CHANGES IN GROWTH OF TROPICAL FORESTS: EVALUATING POTENTIAL BIASES

O. L. Phillips,[1,10] Y. Malhi,[2] B. Vinceti,[2] T. Baker,[1] S. L. Lewis,[1,2] N. Higuchi,[3] W. F. Laurance,[4,5] P. Núñez Vargas,[6] R. Vásquez Martinez,[7] S. Laurance,[4] L. V. Ferreira,[4] M. Stern,[8] S. Brown,[9] and J. Grace[2]

[1]*Centre for Biodiversity and Conservation, School of Geography, University of Leeds, UK*
[2]*Institute of Ecology and Resource Management, University of Edinburgh, Scotland, UK*
[3]*Departamento de Silvicultura Tropical, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brasil*
[4]*Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), Manaus, AM, Brasil*
[5]*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama*
[6]*Herbario Vargas, Universidad Nacional San Antonio Abad del Cusco, Cusco, Perú*
[7]*Proyecto Flora del Perú, Jardín Botánico de Missouri, Jaen, Cajamarca, Perú*
[8]*New York Botanical Garden, New York, New York, USA*
[9]*Winrock International, Corvallis, Oregon, USA*

Abstract. Over the past century almost every ecosystem on Earth has come under the influence of changes in atmospheric composition and climate caused by human activity. Tropical forests are among the most productive and extensive ecosystems, and it has been hypothesized that both the dynamics and biomass of apparently undisturbed, old-growth tropical forests have been changing in response to atmospheric changes. Long-term forest sample plots are a critical tool in detecting and monitoring such changes, and our recent analysis of pan-tropical-forest plot data has suggested that the biomass of tropical forests has been increasing, providing a modest negative feedback on the rate of accumulation of atmospheric CO_2. However, it has been argued that some of these old forest plot data sets have significant problems in interpretation because of the use of nonstandardized methodologies.

In this paper we examine the extent to which potential field methodological errors may bias estimates of total biomass change by detailed examination of tree-by-tree records from up to 120 Neotropical plots to test predictions from theory. Potential positive biases on measurements of biomass change include a bias in site selection, tree deformities introduced by the measurement process, poor methodologies to deal with tree deformities or buttresses, and nonrecording of negative growth increments. We show that, while it is important to improve and standardize methodologies in current and future forest-plot work, any systematic errors introduced by currently identified biases in past studies are small and calculable. We conclude that most tropical-forest plot data are of useful quality, and that the evidence does still weigh conclusively in favor of a recent increase of biomass in old-growth tropical forests.

Key words: Amazon rain forest; basal area; bias, evaluating; buttresses; carbon sink; climate change, global; forest plot data; forest-plot-based estimates of biomass; Neotropics; tree growth; tropical forests, changing dynamics.

INTRODUCTION

Recently we analyzed results of tree measurements from long-term permanent sample plots in tropical forests, and concluded that in the Neotropics there has been a late 20th century trend toward increased biomass in old-growth forests (Phillips et al. 1998*a*). The biomass increase pointed to a sink for atmospheric CO_2 in South American forests of 0.5–1 Pg C/yr (1 Pg = 10^{15} g), equivalent to the fossil-fuel emissions of the European Union. Earlier plot-based analyses also suggested that tropical tree populations experienced increased rates of mortality and recruitment (''turnover'')

in the latter part of the last century (Phillips and Gentry 1994, Phillips 1996). Meanwhile, researchers using micrometeorological techniques and inverse modeling of atmospheric CO_2 concentrations reported that tropical ecosystems as a whole probably contribute a C sink of 1–3 Pg/yr (Grace et al. 1995, Malhi et al. 1998, Rayner et al. 1999, Bousquet et al. 2000). These findings are broadly consistent with modeling and laboratory studies that imply changes in the physiology and productivity of forests in response to global atmospheric change, such as increasing CO_2 concentrations (e.g., Lloyd 1999, Norby et al. 1999). In sum, recent empirical research suggests that apparently undisturbed tropical forests, far from areas of deforestation, are undergoing secular changes, and these changes have a plausible basis in the effects of atmospheric change on plant

ecophysiology (cf. Malhi and Grace 2000). We call this the ''changing dynamics of tropical forests hypothesis'' (CDTF).

The CDTF hypothesis challenges the conventional ecological assumption that old-growth forests should be at some kind of dynamic equilibrium, as these forests may have been affected by changing atmospheric composition since before tropical forests were first studied. The notion of a carbon sink in old-growth forests in particular is controversial. For example, inverse models of atmospheric-CO_2 sinks and sources suffer from the low global density of atmospheric-CO_2 measurement sites (Bousquet et al. 2000) and apparently wide year-to-year variation in planetary carbon metabolism—so estimates remain poorly resolved spatially and temporally. It has also been suggested that the eddy-covariance results may be explained by spatial bias of measurements toward sites accumulating biomass (e.g., Keller et al. 1996), or incomplete measurement of rates of nighttime CO_2 efflux from forest to atmosphere (Moncrieff et al. 1996, Malhi et al. 1999). The controversies surrounding long-term plot data center around whether artifactual errors of experimental design, measurement, or interpretation can explain some or all of the observed patterns (e.g., Phillips 1995, 1996, Sheil 1995*a, b,* Condit 1997, Phillips and Sheil 1997, Hall et al. 1998, Phillips et al. 1998*b*). In this paper we address some potential errors associated with plot-based evidence for a biomass change in neotropical forests, the subject of a recent critique (Clark 2002), and focus on theoretical and empirical aspects of what we believe to be the most plausible sources of error, as well as those that Clark has highlighted. We then propose a strategy for moving the debate forward. What are the post-hoc tests needed to detect and quantify possible biases and errors? And what are the most practical plot-based approaches to clarify the spatial, environmental, and temporal distribution of the C balance of biomass in old-growth tropical forests?

Artifacts, Errors, and Biases: a Brief Overview

A range of methodological issues may affect plot-based estimates of biomass change. If these generate erroneous information or cause misinterpretation of information, these may produce artifactual results. Some may tend to simply increase the error term of stand-level change estimates, while others may actually bias the estimate positively or negatively (cf. Sheil 1995*b*). In any single plot study, several kinds of methodological errors and biases could be operating, so, unless studies were specifically designed to experimentally test the contribution of each individual issue, quantifying the significance of each is difficult. However, the estimates of net stand-level change are only composite results of changes in underlying structure and processes (e.g., spatial distribution of basal area, and rates of growth, recruitment, and mortality, all of which in turn

may vary as functions of, for example, tree size, species, and functional behavior). Each artifact that can affect stand-level change will therefore likely do so in a unique way by biasing estimates of one or more of the underlying processes, and thus should leave a unique ''footprint'' in the data structure. This makes it possible to use insights from ecological theory and mathematical simulations to predict and model the likely pattern(s) such an artifact would cause in the plot data, and to explicitly test for such pattern(s) in the data. This is the approach we adopt in this paper.

We have compiled a list of methodological issues that have been argued to cause a systematic negative or positive bias in plot-based estimates of basal area change (Table 1), based on our own work and other published and unpublished sources, including comments received by us before and after the publication of Phillips et al. (1998*a*). In that paper we selected an allometric equation based on 319 trees harvested in a Central Amazonian study that modeled stand biomass as a function of stand basal area, and used that relationship to express our basal-area change results in biomass terms. In the following evaluation, we specifically exclude possible artifacts that might impact biomass estimates that might derive from our choice of allometric equation, and the methods used to generate these allometric relationships themselves. These issues are dealt with elsewhere, for example by Chambers et al. (2001), who conclude that there is remarkable similarity in diameter/biomass relationships among most lowland tropical forests that have been evaluated. Furthermore, it is not clear that such methodological variations would cause a systematic bias (positive or negative) in estimates of biomass change.

The discussion that follows is unlikely to be exhaustive, but we believe it represents a summary of the major concerns that investigators have. For each methodological issue, we infer the likely direction of bias it would cause, and propose a test or tests for detecting such an artifact.

Did We Overestimate the Increase in Biomass?

A recent critique (Clark 2002) focuses solely on the possibility that forest-wide basal-area changes, and therefore forest carbon sinks, have been overestimated, but clearly bias in *either* direction is plausible a priori. The important question is: Are these processes significant *in practice*? Have we erroneously overestimated (or underestimated) the global C sink provided by biomass in old-growth forests?

To specifically address the issues Clark raises, in this paper we focus our analysis on specific sources of ''positive'' bias, i.e., those that might have led to a significant overestimate. A future paper will attempt to address the possible sources of negative bias (see Table 1). It is however worth pointing out here that many of these biases, both negative and positive, appear intu-

O. L. PHILLIPS ET AL.

TABLE 1. Possible sources of bias on forest basal-area change estimates.

Source of error/bias	Issue	Description	Results should also show†
A) Negative bias			
Site-selection bias	"Majestic-forest bias"	Biased selection of mature-phase, gap-free sites in the landscape	Decline in number of big trees with increasing time Mortality and recruitment increase with increasing time Basal area correlates negatively with plot size
Site-selection bias	"Progressive fragmentation and edge effects"	Biased selection of accessible sites vulnerable to fragmentation and edge-effects	Mortality correlates with increasing time Mortality and negative changes in basal area correlate with fragment size and/or distance to edge
The process of the research itself	Methodological impact on vegetation (~ "Heisenberg uncertainty principle")	For example, researchers compacting soil, tagging trees, climbing and collecting trees, drawing attention of others to plot, etc.	Growth negatively correlated with time Mortality positively correlates with time Climbed or collected trees have depressed growth and elevated mortality. Infection rates of climbed/collected trees positively correlate with time.
Field measurement errors	Incomplete recensusing	New recruits may be missed, and some surviving trees may be missed and assumed dead ("ghost mortality")	Apparent sudden "recruitment" of large trees
Field measurement errors	Improved measurements of buttressed trees	Methods for measuring buttressed trees typically improve with time, with researchers more likely to measure around buttresses in initial censuses.	Apparent sudden loss of basal area of some individual large trees
Post-measurement data checking	Reducing extreme increments	Exceptional increments (e.g., >75 mm/yr) eliminated a priori or reduced in case measurement is in error	Effect only on the latest census interval (since most trees discovered to have been rounded-down incorrectly previously may be re-corrected at subsequent censuses)
Publication bias	Selective reporting of plots	Catastrophic disturbances (cyclones, fire, flood, etc.) during census period increases interest in reporting results	Negative changes in basal area explicitly linked by authors to catastrophic events
B) Positive bias			
Site-selection bias	"Immature-forest bias"	Biased selection of successional forest	Stem density declines as basal area increases (self-thinning)
The process of the research itself	Methodological impact on vegetation ("Heisenberg uncertainty principle," e.g., "nails")	Increasing swelling around nail used to place tag on tree	Effect increases with time No evidence of increase in recruitment No evidence of researchers moving point of measurement
Field measurement errors	"Buttress creep"	Bole irregularities move up with time, becoming more likely to affect point of measurement with increasing time	Effect increases with time Effect especially marked in trees with large diameter No evidence of increase in recruitment No evidence of researchers moving point of measurement
Field measurement errors	"Basal-area inflation"	"[D]isproportionately rapid radial increment of buttresses . . . bole irregularities will compound the overestimation of [stand] biomass increase" (Clark 2001; but see text below)	Effect especially marked in trees with large diameter Effect increases with increasing time Some trees with implausibly large diameters

TABLE 1. Continued.

Source of error/bias	Issue	Description	Results should also show†
Post-measurement data checking	"Rounding-up negative increments"	In evaluating changes in diameter, "false negatives" are rounded up to zero, but "false positives" are kept because they cannot be distinguished from trees that have genuine increases in diameter	Effect size small and diminishes with increasing length of interval No negative increments in researchers' tree-by-tree data sets Effect mostly on smallest size classes (since small understory light-limited trees most likely to show little or no real growth)

† If the source has an artifactual negative (A) or positive (B) impact on the estimates of forest basal-area change, then the results should also show these characteristics.

itively credible. Some of these have been the main focus of critiques of the changing dynamics of tropical forests (CDTF) hypothesis cited above (see *Introduction*), while others are actively debated in other contexts—particularly the possibility of progressive fragmentation and edge effects affecting permanent sample plots (e.g., Laurance 2000).

Site-selection bias: "Immature Forest Bias"

Potentially, biased selection of nonmature sites in the landscape could lead to a bias in the forest-wide estimate of biomass change. If mature-phase forest were somehow avoided when many plots were established, the tendency would be for plots to accumulate biomass simply as a result of normal successional processes. This seems unlikely; many critiques of the CDTF hypothesis focus on the opposite concern that ecologists may be biased toward selecting especially large and majestic-looking stands (e.g., Sheil 1996, Condit 1997, Phillips et al. 1997). We have also specifically excluded obviously immature forests from our earlier analyses. Yet most tropical forest locations have probably experienced severe anthropogenic or natural disturbance at least once within the Holocene (e.g., Sanford et al. 1985, Meggers 1994, Clark 1996, Netherley 1997), and in Peruvian Amazonia alone 120 000 km² of forest are situated within geomorphological floodplains aggrading in modern, Holocene times (Salo et al. 1986, Rasanen et al. 1992) so it would be inappropriate to exclude sites from our analysis simply on the basis of prior disturbance. We need to ask whether recovery from disturbance could itself explain our results—whether as an artifact driven by biased selection of successional sites, or as a genuine region-wide phenomenon of forest "rebound" from earlier large-scale disturbances.

To explore these possibilities we propose two tests. First, even-aged forest stands recovering from major disturbance (primary or secondary succession) undergo self-thinning with smaller trees being out-competed by larger individuals, so that increasing basal area should coincide with decreasing stem number. The self-thinning rule ($B = a\ N^{-0.5}$; where B = biomass, a is a constant, and N = stems per unit area) is a result of competition between growing stems, and has been demonstrated empirically and theoretically for mono-specific and multispecies stands in temperate and tropical forests (e.g., Kohyama 1992, Drake and Mueller Dombois 1993, Runkle 1998, Kiyoshi and Kihachiro 1999). In species-rich tropical forests the process may well be more complicated, with many individuals of shade-tolerant species surviving for long periods of time in a suppressed state. Hence, tree density in some successional tropical forests may be predicted to decrease only after a timelag. This might be difficult to detect with our data, since intervals of 10–20 yr are still relatively short with respect to tree life spans. However, more immediate "self-thinning" effects should still be seen among those dominant and codominant canopy trees undergoing two-way competition for growing space. The second test that we propose is that biomass accumulation rates recorded should fall broadly within the range of rates of biomass accumulation derived from direct studies of late secondary successional sites of known age. In other words, if experimental lowland tropical sites known to be younger than our lowland tropical sites accumulate biomass much more slowly than our sites, then the biomass increase at our sites is unlikely to be driven by secondary succession.

The results of our first test are shown in Fig. 1. Many stands with recent accumulation of basal area are not undergoing self-thinning. In fact, the opposite has occurred in the 10 plots located on the Holocene floodplain, since the sites which gained most basal area have also experienced the largest increase in stem density, with particularly high rates of recruitment into the 10-cm diameter class (Fig. 1a) (Pearson's $r = 0.78$, $P < 0.01$). The pattern is equally apparent for those dominant and codominant canopy trees, defined as trees ≥ 50 cm diameter, whose stem density has increased as total stand basal area has increased (Fig. 1b) (Pearson's $r = 0.88$, $P < 0.001$). These results are contrary to the prediction of the self-thinning rule applied to an even-aged late-successional forest accumulating biomass, as a cohort of successional large canopy trees would be
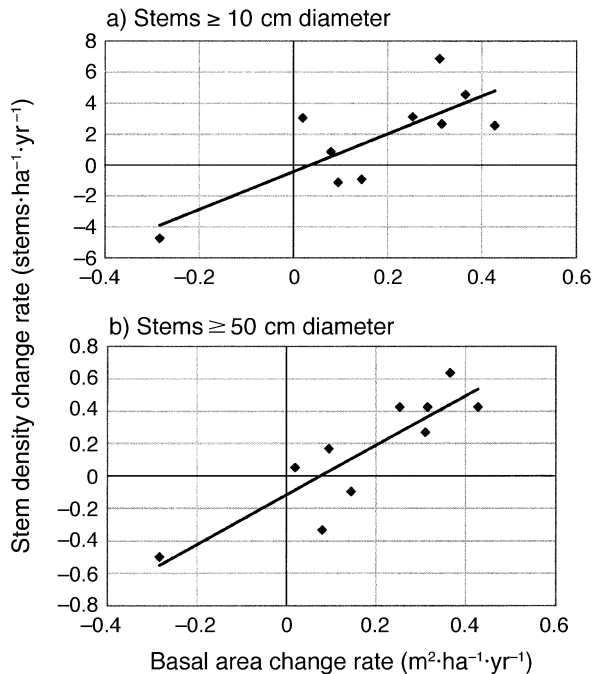
FIG. 1. Rate of change in stem density of Amazon forest sites in the Holocene floodplain as a function of the rate of change in stand basal area (O. J. Phillips, R. Vásquez Martinez, P. Núñez Vargas, and M. Stern, *unpublished data.*) Stem density change rates are a positive function of basal area change rates, indicating that the sites do not host secondary successional forests.

expected to increasingly suppress smaller trees and compete with one another.

The second test is more difficult to apply because there are few reliable measures of biomass accumulation in late successional forests to compare with, and we currently have no way to precisely know the age of the forests. We do know however that most secondary forests acquire at least 50% of aboveground biomass within 30 yr and the rate of increase declines rapidly with age (e.g., Brown and Lugo 1990, Hughes et al. 1999, Johnson et al. 2000, Salimon and Brown 2000). We also know that an oxbow lake close to site 21 in Phillips et al. (1998a) was independently estimated to be ~900 yr old (M. Silman, *personal communication*, M. Bush and M. Silman, *unpublished manuscript*). As site 21 is on an older surface than the lake itself, and is within the floodplain belt of the most rapidly migrating river in our data set (Río Manú) (Gentry and Terborgh 1990), it is plausible to suggest that all of our sites are at least 900 yr old. We have simulated biomass accumulation rates for late secondary succession using an exponential model (Salimon and Brown 2000) fitted to secondary forests in Acre (southwest Brazil) ($6.2 \times e^{-0.025t}$ kg·ha^{-1}·yr^{-1}, where t is the time elapsed since succession initiated), and infer that after just 300 yr maturing secondary forests may only accumulate ~3 kg·ha^{-1}·yr^{-1}, equivalent to just 0.0014%

of biomass, as a result of successional processes. This rate would be too small to detect using tree plots and is more than two orders of magnitude less than the mean rate of increase recorded in our Neotropical sites (Phillips et al. 1998a). Other exponential models of aboveground biomass accumulation suggest that biomass of secondary forests can attain that of primary forests within as little as 70–100 yr, and that the rate of accumulation is a positive function of soil nutrient concentrations (Brown and Lugo 1990, Hughes et al. 1999). Holocene floodplain soils from our sites have exceptionally high nutrient concentrations by Amazonian standards (e.g., Clinebell et al. 1995, Pitman 2000), so it is particularly unlikely that successional processes after many hundreds of years can account for observed biomass increase in the Holocene floodplain sites. In sum, evidence from analysis of the pattern of change in our sites and rates of biomass accumulation in dated successional sites shows that an "immature forest bias" is an extremely unlikely explanation of our results.

Research artifact: "Nails"

Localized swelling of trees around nails could cause an error in biomass change estimates if nails are located close to point of measurement (POM), and if remeasurement teams are careless in failing to shift the POM in response. This cannot explain the tendency for sites to experience increased recruitment rates (Phillips 1996), but could conceivably still contribute to the apparent biomass increase. To do so, the effect should increase, possibly linearly or exponentially, with time since plot establishment, as the original tags and nails become increasingly enveloped by wound tissue. In fact, no such trend is apparent across all Neotropical plots (Fig. 2).

Field measurement errors: "Buttress creep"

Similarly, the tendency of some stems to progressively deform from below could cause a positive bias in net change estimates if the deformity begins to affect the POM during the monitoring period, and if remeasurement teams are careless in failing to shift the POM in response. Over time, an increasing number of POMs would become affected by stem deformities. However, as with the potential artifact caused by nails, such an effect cannot in itself explain the finding of increased recruitment rates. Similarly, it would be expected to generate a linear or exponential apparent increase in annual net basal-area change with time since plot establishment, which is not the case in our data (Fig. 2).

Field measurement errors: "Basal-Area Inflation"

A further problem for plot-based estimates of forest structure and change could be a tendency for some foresters and ecologists to measure trees at a standard 1.3 m regardless of any stem deformity. This would clearly cause a positive bias in estimated basal area and
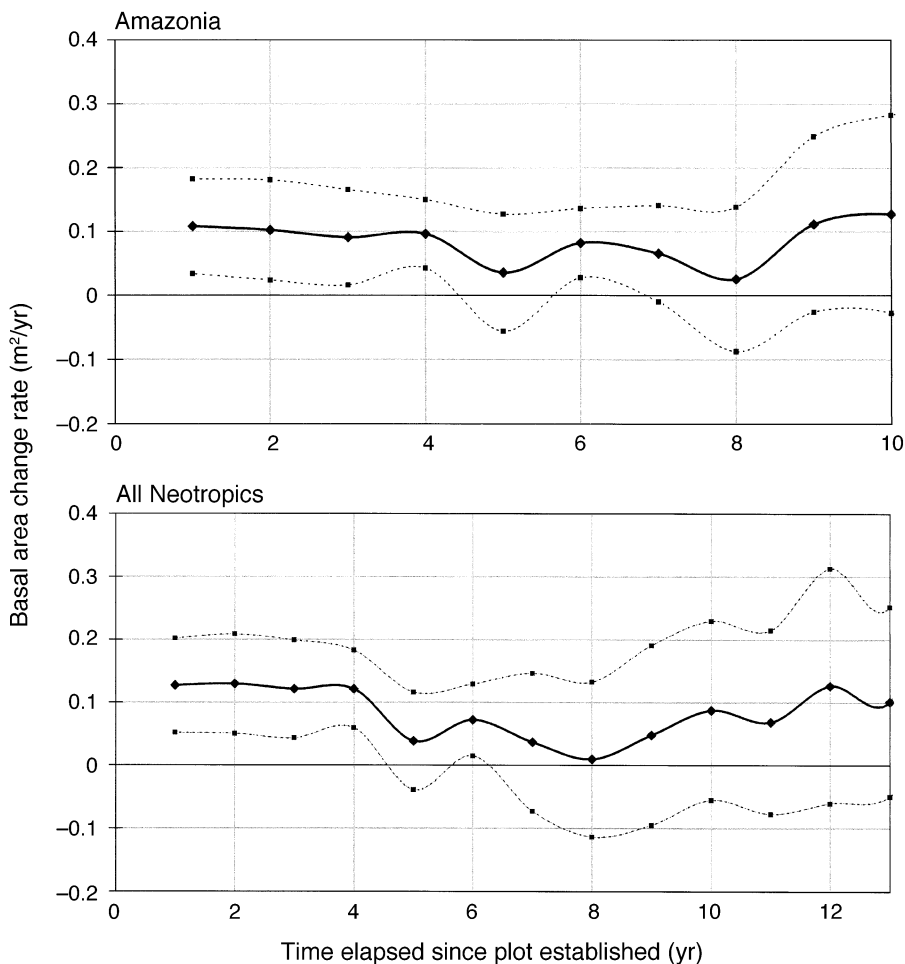
FIG. 2. Annual basal-area change rate measured as a function of time elapsed since the plot was established, showing mean and upper and lower 95% confidence intervals of rate of change in each year.

biomass, but it has also been suggested it would also cause a positive bias in the estimated *net change* of basal area and biomass (Clark 2002).

However, it is difficult to believe that Neotropical foresters and ecologists would, in mass, commit the error of measuring tree "diameter" at 1.3 m height regardless of the degree of buttressing encountered. They may take it for granted that their readers are aware of this, too, and therefore do not always make this explicit in publications (absence of published evidence is not evidence of absence), but if they did make this mistake it is more likely that they would have done so in the past than more recently, since good practice has spread and plot methods have become increasingly standardized. Indeed, Clark (2002) reports that at La Selva this is exactly what happened—in the 1960s some trees were apparently measured "around buttresses" but by the 1980s all trees were measured above buttresses. Similarly, when the 50-ha plot at Barro Colorado Island, Panama, was established in 1982 this mistake was made for some trees, but by 1985 the correct

protocol was used (R. Condit, *personal communiction* [1997]). Thus, it seems likely that such a measurement error if unreported would act as a *negative* bias on the basal-area change measured (cf. Table 1A). Our experience is that most tropical foresters and ecologists are aware of the problem of buttresses and make efforts to measure stem diameter above buttresses, and that the mensuration methodologies adopted become progressively more robust with successive censuses. To our knowledge at no site within our data set—other than La Selva in 1969—are buttressed trees measured directly around the buttresses. Any statistical comparison of 1.3-m sites vs. above-buttress sites is therefore groundless. In Clark's (2002) critique, several Venezuelan sites analyzed by Phillips et al. (1998a) are characterized as being measured around buttresses, but at the Venezuelan sites 35–38 and 44–50 in the more recent censuses most trees were definitely measured above buttresses (A. Torres Lezama [University de los Andes], 1999 *personal communication* to S. Brown reporting measurements by A. D. Jesus and others since

J. P. Veillon retired). For pre-1978 Venezuelan censuses that include data published by Veillon (1985), there is an apparent disagreement—with trees either (always?) measured at 1.3 m (Clark 2002: J. P. Veillon, *personal communication*), or increments of trees with very tall buttresses based on the average increment of non-buttressed trees in the diameter class (D. B. Clark, *personal communication* [1999, reporting J. P. Veillon comment to D. A. Clark]), or always measured above buttresses (A. Torres Lezama, *personal communication*). J. P. Veillon retired in 1978, but most of the Venezuelan site data we analyzed ran until after 1978, so if there is any effect of any change in measurement technique on net basal-area change estimates at these sites, it is likely to be negative. This suggests that our estimates of biomass increase in Venezuelan forests (Phillips 1998*a*) may have erred on the conservative side.

Regardless of such concerns, it is also possible to test empirically the combined potential impact of several field-measurement errors (e.g., buttress creep *and* basal-area inflation) on our biomass change estimates, by evaluating net change by size class, since buttresses are disproportionately large and frequent on larger diameter trees (e.g., Clark 2002) and so any associated measurement errors must be disproportionately significant here as well. To quantify the proportion of the net biomass accumulation attributable to different size classes, we examined net basal-area change for all 34 plots (from sites 8–10, 16–38, 44, and 45 in Phillips et al. [1998*a*]) where we have full tree-by-tree data sets. There is large among-plot variation in net basal-area change for all size classes, but gains are clearly not restricted to the largest classes. On average, basal area has accumulated throughout the size classes (for small trees 10–30 cm diameter, by 0.033 ± 0.026 $m^2 \cdot ha^{-1} \cdot yr^{-1}$ [mean ± 95% CI]; for medium-sized trees 30–60 cm diameter, by 0.029 ± 0.033 $m^2 \cdot ha^{-1} \cdot yr^{-1}$; for large trees 60–90 cm diameter, by 0.009 ± 0.045 $m^2 \cdot ha^{-1} \cdot yr^{-1}$; and for very large trees >90 cm diameter by 0.028 ± 0.037 $m^2 \cdot ha^{-1} \cdot yr^{-1}$). Finally, if such an effect were operating, it should generate an increase in apparent basal-area change rates with increasing time since plot establishment, which is not shown by the data (Fig. 2).

Yet it is worth exploring this issue further, as no forester can claim to always measure every tree diameter accurately! We need to ask whether such inevitable inaccuracies could cause systematic biases—and, if so, by how much.

How does poor measurement of basal area affect estimates of basal-area change?—If poor measurement strategies do introduce a systematic bias in basal area, as suggested by Clark (2002), it is interesting to explore what effect such a bias would have on estimates of *rate of change* of basal area. At first glance an overestimate of plot basal area by, say, 20% may seem to render impossible a detection of change in basal area between censuses of, say, 5%. However, we show below that measurements of change of basal area are surprisingly robust, and, crucially, that overestimates in basal area do not erroneously cause equilibrium forests to appear to be accumulating basal area.

To examine the possible effects of measurement error we will use 1-ha inventory data from eight plots where we are very confident, through direct experience, that the trees have been censused with good methodology. We use three plots (hereafter referred to as "Bio1," "Bio2," and "Bio3": original plot numbers T0-B1SB2, T0-B2SB3, and T0-B4SB5) from the BIONTE (biomass and nutrient experiment) project near Manaus, central Amazonia (Carvalho et al. 1998); four plots (BDF1 to BDF4: original BDFFP reserve numbers 1201(1), 1113, 1109, and 1102) from the BDFF (Biological Dynamics of Forest Fragments) project, also near Manaus (Laurance et al. 1998); and one plot (Tamb: original plot number 0) from Tambopata, Peru (Phillips et al. 1994*a, b*). We take data from the initial and final censuses, with the gap between these censuses being >10 yr in all plots. A ninth, slightly artificial, "equilibrium" plot was also generated by removing two trees from the Bio4 plot data; this "equilibrium" plot had the same basal area in the first and second recensus.

To mimic the effects of errors we introduce a set of "measurement errors" to these data sets. We define two functions P_{dbh} and S_{dbh}, both of which are functions of dbh (tree diameter at breast height [1.3 m]). P_{dbh} describes the probability of there being an error in the measurement of dbh in any particular tree, and S_{dbh} describes the size of that error. The possible scenarios to dbh we introduce for each of these functions are as follows:

1) P_{exp}, S_{exp}—An exponential increase of probability and size of error with increasing dbh, with all trees larger than 50 cm having a measurement error, with $P = 0.09 \exp(0.05 \times dbh)$ [where $P \leq 1$], an exponential increase from 5% for trees of dbh 10 cm to 100% for all trees with dbh >50 cm, and $S = 0.008 \exp(0.05 \times dbh)$, an exponential increase from 3.5% for dbh = 30 cm to 100% for dbh >95 cm.

2) P_{con}, S_{con}—The probability of measurement error is fixed (i.e., constant) at 30% for all trees, and the size of the error is fixed at +30%.

3) P_{con}, S_{lin}—The probability of error is fixed at 30%, but the size of the error increases linearly with dbh from 5% at dbh = 10 cm to 30% at dbh = 120 cm.

4) P_{lin}, S_{con}—The probability of error increases linearly with dbh (as for S in (3)), but the size of the error is fixed at 30%.

5) P_{lin}, S_{lin}—Both probability and size of error increase linearly with dbh, as in (3) and (4) above.

For example, error scenario P_{lin}, S_{lin} assumes that a tree of dbh 120 cm would have a 30% chance of being erroneously measured, and that the magnitude of the error would be a 30% overestimate of dbh. This could

TABLE 2. The impacts of flawed measurement methodologies on estimates of forest structure and structural change, for nine tropical forest plots.

Error scenario†	Basal area, BA	BDFFP				BIONTE project			Equil.	Tamb.
		BDF1	BDF2	BDF3	BDF4	Bio1	Bio2	Bio3		
Original data	Initial	27.2	24.5	28.5	28.1	27.8	30.0	27.6	27.6	27.3
	Final	26.9	25.7	27.6	22.5	30.4	33.2	28.2	27.6	28.5
	Change between censuses (%)	−1.1	4.6	−2.9	−19.9	9.2	10.6	2.1	0.0	4.3
	Effect of error scenario (%)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
P_{exp}, S_{exp}	Initial	33.0	27.2	36.2	56.5	48.3	33.0	36.7	36.7	34.5
	Final	32.9	28.4	35.4	43.4	52.3	36.2	37.6	36.5	37.7
	Change between censuses (%)	−0.3	4.6	−2.2	−23.3	8.1	9.9	2.5	−0.7	9.2
	Effect of error scenario (%)	21.2	10.8	27.1	101.3	73.7	9.8	33.2	33.3	26.3
P_{con}, S_{con}	Initial	32.9	29.5	34.2	33.9	33.6	36.3	33.2	33.4	33.0
	Final	32.5	30.9	33.3	27.1	36.6	40.2	33.9	33.4	34.4
	Change between censuses (%)	−1.2	4.7	−2.8	−19.8	9.2	10.7	2.1	0.0	4.3
	Effect of error scenario (%)	20.8	20.4	20.2	20.6	20.6	21.0	20.6	21.2	20.8
P_{con}, S_{lin}	Initial	29.6	26.5	31.1	30.8	30.4	32.5	30.0	30.1	29.7
	Final	29.3	27.7	30.2	24.5	33.1	35.9	30.5	29.9	30.9
	Change between censuses (%)	−1.3	4.5	−3.1	−20.6	9.0	10.5	1.8	−0.4	3.9
	Effect of error scenario (%)	8.9	8.0	9.3	9.7	9.2	8.2	8.7	9.0	8.9
P_{lin}, S_{con}	Initial	30.2	26.8	31.8	31.6	31.0	33.0	30.7	30.6	30.4
	Final	29.8	28.0	30.7	24.9	33.8	36.4	31.2	30.4	31.5
	Change between censuses (%)	−1.4	4.4	−3.4	−21.2	9.0	10.2	1.6	−0.7	3.5
	Effect of error scenario (%)	11.0	9.3	11.6	12.6	11.6	10.0	11.3	11.0	11.3
P_{lin}, S_{lin}	Initial	28.8	25.5	30.4	30.3	29.8	31.3	29.2	29.3	28.9
	Final	28.5	26.7	29.4	24.0	32.5	34.6	29.8	29.2	30.2
	Change between censuses (%)	−1.2	4.6	−3.0	−20.7	9.0	10.4	1.9	−0.4	4.3
	Effect of error scenario (%)	5.8	4.1	6.7	8.1	7.0	4.4	5.9	6.3	6.0

Notes: Inventory data are from forest plots from BDFFP (Biological Dynamics and Forest Fragments Project) near Manaus, central Amazonia (Laurence et al. 1998), BIONTE (Biomass and Nutrient Experiment), near Manaus (Carvalho et al. 1998), and Tambopata, Peru (Phillips et al. 1994*a, b*); the equilibrium plot (Equil.) is Bio4 minus two trees, thereby having the same BA in the first and second censuses.

† P describes the probability of there being an error in the measurement of diameter at breast height, and S describes the size of that error. For details of the different error scenarios, see *Did we overestimate. . .: Field measurement errors: ''basal-area inflation'': How does poor measurement. . .?*

mimic, for example, the effect of overestimate of dbh around trees with buttresses, at a site where large trees are more likely than small trees to have buttresses at 1.3 m height. Note that these are fairly pessimistic scenarios: any forestry survey where 30% of large trees were being wrongly measured by 30% would conventionally be regarded as flawed.

For each error plot, we create an ''erroneous first census'' data set for the first census as described above, using a random number generator to decide whether any individual tree is erroneously measured (according to P_{dbh}), and, if it is erroneously measured, ascribing a measurement error of magnitude S_{dbh}. For the second census, we assume that the error persists for each individual tree (i.e., that the error is a systematic error related to tree geometry), and scale the error proportionally with actual tree growth, thus generating an

''erroneous second census'' data set. We use a Monte Carlo approach and repeat this exercise 100 times for each plot using different values from the random-number generator, thus generating a different distribution of errors amongst the tree population in each run. We then compile mean statistics for each error scenario, and for each plot.

Table 2 shows that these flawed methodologies result in overestimates of basal area of between 4% and 101%, according to error methodology and forest structure. The mean basal-area overestimate for individual plots ranges from 10% (BDF2 and Bionte 2) to 30% (BDF4). This difference is related to forest structure—not surprisingly, plots with a greater preponderance of small trees are more immune to the error scenarios proposed here.

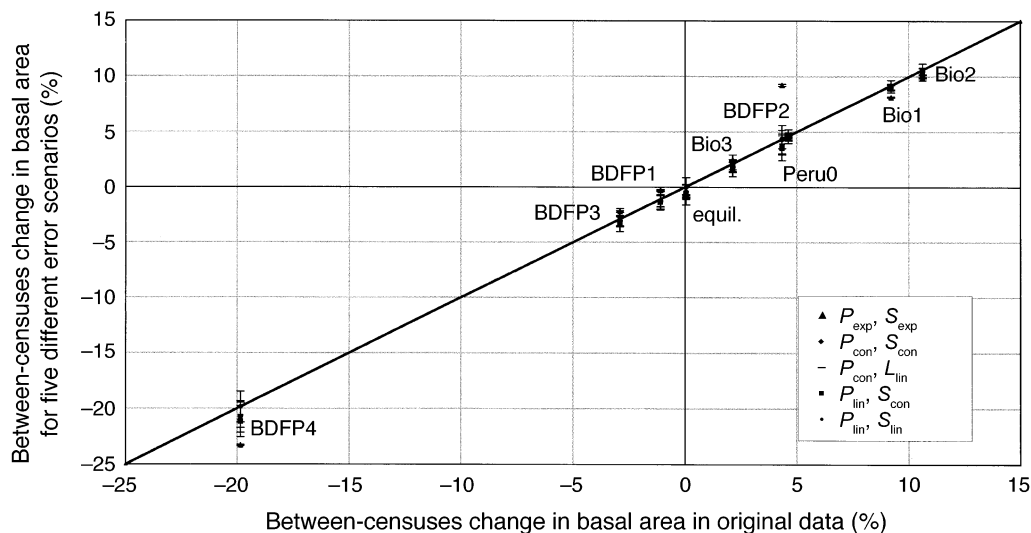The impact in terms of rate of change of basal area

FIG. 3. Percentage basal-area change between first and last census in the nine plots in Table 2 under five different error scenarios, compared with the percentage basal-area change in the original ("error-free") data. Results are shown for eight different tropical forests plots, and for an artificial "equilibrium" forest. Data are means ± SD.

(BA) in shown in Fig. 3. The *x*-axis shows the fractional change in basal area between the original "correct" censuses (fraction change in BA = [final BA − initial BA]/initial BA). The plots chosen show a range of behaviors, with changes in basal area of the plots ranging from a gain of 10% (Bio1 and Bio 2) to a loss of 20% (BDF2). The "equilibrium" plot shows no change in basal area. The *y*-axis shows the mean fractional change in basal area in the artificially generated "erroneous" censuses for each plot and for each error scenario. The error bars show the standard deviation (1 SD) of the results derived from 100 reruns. Clearly, the means of all plots, independent of error scenario, fall on a 1:1 line. Note in particular that the plot that is in equilibrium remains in equilibrium, in terms of basal area, and hence by implication biomass and net C balance. Thus, even if this measurement error were frequent and substantial, it would be very difficult to erroneously infer a C sink where none exists. However, although the *fractional* change in basal area is not affected by the erroneous measurements, as the *initial* basal area is inflated by the erroneous census (as shown in Table 2), the *absolute* change in basal area is also inflated in exact proportion to the inflation in basal area. Thus, if basal area is inflated by 10% through erroneous measurement, the estimated "C sink" in biomass is inflated by 10%. There are random errors associated with the particular distribution of erroneous measurements (as indicated by the error bars), but any systematic error is exactly proportional to the error in basal area.

Thus, even if erroneous measurements around buttresses are common (and we have given evidence above that they are not), they only have a modest effect on the net magnitude of the predicted C sink. This error

should be avoided and corrected for where possible, but it is unlikely that measurement errors can explain the increases in basal area measured in the plots rejected by Clark (2002) as being apparently erroneously measured, and data from these plots should not be rejected.

The result from the preceding analysis is more generally applicable. *Any* systematic bias on overall basal area of *x*% will produce a systematic bias in estimated basal-area increase (or decrease) of *x*%. It will *not* systematically bias a plot that is actually in equilibrium to appear as a plot that is increasing in basal area. Thus we reach the perhaps surprising conclusion that any poorly measured plot can still give a reasonably reliable estimate of change in basal area, *as long as the nature of the type of measurement error does not change systematically with time.*

Post-measurement error: "Rounding up negatives"

Bias could be generated by incorrectly assuming either in the field or at the post-measurement analysis stage that negative values in diameter growth "must" be showing zero growth, so these are entered into the data set as zero growth. If this explained the apparent increase in basal area, we would expect small trees to account for the majority of the increase, because the rounding error affects a greater proportion of smaller stems than larger stems. However, increased growth has occurred in all size classes (see *Field measurement errors: Basal area inflation*, above).

The impact of "rounding up negatives" can be investigated by plotting the size-frequency distribution of diameter growth of stems between successive measurement periods. If there is a bias the data will show an overrepresentation of trees exhibiting no growth,
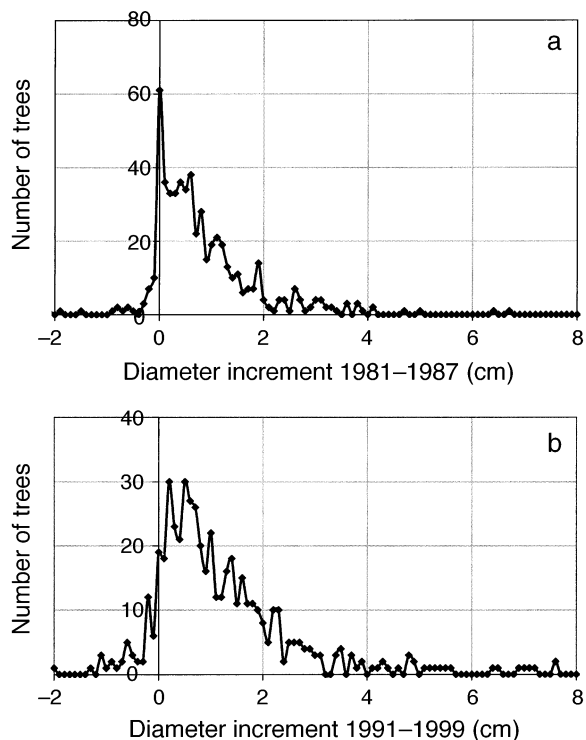
FIG. 4. Size-frequency distribution of diameter growth of stems between successive measurement periods, shown for plot 1101 of the BDFF project. (a) Data between 1981 and 1987 indicate a bias towards recording of zero-growth increments; (b) between 1991 and 1997 an improvement in methodology is evident.

and an underrepresentation of trees with small negative growth values. This is shown for plot 1101 from the BDFFP between the first and second censuses (1981, 1987), which shows a small amount of bias (Fig. 4). This bias can be approximately quantified and compared to other measurement periods, forest plots, or synthetic stands, by plotting a size-frequency distribution of the annual change in basal area of stems alive at both censuses, as the area under this graph is related to the change in basal area of the plot due to tree growth (area > zero growth minus area < zero growth equals net change). The area associated with the overrepresentation of trees with zero growth is the amount of bias.

The plots we have made preliminary checks on show later size-frequency distributions that are more accurate (cf. BDFFP 1981–1987 and 1991–1999 distributions, Fig. 4), presumably as good practice and the importance of very accurate results has spread. This improvement of methodology over time would lead to an apparent decrease in biomass over time, rather than an increase. In these plots there is also some evidence that censuses that inflate the number of stems with zero growth also document fewer stems with small positive growth than expected from the size-frequency distribution, presumably as a result of rounding this growth

down to zero. Hence the bias may be even smaller that suggested above.

MOVING FORWARD

In sum, our analysis of the data set shows that the potential artifacts (of site selection, the research intervention, measurement methods, and post-measurement analysis) are very unlikely to be driving the apparent increase in biomass in Neotropical plots. The rate of change in biomass in these plots is too rapid to be explained by late-successional aggradation, it coincides with an increase in recruitment rates, it is independent of time elapsed since plot establishment, and the biomass increment is, on average, spread across all size classes of trees. Results of simulation of measurement errors applied to real and synthetic stand data are consistent with the conclusion from actual patterns of change recorded in plots, providing further evidence that systematic measurement errors are unlikely to be responsible for the apparent biomass increase. Old-growth Neotropical forest plots have on average accumulated substantial biomass, indicating that mature neotropical forests are functioning as a C sink.

Our experience and analysis leads us to a relatively optimistic view of the quality of tropical-forest science in terms of its value for deriving growth-increment and biomass-increment data. However, identifying and testing for potential artifacts remains important. Although good-practice forest-measurement techniques are widespread, better assessment is still needed of the potential impacts of measurement errors and other possible sources of error in scaling up from plots to landscapes. Improved accuracy of biomass change estimates can be achieved by using more sophisticated allometric relationships that relate individual tree diameters to biomass, rather than relying on stand-level basal area and biomass relationships. This will require intensive work, with diameter/biomass relationships generated at several sites. Similarly, additional intensive analysis is warranted of how changes in growth, biomass accumulation, and population dynamics are distributed over different size classes and functional groups.

An even greater strategic issue is the need to clarify how the C balance of old-growth tropical forests is distributed in space and time. Addressing this requires a major, coordinated, long-term international scientific effort. An idealized tropical-forest network would span the environmental space (i.e., cover the range of climate regimes and soil types), in a stratified random fashion, while having sufficient spatial-sampling density to cover sites with similar environments in different geographical areas. These would help to tease out possible spatial effects, such as historically determined phytogeographical patterns. In practice, logistical concerns may constrain a sampling strategy, but it should still be possible to identify major gaps in environmental space and geographical space that are not covered by permanent sample plots (PSPs), and fill them with rep-

licated PSPs using standard measurement protocols. We are currently conducting such a sample program in underrepresented areas of Amazonia as part of the RAINFOR project (Y. Malhi, O. L. Phillips, T. Baker, S. Almeida, and 22 others, *unpublished manuscript*); in future this approach may be extended to other tropical regions. In addition, for the tropics as a whole, we are currently searching for published or unpublished PSP data, to quantify biases and assess turnover and biomass changes with expanded data sets. These will also be used to begin distinguishing between different mechanisms that may be changing forests dynamics. We would warmly welcome the involvement of readers who are involved in PSP projects and want to be part of these global scientific efforts. Please contact Y. Malhi or O. L. Phillips for the trans-Amazonian RAINFOR project, or S. L. Lewis for the global analysis of PSP data (details of these projects are available on the Internet).[11]

Networks such as these will help elucidate the mechanisms driving changes in old-growth forests. They have the potential to provide unique and valuable information on the effects of global change that will continue to affect tropical forests over the coming century (whether in the form of climate change, biodiversity loss, fragmentation, or CO_2 fertilization), and also on the feedback between tropical forests and the global climate through their influence on the C cycle (Cox et al. 2000, White et al. 2000). This is information that will be crucial to the understanding and protection of this important yet threatened biome.

Literature Cited

Bousquet, P., P. Peylin, P. Ciais, C. Le Quere, P. Friedlingstein, and P. P. Tans. 2000. Regional changes in carbon dioxide fluxes of land and oceans since 1980. Science **290**:1342–1346.

Brown, S., and A. Lugo. 1990. Tropical secondary forests. Journal of Tropical Ecology **6**:1–32.

Carvalho, J. A., N. Higuchi, T. M. Araujo, and J. C. Santos. 1998. Combustion completeness in a rainforest clearing experiment in Manaus, Brazil. Journal of Geophysical Research—Atmospheres **103**(D11):13195–13199.

Chambers, J. Q., J. dos Santos, R. J. Ribeiro, and N. Higuchi. 2001. Tree damage, allometric relationships, and aboveground net primary production in central Amazon forest. Forest Ecology and Management **5348**:1–12.

Clark, D. A. 2002. Are tropical forests an important global carbon sink?: revisiting the evidence from long-term inventory plots. Ecological Applications **12**:3–7.

Clark, D. B. 1996. Abolishing virginity. Journal of Tropical Ecology **12**:735–739.

Clinebell, R., O. L. Phillips, A. H. Gentry, N. Stark, and H. Zuuring. 1995. Prediction of tree and liana species richness in Neotropical forests using soil and climatic data. Biodiversity and Conservation **4**:56–90.

Condit, R. 1997. Forest turnover, diversity, and CO_2. Trends in Ecology & Evolution **12**:249–250.

Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature **408**:184–187.

Drake, D. R., and D. Mueller Dombois. 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. Ecology **74**:1012–1019.

Gentry, A. H., and J. Terborgh. 1990. Composition and dynamics of the Cocha Casha ''mature'' floodplain forest. Pages 542–564 *in* A. H. Gentry, editor. Four Neotropical rain forest. Yale University Press, New Haven, Connecticut, USA.

Grace, J., J. Lloyd, J. McIntyre, A. C. Miranda, P. Meir, H. S. Miranda, C. Nobre, J. Moncrieff, J. Massheder, Y. Malhi, I. Wright, and J. Gash. 1995. Carbon dioxide uptake by an undisturbed tropical rain-forest in Southwest Amazonia, 1992 to 1993. Science **270**:778–780.

Hall, P., P. S. Ashton, R. Condit, N. Manokaran, and S. P. Hubbell. 1998. Signal and noise in sampling tropical forest structure and dynamics. Pages 63–77 *in* F. Dallmeier, editor. Measuring and monitoring biological diversity. Smithsonian Institution Press, Washington, D.C., USA.

Hughes, R. F., J. B. Kauffman, and V. J. Jaramillo. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology **80**:1892–1907.

Johnson, C. M., D. J. Zarin, and A. H. Johnson. 2000. Post-disturbance aboveground biomass accumulation in global secondary forests. Ecology **81**:1395–1401.

Keller, M., D. A. Clark, D. B. Clark, A. M. Weitz, and E. Veldkamp. 1996. If a tree falls in the forest. . . . Science **273**:201.

Kiyoshi, U., and K. Kihachiro. 1999. Long-term growth dynamics of natural forests in Hokkaido, northern Japan. Journal of Vegetation Science **10**:815–824.

Kohyama, T. 1992. Density–size dynamics of trees simulated by a one-sided competition multispecies model of rainforest stands. Annals of Botany **70**:451–460.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? Trends in Ecology & Evolution **15**:134–135.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032–2040.

Lloyd, J. 1999. Current perspectives on the terrestrial carbon cycle. Tellus Series B—Chemical and Physical Meteorology **51**:336–342.

Malhi, Y., D. D. Baldocchi, and P. G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell and Environment **22**:715–740.

Malhi, Y., and J. Grace. 2000. Tropical forests and atmospheric carbon dioxide. Trends in Ecology & Evolution **15**:332–337.

Malhi, Y., A. D. Nobre, J. Grace, B. Kruijt, M. G. P. Pereira, A. Culf, and S. Scott. 1998. Carbon dioxide transfer over a central Amazonian rain forest. Journal of Geophysical Research **D24**:31593–31612.

Meggers, B. 1994. Archeological evidence for the impact of mega-Niño events on Amazonia during the past two millennia. Climatic Change **28**:321–338.

Moncrieff, J. B., Y. Malhi, and R. Leuning. 1996. The propagation of errors in long-term measurements of land–atmosphere fluxes of carbon and water. Global Change Biology **2**:231–240.

Netherly, P. 1997. Loma y ribera: patrones de asentamiento prehistóico en la Amazonía ecuatoriana. Fronteras de la Ciencia **1**:33–54.

Norby, R. J., S. D. Wullschleger, C. A. Gunderson, D. W. Johnson, and R. Ceulemans. 1999. Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell and Environment **22**:683–714.

Phillips, O. L. 1995. Evaluating turnover in tropical forests: response to Sheil. Science **268**:894–895.

Phillips, O. L. 1996. Long-term environmental change in tropical forests: increasing tree turnover. Environmental Conservation **23**:235–248.

Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. Science **263**:954–958.

Phillips, O. L., A. H. Gentry, C. Reynel, P. Wilkin, and C. Gálvez Durand B. 1994*a*. Quantitative and Amazonian conservation. Conservation Biology **8**:225–240.

Phillips, O. L., P. Hall, A. H. Gentry, R. Vásquez, and S. Sawyer. 1994*b*. Dynamics and species richness of tropical forests. Proceedings of the National Academy of Sciences (USA) **91**:2805–2809.

Phillips, O. L., P. Hall, S. A. Sawyer, and R. Vásquez. 1997. Species richness, tropical forest dynamics and sampling: response to Sheil. Oikos **79**:183–187.

Phillips, O. L., Y. Malhi, N. Higuchi, W. F. Laurance, P. Núñez V., R. Vásquez M., S. G. Laurance, L. V. Ferriera, M. Stern, S. Brown, and J. Grace. 1998*a*. Changes in the carbon balance of tropical forest: evidence from long-term plots. Science **282**:439–442.

Phillips, O. L., P. Núñez V., and M. Timaná. 1998*b*. Tree mortality and collecting botanical vouchers in tropical forests. Biotropica **30**:298–305.

Phillips, O. L., and D. Sheil. 1997. Forest turnover, diversity, and CO_2: further comments. Trends in Ecology & Evolution **10**:404.

Pitman, N. 2000. A large-scale inventory of two Amazonian tree communities. Dissertation. Botany School, Duke University, Durham, North Carolina, USA.

Rasanen, M., R. Neller, J. Salo, and H. Jungner. 1992. Recent and ancient fluvial deposition systems in the Amazonian foreland basin, Peru. Geological Magazine **129**:293–306.

Rayner, P. J., I. G. Enting, R. J. Francey, and R. Langenfelds. 1999. Reconstructing the carbon cycle from atmospheric CO_2, delta C^{13} and O_2/N_2 observations. Tellus B **51**:213–232.

Runkle, J. R. 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. Ecology **79**:1768–1780.

Salimon, C. I., and I. F. Brown. 2000. Secondary forests in western Amazonia: significant sinks for carbon released from deforestation? Interciencia **25**:198–202.

Salo, J., R. Kalliola, I. Hakkinen, Y. Makinen, P. Niemela, M. Puhakka, and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature **322**:254–258.

Sanford, R. L., J. Saldarriaga, K. E. Clark, C. Uhl, and R. Herrera. 1985. Amazon rainforest fires. Science **227**:53–55.

Sheil, D. 1995*a*. Evaluating turnover in tropical forests. Science **268**:894.

Sheil, D. 1995*b*. A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. Forest Ecology and Management **77**:11–34.

Sheil, D. 1996. Species richness, tropical forest dynamics and sampling: questioning cause and effect. Oikos **77**:587–509.

Veillon, J. P. 1985. El crecimiento de algunos bosques naturales de Venezuela en relación con los parámetros del medio ambiente. Revista Forestal Venezolana **29**:5–121.

White, A., M. G. R. Cannell, and A. D. Friend. 2000. CO_2 stabilization, climate change and the terrestrial carbon sink. Global Change Biology **6**:817–833.