**Reports**

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

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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 global C cycle (3, 4). 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,
Neotropical forests are heterogeneous (20), and our dataset spans much of the natural variation in Amazonian forests (27). 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 ha⁻¹ year⁻¹) (2) and near Manaus (5.9 t 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 a/b, where a = the cumulative time elapsed since the first year and b = the mean monitoring period per site up to each year end.
Deforestation, logging (35), increased fragmentation and edge-effect mortality (23), 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**


2. H. Tuomisto et al., *Science* 265, 351 (1991). This exclusion was conservative; biomass in the two cyclostome-fors"


5. A. E. Lugo, *Can. J. For. Res.* 12, 349 (1982). We excluded plots in the BIONTE study area in which the BIONTE study plots of 3 ha by 1 ha (site 8), or are characterized by deforestation before or during the inventory period. However, we are not aware of any cases of abandoning tropical forest plots after catastrophic loss, and monitoring the impacts of such natural catastrophic events would presumably be of extra scientific value (see also [9]).

6. As an example, we take the BIONTE study area in central Amazonia where diameter/biomass relationships have been derived from recent inventory plots. In the BIONTE study plots of 3 ha by 1 ha (site 8), mean biomass is 353 t ha−1. Biomass of the five largest trees was 17.2, 13.0, 9.4, 8.0, and 7.8 t. Thus, the loss of only one of these large trees would represent a loss of 1.6, 1.2, 0.9, 0.8, and 0.8% of the total inventoried biomass (equivalent to 4.9 to 2.2%, respectively, of total biomass in 1 ha). Although some trees are very long-lived (e.g., H. Tuomisto, *Science* 278, 1905 (1993). We excluded a priori any plots in fragments <100 ha, but some Neotropical sites are in larger islands or narrow peninsulas of forest (sites 1, 42, 43), are close to forest edges abutting on large areas that have been deforested before or during the monitoring periods (sites 2, 34), or are characterized by deforestation before or during the inventory period. However, we are not aware of any cases of abandoning tropical forest plots after catastrophic loss, and monitoring the impacts of such natural catastrophic events would presumably be of extra scientific value (see also [9]).

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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 carbon dioxide at a rate of about 3 Pg C year\(^{-1}\) (1–3). Atmospheric CO\(_2\) concentrations in the Northern Hemisphere are about 3 parts per million (ppm, mole fraction in dry air) greater than those in the Southern Hemisphere. Fossil CO\(_2\) is released predominantly at northern latitudes (Table 1), which should result in a north-to-south decrease of 4 to 5 ppm in the concentration of atmospheric CO\(_2\) (4). A

Northern Hemisphere sink is implied because the observed gradient is smaller than this. The original studies disagreed on whether the sink was predominantly oceanic (1) or terrestrial (2). Recent studies with atmospheric 13C/12C ratios (5) 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 zonal atmospheric transport than by the slower meridional transport (weeks instead of ~1 year for interhemispheric exchange). Sec-