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 CO_2, O_2, 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,

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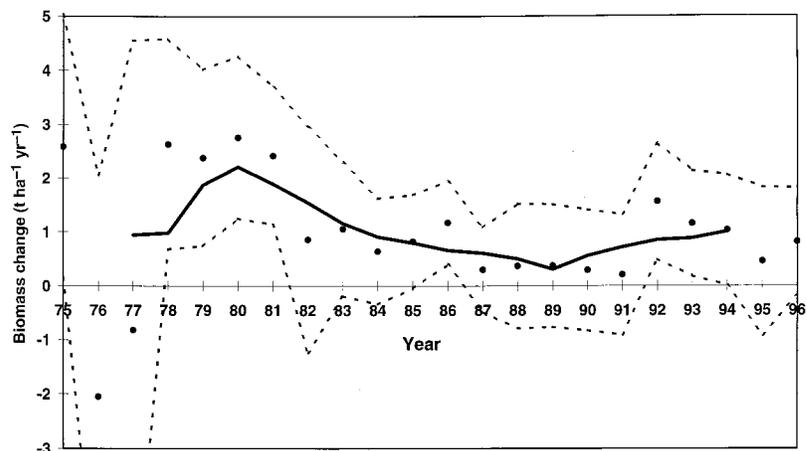*To whom correspondence should be addressed. E-mail: O.Phillips@geog.leeds.ac.uk (O.L.P); YMalhi@ed.ac.uk (Y.M.)

Fig. 1. Annual aboveground biomass change in Amazonian forests, 1975–96. Mean (solid circles), 95% confidence intervals (dotted line), and 5-year moving average (solid line) are shown.

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 CO_2 (*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-
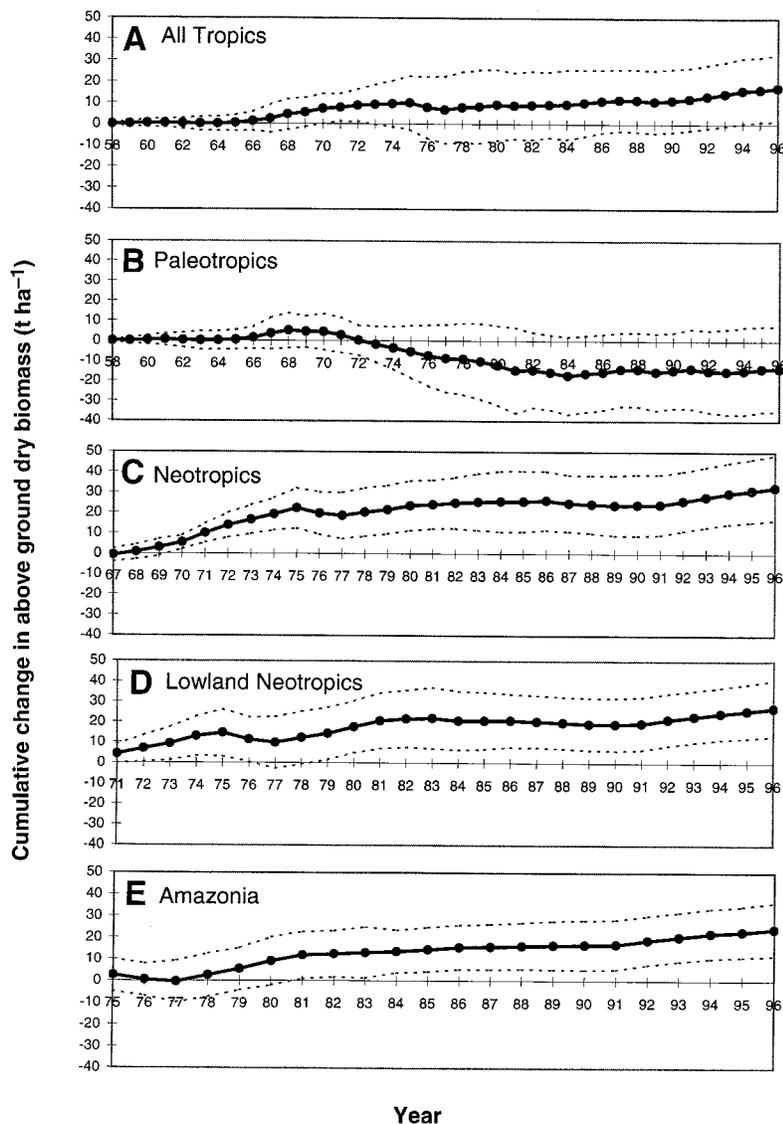
Fig. 2. Cumulative aboveground net biomass change (tons per hectare per year) in humid forests in: (**A**) the Tropics since 1958; (**B**) the Paleotropics (tropical Africa, Asia, Australia) since 1958; (**C**) the Neotropics (tropical Central and South America) since 1967; (**D**) the lowland Neotropics 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.

creases 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 CO_2, 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

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8. Sequential basal area data were sourced in three ways: (i) from unpublished plots in Peru, Brazil, and Venezuela censused by the authors and colleagues; (ii) by asking others responsible for monitoring mature plots for permission to use their unpublished data; and (iii) from the literature. Basal area (*BA*, in square meters) is related to diameter (*D*, in meters) by $BA = \Pi (D/2)^2$.
9. Mature tropical forest data were included where living trees ≥10 cm in diameter were measured either at 1.3 m (nonbuttressed 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 recensused immediately after cyclones hit or else are established in areas recovering from cyclones [see also review by E. V. J. Tanner, J. R. Healey, V. Kapos, *Biotropica* **23**, 513 (1991)]. This exclusion was conservative; biomass increased in the two cyclone-forest sites with published long-term basal area data [T. R. Crow, *ibid.* **12**, 42 (1980); D. I. Nicholson, N. Henry, J. Rudder, *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.
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11. "Humid tropics" includes forest receiving >1500 mm precipitation annually; "lowlands" includes forest <500 m above mean sea level; "Amazonia" includes humid forest within the phytogeographical region of Amazonia, encompassing Amazonian Brazil, Colombia, Ecuador, Peru, Bolivia, the Guianas, and contiguous moist forest in Venezuela, excluding nonforest vegetation.
12. Data table and data references are available as supplementary material at the *Science* Web site. (www.sciencemag.org/feature/data/976299.shl)
13. Mean individual plot size per site = 1.87 ha; data from plots <0.2 ha were pooled.
14. Excessive declines or increases in diameter of trees reported in individual censuses indicate human measurement error and were corrected by interpolating between prior and subsequent censuses.
15. The relationship between tree basal area (*BA*, in square meters per hectare) and fresh aboveground biomass of trees ≥10 cm diameter (*AGFB*, in tons per hectare) has the linear form $AGFB = 66.92 + 16.85(BA)$, with $r^2 = 0.85$, based on destructive harvesting of 319 trees at site 9. The relationship was tested and found to be appropriate at another site in eastern Amazonia [T. M. Araujo, N. Higuchi, J. A. Carvalho Jr., *An. Acad. Bras. Cienc.* (1996)]. Correction factors were included for the biomass of trees with diameter <10 cm (× 1.062), on the basis of the biomass-DBH (diameter at breast height) distribution, and for lianas with diameter ≥1 cm (× 1.037), on the basis of liana/tree biomass comparisons in Amazonian forests [E. E. Hegarty and G. Caballé, in *The Biology of Vines*, F. E. Putz and H. E. Mooney, Eds. (Columbia Univ. Press, New York, 1991), pp. 313–336]. Other generally minor components of plant biomass such as stranglers, epiphytes, shrubs, and herbs were not considered. The proportion of water in *AGFB* (40%) was determined from the destructive sampling of 38 trees and the partial sampling of 100 trees at site 9.
16. Neotropics: $n = 50$ sites, 38 with positive change, $P < 0.001$; lowland Neotropics: $n = 45$ sites, 34 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.
17. All tropics: $n = 68$ sites, 48 with positive change, $P < 0.01$; Paleotropics: $n = 18$ sites, 10 with positive change, not significant. P values are for two-tailed binomial tests.
18. For years in which ≥5 sites were monitored, the mean change was positive in 24 of 30 years 1967–96 for the Neotropics ($P < 0.01$), in 21 of 26 years 1971–96 for the lowland Neotropics ($P < 0.01$), in 20 out of 22 years 1975–96 for Amazonia ($P < 0.001$), in 13 of 30 years 1958–87 for the Paleotropics (not significant), and in 36 of 41 years since 1956 for all tropical forests ($P < 0.001$). P values are for two-tailed binomial tests.
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21. Nonflooded forests on low- to medium-fertility pre-Holocene substrates cover 65 to 70% of Amazonia [J. M. Pires, in *Tropical Forest Ecosystems* (UNESCO, Paris, 1978), pp. 607–627] and comprise 70% of our Amazonian sites. Other extensive Amazonian forest types (on alluvial, white sand, and swampy substrates) feature in the dataset in proportion to their region-wide abundance.
22. Estimates of humid tropical forest areas vary according to definition. We use the 1990 area estimates from the Food and Agricultural Organisation [*FAO Forestry Paper 112* (FAO, Rome, 1993)], combining areas described as tropical rain forest, moist deciduous forest, and hill and montane forest to calculate humid Neotropical forest area in the lowlands (7,486,150 km²) and in total (8,705,100 km²). Our estimate of lowland Amazonian forests (7,116,280 km²) is based on combining the lowland humid forest

figures for Brazil, Bolivia, Colombia, Ecuador, French Guyana, Guyana, Peru, Suriname, and Venezuela. The area is dominated by the Amazonian hylaea, but also includes small areas of lowland forest along the Pacific and Atlantic coasts.
23. See also R. O. Bierregaard, T. E. Lovejoy, V. Kapos, A. Santos, R. Hutchings, *Bioscience* **42**, 859 (1992); O. L. Phillips, *Science* **268**, 894 (1995); D. Sheil, *ibid.*, p. 894; *For. Ecol. Manage.* **77**, 11 (1995); R. Condit, *Trends Ecol. Evol.* **12**, 249 (1997); L. V. Ferreira and W. F. Laurance, *Conserv. Biol.* **11**, 797 (1997); O. L. Phillips and D. Sheil, *Trends Ecol. Evol.* **12**, 404 (1997); O. L. Phillips, P. Nuñez V., M. Timaná, *Biotropica*, in press.
24. Fragmented Amazonian forests can experience precipitous declines in biomass after isolation [W. F. Laurance *et al.*, *Science* **278**, 1117 (1997)], and edge effects have been suggested to extend up to 1000 m in from forest margins [D. Skole and C. Tucker, *ibid.* **260**, 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 both these conditions. The mean rate of biomass change in these sites is −0.42 t ha⁻¹ year⁻¹.
25. If plots measuring a catastrophic loss were somehow excluded from the study, they would have been done so a priori or post priori. A mechanism for a priori exclusion would be that forest vulnerable to catastrophes is selected against when plots are established, but it is difficult to see what criteria could be used to make such an assessment. For example, while multiple tree-falls covering large areas do occasionally occur, where they will occur is unknowable. Moreover, any such tendency may select against young stands obviously recovering from disturbances (for example, gaps regenerating after local flooding) and bias our results instead to the parts of the landscape gaining C less rapidly. A mechanism for post priori exclusion would be that plots suffering catastrophic losses are abandoned and not reported. 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)].
26. As an example, we take the BIONTE study area in central Amazonia where diameter/biomass relationships have been derived for individual tree species. 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 one of these large trees would only 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 [J. Q. Chambers, N. Higuchi, 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 by 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 [O. L. Phillips, P. Hall, A. H. Gentry, S. A. Sawyer, R. Vásquez, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 2805 (1994); O. L. 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.
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33. For example, D. S. Schimel *et al.*, *Global Biogeochem. Cycles* **10**, 677 (1996); P. M. Vitousek *et al.*, *Ecol. Appl.* **7**, 737 (1997). Tropical forest tree growth has been shown experimentally to increase after N and P fertilization [E. V. J. Tanner, V. Kapos, W. Franco, *Ecology* **73**, 78 (1992)].

34. We assumed that: (i) 48% of biomass is in the form of C {based on burning experiments near Manaus, central Amazonia [J. A. Carvalho Jr., J. M. Santos, J. C. Santos, M. M. Leitão, N. Higuchi, *Atmos. Environ.* **29**, 2301 (1995); J. A. Carvalho Jr., N. Higuchi, T. M. Araujo, J. C. Santos, *J. Geophys. Res.* **103**, 13195 (1998)]}; (ii) that the ratio of aboveground biomass to root biomass is 3:1 {the average value of three studies in Brazilian Amazonia [P. Fearnside, *Emissão e Sequestro de CO₂* (Companha Vale do Rio Doce, Rio de Janeiro, 1994), pp. 95–124]}, consistent with a global analysis of root biomass allocation [M. A. Cairns, S. Brown, E. Helmer, G. Baumgardner, *Oecologia* **111**, 1 (1997)]; and (iii) that root biomass increased in proportion to aboveground biomass. We ignored C stocks in fine litter, dead wood, and soil, which may also have changed.

35. Although PSP data address the problem of spatial variability that can limit extrapolation of eddy covariance studies, they clearly cannot assess the behavior of necromass and belowground C pools, which might be expected to increase together with biomass. A combination of eddy covariance and biomass studies may provide a useful tool in the future to examine belowground processes.

36. The "missing" sink was recently estimated at ~1.4 Gt [D. S. Schimel, *Global Change Biol.* **1**, 77 (1995)]. By comparison, deforestation in Brazilian Amazonia was estimated to yield a net C emission of 0.34 Gt in 1990 [P. M. Fearnside, in *Biomass Burning in South America, Southeast Asia, and Temperate and Boreal Ecosystems, and the Oil Fires of Kuwait*, J. S. Levine, Ed. (MIT Press, Cambridge, MA, 1996), pp. 606–617]. Deforestation in the whole Neotropics was estimated to yield 0.6 ± 0.3 Gt C annually between 1980 and 1990 [R. A. Houghton, in *Forest Ecosystems, Forest Management and the Global Carbon Cycle*, M. G. Apps and D. T. Price, Eds., *NATO ASI Ser. I Global Environ. Change*, vol. 40 (Springer-Verlag, Heidelberg, Germany, 1996)].

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40. We gratefully acknowledge help in Peru from the late A. H. Gentry, as well as M. Aguilar, C. Díaz, C. Grández, N. Jaramillo, M. Jarrell, K. Johnson, D. Milanowski, R. Ortíz, S. Rose, J. Terborgh, A. Vásquez, and the logistical support of INRENA, ACEER, Cuzco Amazonico Lodge, Explorama Tours, Instituto de Investigaciones de la Amazonía Peruana, Peruvian Safaris, Universidad Nacional de la Amazonía Peruana (Iquitos), and Universidad Nacional de San Antonio Abad del Cusco (Cusco and Puerto Maldonado). In Brazil, we acknowledge the help of R. J. Ribeiro, Y. Biot, P. Delamonica, C. Gascon, and other BIONTE and BDFFP project members. We thank J. Terborgh, R. Foster, R. Condit, S. Lao, S. P. Hubbell, M. D. Swaine, D. Nicholson, R. Keenan, T. Richards, J. N. M. Silva, J. P. Veillon, J. Comiskey, and R. Moraes de Jesus for kindly making data available and for other help. Peruvian field research was supported by the American Philosophical Society, National Geographic Society (grant 5472-95), NSF (BSR-9001051), World Wide Fund for Nature (WWF)–U.S./Garden Club of America, Conserva-

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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 CO_2 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 $^{13}C/^{12}C$ 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 rapid zonal atmospheric transport than by the slower meridional transport (weeks instead of ~1 year for interhemispheric exchange). Sec-

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