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Changes in the Carbon Balance of Tropical Forests: Evidence from Long-Term Plots

Oliver L. Phillips,* Yadvinder Malhi,* Niro Higuchi, William F. Laurance, Percy V. Núñez, Rodolfo M. Vásquez, Susan G. Laurance, Leandro V. Ferreira, Margaret Stern, Sandra Brown, John Grace

The role of the world's forests as a "sink" for atmospheric carbon dioxide is the subject of active debate. Long-term monitoring of plots in mature humid tropical forests concentrated in South America revealed that biomass gain by tree growth exceeded losses from tree death in 38 of 50 Neotropical sites. These forest plots have accumulated 0.71 ton, plus or minus 0.34 ton, of carbon per hectare per year in recent decades. The data suggest that Neotropical forests may be a significant carbon sink, reducing the rate of increase in atmospheric carbon dioxide.

Tropical forests contain as much as 40% of the C stored as terrestrial biomass (1) and account for 30 to 50% of terrestrial productivity (2). Therefore, a small perturbation in this biome could result in a significant change in the C sink in mature Amazonian forests (5, 6). Recent micrometeorological research suggests that there is a net C sink in mature Amazonian forests (5, 6), but the ability to draw firm conclusions is hampered by the limited spatial and temporal extent of these measurements. Another approach, applying atmospheric transport models to measured global distributions of CO₂, O₂, and their isotopes (7), has yielded conflicting results. We report a third approach to explore the role of mature tropical forests in the global C cycle, namely, the use of permanent sample plots (PSPs). PSPs, established by foresters and ecologists to monitor tree growth and mortality, have the potential to yield C accumulation estimates that are at once both geographically extensive and of high spatial and temporal resolution.

We compiled data on basal area (cross-sectional area of trees per unit ground area) from mature tropical forest plots (8) that meet appropriate a priori criteria (9). Basal area of trees is a well-substantiated surrogate measure of total biomass in tropical forests (10), so changes due to tree growth and mortality provide an effective measure of changes in biomass. We tested for changes in mature tropical forest biomass in each of four nested regions: the humid tropics (153 plots), the humid Neotropics (120 plots), the humid lowland Neotropics (108 plots), and Amazonia (97 plots) (11). These plots represent more than 600,000 individual tree measurements tropics-wide.

We conducted two analyses with the information available. For each region, we first calculated the mean rate of change in tree basal area across sites, based on the difference between the initial and final census at each geographically distinct site (12). Sites may contain one or more floristically and edaphically similar plots (13). In the second analysis, we estimated basal area change as a function of calendar year and derived an estimate of regional net accumulated biomass through time. Data for this approach were derived for each site by first computing differences between each successive census, then by linear interpolation between successive censuses for years when measurements were not taken, and finally for each year by averaging change across all contributing plots. Measurement errors were corrected by comparing multiple measurements of the same tree over time (14). Basal area values were converted to aboveground biomass estimates by using an allometric model developed for lowland forest in central Amazonia and by using correction factors to account for the biomass of lianas and small trees (15).

Biomass has increased in mature forest sites in the humid Neotropics (1.11 ± 0.54 t ha⁻¹ year⁻¹; mean ± 95% confidence intervals), the humid lowland Neotropics (1.08 ± 0.59 t ha⁻¹ year⁻¹), and in Amazonia (0.97 ± 0.58 t ha⁻¹ year⁻¹) (16). The entire pantropical dataset also shows an increase in biomass (0.77 ± 0.44 t ha⁻¹ year⁻¹), but the signal is dominated by the Neotropical pattern, and there has not been a significant change in Paleotropical sites (tropical Africa, Asia, Australia) (−0.18 ± 0.59 t ha⁻¹ year⁻¹) (17). In the Neotropics (tropical Central and South America), the mean value of biomass change has been positive for most years since widespread PSP monitoring began (18). In Amazonia, where most inventories are located, plots have on average gained biomass in most years since at least the late 1970s (Fig. 1). By 1990, mature forest sites in all three nested Neotropical regions had on average accumulated substantial biomass (Fig. 2).

These results show that (i) there is considerable spatial and temporal variability in rates of biomass change, yet (ii) on average,
plots have gained biomass, and (iii) the increase has been especially marked in lowland Neotropical sites. There has been no statistically detectable change in biomass in African and Asian plots, but our coverage of these areas (18 sites) is sparser than in the Neotropics (50 sites), so we concentrate our discussion on the Neotropics. If the difference between Neotropical and Paleotropical forests is genuine, it may reflect differing climatic factors or perhaps greater human disturbance in the more densely populated Paleotropics (19).

Before extrapolating these results to the biomass of Neotropical forests as a whole, it is important to consider whether the PSPs were representative of the broader region. Neotropical forests are heterogeneous (20), and our dataset spans much of the natural variation in Amazonian forests (21). The number of extra-Amazonian lowland and montane samples also corresponds to the approximate coverage of each region (22). Recent debate (23) has centered on two potential problems in monitoring: (i) research activity having a negative impact on tree survivorship and growth and (ii) plots becoming increasingly subject to edge effects as surrounding forest is fragmented (24). These effects would increase mortality relative to growth, thus causing a decline in measured biomass—the opposite of our result. A further possibility is that there could be a bias in the PSPs compared to the surrounding forest, by systematic avoidance or underreporting of forests that underwent natural catastrophic disturbances or smaller scale disturbance due to localized tree death. Although it is difficult to quantify such a bias, there is little evidence for it in our dataset (25), and the increase in biomass is larger than can be accounted for simply by the dynamics of a few large trees (26).

Our results are therefore indicative of a widespread increase in the biomass of surviving Neotropical forests over recent decades. There are a number of mechanisms that may explain this change: (i) a response to continental-scale cyclical climate change; (ii) recovery from widespread disturbance, either natural or anthropogenic; (iii) enhanced forest productivity due to a secular change in climate or increased nutrient availability.

Because Earth’s climate fluctuates, forest stocks of C might be responding to past climatic events. The El Niño–Southern Oscillation (ENSO) may be one long-term driver of cyclical changes in forest dynamics (27). In El Niño years, most of Amazonia receives below-normal rainfall (28), but our data show that Amazon forests gained biomass before, during, and after the intense 1982–83 ENSO (Fig. 1). It is possible that regional forest biomass is recovering from earlier greater disturbances, either from drought or from the impacts of indigenous peoples who have experienced steep population declines since the 16th century (29). The biomass increase could also be a response to recent anthropogenic global change. There is some evidence for an increase in temperate and tropical forest productivity (30), and even mature ecosystems may gain biomass if plant productivity is stimulated (4). Candidate factors for nutrient fertilization include increasing atmospheric CO2 (31) and increased N and P deposition from Saharan dust (32) and biomass burning (33).

To estimate regional C sequestration rates, we first converted aboveground biomass into C stocks, using allometric data obtained in central Amazonia (34). The increase in biomass on Amazonian plots is equivalent to a net uptake of 0.62 ± 0.37 t C ha\(^{-1}\) year\(^{-1}\). Multiplying this by the estimated area of humid forest in lowland Amazonia (22) produces a mature forest biomass C sink of 0.44 ± 0.26 Gt C year\(^{-1}\). Similarly, the estimated annual C sink in lowland Neotropical humid forest is 0.52 ± 0.28 Gt C; it is 0.62 ± 0.30 Gt C for all mature humid neotropical forests. Our method suggests a lower C uptake rate than estimates from eddy covariance studies in Rondônia (1.0 t C ha\(^{-1}\) year\(^{-1}\)) (2) and near Manaus (5.9 t C ha\(^{-1}\) year\(^{-1}\)) (6). The discrepancy may reflect the limited spatial and temporal extent of eddy covariance measurements, or else be indicative of significant in-

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**Fig. 2.** Cumulative aboveground net biomass change (tons per hectare per year) in humid forests in: (A) the Tropics since 1958; (B) the Paleotropics (tropical Africa, Asia, Australia) since 1958; (C) the Neotropics (tropical Central and South America) since 1967; (D) the lowland Neotropics since 1971; (E) Amazonia since 1975. Annual mean (solid line) and 95% confidence interval (dotted line) values are based on the cumulative changes in individual sites since the first year and are scaled by \(ab\), where \(a\) = the cumulative time elapsed since the first year and \(b\) = the mean monitoring period per site up to each year end.
increases in the necromass and soil pools (35), which are not accounted for in our analysis. Our results suggest that mature Neotropical forest biomass may account for ~40% of the so-called "missing" terrestrial C sink (36). Hence, intact forests may be helping to buffer the rate of increase in atmospheric CO2, thereby reducing the impacts of global climate change. However, the C sink in mature forests appears vulnerable to several factors. There is likely to be an upper limit to the biomass a forest stand can hold. Moreover, deforestation, logging (37), increased fragmentation and edge-effect mortality (23, 24), regional drying and warming (38), and possible intensification of El Niño phenomena (39) may limit and even reverse the sink provided by mature forest. A dedicated large network of permanent biomass plots could provide vital insight into the future role of tropical forests in the global C cycle.

References and Notes
12. Sequential basal area data were sourced in three ways: (i) from unpublished plots in Peru, Brazil, and Venezuela centers with authors and colleagues; (ii) by asking others responsible for monitoring mature forest plots for permission to use their unpublished data; and (iii) from the literature. Basal area (BA, in square meters) was related to diameter (D, in millimeters) by BA = π(D/2)^2.
13. Mature tropical forest data were included where living trees ≥10 cm in diameter were measured either at 1.3 m (nontubestored trees) or immediately above buttress roots. Sites that experienced natural disturbances before or during the inventory period were generally included, but cyclone-prone forests (such as Puerto Rico or Australia) were excluded to avoid biases in timing; most such plots were either recently seeded after cyclones hit or else are established in areas recovering from cyclones (see also review by E. V. J. Tanner, J. H. Healy, V. Kapo, Biotropica 23, 513 (1991)). This exclusion was conservative; biomass increased in the two cyclone-prone forest sites with published long-term basal area (T. R. Crow, ibid. 12, 42 (1980); D. J. Nicholson, N. Henry, J. Ruddler, Proc. Ecol. Soc. Aust. 15, 61 (1988)).
14. Plot sizes in fragments ≤100 ha and that suffered mass mortality by logging or deforestation before or during the inventory period were also excluded.
16. T. R. Crow, ibid. 12, 42 (1980); D. J. Nicholson, N. Henry, J. Ruddler, Proc. Ecol. Soc. Aust. 15, 61 (1988). Plots in forest fragments ≤100 ha and plots that suffered mass mortality by logging or deforestation before or during the inventory period were also excluded.
17. All tropics: n = 68 sites, 48 with positive change, P < 0.01; lowland Neotropics: n = 40 sites, 30 with positive change, P < 0.01; Amazonia: n = 40 sites, 30 with positive change, P < 0.01. P values are for two-tailed binomial tests; the one Amazon site with no change was treated as negative change.
18. All tropics: n = 68 sites, 48 with positive change, P < 0.01; lowland Neotropics: n = 40 sites, 30 with positive change, P < 0.01. P values are for two-tailed binomial tests.
21. Nonflooded forests on low- to medium-fertility pre-Amazonian sites. Other extensive Amazonian forest sites with published long-term basal area data [T. R. Crow, ibid. 12, 42 (1980); D. I. Nicholson, N. Higuchi, J. A. Carvalho Jr., An. Acad. Bras. Cienc. (1996)]. Corrections for factors were included for the biomass of trees with DBH < 50 cm, for the basal area of the biomass-DH (diameter at breast height) distribution, and for lianas with diameter ≤1 cm (1307). On the basis of these factors, the overall biomass of tropical forests (including nonbuttressed trees) is an underestimate of 1.6, 1.2, 0.9, 0.8, and 0.8% of the total inventory biomass (equivalent to 4.9 to 2.2%, respectively, of total biomass in 1 ha). Although some trees may have very long-lived [J. K. Wright, J. P. Schimel, Nature 391, 135 (1998)], the dynamics of the much more numerous smaller trees are more important. In the BIONTE example, the gain of biomass in the 3 ha 1 ha study between 1980 and 1997 was 90.5 t, which represents the equivalent of 5.3 times the biomass of the single largest tree and is spread throughout the study area. On a wider scale, many of the Neotropical plots have recently experienced very high mortality rates and rapid recruitment of small trees [D. O. Phillips, P. Hall, A. H. Gentry, S. A. Sawyer, R. Vásquez, Proc. Natl. Acad. Sci. U.S.A. 91, 2805 (1994); D. O. Phillips, Environ. Conserv. 23, 235 (1996); O. L. Phillips, P. Hall, S. Sawyer, R. Vásquez, Oikos 79, 183 (1997)], which indicates that Neotropical forest dynamics are not dominated by the behavior of a few giant, slow-growing trees.
A Large Terrestrial Carbon Sink in North America Implied by Atmospheric and Oceanic Carbon Dioxide Data and Models

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Atmospheric carbon dioxide increased at a rate of 2.8 petagrams of carbon per year (Pg C year \(^{-1}\)) during 1988 to 1992 (1 Pg = 10\(^{15}\) grams). Given estimates of fossil carbon dioxide emissions, and net oceanic uptake, this implies a global terrestrial uptake of 1.0 to 2.2 Pg C year \(^{-1}\). The spatial distribution of the terrestrial carbon dioxide uptake is estimated by means of the observed spatial patterns of the greatly increased atmospheric carbon dioxide data set available from 1988 onward, together with two atmospheric transport models, two estimates of the sea-air flux, and an estimate of the spatial distribution of fossil carbon dioxide emissions. North America is the best constrained continent, with a mean uptake of 1.7 ± 0.5 Pg C year \(^{-1}\), mostly south of 51 degrees north. Eurasia–North Africa is relatively weakly constrained, with a mean uptake of 0.1 ± 0.6 Pg C year \(^{-1}\). The rest of the world’s land surface is poorly constrained, with a mean source of 0.2 ± 0.9 Pg C year \(^{-1}\).

A number of carbon cycle studies conducted in the last decade have indicated that the oceans and terrestrial ecosystems in the Northern Hemisphere absorb atmospheric CO\(_2\) at a rate of about 3 Pg C year \(^{-1}\) (1–3). Recent studies with atmospheric \(^{13}\)C/\(^{12}\)C ratios (3) and oxygen concentrations (6) concluded that the sink is caused primarily by terrestrial biosphere uptake. Other studies demonstrated increased activity of sufficient magnitude by the terrestrial biosphere in northern latitudes: a longer growing season observed in satellite measurements of surface color (7) and an increase over time of the amplitude of the annual cycle of atmospheric CO\(_2\) concentrations caused by terrestrial vegetation (8).

The partitioning of the Northern Hemisphere terrestrial CO\(_2\) sources and sinks between Eurasia and North America may be estimated by using the west-to-east gradient of atmospheric CO\(_2\) across the continents. The west-east signal is much smaller and more difficult to detect than the north-south signal for two reasons. First, the CO\(_2\) distribution is smoothed more by the relatively rapid zonal atmospheric transport than by the slower meridional transport (weeks instead of ~1 year for interhemispheric exchange). Sec-