

- deepens to 500 m, the diatom blooms do not occur, and production between glacial and interglacial periods changes by up to two to three orders of magnitude [M. N. Shimaraev, N. G. Granin, A. A. Zhdanov, *Limnol. Oceanogr.* **38**, 1068 (1993)] in response to insolation orbital forcing. Through this model, biogenic silica and diatom abundance become two excellent proxies within a multiple proxy data set including magnetic susceptibility, lithogenic flux, pollen-spore composition changes, and diatom assemblage changes.
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  26. Lake Baikal's geographic position in the largest continental interior of the world, unaffected by the type of large-scale glacial ice sheets that greatly disturbed sediments at similar latitudes on North America, Europe, and western and far eastern Siberia, makes it an ideal sedimentary archive in the International Geosphere-Biosphere Program Pole-Equator-Pole (PEP-II) transect through Asia as part of the Past Global Changes (PAGES) program. The purpose of the PAGES PEP transects is to construct a global network of sites on each of the continents that is analogous in some ways to the available array of deep-sea sites. In the case of the PEP sites, potential archives are tied to specific features and boundary conditions of the atmosphere-hydrosphere-cryosphere system. Lake Baikal is positioned to determine the expansion of the Siberian high-pressure system, incursions of the Asian monsoon, and moisture transport emanating from the Barents Sea and other parts of the Arctic.
  27. The BDP-96 Leg II drill site is located at 53°41'48"N, 108°21'06"E. An APC was used to drill in 321 m of water where multichannel seismic reflection profiles showed thick and continuous sedimentary sequences. The APC cores were retrieved in 2-m-long sections in 58-mm-inside diameter plastic liners.
  28. The paleomagnetic study was done on oriented 5-cm<sup>3</sup> subsamples with a stepwise, alternating-field demagnetization, which indicated that a viscous remanence component was removed at demagnetizing fields between 2.5 and 5 mT.
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  35. Spectral analyses were performed with the Arrand program. The evolutive spectra analyses (Fig. 2) were performed with a sliding 400-ky window offset by 100 ky, whereas the spectra shown in Fig. 3, E through H, were obtained on the data set spanning the entire 800-ky period.
  36. The biogenic silica data, generally sampled every 2 cm (~500 years), were placed on the polarity age model (Fig. 1D) and linearly interpolated to an even spacing of 500 years. An inverse correlation method, CORPAC [D. G. Martinson, W. Menke, P. Stoffa, *J. Geophys. Res.* **87**, 4807 (1982)], was used to correlate the Baikal silica record to ODP site 677  $\delta^{18}\text{O}$  (31). The initial coherence *C* between the two records (*C* = 0.23) attained a high degree of coherence (*C* = 0.65) and 43% shared variance after inverse correlation with four coefficients. The mapping function resulting from this correlation (Fig. 1H) shows no sign of major unconformities or of excessive correlation. The biogenic silica analytical method was modified from (42).
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## Biomass Collapse in Amazonian Forest Fragments

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Rain forest fragments in central Amazonia were found to experience a dramatic loss of above-ground tree biomass that is not offset by recruitment of new trees. These losses were largest within 100 meters of fragment edges, where tree mortality is sharply increased by microclimatic changes and elevated wind turbulence. Permanent study plots within 100 meters of edges lost up to 36 percent of their biomass in the first 10 to 17 years after fragmentation. Lianas (climbing woody vines) increased near edges but usually compensated for only a small fraction of the biomass lost as a result of increased tree mortality.

Habitat fragmentation affects the ecology of tropical rain forests in many ways, such as altering the diversity and composition of fragment biotas, and changing ecological processes like nutrient cycling and pollination (1, 2). Recent evidence indicates that fragmentation also alters rain forest dynamics, causing sharp increases in the rates of tree mortality, damage, and canopy-gap formation, apparently as a result of microclimatic changes and increased wind turbulence near forest edges (3). Here we demonstrate that in central Amazonian rain forests, fragmentation is having an equally

measurable effect on above-ground biomass. Given that more than  $15 \times 10^6$  ha of tropical forest are being cleared and fragmented annually (4), a decline of biomass in forest remnants could be a significant source of greenhouse gases such as CO<sub>2</sub>, released upon decay.

The study area, an experimentally fragmented landscape spanning about 20 km by 50 km, is located 80 km north of Manaus, Brazil (2°30'S, 60°W), at an elevation of 100 to 150 m. Between 1980 and 1986 a series of replicate forest patches of 1, 10, and 100 ha in area were isolated by clearing and often burning the surrounding vegetation to create cattle pastures. A total of 39 permanent, square, 1-ha study plots were established in four 1-ha fragments, three 10-ha fragments, and two 100-ha fragments, and 27 identical control plots were located in nearby continuous rain forest. The plots in the fragments were stratified so that edge and interior areas were both sampled. More than 1000 tree species have been identified in the study plots (5).

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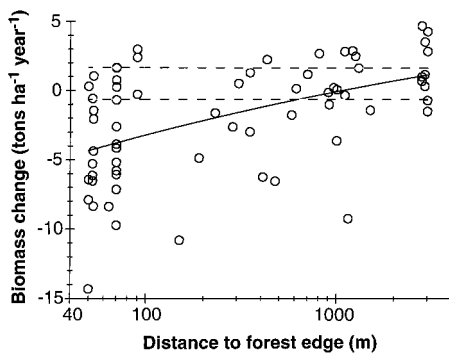
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The plots were initially censused between January 1980 and January 1987, then subsequently censused two to five times, with the last census in early 1997 (mean of 3.6 censuses per plot). Estimates of above-ground dry biomass (AGBM) for each plot were derived by carefully measuring the diameters of all trees  $\geq 10$  cm diameter-at-breast-height (DBH), except for buttress trees, which were measured just above the buttresses. DBH values were cross-checked for outliers (for example, declines of  $>5$  mm or increases of  $>15$  mm per year) by comparing multiple measurements over time of the same tree. DBH measurements were converted to biomass estimates with an allometric model derived by using 319 trees from local rain forests (6). Total AGBM estimates for each plot were adjusted upward by 12% to account for trees of  $<10$  cm DBH (7). Lianas (climbing woody vines) of  $\geq 2$  cm DBH were recorded in 21 of the plots in 1997 and converted to biomass estimates with a DBH-AGBM formula developed for Venezuelan rain forests (8).

We used linear regressions to estimate the rate of change in biomass on each plot (using AGBM as the dependent variable and the number of months since January 1980 as the independent variable). Slope terms for each plot were converted to metric tons of AGBM per hectare per year. The rate of biomass loss was significantly related to the distance of plots from the nearest forest edge (Fig. 1). On average, plots within 100 m of edges lost  $3.5 \pm 4.1$  tons  $\text{ha}^{-1}$  year $^{-1}$  during the first 10 to 17 years after fragmentation, with some plots losing up to 36% of their total AGBM (mean  $\pm$  SD =  $8.8 \pm 10.2\%$ ,  $n = 30$ ). Forest-interior plots



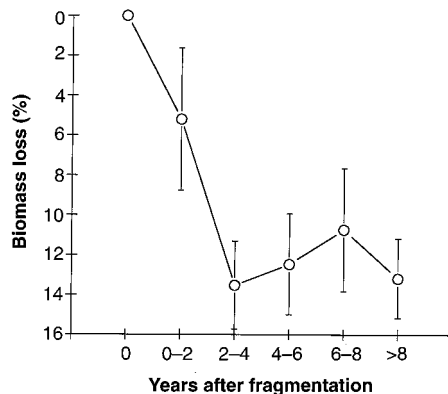
**Fig. 1.** Rate of change in above-ground tree biomass as a function of distance of the plots from the forest edge. The solid line is an exponential curve fitted to the data, and the dashed lines are 95% confidence intervals for 26 forest-interior plots ( $>500$  m from edge). The curve formula is biomass change =  $9.58 - \{22.47 \times \exp[-0.28 \times \log(\text{distance to edge})]\}$ . A linear regression comparing observed and fitted values was highly significant [ $F(1,64) = 21.47$ ,  $R^2$  (coefficient of determination) = 25.1%,  $P = 0.00002$ ].

( $\geq 100$  m from the edge) exhibited no significant changes in AGBM over the time period studied, with 15 plots declining and 21 increasing ( $P = 0.203$ , sign test).

To examine the actual kinetics of biomass loss, we plotted the mean percent decline of AGBM in 16 edge plots that had lost  $\geq 3$  tons  $\text{ha}^{-1}$  year $^{-1}$  since fragmentation (Fig. 2). Mean AGBM dropped sharply within 4 years of fragmentation, then roughly stabilized thereafter. At least within 10 to 17 years of fragmentation, recruitment of new trees ( $\geq 10$  cm DBH) has not offset losses caused by tree mortality.

Lianas, the only other abundant woody plants in the study area, have increased in plots within 100 m of edges, from  $5.4 \pm 0.7$  to  $7.9 \pm 1.7$  tons  $\text{ha}^{-1}$  (9). However, on most edge plots these increases constitute only a small fraction ( $<8\%$ ) of the biomass lost from elevated tree mortality.

Our long-term study, involving more than 137,000 DBH measurements of  $>56,000$  trees, has revealed that the dynamics and biomass of fragmented rain forest are being fundamentally altered. Although growth of lianas and new trees (10) has increased in fragments, these have not offset the sudden loss of AGBM caused by the deaths of many large trees, which contain a disproportionately large fraction of AGBM. It is not yet known whether AGBM in fragments will eventually recover to the levels present before fragmentation or whether fragments will reach a new equilibrium that is lower than that of the original forest. We suspect the latter is more likely because fragmented forests are prone to recurring wind disturbance (3, 11), which can kill and damage many large trees. If this is the case, complex, old-growth rain forests will tend to be replaced by shorter, scrubby forests with smaller volume and biomass. The biomass losses described here are actually underestimates because rates of major tree damage



**Fig. 2.** Mean decline ( $\pm$  SE) in AGBM in 16 study plots before and after forest fragmentation (sample sizes: before fragmentation = 14; 0 to 2 years = 6; 2 to 4 years = 11; 4 to 6 years = 15; 6 to 8 years = 9;  $>8$  years = 11).

(broken crowns or snapped trunks) are nearly as high within 100 m of edges (2.82% per year) as is tree mortality (3.04% per year) (3). Hence, for every tree that dies, another is badly damaged, and a portion of that tree's biomass is lost.

The loss of biomass is a previously unrecognized and unanticipated consequence of habitat fragmentation. Because AGBM declines near forest edges, the magnitude of biomass loss will depend on the spatial pattern of deforestation, which determines the sizes and shapes of forest fragments. Mathematical models suggest edge-related tree mortality and damage will increase sharply once Amazonian fragments fall below 100 to 400 ha in area, depending on fragment shape (3). Fragments in anthropogenic landscapes commonly fall within or below this size range (2), suggesting that the loss of biomass in recently fragmented landscapes could be a significant source of greenhouse gas emissions. Given the rapid rate of forest fragmentation in the tropics (4), such emissions may exacerbate effects of global warming above and beyond that caused by forest clearing per se.

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