Biomass Dynamics in Amazonian Forest Fragments

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Abstract. Habitat fragmentation affects aboveground biomass in Amazonian forests, with potentially important implications for carbon storage and greenhouse gas emissions. We assessed the dynamics of aboveground-biomass stocks by combining long-term (10–19 yr) data on mortality, damage, growth, and recruitment of large (≥10 cm diameter at breast height [dbh]) trees with measurements of nearly all other live and dead plant material (seedlings, saplings, small trees, palms, lianas, downed wood debris, snags, litter) in 50 1-ha plots in fragmented and continuous Amazonian forests.

The key process altering biomass dynamics in fragmented forests is the chronically elevated mortality of large trees, which apparently results from microclimatic changes and increased wind turbulence near forest edges. This, in turn, accelerates the production of necromass and leads to significantly increased wood debris and litter on the forest floor. Near forest edges, frequent canopy disturbance increases the amount of light in the understory, resulting in accelerated tree recruitment, significantly higher biomass of small (5–10 cm dbh) trees, and higher liana densities. Surprisingly, the estimated annual turnover of wood debris increases significantly near forest edges, suggesting that decomposition is occurring more rapidly in fragmented than continuous forests.

These results reveal that habitat fragmentation fundamentally alters the distribution and dynamics of aboveground biomass in Amazonian forests. The rate of carbon cycling probably increases sharply, both because long-lived canopy and emergent trees decline in favor of shorter-lived successional trees and lianas, and because necromass production and turnover both appear to increase. Carbon storage in live vegetation also declines because small successional trees and lianas (which typically have low wood density) store substantially less carbon than do large, old-growth trees. Finally, the decline and rapid decay of live biomass in forest fragments may produce substantial atmospheric carbon emissions, above and beyond that resulting from deforestation per se.

Key words: Amazon; biomass; Brazil; carbon cycling; carbon storage; decomposition; edge effects; greenhouse gases; habitat fragmentation; rainforest.

Introduction

Amazonian forests have a strong influence on the global carbon cycle (Grace et al. 1995, Fearnside 1997, Houghton et al. 2000) and are being cleared and fragmented at alarming rates (Skole and Tucker 1993, National Institute for Space Research [INPE] 2000, Laurance et al. 2001a). Habitat fragmentation affects the ecology of tropical forests in many ways, such as altering the diversity and composition of fragment biotas, and changing ecological processes like seed germination and predation intensity (Lovejoy et al. 1986, Bierregaard et al. 1992, Laurance et al. 2002). Recent studies reveal that fragmentation also alters forest dynamics, causing sharply elevated rates of tree mortality and canopy-gap formation (see Plate 1), apparently as a result of microclimatic changes and increased wind turbulence near forest edges (Laurance et al. 1998b). Large (≥60 cm diameter at breast height [dbh]) trees are particularly vulnerable, dying nearly three times faster within 300 m of forest edges than in forest interiors (Laurance et al. 2000).

Chronically elevated tree mortality in forest fragments has important impacts on ecological and ecosystem processes. For example, increased canopy-gap formation near forest edges leads to accelerated tree recruitment (into the ≥10 cm dbh size class) and a proliferation of disturbance-adapted successional trees (Laurance et al. 1998c) and lianas (Laurance et al. 2001b). Even more notable is an apparent “collapse” of living biomass in forest fragments, as large, old-growth trees decline at the expense of smaller trees and lianas (Laurance et al. 1997). Simulation models suggest that the decline and decomposition of biomass in fragmented tropical forests could be an important source of atmospheric carbon emissions, potentially producing as much as 150 million Mg C annually (Laurance et al. 1998d).

However, the notion that forest fragmentation may increase carbon emissions has been controversial (Cowles 1998, Kauffman et al. 1998, Laurance et al. 1998a) because the biomass-collapse phenomenon has
been documented only for ≥10 cm dbh trees (Laurance et al. 1997). Although such trees comprise the bulk of aboveground biomass in tropical forests (Clark and Clark 1995, Brown 1997; Nascimento and Laurance, 2002), other factors can also influence the magnitude of carbon emissions. In particular, the proliferation of small trees and lianas in fragments might offset biomass losses from mortality of larger trees (Cowles 1998, Kauffman et al. 1998). Moreover, little is known about the production and decomposition of necromass (dead organic material) in fragmented tropical forests (Didham 1998). Thus, assessing the effects of forest fragmentation on carbon storage requires information about the various stocks of live and dead biomass and the dynamics of carbon cycling.

Here we provide a detailed assessment of the impacts of Amazon forest fragmentation on aboveground biomass. To accomplish this, we combine a long-term (10–19 yr) data set on the biomass dynamics of large (≥10 cm dbh) trees with recent measurements of nearly all other live and dead plant material (seedlings, saplings, small trees, palms, lianas, downed wood debris, snags, and litter) in 50 1-ha plots in fragmented and continuous forests. We also employ improved allometric models to quantify the biomass of large trees. These combined data sets allow us to estimate the rates of necromass production and turnover in fragmented and continuous forests, and to determine how fragmentation affects the quantity and distribution of live and dead plant material. These analyses provide a key contribution toward our ultimate goal of understanding how habitat fragmentation affects carbon storage and cycling in tropical forests.

**METHODS**

**Study area and plots**

The study area is an experimentally fragmented landscape spanning ~1000 km² in the central Amazon, 80 km north of Manaus, Brazil (2°30′ S, 60° W), at 50–100 m elevation (Lovejoy et al. 1986). Rainforests in the area are terra firme (not seasonally inundated). Rainfall ranges from 1900 to 3500 mm annually with a pronounced dry season from June to October. The forest canopy is 30–37 m tall, with emergents to 55 m (Laurance 2001). Species richness of trees is very high and can exceed 280 species (≥10 cm dbh) per hectare (Oliveira and Mori 1999). The dominant soils in the study area are xanthic Ferralsols, which are heavily weathered, acidic, and very poor in nutrients such as P, Ca, and K (Chauvel et al. 1987, Laurance et al. 1999). The study area (Fig. 1) is surrounded by large expanses (>200 km) of continuous forest to the west, north, and east. In the early to mid 1980s, forest fragments ranging from 1 to 100 ha in area were isolated by distances of 70–1000 m from surrounding forest by clearing and burning the intervening vegetation to establish pastures in three large (~5000 ha) cattle ranches. Fragments were fenced to prevent encroachment by cattle. Reserves ranging from 1 to 1000 ha in area were delineated in nearby continuous forest to serve as experimental controls. Regrowth forests have regenerated in some cleared areas and are dominated by *Cecropia* spp. or *Vismia* spp.

Since the early 1980s, a long-term study of tree mortality, damage, growth, recruitment, and species composition has been conducted in fragmented and continuous forests in the study area. Over 62 000 trees (≥10 cm dbh) are being monitored at regular (typically 4–6-yr) intervals within 69 permanent, square, 1-ha plots. We randomly selected 50 of these plots for the present study, 30 of which are in nine forest fragments (four 1-ha fragments [four plots], three 10-ha fragments [12 plots], and two 100-ha fragments [14 plots]), with the remaining 20 plots in eight reserves that roughly mimic the spatial arrangement of fragment plots, but in continuous forest. Plots in fragmented and continuous forests are stratified so that edge and interior areas are both sampled.
Forest biomass

All significant components of aboveground live biomass (large trees, small trees, saplings, seedlings, stemless palms, lianas) were estimated in each plot. The relevant field methods, allometric models, and wood-density parameters are detailed elsewhere (cf. Laurance et al. [2001b] for lianas, Nelson et al. [1999] for pioneer trees, and Nascimento and Laurance [2002] for other variables) and briefly summarized here. All data were converted to estimates of aboveground dry biomass on a per-hectare basis.

Large trees.—For each 1-ha plot, biomass of trees ≥10 cm dbh was estimated from our most recent census (1997–1999). Tree diameters were carefully measured at 1.3 m height or above any buttresses. For all but common pioneer species, dbh data were converted to biomass estimates using an allometric model derived by destructively sampling 315 trees in local primary rainforest (Chambers et al. 2001a). This model is a refinement of an earlier model by dos Santos (1996), which overestimates the biomass of large (≥60 cm dbh) trees while underestimating biomass of smaller trees (Chambers et al. 2001a). Because pioneers tend to have lower wood densities and hence less biomass than old-growth species, two additional allometric models were used to estimate biomass for pioneers, the first for Cecropiaceae (principally Cecropia spp. and Pourouma spp.) and the second for Bellucia spp., Vismia spp., and Goupia glabra (Nelson et al. 1999).

Small trees.—The diameters of small trees (5.0–9.9 cm dbh) were recorded from 1999–2000 within 13 subplots that were evenly arrayed over each plot. Separate allometric formulas were used to estimate biomass for primary-forest trees (Nascimento and Laurance, 2002), pioneers (Nelson et al. 1999), and palms (Hughes 1997).

Saplings.—Diameters of saplings (1.0–4.9 cm dbh) were recorded from 1999–2000 within 13 subplots (5 × 5 m) that were evenly arrayed over each plot. Separate allometric formulas were used to estimate biomass for primary-forest trees (Nascimento and Laurance, 2002), pioneers (Nelson et al. 1999), and palms (Hughes 1997).

Seedlings.—Seedlings (>50 cm height but <1 cm dbh) were counted from 1999 to 2000 within 13 samples (2 × 2 m) that were evenly arrayed over each plot. Seedling counts were multiplied by average seedling dry mass to estimate biomass.

Stemless palms.—Abundant stemless palms (principally Attalea spp. and Astrocaryum spp.) were sampled within 13 subplots (5 × 5 m) per plot. To estimate biomass, leaves of individual plants were divided into three size classes (0–2, >2–3, and >3 m height), counted, and then multiplied by an average leaf dry mass.

Lianas.—Lianas (≥1 cm dbh) were measured at 1.3 m height from 1997 to 1999 then converted to biomass estimates using an allometric formula developed in northern Amazonia (Putz 1983). All stems of ≥2 cm dbh in the understory of each plot were measured, whereas smaller (1.0–1.9 cm) stems in the understory were measured in 13 subplots (5 × 5 m) that were evenly arrayed over each plot.
Forest necromass

All significant components of aboveground necromass (downed wood debris, snags, litter) were carefully estimated for each plot. Data were converted to estimates of dry necromass on a per-hectare basis.

Downed coarse debris.—Coarse wood debris (≥10 cm diameter) on the forest floor and understory was measured in 1999–2000 using the planar-intersect method (Van Wagner 1968, Brown 1974). Debris was sampled along 26, 15 m long transects that were evenly arrayed across each plot. Debris was separated into sound and rotten classes, and necromass was estimated using formulas in Brown (1974) and mean wood-density values for sound and rotten wood (Nascimento and Laurance, 2002).

Downed fine debris.—Fine wood debris (2.5–9.9 cm diameter) was also estimated in 1999–2000 with the planar-intersect method, using 26, 5 m long transects that were evenly arrayed across each plot. Dry necromass was estimated using a formula in Brown (1974) and mean wood-density for fine debris (Nascimento and Laurance, 2002).

Snags.—Plots were surveyed in 1999–2000 to identify standing dead trees (≥10 cm dbh). Dry necromass was estimated using the formula of Chambers et al. (2001a), with values reduced by 10% to compensate for the loss of leaves, twigs, and small branches (Delaney et al. 1998). For snags with broken boles, a taper function was used to estimate tree volume, which was then multiplied by the mean density of sound wood to yield a necromass estimate (Nascimento and Laurance, 2002).

Litter.—Litter standing crop was quantified during the 2001 wet season using 26 samples (50 × 50 cm) that were evenly arrayed over each plot. All material above the soil surface was removed (leaves, twigs of <2.5 cm diameter, fruits, fine live roots) and weighed in the field. A portion of the sample was oven dried and the ratio of dry to wet litter weight was used to estimate litter dry mass.

Biomass dynamics

Three parameters were derived to estimate the rates of biomass production, mortality, and decomposition on each plot. “Tree recruitment and growth” describes the mean annual production of new large-tree (≥10 cm dbh) biomass, which comprises >80% of aboveground biomass in intact forests of the study area (Nascimento and Laurance, 2002). “Coarse-debris production” describes the average rate at which coarse wood debris—the dominant component of aboveground necromass (Delaney et al. 1998, Chambers et al. 2000, 2001a)—is produced annually. Finally, “coarse-debris turnover” describes the mean fraction of coarse wood debris that decomposes each year (Delaney et al. 1998).

Tree recruitment and growth.—The mean annual biomass increment from recruitment of new trees (into the ≥10 cm dbh size class) and growth of existing large trees was determined using forest-mensuration data collected between the early to mid 1980s and 1999 (three to six censuses per plot over intervals of 10.3–18.5 yr). The allometric formulas of Chambers et al. (2001a) and Nelson et al. (1999) were used to derive aboveground biomass for primary and pioneer species, respectively, based on recruitment and growth data. Values for each plot were increased by 20% to compensate for major structural damage to trees (branch fall and crown loss; cf. Chambers et al. 2001a).

Coarse-debris production.—Mean annual production of coarse wood debris was estimated for each plot by (1) determining the annual production of total necromass from mortality of large trees (using the long-term data set described above), (2) increasing this value by 20% to account for necromass production from tree structural damage (Chambers et al. 2001a), and (3) multiplying this quantity by 0.85, which is the estimated fraction of tree mass that is ≥10 cm in diameter, based on destructive sampling of 29 trees in the central Amazon (Chambers et al. 2000).

Coarse-debris turnover.—This parameter was derived by dividing average coarse-debris production by the standing stock of coarse wood debris (the sum of coarse downed wood debris plus snags; cf. Delaney et al. 1998).

Edge distance and slope

Because fragmentation effects on tree mortality and forest biomass in the recently isolated forests (<20 yr) of the study area are strongly influenced by the distance of plots to forest edge (cf. Laurance et al. 1997, 1998a, b, c, d, 2000, 2001b), this study focuses on edge-distance as a key landscape variable. Edge distances (which ranged from 53 to 3000 m, measured from the plot center) were log_{10}-transformed to help linearize the relationship with response variables.

Slope was also used as a potential predictor, because the 50 plots vary considerably in slope (0–43°) and a previous study showed that increasing slope has a negative effect on large-tree biomass and soil-fertility parameters (clay content, organic matter, N, K, Mg, total exchangeable bases, aluminum saturation) in central Amazonian terra-firme forests (Laurance et al. 1999).

Slope data were the average of 25 clinometer measurements (determined by sighting along the maximum slope at a vertical stake that was marked at eye level and held 10 m from the observer) that were evenly arrayed across each plot.

Statistical analysis

Interrelationships among the 14 biomass and necromass parameters in fragmented and continuous forests were assessed using nonmetric multidimensional scaling (NMDS), a robust ecological ordination method, with the PC-ORD package (McCune and Mefford...
The number of ordination axes was determined by examining the relationship between stress and number of axes, and by using randomization tests to confirm that each axis in the final analysis explained significantly more variation than expected by chance. All variables were standardized by the relativization by maximum method (Noy-Meir et al. 1975) prior to analysis. Sorensen’s distance measure was used (comparable results were obtained with different distance metrics and ordination techniques, indicating that the observed patterns were insensitive to the methods used).

Product–moment correlations and linear regressions were used to assess the influence of distance to forest edge and slope on the ordination axes and each original variable. When conducting multiple simultaneous correlations, Bonferroni corrections were employed to reduce the likelihood of spurious correlations, using an experiment-wise error rate of 0.15 (cf. Chandler 1995).

**RESULTS**

**Ordination analysis**

The ordination revealed three major gradients in the data set (Table 1). A randomization test ($n = 50$ runs) confirmed that all three axes explained significantly more variation than expected by chance ($P < 0.02$ in all cases). The first axis captured over half (50.5%) of the total variation and described a gradient between sites with heavy tree mortality, low biomass of large trees, and high coarse-debris production, and those with opposite values. Sites with high mortality also had significantly increased tree recruitment and growth, increased coarse-debris turnover, more saplings and small trees, and fewer stemless palms.

The second axis captured 21.9% of the total variation and described a gradient between sites with increased tree mortality, more coarse and fine debris, greater coarse-debris production, more stemless palms, and sites with many saplings and lianas. The third axis captured 10.5% of the variation and described a gradient in snag biomass.

When the plots were arrayed in ordination space (Fig. 2), there was an obvious difference between plots near forest edges and those in interiors. When ordination scores were compared for edge (plot center <300 m from edge) vs. interior (>300 m from edge) plots, there were highly significant differences for axes 1 ($t = -5.05, P < 0.0001$) and 2 ($t = 2.69, P < 0.01$), but not for axis 3 ($t = -0.15, P > 0.8$; all $t$ tests, df = 45 in all cases). In addition, both axis 1 ($F_{1,45} = 15.77, R^2 = 26.0\%, P = 0.0003$) and axis 2 ($F_{1,45} = 13.63, R^2 = 23.3\%, P = 0.0006$) were strongly correlated with distance to forest edge (Fig. 3). Thus, the two most important axes of variation in the study plots were both associated with edge–interior gradients.

Slope had no significant effect on the ordination axes when simple linear regressions were used ($F_{1,45} < 0.5, P > 0.50$ for all axes). Slope also was a nonsignificant predictor when it was included as a second variable along with edge distance in multiple regression models.

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**Table 1.** Product-moment correlations between 14 biomass variables and three ordination axes produced by nonmetric multidimensional scaling.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Axis 1</th>
<th>Axis 2</th>
<th>Axis 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large-tree biomass</td>
<td>-0.640†</td>
<td>-0.085</td>
<td>-0.210</td>
</tr>
<tr>
<td>Large-tree mortality rate</td>
<td>0.839‡</td>
<td>-0.494‡</td>
<td>0.217</td>
</tr>
<tr>
<td>Growth and recruitment of large trees</td>
<td>0.61‡</td>
<td>-0.360</td>
<td>0.207</td>
</tr>
<tr>
<td>Production of coarse wood debris</td>
<td>0.824‡</td>
<td>-0.571‡</td>
<td>0.208</td>
</tr>
<tr>
<td>Turnover of coarse wood debris</td>
<td>0.652‡</td>
<td>-0.122</td>
<td>0.364</td>
</tr>
<tr>
<td>Coarse downed-wood debris</td>
<td>0.388</td>
<td>-0.489‡</td>
<td>0.090</td>
</tr>
<tr>
<td>Fine downed-wood debris</td>
<td>0.113</td>
<td>-0.476‡</td>
<td>0.056</td>
</tr>
<tr>
<td>Snag biomass</td>
<td>-0.197</td>
<td>-0.047</td>
<td>-0.912‡</td>
</tr>
<tr>
<td>Litter biomass</td>
<td>0.208</td>
<td>-0.134</td>
<td>0.368</td>
</tr>
<tr>
<td>Seedling biomass</td>
<td>-0.131</td>
<td>0.144</td>
<td>0.236</td>
</tr>
<tr>
<td>Sapling biomass</td>
<td>0.557†</td>
<td>0.420†</td>
<td>0.219</td>
</tr>
<tr>
<td>Small-tree biomass</td>
<td>0.733†</td>
<td>0.100</td>
<td>0.246</td>
</tr>
<tr>
<td>Stemless-palm biomass</td>
<td>-0.528†</td>
<td>-0.500†</td>
<td>0.066</td>
</tr>
<tr>
<td>Liana biomass</td>
<td>0.107</td>
<td>0.582†</td>
<td>-0.227</td>
</tr>
<tr>
<td>Variation explained‡</td>
<td>50.5%</td>
<td>21.9%</td>
<td>10.5%</td>
</tr>
</tbody>
</table>

† Significant correlations, using a Bonferroni-adjusted alpha value ($P = 0.0036$).
‡ Coefficients of determination are based on the correlations between ordination distances and distances in the original $n$-dimensional space.
**Simple correlations**

The influence of edge effects and slope on the individual biomass variables was further assessed using product–moment correlations (Table 2). Distance to edge and slope were not significantly correlated ($r = -0.136, df = 48, P = 0.35$), so their effects could be assessed independently.

Slope had no significant effects on any biomass variable. However, even with the stringent Bonferroni correction ($P < 0.0088$), many biomass parameters varied as a function of distance to forest edge. Plots near edges had significantly higher tree mortality and greater production of coarse wood debris (Fig. 4), more downed coarse and fine wood debris, greater biomass increment from recruitment and growth of large trees, and higher...
densities of small (5–9.9 cm dbh) trees. Two additional variables, litter and turnover of coarse wood debris (Fig. 4), also increased near edges but at a lower level of significance ($P = 0.046$ and $P = 0.018$, respectively). Although snag mass did not change significantly near edges, the proportion of coarse wood debris comprised by snags was somewhat lower near edges ($r = 0.274$, df = 48, $P = 0.055$, using arcsine-transformed proportions).

We also assessed the influence of edge and slope on two composite variables: total understory biomass (seedlings, saplings, small trees, stemless palms, lianas) and total necromass (downed wood debris, snags, litter). Neither variable was influenced by slope. Distance to edge had no significant effect on total understory biomass, but total necromass increased significantly near edges (Table 2).

**Direct comparisons of edges vs. interiors**

The mean values of the various biomass components in fragmented and continuous forests (Table 3) are important for parameterizing models of carbon and nutrient cycling and ecosystem productivity (Potter et al. 1993, Chambers et al. 2000, 2001a, b, Clark et al. 2001). Relative to forest interiors, plots near edges (<300 m from edge) had highly significant ($P < 0.01$) increases in tree mortality, biomass increment from growth and recruitment of trees, production and turnover of coarse wood debris, standing stocks of coarse downed wood debris, and total necromass. There also were significant ($P < 0.05$) increases near edges in the biomass of small (5.0–9.9 cm dbh) trees, fine downed wood debris, and coarse wood debris (coarse downed debris and snags). Finally, although litter did not differ significantly when plots at $<300$ m vs. $>300$ m from edges were compared, it did differ when plots $<100$ m vs. $>100$ m from edges were contrasted ($t = -2.55$, df = 48, $P = 0.014$; $t$ test).

**Estimating carbon emissions**

A preliminary estimate of the increase in carbon emissions from forest fragmentation can be generated from our data. This can be achieved by estimating the mean loss of aboveground biomass from large-tree mortality and damage and changes in the density of light-wooded pioneer species, subtracting increases in necromass and understory biomass, and then determining the fraction of decomposing necromass that is likely to be emitted as carbon emissions. In our analysis we assume that fragmentation does not lead to a significant change in belowground carbon storage, although it must be emphasized that information about this process in fragmented rainforests is almost nonexistent.

The magnitude of biomass losses from large trees was estimated by comparing the initial (prefragmentation) and final measurements of tree biomass for each plot to quantify changes during the first 10–17 yr after fragmentation (Fig. 5). This interval is more than sufficient for edge-related biomass losses to occur; by 6–9 yr after fragmentation, biomass declines from increased tree mortality are gradually balanced by increased recruitment and growth, so that the forest apparently achieves a new equilibrium with lower large-tree biomass than it originally had (Laurance et al. 1997). For our 29 plots within 300 m of edges, live biomass of large trees declined by an average of 22.7 (±31.8) Mg/ha.

Plots within 300 m of edges averaged 1.7 and 10.1 Mg/ha more understory biomass and necromass, respectively, than did plots further from edges (Table 3). These values are lower than the biomass losses from...
large-tree mortality and suggest a net biomass decline of 10.9 Mg/ha within 300 m of edges. Assuming that 50% of biomass is carbon and that at least three-quarters of decomposition loss results from wood respiration (principally from fungal and microbial decomposers) that directly produces C emissions (Chambers et al. 2001b), this implies a net flux of at least 4.1 Mg C/ha to the atmosphere within 300 m of forest edges. The remaining biomass (about 1.4 Mg C/ha) would be exported to soils and streams in the form of wood particles and leachates, and a significant fraction of this is likely to be quickly respired to the atmosphere (e.g., Richey et al. 2002). The overall C emissions are thus predicted to be on the order of 4–5 Mg/ha within 300 m of forest edges.

**Discussion**

Distribution of aboveground biomass

Our findings demonstrate that habitat fragmentation substantially alters the quantity and distribution of aboveground biomass in Amazonian forests. As a result of sharply elevated tree mortality and necromass production, wood debris and litter increase significantly in the forest understory. Because of frequent canopy disturbances that increase light in the understory, the biomass of small (5–9.9 cm dbh) trees increases significantly, and there is a corresponding increase in the biomass increment from recruitment and growth of large (≥10 cm dbh) trees.

The net effect of these changes is a forest in which biomass is being lost from large, old-growth trees and partially redistributed to necromass and smaller trees. Surprisingly, there was no significant increase in total understory live biomass near forest edges, despite an observed increase in small trees, because the other understory plants (seedlings, saplings, palms, lianas) did not respond positively to forest edges. Lianas increase in density near forest edges but not in biomass (at least in our study area, where forests have been fragmented for <20 yr), because forest edges support many small, actively growing lianas (Laurance et al. 2001b).

Despite increased tree mortality near edges, there was no significant difference during our most recent survey (1997–1999) in the biomass of large trees between edge and interior plots (Table 3). This is not overly surprising, however, given that there was pronounced variation in large-tree biomass among our 50 study plots prior to forest fragmentation, with estimates ranging from 228 to 420 Mg/ha. This is partly a result of natural variability in soil fertility and topography, which significantly influences forest biomass (Laurance et al. 1999) and tends to obscure a simple relationship between tree biomass and distance to forest edge. The advantage of a long-term study such as ours, in which tree biomass was determined prior to fragmentation, is that the confounding effects of such marked natural variability can be effectively eliminated. When such confounding effects are removed, the strong impact of forest edges on tree biomass becomes obvious (Fig. 5).

In recently fragmented forests, edge effects clearly play a dominant role in biomass dynamics, but the spatial scales of different edge-related alterations vary considerably (e.g., Lovejoy et al. 1986, Didham and Lawton 1999, Laurance et al. 2002). Mortality of large trees is elevated as far as 300 m from forest edges (Laurance et al. 1998b, 2000), apparently because wind turbulence can be increased as far as several hundred meters downwind from forest edges (reviewed in Laurance 1997). Other edge phenomena, such as increased litter stocks (Table 3) and litterfall, occur over smaller scales (<100 m from edges) and probably result from edge-related changes in forest microclimate (Didham 1998, Carvalho and Vasconcelos 1999, Didham and Lawton 1999).

**Biomass dynamics**

In fragmented forests, the rate of carbon cycling probably increases substantially, for two reasons. First, high mortality rates of trees lead to a general decline of large, old-growth trees and an increase in shorter-lived successional trees and lianas (Laurance et al. 1998c, 2000, 2001). The pioneer tree *Cecropia scidophylla*, for example, has increased 33-fold in density since our study area was fragmented (Laurance et al. 1998b). The residence time of carbon is clearly much greater in large trees (some of which can live for over 1000 years; Chambers et al. 1998) than successional species, which exhibit relatively rapid population turnover (Condit et al. 1995). Even among nonpioneers, recruitment and growth rates tend to increase near edges, presumably because of increased light resulting...
from frequent treefall gaps and lateral light penetration near edges.

Second, necromass production and turnover both apparently increase in fragmented forests (Fig. 4). These processes will tend to accelerate carbon cycling because the residence times of wood debris and litter are considerably shorter than that of live trees (Delaney et al. 1998, Chambers et al. 2000). While greater necromass production was expected given the chronically elevated tree mortality in fragments, increased turnover is surprising because it implies that decomposition rates rise near forest edges. In the only published study of decomposition in tropical forest fragments, Didham (1998) found that short-term turnover of leaf litter exhibited no consistent relationship with edge distance.

There are several plausible explanations for the apparently increased necromass turnover in fragments. The first is that it is simply an artifact of the indirect method used to estimate turnover, which involved comparing long-term data on coarse wood debris production with a one-time measurement of coarse-debris stocks. This technique, which was also used by Delaney et al. (1998) in a large-scale study of turnover rates, might yield biased estimates if necromass production varied substantially over time. However, while tree mortality is patchy and episodic, there is no evidence that average mortality rates have declined over time in our individual forest fragments (Laurance et al. 1998b).

There was, moreover, a highly significant linear relationship for our plots between long-term mortality rates and recent rates from our latest census interval ($F_{1,49} = 67.1, R^2 = 58.3\%, P < 0.00001$; slope not significantly different from 1.0), suggesting that the observed trend in turnover is real. Finally, it is noteworthy that our average turnover estimate in forest interiors ($0.12 \pm 0.04$ yr$^{-1}$) is not greatly dissimilar from that derived for the same plots by Chambers et al. (2000), based on direct observations of decomposition in 155 randomly selected dead trees ($0.17$ yr$^{-1}$). Thus, while experimental decomposition studies (e.g., Harmon et al. 1995) in forest fragments are needed to verify our findings, we have some confidence that necromass turnover actually increased near forest edges.

Why should turnover increase near edges? There are several possible reasons. Pioneer trees, for example, proliferate near edges and usually decompose more rapidly than old-growth trees, because they are generally small with low wood density, factors that increase decomposition (Chambers et al. 2000). Many pioneers also have low concentrations of secondary compounds that inhibit decomposers (Coley 1983). Wood- and litter-consuming invertebrates, such as termites and beetles, change in abundance, diversity, and guild composition near forest edges and might influence decomposition rates (de Souza and Brown 1994, Didham et al. 1998). Although reduced moisture near edges (Kapos 1989, Didham and Lawton 1999) could slow fungal activity (especially if moisture falls below 0.5 g H$_2$O/cm$^2$ of wood; Chambers et al. 2001b), temperature increases near edges (up to 3.2°C; Didham 1998) might have an opposite effect because metabolic rates of decomposers are expected to rise exponentially with temperature (Chambers et al. 2000). Finally, the fraction of coarse wood debris comprised by snags declined somewhat near edges, and this might increase turnover because snags have lower moisture and decomposition rates than do downed trunks (Chambers et al. 2001b).

**Estimating carbon emissions**

Our results suggest that forest fragmentation leads to the net production of 4–5 Mg/ha of atmospheric carbon emissions within 300 m of forest edges. Thus, for every 100 m of forest edge created, roughly 12–15 Mg of carbon emissions are expected. Given that hundreds of thousands of kilometers of forest edge are being created by deforestation in the Amazon (cf. Skole and Tucker 1993, INPE 2000), the overall emissions from such edge-related processes could be considerable.

In deriving our estimate, we assumed that belowground carbon storage is minimally affected by forest fragmentation. Carbon inputs to the soil surface might increase near forest edges as a result of greater wood debris and litter production, but a large fraction of this is likely to decompose quickly in the soil (e.g., Townsend et al. 1995) or as organic leachates in streams and rivers (e.g., Richey et al. 2002). Moreover, carbon stored in live roots could actually decline near edges, because the biomass of coarse tree roots is generally proportional to aboveground tree biomass (Klinge and Rodriguez 1973, Jordan and Uhl 1978, Saldarriaga et al. 1988). For these reasons, we believe that changes in belowground storage are unlikely to offset edge-related carbon emissions and might even increase emissions marginally (cf. Palm et al. 2000).

It must also be emphasized that our study area is an experimental landscape in which many common land-use activities that increase forest degradation (e.g., logging, hunting, forest burning) are controlled. In addition, despite efforts to maintain clearings around our fragments, regrowth forest has proliferated in many formerly cleared areas, reducing edge-related tree mortality and microclimatic alterations (Didham and Lawton 1999, Mesquita et al. 1999); nevertheless, regrowth on abandoned pastures is a common feature of fragmented landscapes in the Amazon. Thus, in at least some other Amazonian landscapes, the impacts of forest fragmentation on biomass and carbon emissions are likely to be greater than those observed in our study area.

**Ecological effects of altered biomass dynamics**

Fundamental changes in aboveground biomass and carbon cycling could have diverse effects on frag-
mented communities. As a result of increased tree mortality, forest structure will be altered, with taller, structurally complex forests tending to be replaced by shorter, scrubbiest forests with lower volume and live biomass. Very large (>60 cm dbh) trees are critical sources of fruits, flowers, and shelter for animals, and their decline in fragments could have important effects on animal populations (Laurance et al. 2000). The elevated production of wood debris and litter may increase seedling mortality (Scariot 2001) and depress seed germination (Bruna 1999) near forest edges, while dense litter and debris near edges will provide increased habitat and food resources for some animals (e.g., wood-feeding termites [de Souza and Brown 1994], wood-boring beetles [Didham et al. 1998], twig-nesting ants [Carvalho and Vasconcelos 1999], some small mammals [Malcolm 1997]). Nutrient cycling will probably accelerate in fragments because of higher necromass production and turnover, and could have important effects on biotic and ecosystem processes given that Amazonian soils are often severely nutrient limited (Brown 1987, Chauvel et al. 1987).

Perhaps the most alarming consequence of biomass alterations in fragmented forests is increased fire vulnerability. The accumulation of wood debris and litter, in concert with drier, hotter conditions near edges, can substantially increase the likelihood of surface fires (Uhl and Kauffman 1990, Kauffman et al. 1995). Such fires commonly penetrate into fragments when adjoining cattle pastures are burned to control weeds (Cochrane et al. 1999, Nepstad et al. 1999). In the eastern Amazon, increased fire frequency is detectable inside forests within at least 2400 m of forest edges, indicating that fires there are operating as a large-scale edge effect (Cochrane and Laurance 2002). Because fire is nearly foreign to rainforests, plant mortality from even low-intensity burns is very high (Uhl and Kauffman 1990, Cochrane et al. 1999) and fragment margins often collapse over time with repeated burning (Gascon et al. 2000, Cochrane and Laurance 2002). The net effect is that in much of the Amazon, fragmentation and fire operate synergistically, leading to even greater forest destruction and atmospheric carbon emissions.

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Literature Cited


