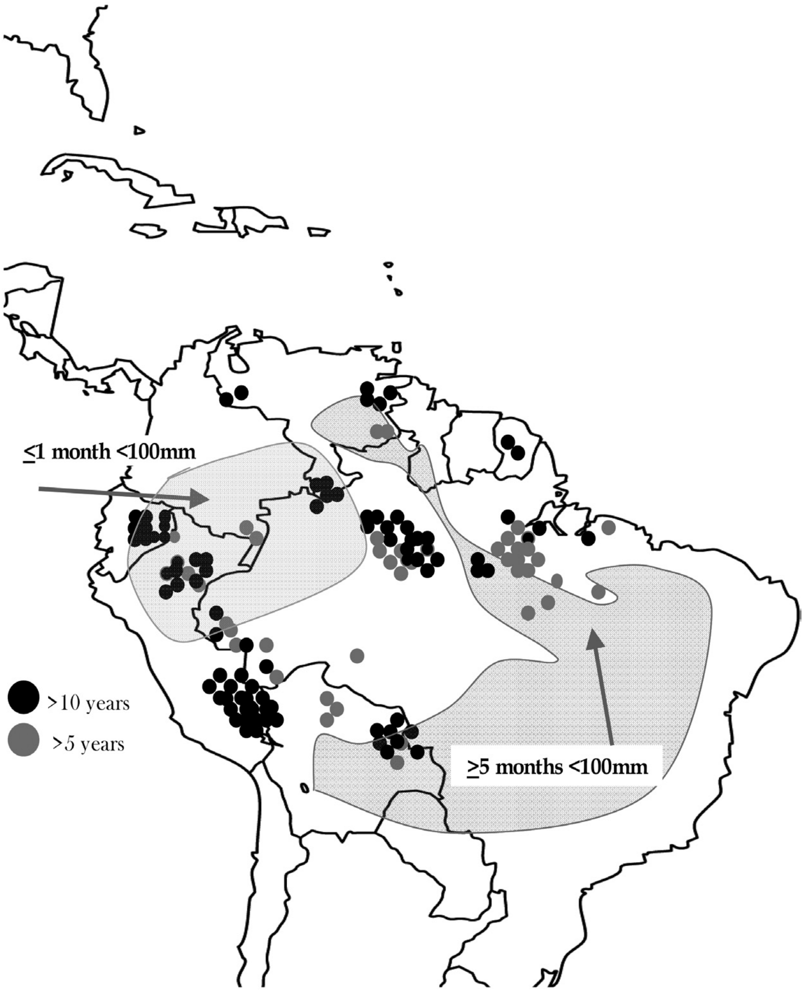


Figure 1. Plot locations used in this study. Symbols represent approximate locations of each plot; gray circle for plots monitored for 5–10 years, black for those with ≥10 years of monitoring. The approximate extent of seasonal and highly seasonal areas within South America north of the tropic of Capricorn and excluding local rain shadow climates are indicated.

issues relating to collating and analyzing plot data are omitted from this chapter for reasons of space but are discussed in detail elsewhere [*Phillips et al.*, 2002a, 2002b; *Baker et al.*, 2004a, 2004b; *Malhi et al.*, 2002, 2004; *Lewis et al.*, 2004b; *Phillips et al.*, 2004]. Scaling from individual tree to biomass is based on the diameter-based allometric equations detailed by *Baker et al.* [2004a, 2004b]. In brief, we used an equation developed for the Manaus area [*Chambers et al.*, 2001a], modified by taking account of the taxon-specific wood density of each tree relative to the mean wood density of trees in the Manaus region. Alternatively, biomass can be estimated by universal, tropical forest equations such as those of *Chave et al.* [2005]. The Manaus equation is based on a smaller sample size but has the advantage of being local. For simplicity, we do not show results using universal equations here, but note that while different methods certainly result in systematic differences in "biomass" estimates [e.g., *Chave et al.*, 2003; *Peacock et al.*, 2007], the rates of biomass "change" calculated across Amazonia appear largely insensitive to the equation used [*Baker et al.*, 2004a]. We summarize findings from old-growth forests in terms of (a) structural change, (b) dynamic-process change, and (c) functional change, over the two to three decades up to ~2002. Results assembled after this manuscript was prepared [*Phillips et al.*, 2004] update some of the pattern documented here for the early twenty-first century.

4. RESULTS AND DISCUSSION

4.1. Structural Changes

Among 59 long-term old-growth Amazonian plots with full tree-by-tree data, there has been a significant increase in aboveground biomass between the first measurement (mean date 1988) and the last measurement (mean date 2000). For trees $\geq$10 cm diameter, the increase has been 0.62 ± 0.23 t of carbon per hectare per year (mean ± 95% confidence interval) [*Baker et al.*, 2004a]. Across all 59 plots, the aboveground biomass change is normally distributed and shifted to the right of zero (Figure 2a). The estimate of a net increase of 0.62 ± 0.23 t C ha^{-1} a^{-1} is statistically indistinguishable from the 0.54 ± 0.29 t C ha^{-1} a^{-1} estimated by *Phillips et al.* [1998] for the lowland Neotropics using 50 sites up to 1996.

There are various possible ways by which these plot-based measures can be scaled to the whole of Amazonia and South America. Here we adopt a relatively simple approach; while we acknowledge it is not perfect, we believe it is reasonable especially given the various uncertainties, not all quantifiable, for example, in terms of nontree carbon, belowground biomass, area of each forest type, and degree of human disturbance. Thus, we assume that our measurements are representative of the wider forest landscape, and that other biomass and necromass components are also increasing proportionally but that soil carbon stocks are static, and estimate the magnitude of the South American carbon sink by multiplying the plot-based rate by a series of correction factors to account for biomass of lianas, trees <10 cm diameter, necromass, and belowground carbon, and a mid-range estimate of the surviving neotropical forest area for year 2000 (7.8×10^6 km^2, Table 1). This yields a total estimated South American forest sink of 0.79 ± 0.29 Pg C a^{-1}. If tropical forests elsewhere are behaving similarly, the combined old-growth tropical forest sink would be 1.60 ± 0.58 Pg C a^{-1}, before allowing for any possible net change in soil carbon stock, and not counting less extensive forest areas in central America, Australia, and Oceania. This depends on various assumptions but represents the best available bottom-up estimate of the biomass carbon balance of mature tropical forests given current knowledge, pending syntheses of detailed biometric studies across the other tropical continents. It is consistent with evidence from recent inversion-based studies, showing the tropics are either carbon neutral or sink regions, despite widespread deforestation [*Denman et al.*, 2007, p. 522].

We present a range of estimates in Table 1, broken down by biomass component, forest area estimation methodology, and continent. Clearly, these estimates depend on (1) measurement techniques; (2) how representative the plots are of forests in South America and the rest of the tropics; (3) assumptions about the extent of mature, intact forest remaining; and (4) the extent to which we have sampled the regional-scale matrix of natural disturbance and recovery. Moreover, they represent average annual estimates for the late twentieth century, forest plots are generally not measured sufficiently frequently in enough places to estimate biome carbon balance on a year-by-year basis.

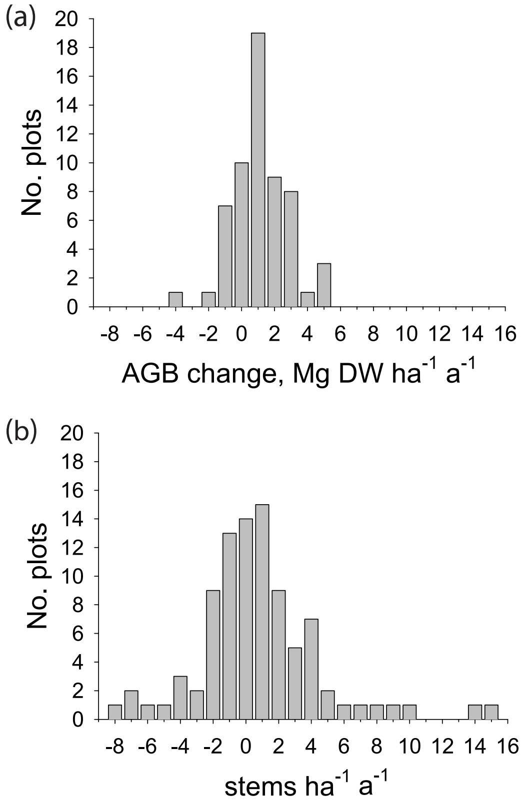


Figure 2. (a) Aboveground biomass change (dry weight) of trees greater than 10 cm diameter in 59 Amazonian plots, based on initial and final stand-biomass estimates calculated using an allometric equation relating individual tree diameter to biomass, and incorporating a correction factor to account for variation in wood density among species [from *Baker et al.*, 2004a]. As would be expected in a random sample of small plots measured for a finite period, some sites show a decline in biomass during that period indicating that at that particular point in space and time tree mortality has exceeded tree growth. However, the mean and median are shifted significantly to the right ($P < 0.01$). (b) Stem number change in 91 plots from across South American tropical forests. Stems were counted during the first and final censuses of each plot (plots are the same as used by *Phillips et al.* [2004]). The mean and median are shifted significantly to the right ($P < 0.05$).

Table 1. Estimated Recent Net Carbon Sink in Different Components of Biomass and Different Geographical Regions Across the World's Major Tropical Forests[a]

	Land Cover Class	Forest Area (ha 10^6)	Coarse Aboveground Biomass (Trees ≥10 cm dbh) Increase		Aboveground Biomass Increase Trees ≤10 cm and Lianas ≥1 cm	Coarse Necromass Increase	Total Aboveground Biomass and Necromass Increase		Belowground Biomass Increase	Total Biomass and Necromass Increase	
			Mean	CI	Mean	Mean	Mean	CI	Mean	Mean	CI
South America											
GLC2000	humid tropical forest	630.5	392.2	142.4	38.8	49.8	480.9	174.6	159.4	*640.3*	*232.4*
	dry tropical forest	146.7	91.3	33.1	9.0	11.6	111.9	40.6	37.1	*149.0*	*54.1*
	flooded tropical forests	25.3	15.7	5.7	1.6	2.0	19.3	7.0	6.4	*25.7*	*9.3*
	total	*802.5*	*499.2*	*181.2*	*49.4*	*63.4*	*612.1*	*222.2*	*202.9*	*815.0*	*295.8*
FRA CS	closed forest	858.3	533.9	193.8	52.9	67.8	654.6	237.6	217.0	*871.7*	*316.4*
	open forest	68.9	42.9	15.6	4.2	5.4	52.5	19.1	17.4	*70.0*	*25.4*
	total	*927.2*	*576.8*	*209.4*	*57.1*	*73.3*	*707.2*	*256.7*	*234.5*	*941.6*	*341.8*
FRA RS	*forest total*	*780.2*	***485.4***	***176.2***	*48.1*	*61.6*	*595.1*	*216.0*	*197.3*	***792.3***	***287.6***
Africa											
GLC2000	humid tropical forest	232.7	144.8	52.5	14.3	18.4	177.5	64.4	58.8	*236.3*	*85.8*
	dry tropical forest	415.1	258.2	93.7	25.6	32.8	316.6	114.9	105.0	*421.6*	*153.0*
	flooded tropical forests	13.1	8.1	3.0	0.8	1.0	10.0	3.6	3.3	*13.3*	*4.8*
	total	*660.9*	*411.1*	*149.2*	*40.7*	*52.2*	*504.1*	*183.0*	*167.1*	*671.2*	*243.6*
FRA CS	closed forest	352.7	219.4	79.6	21.7	27.9	269.0	97.6	89.2	*358.2*	*130.0*
	open forest	288.9	179.7	65.2	17.8	22.8	220.3	80.0	73.1	*293.4*	*106.5*
	total	*641.6*	*399.1*	*144.9*	*39.5*	*50.7*	*489.3*	*177.6*	*162.2*	*651.6*	*236.5*
FRA RS	*forest total*	*518.5*	*322.6*	*117.1*	*31.9*	*41.0*	*395.5*	*143.6*	*131.1*	***526.6***	***191.1***
Asia											
GLC2000	humid tropical forest	230.6	143.5	52.1	14.2	18.2	175.9	63.8	58.3	*234.2*	*85.0*
	dry tropical forest	144.8	90.1	32.7	8.9	11.4	110.4	40.1	36.6	*147.1*	*53.4*
	flooded tropical forests	13.5	8.4	3.0	0.8	1.1	10.3	3.7	3.4	*13.7*	*5.0*
	total	*388.9*	*241.9*	*87.8*	*24.0*	*30.7*	*296.6*	*107.7*	*98.3*	*395.0*	*143.4*
FRA CS	closed forest	416.2	258.9	94.0	25.6	32.9	317.4	115.2	105.2	*422.7*	*153.4*
	open forest	58.3	36.3	13.2	3.6	4.6	44.5	16.1	14.7	*59.2*	*21.5*
	total	*474.5*	*295.2*	*107.2*	*29.2*	*37.5*	*361.9*	*131.4*	*120.0*	*481.9*	*174.9*
FRA RS	*forest total*	*272.0*	*169.2*	*61.4*	*16.8*	*21.5*	*207.5*	*75.3*	*68.8*	***276.2***	***100.3***

Table 1. (continued)

	Land Cover Class	Forest Area (ha 10^6)	Coarse Aboveground Biomass (Trees ≥10 cm dbh) Increase		Aboveground Biomass Increase Trees ≤10 cm and Lianas ≥1 cm	Coarse Necromass Increase	Total Aboveground Biomass and Necromass Increase		Belowground Biomass Increase	Total Biomass and Necromass Increase	
			Mean	CI	Mean	Mean	Mean	CI	Mean	Mean	CI
Global											
GLC2000	humid tropical forest	1093.8	680.5	247.0	67.4	86.4	834.2	302.8	276.6	*1110.8*	*403.2*
	dry tropical forest	706.6	439.6	159.6	43.5	55.8	538.9	195.6	178.7	*717.6*	*260.5*
	flooded tropical forests	51.9	32.3	11.7	3.2	4.1	39.6	14.4	13.1	*52.7*	*19.1*
	total	*1852.3*	*1152.3*	*418.3*	*114.1*	*146.3*	*1412.7*	*512.8*	*468.4*	1881.1	682.9
FRA CS	closed forest	1627.2	1012.3	367.5	100.2	128.6	1241.1	450.5	411.5	*1652.5*	*599.9*
	open forest	416.1	258.9	94.0	25.6	32.9	317.4	115.2	105.2	*422.6*	*153.4*
	total	*2043.3*	*1271.1*	*461.4*	*125.8*	*161.4*	*1558.4*	*565.7*	*516.7*	2075.1	753.3
FRA RS	*forest total*	*1570.7*	*977.1*	*354.7*	*96.7*	*124.1*	*1198.0*	*434.9*	*397.2*	**1595.1**	**579.1**

[a]We take the net gain in aboveground coarse biomass (trees ≥10 cm dbh) recorded in Amazonia (0.62 ± 0.22 t C ha^{-1} a^{-1}), and scale by the estimated ratio of trees ≤10 cm dbh and lianas ≥1 cm dbh to trees ≥10 cm dbh in Amazonia (=0.099, [*Phillips et al*., 1998]), by the most comprehensive estimate of coarse necromass: aboveground coarse biomass ratio available for Amazonia (=0.127) [*Chao et al*., 2009], and by the latest estimate of belowground: aboveground biomass ratio (=0.370) (N. Higuchi et al., unpublished central Amazonian estimate, 2008). Values for each region are estimated by assuming the same allometry and behavior as Amazonian forests. Forest area estimates are taken from *Mayaux et al.* [2005]. Abbreviations are GLC, global land cover; FRA CS, *Food and Agriculture Organization* (*FAO*) [2000] country statistics; FRA RS, *FAO* [2000] remotely sensed values. Scaled-up estimates based on FRA RS highlighted in bold are mentioned in the text. Units for biomass stock increases are 10^6 t C a^{-1}. Totals for each continent are given in italics.

The finding of increased biomass has proved controversial [cf., for example, *Clark*, 2002; *Phillips et al.*, 2002a, 2002b; *Wright*, 2005; *Lewis et al.*, 2006a]. While there is no space here to review the debate fully, one important aspect concerns the role of recent disturbance and the role of coarse woody debris (CWD) in total aboveground carbon balance. Results from a single LBA site in eastern Amazonia (Tapajos) show that over intervals of a few years, atmospheric carbon fluxes from CWD may exceed biomass gains [*Rice et al.*, 2004]. Clearly, recent disturbances can drive patterns of local biomass change, which is a key reason why long-term monitoring over decades is so valuable. However, the LBA-Tapajos site has uniquely abnormally high values of CWD [*Palace et al.*, 2007; *Chao et al.*, 2009] and at least twice as much as at most sites in western Amazonia where CWD flux rates (mortality and decomposition) are also faster [*Baker et al.*, 2007]. Even if it were possible to accurately track CWD inventories through time at our sites, their impact on our Amazonia-wide long-term aboveground carbon balance estimate would be small, unless there have been recent, large, region-wide secular changes in the rate of CWD production or decomposition.

Have such changes occurred? We find that mortality has indeed increased on average over recent years (see next section); this would imply an additional carbon sink, not a source, in necromass (see Table 1), but because CWD averages only ~12% of biomass and has short residence times [*Baker et al*., 2007], the additional carbon sink it represents must be small. Still, it could be argued that our turn-of-the-century Amazonian mature forest plots could be recovering from unobserved, earlier megadisturbances. By definition, such a suggestion is impossible to falsify completely, but it is inconsistent with the evidence of other, simultaneous structural and dynamic changes including increasing growth rates (see below) and the fact that episodic climate anomalies have occurred during the monitoring period itself, including a drought associated with the strong 1997–1998 El Niño. (The 2005 drought, particularly severe in southwestern Amazonia, struck after the monitoring period analyzed here). Long-term forest rebound from much earlier human disturbances also merits consideration [e.g., *Phillips et al.*, 1998], but recent analyses suggest that such disturbances were only localized [*Bush et al.*, 2007]. In any case, given known rates of secondary succession [e.g., *Hughes et al.*, 1999] and atmospheric CO_2 evolution [*Nevle and Bird*, 2008] recovering forest equilibrated in biomass terms within two centuries of the Spanish conquest (see *Phillips et al.* [2002a, 2002b] for more discussion).

It is important to note that biomass increase is not the only structural change recorded in Amazonia. Across the 91 RAINFOR plots where we have tracked populations, there has also been a small increase in stem density between the first and last measurements, of 0.84 ± 0.77 stems ha^{-1} a^{-1} (Figure 2b; paired *t* test, $t = 2.12$, $P = 0.037$), an annual increase of 0.15 ± 0.13% [*Phillips et al.*, 2004]. Across all plots, stem-change rates are approximately normally distributed and slightly shifted to the right of zero (Figure 2b). The same test using the smaller set of 59 plots where we have tracked biomass shows a similar increase in stem density (0.16 ± 0.15% per year), while a longer-term subset of plots (50 plots from *Lewis et al.*, 2004b) shows a slightly larger increase (0.18 ± 0.12% per year). These increases in stem density, while proportionally smaller than the biomass changes, run counter to expectations if the plots were in an advanced state of secondary succession [e.g., *Coomes and Allen*, 2007]. They falsify the hypothesis that the generalized biomass increase across Amazonian plots can be explained as a result of disturbance recovery.

For practical reasons, the pan-Amazon sample is nonrandomly distributed. It is possible to test whether this spatial bias might be driving the result by assessing whether we have oversampled unusually heavily regions that happened to be gaining biomass and undersampled those that happened to lose biomass. At smaller scales, this appears unlikely, since the long-term mean net gain is almost identical whether the sampling unit is taken to be the “plot” (as here) or a larger unit such as a “landscape cluster of plots” [*Phillips et al.*, 2009]. At larger scales, the climate- and soil-environmental space is well-covered, but the network still leaves large expanses of Brazilian Amazonia unsampled (Figure 1). Concerted monitoring efforts in these regions are clearly needed to reduce this source of uncertainty.

4.2. Dynamic Changes

An alternative way of examining forest change is to look for changes in the processes (growth, recruitment, death), as well as the structure (biomass, stem density): are these forests simply gaining mass, or are they becoming more dynamic too? We measured the dynamics of forests in two ways. First, we can examine changes in stem population dynamics. By convention [*Phillips and Gentry*, 1994], we estimate stem turnover between any two censuses as the mean of annual mortality and recruitment rates for the population of trees ≥10 cm diameter. Second, we examine changes in biomass fluxes of the forest, in terms of growth of trees and the biomass lost with mortality events. These stand-level rates of biomass growth and biomass loss should be approximately proportional to the rate at which surviving and recruiting trees gain basal area and the rate at which basal area is lost from the stand through tree death [*Phillips et al.*, 1994].

Among 50 old-growth plots across tropical South America with at least three censuses (and therefore at least two consecutive monitoring periods that can be compared), we find that all of these key ecosystem processes, stem recruitment, mortality, and turnover, and biomass growth, loss, and turnover, are increasing significantly (Figure 3), between the first and second monitoring periods [*Lewis et al.*, 2004b]. Thus, over the past two decades, these forests have become, on average, faster-growing and more dynamic. Notably, the increases in the rate of the dynamic fluxes (growth, recruitment, and mortality) are about an order of magnitude larger than are the increases in the structural pools (aboveground biomass and stem density) [*Lewis et al.*, 2004b].

These and similar results can be demonstrated graphically in a number of ways. In Figure 4, we plot the across-site mean values for stem recruitment and mortality as a function of calendar year. The increase is not the short-term result of a year with unusual weather: recruitment rates have on average consistently exceeded mortality rates, and mortality

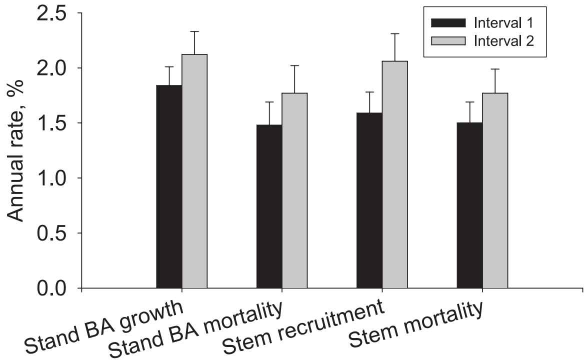


Figure 3. Annualized rates of stand-level basal-area growth, basal-area mortality, stem recruitment, and stem mortality from plots with two consecutive census intervals, each giving the mean from 50 plots with 95% confidence intervals. Paired *t* tests show that all of the increases are significant. The average mid-year of the first and second censuses was 1989 and 1996, respectively [from *Lewis et al.*, 2004b].

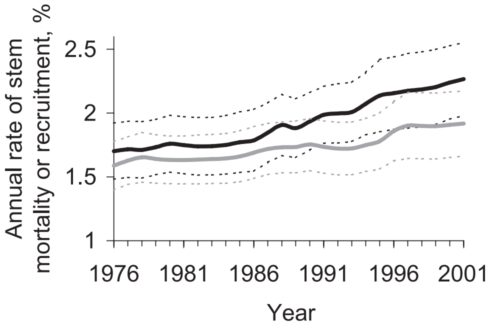


Figure 4. Mean and 95% confidence intervals for stem recruitment and mortality rates against calendar year, for plots arrayed across Amazonia. Rates for each plot were corrected for the effects of differing census-interval lengths, for “site-switching” (changes through time in the plots being measured), and for “majestic-forest bias” (potential avoiding of gaps when establishing plots). A detailed justification methodology for these corrections is given by *Phillips et al.* [2004]; all trends hold if these corrections are not applied. Black indicates recruitment, gray indicates mortality, solid lines are means, and dots are 95% confidence intervals [from *Phillips et al.*, 2004].

appears to lag recruitment [*Phillips et al.*, 2004; *Lewis et al.*, 2004b].

For the 50 plots which have two consecutive census intervals, we can separate them into two groups, one fast-growing and more dynamic (mostly in western Amazonia), and one slow-growing and much less dynamic (mostly in eastern and central Amazonia), which reflects the dominant macroecological gradient across Amazonia [*Phillips et al.*, 2004; *Vieira et al.*, 2004; *ter Steege et al.*, 2006]. Both groups showed increased stem recruitment, stem mortality, stand basal-area growth, and stand basal-area mortality, with greater “absolute” increases in rates in the faster-growing and more dynamic sites than in the slower-growing and less dynamic sites (Figure 5) [*Lewis et al.*, 2004b], but proportional increases in rates that were similar and statistically indistinguishable among forest types [*Lewis et al.*, 2004b]. Increasing growth, recruitment, and mortality has occurred across different forest types and geographically widespread areas.

The simultaneous recent increases in plot dynamic rates, biomass, and stem density raise the following question: for how long has this been going on? Monitoring of Amazonian plots only began in a concerted fashion around 1980. To go much further back in time requires annual dating of growth rates of a large sample of individual trees from different species, something that to our knowledge has been only been done in Amazonia from two locations in terra firme [*Vieira et al.*, 2005], using radiocarbon dating. Although the majority of trees tested did grow faster since 1960 than before 1960, the null hypothesis of no change in growth rate could not be rejected. This technique is complicated by potential ontogenetic variation in growth rates partly related to changing light environments [e.g., *Worbes*, 1999] and could overestimate “stand-level” growth rates in the past because individual trees with slow- and declining growth are more susceptible to mortality [*Chao et al*., 2008] and therefore less likely to survive to the point at which they are dated.

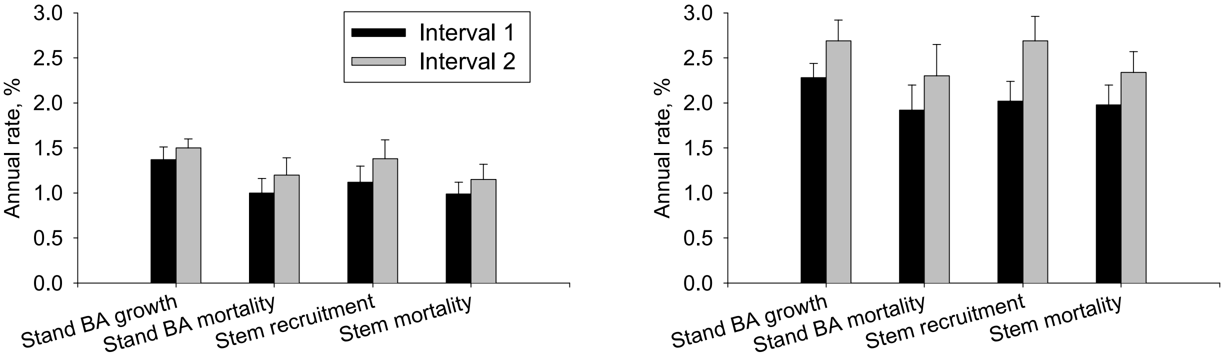


Figure 5. Annualized rates of stand-level basal-area growth, basal-area mortality, stem recruitment, and stem mortality over consecutive census intervals for plots grouped into “slower growing less-dynamic” (left) and “faster growing more-dynamic” (right) forests. Of the slower-dynamics group, 20 of 24 plots are from eastern and central Amazonia, whereas just two are from western Amazonia. Of the faster-dynamics group, 24 of 26 plots are from western Amazonia, with just one from central Amazonia. The remaining three plots are from Venezuela and outside the Amazon drainage basin. Changes have occurred across the South American continent, and in both slower- and faster-dynamic forests [from *Lewis et al.*, 2004b].

4.3. Functional Composition Changes

Changes in the structure and dynamics of tropical forests are likely to be accompanied by changes in species composition and forest function. *Phillips et al.* [2002a, 2002b] studied woody climbers (structural parasites on trees, also called lianas), which typically contribute 10–30% of forest leaf productivity, but are ignored in almost all monitoring studies except in most of our western Amazonian sites. Across the RAINFOR plots of western Amazonia, there has been a concerted increase in the density, basal area, and mean size of lianas (Figure 6) [*Phillips et al.*, 2002b]. Over the last two decades of the twentieth century, the density of large lianas relative to trees increased here by 1.7–4.6% per year. This was the first direct evidence that intact tropical forests are changing in terms of their functional composition. A long-term monitoring study from beyond Amazonia (Barro Colorado Island in Panama) has since reported a substantial increase in absolute and relative liana leaf-fall rates since the 1980s, indicating that lianas are both increasing and becoming more dominant there [*Wright et al.*, 2004]. There is some experimental evidence [*Granados and Körner*, 2002] for tropical lianas to respond more strongly than trees to elevated atmospheric CO_2 concentrations.

Finally, a large cluster of plots in central Amazonia shows consistent changes in tree species composition over the past two decades [*Laurance et al.*, 2004]. Many faster-growing genera of canopy and emergent stature trees increased in basal area or density, whereas some slower-growing genera of subcanopy or understory trees declined. *Laurance et al.* [2004] provide evidence of pervasive changes in central Amazonian forests: growth, mortality, recruitment all increased significantly over two decades (basal area also increased, but not significantly so), with faster-growing genera showing larger absolute and relative increases in growth, relative to slower-growing genera. Further studies are urgently needed to determine whether comparable shifts in tree communities are occurring throughout Amazonia.

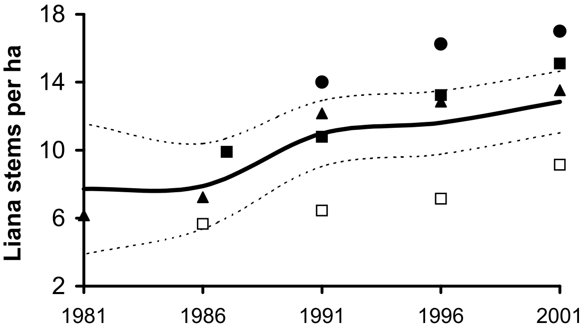


Figure 6. Five-year running means (solid line) with 95% confidence intervals (dashed lines) of liana stem density per hectare (≥10 cm diameter at breast height), with values plotted separately for northern Peru (filled squares), southern Peru (filled triangles), Bolivia (filled circle), and Ecuador (unfilled squares) (adapted from [*Phillips et al.*, 2002b]; see that paper for full details of field and analytical methodology).

5. WHAT IS DRIVING THESE CHANGES?

What could be causing the continent-wide changes in tree growth, recruitment, mortality, stem density, and biomass? Many factors could be invoked, but there is only one parsimonious explanation. The results appear to show a coherent fingerprint of increasing growth [i.e., increasing net primary productivity (NPP)] across tropical South America, probably caused by a long-term increase in resource availability [*Lewis et al.*, 2004a, 2004b]. According to this explanation, increasing resource availability increases NPP, which then increases stem growth rates. This accounts for the increase in stand basal-area growth and stem recruitment rates, and the fact that these show the clearest, most highly significant changes [*Lewis et al.*, 2004b]. Because of increased growth, competition for limiting resources, such as light, water, and nutrients, increases. Over time, some of the faster-growing, larger trees die, as do some of the "extra" recruits (the accelerated growth percolates through the system). This accounts for the increased losses from the system: biomass-mortality and stem-mortality rates increase. Thus, the system gains biomass and stems, while the losses lag some years behind, causing an increase in aboveground biomass and stems. Overall, this suite of changes may be qualitatively explained by a long-term increase in a limiting resource.

The changes in composition can also be explained by increasing resource availability, as the rise in liana density may be either a direct response to rising resource supply rates or a response to greater disturbance caused by higher tree-mortality rates. The changing tree composition in central Amazonian plots [*Laurance et al.*, 2004] is also consistent with increasing resource supply rates, as experiments show that faster-growing species are often the most responsive, in absolute terms, to increases in resource levels [*Coomes and Grubb*, 2000], although others have argued [e.g., *Körner*, 2004; J. Lloyd, personal communication, 2008] that the greatest proportional response should be in understory seedlings and saplings, which are likely to be close to carbon deficit due to shading; a small increase in photosynthetic rate here could therefore have a great proportional impact on carbon balance. There is some experimental evidence to support this view [e.g., *Kerstiens*, 2001; *Aidar et al.*, 2002].

What environmental changes could be increasing the growth and productivity of tropical forests? While there have been widespread changes in the physical, chemical, and biological environment of tropical trees [*Lewis et al.*, 2004a], only increasing atmospheric CO_2 concentrations [*Prentice et al.*, 2001], increasing solar radiation inputs [*Wielicki et al.*, 2002], rising air temperatures, and changing precipitation patterns [*Malhi and Wright*, 2004] have been documented across most or all of Amazonia and could be responsible for increased growth and productivity. For none of these changes, however, do we have overwhelming evidence that the driver has both certainly changed and that such a change is likely to accelerate forest growth [*Lewis et al.*, 2004a]. The increase in atmospheric CO_2 is the primary candidate because of the undisputed long-term increase in CO_2 concentrations, the key role of CO_2 in photosynthesis, and the demonstrated positive effects of CO_2 fertilization on plant growth rates, including experiments on whole temperate-forest stands [*Norby et al.*, 2002; *Hamilton et al.*, 2002; *Lewis et al.*, 2004a]. However, a substantial role for increased insolation [e.g., *Nemani et al.*, 2003; *Ichii et al.*, 2005], or aerosol-induced increased diffuse fraction of radiation [e.g., *Oliveira et al.*, 2007], cannot be ruled out. Elsewhere, we have discussed the candidate drivers in more detail [*Lewis et al.*, 2004a, 2006a, 2006b; *Malhi and Phillips*, 2004, 2005]. Here we do not revisit that discussion, but briefly discuss our philosophy and approach to forest ecology and inference, which has antecedents in peripatetic ecologists of the past from Darwin to Gentry. Ecological science is largely done at individual sites, some of which have become extraordinarily well-known. This is dangerous: there is a natural human tendency to generalize from rather limited personal experience, sometimes exacerbated by the pressure to publish rapidly and to exaggerate the global importance of local research findings. But Amazonia is a very big place indeed. The site-centric approach inevitably colors interpretations and means that the peculiar features of that site including fragmentation, atypical soil conditions, previous cyclones or fires, dominate researchers' findings and interpretations. Our results and those of a recent, parallel study [*Chave et al.*, 2008] show that all sites, if studied intensively enough, will likely reveal strong, local idiosyncratic features which dominate their contemporary ecology, but that no individual site (or even handful of sites) can be satisfactorily used to test for the presence or absence of larger-scale processes. The synoptic challenge is to reveal general patterns that lie beyond the local idiosyncrasies. That will only come from a standardized, geographically distributed, truly long-term, and internationalized science. RAINFOR represents a positive step in that direction.

6. THE FUTURE: POTENTIAL SUSCEPTIBILITY OF AMAZON FOREST TO ENVIRONMENTAL STRESS AND COMPOSITIONAL CHANGES

In sum, then, long-term observations indicate that Amazonia, the world's largest remaining tract of tropical forest, has shown concerted changes in forest dynamics over the past two decades. Such unexpected and rapid alterations, regardless of the cause, were not anticipated by ecologists and raise concerns about other possible surprises that might arise as global changes accelerate in the coming decades. On current evidence, tropical forests are sensitive to changes in incoming resource levels and may show large structural and dynamic changes in the future, as resource levels alter further, temperatures continue to rise, and precipitation patterns shift. The implication of such rapid changes for the world's most biodiverse region is unknown, but could be substantial.

Old-growth Amazonian forests have evidently helped to slow the rate at which CO_2 has accumulated in the atmosphere, thereby acting as buffer to global climate change. The concentration of atmospheric CO_2 is rising at an annual rate equivalent to 3–4 Pg C; this would be significantly greater without the tropical South American biomass carbon sink of 0.5–0.9 Pg C a^{-1}. This subsidy from nature could be a relatively short-lived phenomenon. Mature Amazonian forests may either (1) continue to be a "carbon sink" for decades [*Chambers et al.*, 2001b; *Cramer et al.*, 2001], or (2) soon become "neutral or a small carbon source" [*Cramer et al.*, 2001; *Phillips et al.*, 2002b; *Körner*, 2004; *Laurance et al.*, 2004], or (3) become a "mega-carbon source" [*Cox et al.*, 2000; *Cramer et al.*, 2001]. Given that a 0.4% annual increase in Amazonian forest biomass roughly compensates for the entire fossil-fuel emissions of western Europe (or the deforestation in Amazonia), a switch of mature tropical forests from a moderate carbon sink to even a moderate carbon source would have implications for global climate and human welfare. The ~0.4% annual sink represents the difference between two much larger values: stand-level growth (averaging ~2%) and mortality (averaging ~1.6%), so a small decrease in growth or small increase in mortality would be enough to shut the sink down. There are several mechanisms by which such a switch could occur, apart from the obvious and immediate threats posed by land use change and associated disturbances by fragmentation and fire.

6.1. Photosynthesis/Respiration Changes

Intact forests will remain a sink as long as carbon uptake associated with photosynthesis exceeds the carbon efflux from respiration. Under the simplest scenario of a steady rise in forest productivity over time, it is predicted that forests would remain a carbon sink for decades [e.g., *Lloyd and Farquhar*, 1996]. However, the current increases in productivity, apparently caused by continuously improving conditions for tree growth, cannot continue indefinitely: if CO_2 is the cause, trees are likely to become CO_2 saturated (i.e., limited by another resource) at some point in the future. More generally, whatever the driver for recently accelerated growth, forest productivity will not increase indefinitely, as other factors such as soil nutrients will limit productivity.

Rising temperatures could also shrink the current forest sink or cause forests to become a carbon source in the future. Warmer temperatures increase the rates of virtually all chemical and biological processes in plants and soils (including the enhancement of any CO_2 fertilization effect), until temperatures reach inflection points where enzymes and membranes lose functionality. There is some evidence that the temperatures of leaves at the top of the canopy, on warm days, may be reaching such inflection points around midday at some locations [*Lewis et al.*, 2004a]. Canopy-to-air vapor deficits and stomatal feedback effects may also be paramount in any response of tropical forest photosynthesis to future climate change [*Lloyd et al.*, 1996].

The relationship between temperature changes and respiration is critical. The first global circulation model (GCM) to include dynamic vegetation and a carbon cycle that is responsive to these dynamic changes suggests that under the "business as usual" scenario of emissions, IS92a, atmospheric CO_2 concentrations are 900–980 parts per million by volume (ppmv) in 2100, compared to ~700 ppmv from previous GCMs [*Cox et al.*, 2000, 2004]. These concentrations depend critically on (1) dieback of the eastern Amazonian forests, caused by climate change-induced drought, and (2) the subsequent release of C from soils. The release of C from soils is critically dependent on the assumed response of respiration to temperature and soil moisture and the modeling of soil carbon.

Carbon losses from respiration will almost certainly increase as air temperatures continue to increase. The key question is what form this relationship takes. Carbon gains from photosynthesis cannot rise indefinitely and will almost certainly asymptote. Thus, the sink in intact tropical forests will diminish and eventually reverse. The major uncertainty is "when" this will occur.

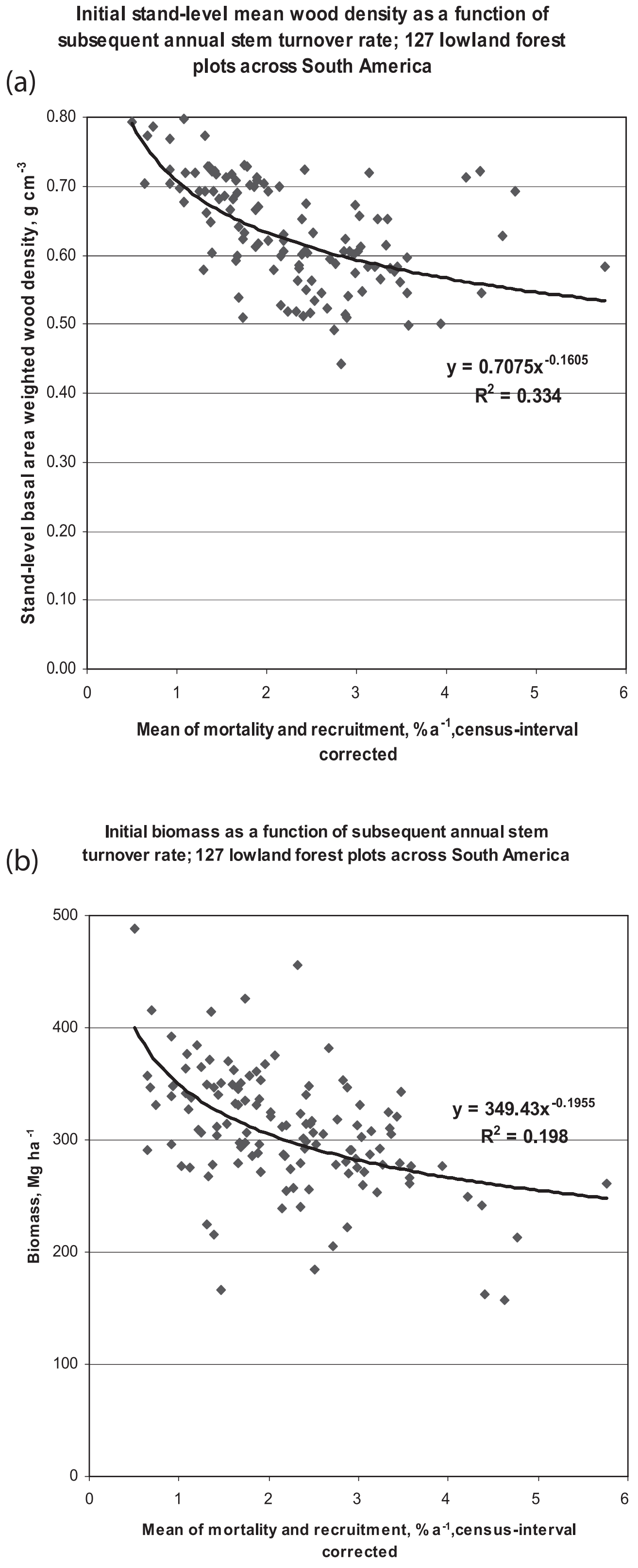
6.2. Moisture Stress

Climate change will alter precipitation patterns. There are critical thresholds of water availability below which tropical forests cannot persist and are replaced by savanna systems; currently, the threshold lies around 1300–1500 mm rainfall per annum [*Salzmann and Hoelzmann*, 2005], but this could increase with rising temperatures. Thus, increasing temperatures and/or changing precipitation patterns may cause shifts in vegetation from carbon-dense tropical forests, to carbon-light savanna systems. The degree to which Amazonian forests may or may not be ecophysiologically resilient to extreme temperatures is a subject of active research, reviewed by *Lloyd et al.* [this volume].

What is the evidence, so far, of drought impacting Amazonian forests? The temporal resolution of RAINFOR plots has generally been insufficient to allocate growth and mortality rates to individual years. Nevertheless, among the 10 longest-running plots (initiated in the 1970s or earlier), the severe 1982–1983 El Niño event apparently did not greatly affect forest dynamics [*Phillips*, 1995]. Where there are annual or higher-resolution records, there is some evidence of short-term stand-level rates responding to moisture stress, with growth decreasing markedly in the dry season near Rio Branco, Acre [*Vieira et al.*, 2004] and mortality temporarily increasing during the 1997–1998 El Niño near Manaus [*Williamson et al.*, 2000]. However, the impact on growth rates of moderate dry conditions in Amazonia may not always be negative. There is some evidence from leaf and branch level [e.g., *Graham et al.*, 2003] and at regional scales [*Huete et al.*, 2006] to suggest that neotropical moist forests may be as light limited as they are moisture-limited. If so, while droughts reduce productivity and exacerbate fire risk in more marginal forest locations, more cloud-free rainless days would enhance productivity in some cloudier locations. In a separate study [*Phillips et al.*, 2009], we report the results of intensive recensusing following the 2005 drought to assess just how sensitive Amazonian forests are to drought across the whole basin.

6.3. Compositional Change

Biodiversity change has inevitable consequences for climate change because different plant species vary in their ability to store and process carbon. Yet most models that project the future carbon balance in Amazonia (and future climate-change scenarios) make no allowance for changing forest composition. Representation of composition is challenging, both because of the computational complexities in integrating ecological processes into ecophysiology-driven models and because the ecological data themselves are sparse. But representing composition better, and its potential for change, is important. Lianas, for example, ignored in all forest models, often contribute little to forest biomass but heavily to productivity [*Schnitzer and Bongers*, 2002], while killing trees [*Phillips et al.*, 2005] and preferentially infesting denser-wooded species [*van der Heijden et al.*,



2008]; their recent increase suggests that the tropical carbon sink might shut down sooner than current models suggest. Large changes in tree communities could also lead to net losses of carbon from tropical forests [*Phillips and Gentry*, 1994; *Körner*, 2004]. One way this could happen is a shift to faster-growing species, driven by increasing tree mortality rates and frequency of gap formation [*Phillips and Gentry*, 1994; *Phillips et al.*, 2004]. Such fast-growing species generally have lower wood specific gravity, and hence less carbon [*West et al.*, 1999], than shade-tolerant trees. Better effort to detect whether or not such changes are occurring is clearly a priority for future monitoring efforts. The potential scope for such impacts of biodiversity changes on carbon storage is highlighted by *Bunker et al.* [2005], who explored various biodiversity scenarios based on the tree species at Barro Colorado Island: if slower-growing tree taxa are lost from an accelerated, liana-dominated forest, as much as one third of the carbon storage capacity of the forest could be lost. In Amazonia, a basin-wide annual decrease in mean wood specific gravity of 0.4% would cancel out the carbon sink effect. There is currently a ~20% difference in mean wood density of the faster forests in the west, compared with slower forests in the east (Figure 7) [*Baker et al.*, 2004b], and because these faster forests also have lower basal area, the differences in terms of biomass carbon stored are greater still (Figure 7) [*Lewis et al.*, 2006b]. Concerted compositional changes driven by greater resource supply, increased mortality rates, and possible selection for faster-growing trees which escape lianas, may shut down the carbon sink function of tropical forests earlier than ecophysiological analyses predict.

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Figure 7. Biomass as a function of mean stand-level wood density, for 127 lowland forest plots across South America. Note that faster forests have lower wood density and much lower biomass.

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T. R. Baker, K.-J. Chao, S. L. Lewis, and O. L. Phillips, Earth and Biosphere Institute, School of Geography, University of Leeds, Leeds LS2 9JT, UK. (o.phillips@leeds.ac.uk)

N. Higuchi, Laboratório de Silvicultura Tropical, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil.

S. Vieira, Laboratório de Ecologia Isotópica, USP, CENA, BR-13400970 Piracicaba, SP, Brazil.