If a Tree Falls in the Forest...

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Scientists conventionally see old-growth tropical rain forests as steady-state systems (*1*). Recently, Grace *et al.* (*2*) challenged this view when they estimated substantial carbon uptake by a remote Amazon forest in Rondonia, Brazil. They surmounted formidable logistical problems and used the eddy covariance technique to measure CO_2 flux from a tower 15 m above the forest canopy over the course of 55 days. With selected data, they parameterized a state-of-the-art physiological model and ran it with a year's worth of meteorological data to calculate a net carbon uptake by the forest of 100 g m^{-2} per year. Extrapolated over the Amazon region, this yields a surprising carbon uptake of 0.6 Gt (gigatons) per year. Are tropical forests sequestering a large portion of the "missing carbon" (1.4 Gt per year) (*3*) in the global carbon budget? The role of CO_2 in global climate is a compelling reason to explore these findings.

Understanding carbon exchange in tropical forests requires us to consider both temporal and spatial variability. Forest carbon budgets are greatly affected by daily weather. Cloudiness, rains, and drought modify the balance between photosynthesis and respiration. Fan *et al.* (*4*) previously measured net carbon uptake by an Amazon forest, but as they noted, their measurements were biased toward fair-weather periods. Grace and colleagues (*5*) noted a possible bias in their model estimate based on data selected when leaves were dry and light was nearly constant. Interannual weather shifts also influence tropical forest productivity (*6*). In Panama, annual tree mortality was approximately 50% higher during 3 years including the 1983 El Niño Southern Oscillation (ENSO) than in the following 5 years (*7*). Today's carbon uptake by Amazon old growth might reflect recovery from 1983. Alternatively, Grace *et al.* (*2*) noted that the atypically cool conditions after Mount Pinatubo's eruption may have affected the carbon exchange they measured.

On a longer time scale, tropical forests may be recovering from past events such as the devastating ENSO about 400 years ago that brought severe drought to the Amazon and likely produced extensive tree death and widespread fires (*8*), much as the 1983 ENSO set Borneo ablaze (*9*). Soil charcoal indicates large-scale fires in the Amazon 250 to 400 years ago (*10*). Recovery from earlier climatic stress may explain the current biomass increase of emergents in a Central American rain forest (*11*).

A leafless emergent towers over old-growth forest on Barro Colorado Island, Panama. Tropical rain forest landscapes span a broad gradient of soil types, successional stages, and anthropogenic influences, complicating assessment of regional carbon budgets. [Photo: D. B. Clark]

Human activities have left their imprint on vast areas of tropical forests currently considered mature. Studies in Venezuela and Panama document maize agriculture where a forest now stands (*12*). The harvesting of larger trees may have depressed carbon stocks and increased many tropical forests' capacity for carbon gain (*13*). Because rivers route human activity, it is plausible that the Grace *et al.* (*2*) study site, located only 1 km from the Ji-Parana River, experienced significant past human impacts.

Tower-based measurements can be greatly affected by the spatial heterogeneity (*14*) and high turnover rate (*15*) of tropical rain forests. Emergent trees, perhaps five per hectare (ha), contain 10 to 40% of the aboveground biomass (*11, 16*). Annual mortality of such giant trees in a Costa Rican forest was only 0.6% (*11*). At this rate, within 200 m of the tower (13 ha), the area most affecting flux measurements (*17*), one giant would die about every 2.5 years. Containing perhaps 10 tons of carbon, a falling emergent could bring down smaller trees, lianas, and epiphytes. As a result, more than 75 g m^{-2} in the 13 ha, could be lost in a few years. The death of a giant tree near a tower would greatly alter measured carbon exchange. Who would risk putting a 45-m tower and $100,000 of instrumentation near a senescent emergent?

Multiple approaches will be necessary to develop regional carbon budgets of tropical forests. The eddy covariance studies must be replicated and compared to mensuration of replicated forest plots stratified to cover underlying variations of climate and soil across the landscape. We need better accounting of human impacts and of large-scale disturbances and subsequent recovery within young- and old-growth forests. Quantifying responses to global changes such as CO_2 fertilization and climate shifts will require standardized long-term data and perhaps field experiments using free air carbon enrichment. New methods such as radar remote sensing and aircraft-based atmospheric sampling promise a future ability for larger area integrating measurements of biomass and productivity for tropical forests. Grace *et al.* (*2*) have now called into question the steady-state assumption for "undisturbed" tropical forests. Determining whether or not tropical forest ecosystems are indeed important global carbon sinks will require an understanding of their historical and spatial complexity.

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References and Notes

1. E. Salati and P. B. Vose, *Science* **225**, 129 (1984).
2. J. Grace *et al.*, *ibid.* **270**, 778 (1995).
3. D. S. Schimel, *Global Change Biol.* **1**, 77 (1995).
4. S.-M. Fan *et al.*, *J. Geophys. Res.* **95**, 16,851 (1990).
5. J. Grace *et al.*, *Global Change Biol.* **1**, 1 (1995).
6. D. A. Clark and D. B. Clark, *J. Ecol.* **82**, 865 (1994).
7. R. Condit, S. P. Hubbell, R. B. Foster, *Ecol. Monogr.* **65**, 419 (1995).
8. B. J. Meggers, *Clim. Change* **28**, 321 (1994).
9. M. Leighton and N. Wirawan, in *Tropical Rain Forests and the World Atmosphere*, G. T. Prance, Ed. (Westview, Boulder, CO, 1986), pp. 75–102.
10. R. L. Sanford Jr., J. Saldarriaga, K. E. Clark, C. Uhl, R. Herrera, *Science* **227**, 53 (1985).
11. D. B. Clark and D. A. Clark, *For. Ecol. Manage.* **80**, 235 (1996).
12. A. C. Roosevelt, *Parmana: Prehistoric Maize and Manioc Subsistence Along the Amazon and Orinoco* (Academic Press, New York, 1980); M. B. Bush and P. A. Colinvaux, *Ecology* **75**, 1761 (1994).
13. A. E. Lugo and S. Brown, *For. Ecol. Manage.* **54**, 239 (1992).
14. H. Tuomisto *et al.*, *Science* **269**, 63 (1995).
15. G. S. Hartshorn, in *Four Neotropical Rainforests*, A. H. Gentry, Ed. (Yale Univ. Press, New Haven, CT, 1990), pp. 585–599.
16. I. F. Brown *et al.*, *For. Ecol. Manage.* **75**, 175 (1995).
17. P. H. Schuep *et al.*, *Boundary Layer Meteorol.* **50**, 355 (1990).
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