

Biomass Decline in Amazonian Forest Fragments

The report by William F. Laurance *et al.* about the destruction of Brazilian rain-forest trees along the edges of clearings (1) contains important information about the tree loss in the “edge effect” of such clearings, but their experimental design seems to artificially inflate the effect they observed, which may call into question some of their results.

Laurance *et al.* estimated biomass in sections of forest on the basis of tree diameter at breast height (DBH), which is a commonly accepted measurement. DBH was used to calculate dry aboveground biomass (AGBM) by an allometric model based on trees from the local forest. Trees of less than 10 cm DBH were excluded from the analysis. Although I do not have firsthand experience with tropical forests, my experience in temperate forests suggests that this method of measuring biomass introduces a bias toward measuring losses while under-sampling the gains that partly offset the losses.

The floor of a dense, closed forest is often dominated by the trunks of large trees. Few saplings and little foliage occur near the forest floor because of light limitation. The trunks are tall and most of the limbs occur high in the canopy, where light levels are highest. The similar geometry of the different individuals facilitates estimation of biomass on the basis of a simple measurement such as DBH. When a clearing is made or an individual tree falls, however, the characteristics of the trees in the vicinity change. First, many seedlings spring up in the area that has opened up, and quickly grow up into saplings. These young trees are rapidly accumulating biomass, but would not be counted by the techniques used in this paper until they reached a size of 10 cm DBH. Given the fact that 15 mm/year increase in DBH was considered an outlier, we may assume that 10 mm/year is close to the maximum growth rate exhibited by trees in the area. Over the 10 to 17 years of the study (1), the maximum size one could expect the fastest growing new growth to reach would be 10 to 17 cm diameter at ground level, and even smaller at breast height. This small size class is precisely the class that was excluded from the study, which effectively eliminates one of the largest potential sources for new biomass accumulation. In addition, the branches of some types of trees on the edges of clearings proliferate and grow toward the light, resulting in a change in the geometry of the tree and an increase in biomass well above the ground. This effect would also have been completely missed by measuring DBH.

The effect reported by Laurance *et al.* appears real in terms of the loss of biomass in the large, old trees, but, given their tech-

niques, it would not seem valid to use these data as a realistic estimate of the actual net loss in biomass or as a fair indicator of the level of “biomass collapse.”

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Deforestation alters tropical ecosystems in many ways (1). William F. Laurance *et al.* suggest that “the loss of biomass in recently fragmented landscapes could be a significant source of greenhouse gas emissions” (2, p. 1118). They base their conclusions on comparisons of aboveground biomass in fragmented and intact forests. These measurements were limited to live standing trees greater than 10 cm DBH and vines—that is, the overstory. Forest floor litter, wood debris, and trees of less than 10 cm DBH—the understory—were not measured. Although we agree that their data point to a change in forest structure, the data seem inadequate to ascertain losses of AGBM and carbon pools.

Laurance *et al.* likely overestimate losses of AGBM because they assume (i) that the ratio of understory biomass is a constant 12% of the overstory and (ii) that losses in overstory pools result in total biomass losses. But do changes in forest structure (loss of large trees) necessarily equate to changes in AGBM? To ascertain aboveground biomass changes associated with fragmentation, repeated measures of all components of AGBM are necessary so that losses through decomposition and increases through forest regrowth can be accounted for.

One of us (D.L.C.) used data from 20 tropical forest plots (of 0.79 ha each) in Rondonia, Brazil, to examine the relationship between

overstory and understory biomass pools (3). At these sites, mean AGBM was 341 ± 14 megagrams per hectare. We found a statistically significant negative correlation between the understory:overstory biomass ratio and the overstory tree biomass (Fig. 1). The use by Laurance *et al.* of a constant of 12% erroneously exacerbates differences in AGBM between forests with high and low overstory tree biomass (that is, intact and fragmented forests). A more appropriate methodology would be to use an equation (Fig. 1) to calculate biomass of the understory. Doing so, we estimate that the losses of overstory biomass observed in the report would be offset by increases in understory biomass. Other Amazonian studies report understory biomass to range from 29 to 84 megagrams per hectare (8 to 26% of the AGBM) (3, 4). At least some woody debris is persistent in this fragmented ecosystem (5). Rather than the ecosystem losses suggested by Laurance *et al.*, these structural changes could represent a shift from overstory to understory carbon pools for the duration of their study.

We do not wish to minimize the need to investigate influences of forest fragmentation on dynamics of terrestrial carbon pools in the Amazon, but a complete inventory of ecosystem pools in experimental plots (above- and belowground) is necessary for one to draw reliable conclusions in such a study.

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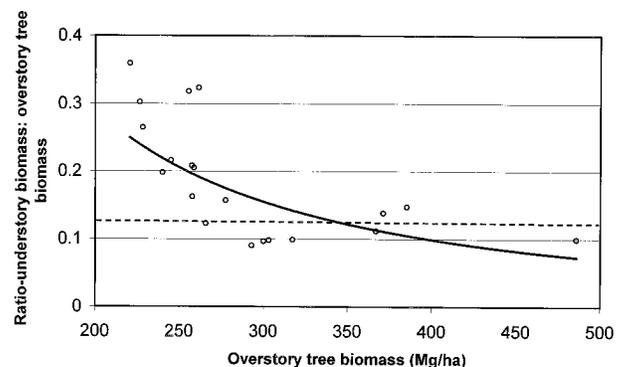
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References and Notes

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Fig. 1. Relation of the understory:overstory biomass ratio to the overstory biomass. $R^2 = 0.48$ $y = 10932 x^{-1.5539}$. Overstory trees are greater than 10 cm DBH. Dotted line represents the 12% constant ratio used by Laurance *et al.* (1) to calculate understory biomass.



Response: Cowles and Kauffman *et al.* raise some relevant questions about our “biomass collapse” phenomenon in Amazonian forest fragments (1). Cowles argues that densities of seedlings and small (<10 cm DBH) trees often increase near forest edges and in treefall gaps, and that these increases may partly compensate for biomass losses caused by the deaths of large trees. He further suggests that changes in tree geometry (particularly the tendency for tree branches near edges to grow toward light) could alter the relationship between tree DBH and AGBM, which we used to estimate biomass changes in our study plots.

Kauffman *et al.* use a similar argument, but with two important additions. First, they suggest that AGBM losses near forest edges may be offset not only by increased growth of understory plants (small trees, saplings, and so forth), but also by accumulating necromass (woody debris and litter). Second, they provide empirical data from a study in southern Amazonia (about 1000 km southeast of our study area), which shows that understory and overstory biomass were negatively correlated in their study plots. Here we respond to the points raised by Cowles and Kauffman *et al.* and argue that the effects they describe are likely to be of limited importance.

1) Are biomass losses near forest edges offset by increased growth of understory plants? The most important issue is whether other living components of the forest compensate for biomass loss near forest edges. To test this possibility, we estimated AGBM of the two largest components of biomass, small (<10 cm DBH) trees and lianas (2), in a representative subset of our 1-ha study plots that were stratified with respect to distance

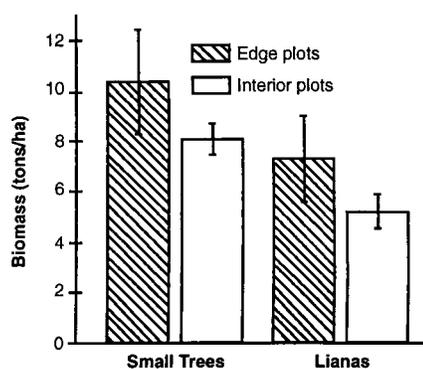


Fig. 1. Estimated aboveground dry biomass for small trees and lianas (woody vines) in the central Amazon ($\bar{X} \pm SD$). Edge plots are located ≤ 100 m from the nearest forest edge, while interior plots are > 100 m from the edge [sample sizes for 1-ha plots: small trees at edge ($n = 8$) and interior ($n = 5$); lianas at edge ($n = 31$) and interior ($n = 19$)].

from forest edge (Fig. 1). Although small trees and lianas both increased near edges, the magnitudes of changes were remarkably small—only 2.2 and 2.1 metric tons ha^{-1} , respectively. Collectively, these increases comprise $< 12\%$ of the 36.1 tons ha^{-1} of living biomass lost on average from mortality and damage of large trees (3), indicating that understory plants compensated for only a small proportion of biomass losses.

2) Could changes in tree geometry, such as lateral crown growth in response to nearby treefall gaps, alter the relationship between above-ground tree biomass and DBH? Such effects would be minor. If a tree were suddenly to expand its crown area and thus increase its photosynthetic capacity, these changes would likely be linked to faster growth of its roots and trunk, which would be reflected in incremental increases in its DBH.

Moreover, trees growing on forest edges are typically shorter than those growing in forest interiors (personal observations), suggesting that edge trees could actually contain less—not more—biomass than forest-interior trees of comparable DBH.

3) Does understory biomass increase as overstory biomass declines? About two-thirds of the understory biomass (in figure 1 in the comment by Kauffman *et al.*) is dead material (4). Tropical rain forests are typically warm and moist, and support a diverse community of fungi, termites, and bacteria that lead to relatively high rates of dead wood (5) and leaf litter (6) decomposition. In our estimates of carbon flux from tropical forest fragmentation (7), we assumed that dead trees constitute “committed carbon emissions,” a common practice in studies of land-use change (8). This assumption is probably valid even if some dead trees require a decade or more to decompose completely because evidence from our 19-year study suggests that the substantial loss of living biomass among large trees in Amazonian fragments is a permanent phenomenon (1, 9).

4) There are important changes in fragment plant composition—not yet incorporated into our model—that probably cause further biomass declines. Many of the disturbance-adapted trees and vines that proliferate in our fragments (1, 10) have lower wood densities, and thus lower carbon contents, than the old growth species they are replacing (for example, the hyperabundant pioneer *Cecropia sciadophylla* has 50 to 65% less biomass than primary forest trees of similar diameter) (11). Also, seedlings of old growth trees decline near forest edges (12), and this could lead to further biomass losses in fragments.

5) Finally, our estimate of carbon emissions (7) is conservative for two additional

reasons: First, most fragments we studied were surrounded by regrowth forest 5 to 15 m in height, which probably reduced effects of desiccation and wind damage common in abrupt edge situations; second, we assumed that tree mortality and damage rates increased only within 100 m of edges (7), whereas modest but significant increases were actually detected up to 300 m. In summary, these conservative assumptions, combined with the fact that small trees and vines compensated for only a small fraction ($< 12\%$) of the living biomass lost from the death and damage of large trees (Fig. 1), suggest that biomass collapse in forest fragments is a real—and worrisome—phenomenon.

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2. For trees of 5 to 9.9 cm DBH, AGBM was estimated by measuring DBH of all trees within 13 1-ha plots, then using an allometric formula developed by J. dos Santos [thesis, National Institute for Research in the Amazon (1996)]. Trees of 1 to 5 cm DBH were sampled within the same 13 plots using 25 regularly spaced 5 m by 5 m quadrants per plot, with AGBM values estimated using an allometric formula developed by R. F. Hughes [thesis, Oregon State University (1997)]. AGBM for lianas (≥ 2 cm DBH) was estimated by measuring DBH of all lianas within 50 1-ha plots, then using an allometric formula developed by F. E. Putz [*Biotropica* **15**, 185 (1983)].
3. Derived by multiplying the mean rate of biomass loss [10.6%; see (7)] by the average AGBM of large trees in our study area (340.6 tons ha^{-1}).
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11. The formula we used to estimate AGBM of large trees [dos Santos, 1996 (see 2)] overestimates *C. sciadophylla* biomass by 50 to 65% when compared to values from an allometric model developed specifically for that species [R. G. Mesquita, thesis, University of Georgia (1995)].
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