

Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia

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ABSTRACT. Forest edges bordering on pasture were created by cutting and burning the surrounding Amazonian lowland rain forest in the dry season (June) of 1990. Litterfall was measured for 3.5 y along transects 10, 50, 100 and 250-m into the forest from the forest edge. Litterfall along the 10-m transects increased by up to 2.5 times that on spatial controls (250-m transects) in the dry season in which the edge was created. In the second dry season after edge creation litterfall at 10-m was lower than on controls, after which it returned to control rates in the second wet season, 1.5 y after edge creation. Litterfall 50-m into the forest was less affected; there was a smaller rise in the dry season in which the edge was cut, and no significant effects after that. At 100-m there was no effect of edge creation on litterfall. Phosphorus concentrations in litterfall were elevated along 10-m transects, 10–12 wk after edge creation, possibly because of reduced retranslocation prior to abscission. The changes in litterfall described here are inextricably linked to the biomass collapse, which occurs near forest-fragment edges in the same area.

KEY WORDS: Amazon, edges, fragments, litterfall, mineral nutrients, tropical rainforest

INTRODUCTION

Many areas of the Brazilian Amazon have become a mosaic-like pattern of pasture, secondary forest at various stages of succession and primary forest.

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The total area of forest cover has been reduced and the proportion of forest edge to forest area has increased. This paper describes the impact of edge formation on litterfall rates and litterfall nutrient concentrations in the forest abutting a newly deforested area. These are components of the 'edge effect' (the suite of changes, which occur in the primary forest as a result of 'edge' creation, where an 'edge' is the boundary between the primary vegetation and converted vegetation, for example pasture, secondary forest, a road or a powerline). The quantification of litterfall rates, and the analysis of the quality of litterfall are potential keys to discovering fundamental changes which might occur in a forest when it is disturbed.

There are few or no published accounts of the response of litterfall rates to large-scale disturbance in lowland tropical forests (Proctor 1983, 1984). Some work has been done in treefall gaps in tropical and temperate forests. In New Guinean montane forest no difference was found between rates of litterfall in a single large treefall gap and those in the nearby understorey (Edwards 1973). In a southern Appalachian montane forest litterfall rates decreased considerably along the edge to centre-gap gradient, and were dependent upon gap size; the authors concluded that forest management practices which alter the size and frequency of gaps could also affect nutrient cycling patterns (Shure & Phillips 1987). No measurements were reported for patterns of litterfall neighbouring the gaps.

Observations during the mist netting of birds, in the same area as the current study, suggested that there might be an increase in litterfall rates in the forest immediately after the creation of forest–pasture edges (R. Bierregaard, *pers. comm.*). In addition litterfall nutrient concentrations might be higher closer to the edge of a recently formed forest fragment (compared to litterfall further into such a fragment) for several reasons. Firstly, the canopies of trees nearer to the edge of the fragment are subjected to greater wind force and to more severe changes in microclimate compared to trees further from the edge (Kapos 1989, Sizer 1992) which could lead to leaves being lost prematurely, before the normal retranslocation of nutrients from the leaves is complete. Secondly, some of the roots of the trees growing along the edge of a forest fragment extend out under the cleared area. The water percolating through the soil in the cleared area might have higher nutrient concentrations than that in the forest, especially after burning (Uhl & Jordan 1984). This might lead to higher rates of nutrient uptake by the trees, and increased foliar nutrient concentrations near to the edge of the fragment. Finally, when the forest that has been cleared to create pasture is burned, some of the smoke and ash is carried by the wind through the forest and is deposited on the leaves of the plants and on the litter layer.

A field study was designed to answer two questions. (1) Is there a change in the rate of litterfall near to the edge of a new forest fragment, and if so to what distance from the edge, when and for what period of time? (2) Does the

litter falling near to the edge of the fragment have higher nutrient concentrations than that falling in the interior of the fragment?

STUDY AREA

The fieldwork was performed in the 100-ha fragment (no. 2303) at Dimona, one of the scientific reserves of the Biological Dynamics of Forest Fragments Project *c.* 80 km north of the city of Manaus, in the State of Amazonas (see figure in Lovejoy & Bierregaard 1990). At the start of the research two sides of the 100-ha fragment were contiguous with continuous primary forest; it was along those two edges that the litterfall study was made (Figure 1 in Sizer & Tanner 1999). On day 45 (11 June 1990, the start of litterfall collection, is day zero) after the third litterfall collection, forest cutting started along the two edges. The process took several weeks and the dry slash was burned between days 87 and 101 (6 and 20 September 1990).

The mean annual rainfall is *c.* 2200 mm, with higher rates from November to April ($> 300 \text{ mm mo}^{-1}$) and a drier season from June to September ($< 100 \text{ mm mo}^{-1}$). Rainfall during the study period did not differ much from the mean except that the dry season of 1991 was in November and December not August and September (Figure 1). The altitude of the area varies between 80 and 120 m, with a strong microrelief created by streams cutting small valleys up to 30 m deep.

The vegetation is evergreen, non-inundated, lowland rain forest (*terra firme*), typical of much of central Amazonia. The mean canopy height is *c.* 35 m, with occasional emergents rising to *c.* 45–50 m. The dominant families of trees are the Lecythidaceae, Sapotaceae, Burseraceae and Leguminosae. The understorey is relatively open and dominated by palms principally of the genera *Astrocaryum*, *Bactris* and *Syagrus*. The area had the lowest density of understorey shrubs in a comparison of lowland rain forest sites (Gentry & Emmons 1987). Herbs are also rare and although many species of climbers are present they are sparsely distributed and do not appear to be a very significant part of the forest structure at the site. Ferns are abundant only around streams, and *Selaginella* is common in well-lit areas such as treefall gaps and along roadsides. Logging has never been practised at the sites where we collected data, and there was no evidence of human disturbance before the area was converted into a mixture of pastures and forest fragments starting in the early 1980s; though activity by indigenous groups was probably widespread before 1600 AD.

The soil in the area is a yellow latosol, varying considerably in clay and sand content. We avoided very sandy soils when choosing our three study sites (moistened soil could be molded into a ball) because they would have been likely to have different species composition and ecosystem dynamics. The mean pH of homogenized samples (made into a stiff paste with water) from 0–5 cm deep in our study sites, was 4.1.

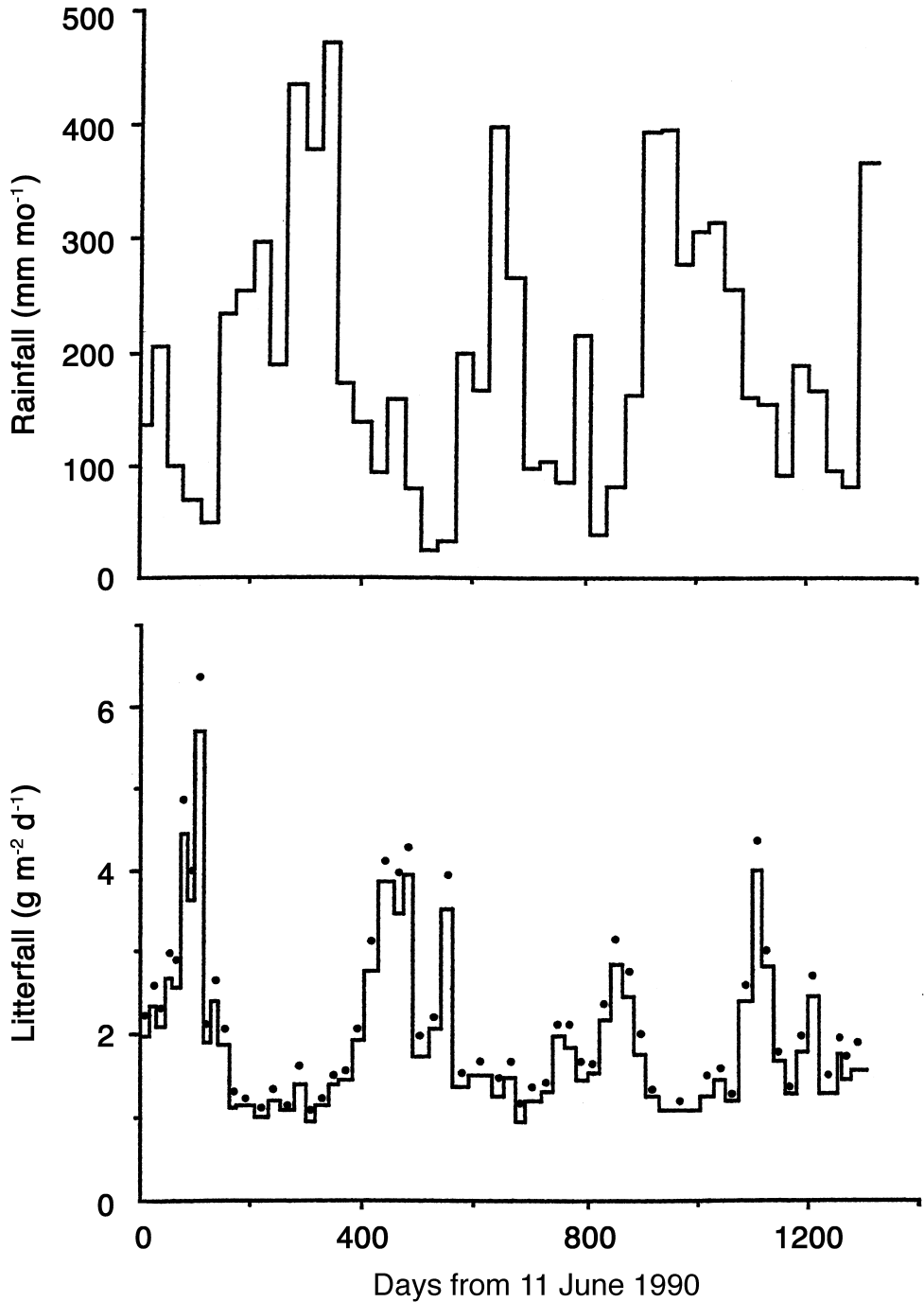


Figure 1. Rates of litterfall (< 5 mm diameter) along transects at 250-m from edges (dots indicate one standard error), and monthly rainfall in the study area. Felling to create edges started between 45 and 59 d from the beginning of litterfall collection (11 June 90), burning of the felled trees was done between 87 and 101 d after 11 June 1990.

METHODS

Live leaves

Between 12 and 17 July 1990 sun-lit live leaves were collected from 70 individual trees, mostly of different species, as they were felled along the ESE side of the fragment (Figure 1 in Sizer & Tanner 1999). Samples of known leaf area were taken from each collection, dried overnight in a field oven, and taken to Cambridge (UK) for nutrient analysis. Twenty of the 70 collections were selected at random for analysis of N, P and K. Twenty individuals were more than sufficient to obtain a representative mean for each nutrient because cumulative mean nutrient concentrations changed less than 5% with each extra individual, after seven individuals had been included (data not shown). Duplicate samples (200 mg) were dissolved in boiling concentrated sulphuric acid, with mercury as a catalyst, and hydrogen peroxide. The resulting solutions were analysed by standard techniques, for nitrogen and phosphorus colorimetry (ChemLab Instrument Methods Sheets CW2-008-11, 1982 and CW2-075-01, 1983), and for potassium flame photometry. A sample of standard leaf litter material was processed with each batch of analyses to check for consistency; and samples of this standard material were analysed by independent laboratories, which confirmed our analyses.

Litterfall

Four transects were set up in each of three study sites parallel to three edges of a soon-to-be-created 100-ha forest fragment (Figure 1 in Sizer & Tanner 1999). The transects were positioned inside the forest, 10, 50, 100 and 250 m from the future edges (the 250-m transects are treated as spatial controls in this study). Along each of the four transects, in each of the three study sites, six 1-m², litterfall traps were randomly positioned. There were thus 18 traps at each distance from the edge and 72 traps in total. Litterfall collections started on 11 June 1990, the traps were emptied on average every 22 d (mean = 21.8, SE = 1.1, n = 60) until 5 January 1994. Litterfall was separated into two categories. Objects > 5 mm diameter including branches and other large objects such as fruits are not considered in this paper. The rest, consisting mainly of leaves, with some small flowers, fruits and twigs, i.e. 'fine' litterfall, is the subject of this paper and is referred to as litterfall without qualification. The litterfall was dried at 65 °C for 48 h, or until constant mass, and weighed.

The litterfall samples from each of the 72 traps at days 30, 101, 129, 252 and 427 were pooled by transect, ground to pass a 1-mm sieve and homogenized. Thus for each collection date a total of 12 'bulk' samples was produced. These 'bulk' samples were analysed for N, P and K in Cambridge (UK) using the same techniques as for leaves.

Estimates of retranslocation of nutrients prior to abscission

Estimates of retranslocation were made using concentration per mass in live leaves and litter. These are only first approximations because they ignore (1)

any carbohydrate retranslocation; (2) any seasonal changes in leaf concentrations; (3) differences between species (mean values were used for both litter and live leaves; and (4) any effects of edge creation on live leaf concentrations (because live leaves were not collected in forest after edge creation). None the less because they were based on 18 traps per distance per time the broad patterns are likely to stand up to future more detailed study.

Statistical analyses

To analyse litterfall rates we first tested for any significant differences between our three sites. Total litterfall per trap was calculated for the whole time period then a two-way ANOVA was used to test for the effects of sites and distance. There was no significant difference between the three sites ($F = 1.61$, $df = 2, 60$; $P > 0.05$), nor was there a significant effect of transect distance from the edge ($F = 2.42$, $df = 3, 60$; $P > 0.05$), though there was a significant interaction ($F = 3.6$, $df = 6, 60$; $P < 0.01$). As there was a significant interaction between site and distance, the data for each site were analysed separately. For each of the three sites we used repeated measures analysis of variance to test whether there was a significant effect of time, of distance, and of an interaction (following the example in section 7.17 in Cochran & Cox 1957). Because there is a limit to the number of repeats which can be analysed in repeated measures ANOVA (number of litter traps [24 traps] – number of treatments [4 distances] > number of repeats; p. 118 in Von Ende 1993) we combined data per trap into seven 6-mo periods, which are approximately the drier and wetter periods in each year. After the repeated measures analysis we tested whether mean rates of litterfall were different between the 250-m transect (spatial controls) and the 100-m, 50-m and 10-m transects for every period; because this involved 21 comparisons in each site (seven periods and three distances) we adjusted our P-values for significance by $0.05/21$. For the three sites combined we present means and standard errors (based on $n = 18$ traps per distance per time), and rates along the 10-m, 50-m and 100-m transects as percentages of rates along the 250-m transect. We did not carry out statistical analyses for the 60 separate time periods.

Litterfall nutrient concentrations of the three 'bulk' samples for each distance and time were analysed by repeated measures ANOVA.

RESULTS

Litterfall rates

Along the 10-m transects there was a marked increase in litterfall in the months following edge creation, it was as much as 2.5 times that along the 250-m transects (Figure 2). The effect was significant over the first 6-mo in two of the three sites (Table 1). In the second 6-mo following edge creation, the wetter half of the year, litterfall along the 10-m transects was similar to that on the 250-m transect (Table 1). In the third 6-mo, the next drier period,

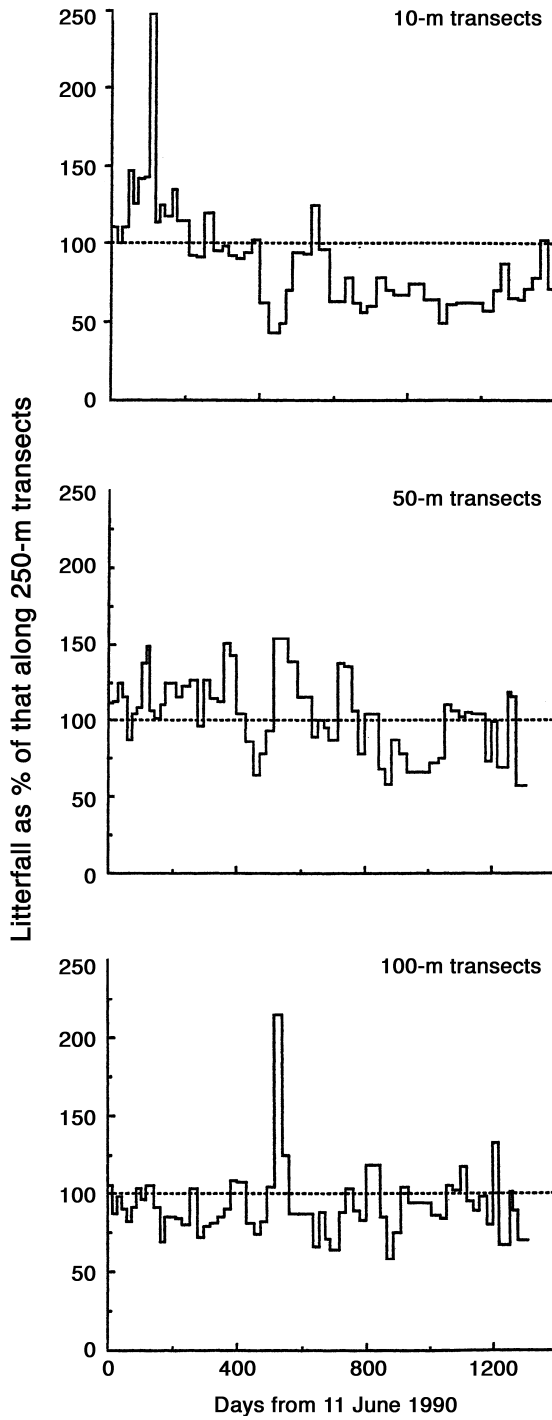


Figure 2. Litterfall along the 10-m, 50-m, and 100-m transects expressed as percentages of that along the 250-m transects.

Table 1. Rates of litterfall ($\text{g m}^{-2} \text{d}^{-1}$, means \pm SE, $n = 6$) for the first three *c.* 6-mo periods from the three study sites (see Methods, litterfall), analysed by repeated-measures analysis of variance. Significant differences between particular transects and 250-m transects at a given time within a site are indicated by: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; these are family P values after Bonferroni correction (0.05/21). There were no significant differences after the first three *c.* 6-mo periods.

Days from 11 June 90	Transects			
	10-m	50-m	100-m	250-m
Site 1				
0–175	***4.55 \pm 0.26	2.69 \pm 0.30	2.63 \pm 0.15	3.01 \pm 0.25
176–359	1.01 \pm 0.14	1.12 \pm 0.15	0.84 \pm 0.05	1.16 \pm 0.13
360–541	**1.38 \pm 0.11	2.34 \pm 0.25	2.87 \pm 0.26	2.60 \pm 0.20
Site 2				
0–175	***4.07 \pm 0.35	**3.87 \pm 0.13	2.55 \pm 0.36	2.28 \pm 0.29
176–359	1.11 \pm 0.19	1.41 \pm 0.11	1.08 \pm 0.16	1.13 \pm 0.16
360–541	*1.25 \pm 0.21	3.25 \pm 0.15	2.76 \pm 0.30	2.70 \pm 0.33
Site 3				
0–175	3.26 \pm 0.27	2.71 \pm 0.23	2.47 \pm 0.16	2.79 \pm 0.28
176–359	1.36 \pm 0.12	1.53 \pm 0.23	0.99 \pm 0.18	1.19 \pm 0.15
360–541	2.80 \pm 0.13	2.42 \pm 0.24	2.43 \pm 0.28	2.57 \pm 0.16

litterfall was lower on the 10-m transects compared to the 250-m transect, (significantly so in the two sites which had significantly higher litterfall one year previously). In the last 2 years of the study there were no significant differences between litterfall on the 10-m transect and that on the 250-m transect.

The 50-m transects showed a weaker effect of edge creation than the 10-m transects. The increase in the first dry season following edge creation was only significant in one of the sites (site 2, Table 1); and in the second dry season litterfall was not significantly different from that on 250-m transects. Along the 100-m transects the pattern of litterfall was not different from that on the 250-m transects (Figure 2).

There was a clear annual seasonality of the rates of litterfall with rates in the dry season 2–2.5 times those in the wet season (Figure 1); all three sites showed a highly significant effect of time ($P < 0.001$).

Live leaves and litterfall nutrient concentrations and retranslocation prior to leaf fall

Live leaves and litterfall along control transects had N, P and K concentrations similar to those from (similar) *terra firme* forest in the Ducke reserve about 80 km away (Table 2).

Phosphorus concentrations of litterfall were 53% higher ($P < 0.05$) at 10-m (0.43 mg g^{-1}) compared with those at 250-m (0.29 mg g^{-1}), in the litter that fell between days 115 and 129 (70 and 84 d after edge formation). This higher concentration may have been due to reduced retranslocation, because before edge creation P concentration in litterfall was 59% lower than that in live leaves but after edge creation it was only 24% lower. More detailed study is needed to test the hypothesis that P retranslocation was reduced following edge creation because there were some variations in N and K concentrations in litterfall for which we have no explanation (Sizer 1992).

Table 2. Mineral nutrient concentrations in live sunlit leaves from 20 randomly chosen individual canopy trees growing ESE of the 100-ha fragment at Dimona in the Central Amazonia, and of litterfall along the control transects; together with data from the Ducke Forest Reserve near Manaus.

	Live leaves (this study), mean and SE	Live leaves (Klinge 1976)
Concentration (mg g ⁻¹)		
N	17.6 ± 0.93	18.4
P	0.58 ± 0.047	0.66
K	3.6 ± 0.31	3.3
Litterfall on control transect (this study)		
Litterfall ('Total'; Klinge & Rodrigues (1968a, b))		
Mass (t ha ⁻¹ y ⁻¹)	8.3	7.4
N	15.0	14.3
P	0.30	0.31
K	1.9	1.7

DISCUSSION

Litterfall rates near to the edge of the forest fragment were increased immediately following edge creation and burning (compared to spatial controls 250-m from the edge); 1 y later they were lower than along spatial controls, after which they returned to rates similar to controls. The effect was variable being seen in only two of three sites and was stronger and lasted longer at 10-m from the edge compared to 50-m from the edge. No effects were detectable at 100-m. Thus the effect was transitory, apparently disappearing after 1.5 y, even on the 10-m transects.

The increase in litterfall was a result of cutting and burning. The timing of the increases in litterfall shows that cutting alone was sufficient to increase litterfall, burning the cut trees seems to further increase litterfall but a separate experiment is necessary to separate the effect of cutting and cutting plus burning. The return of litterfall rates to those on control transects after 1.5 y was probably due to three processes. Firstly, recovery of trees which were initially adversely affected by being exposed along a new edge. Secondly, the growth of shoots from existing stems, which form a 'curtain' of leaves where previously there were only trunks and branches. Thirdly, recruitment of fast growing light-demanders, vines (Laurance *et al.* 2000b) and growth of the advance regeneration (Sizer & Tanner 1999), in the elevated light near edges.

The increased litterfall P, caused by increased litterfall mass and litterfall P concentration, might represent a stress on the trees within 50 m of new forest edges in this ecosystem, which are likely to be P limited (Tanner *et al.* 1998). It would be interesting to see if P fertilization would lower the elevated mortality of trees which occurs near new forest edges in this area (Laurance *et al.* 2000a).

The discovery that effects on litterfall are strong, but reach only 50-m and last for only 1.5 y, is consistent with the effects of edge creation on soil moisture

and microclimate, which are also initially strong and reach 40-m from new edges (Kapos 1989). The effects on air temperature and relative humidity and soil water also decrease with time because the edges are 'sealed' by production of new leaves (Camargo & Kapos 1995). It would be interesting now to discover to what extent the original trees recover from exposure caused by proximity to the new edge, and to what extent the recovery in litterfall rates is due to growth of individuals which were recruited (to tree sizes) after edge creation.

Edge-related changes in litterfall are inextricably linked to the 'biomass collapse' reported by Laurance *et al.* (1997) for the same area; it is likely that death of trees causes both decrease in litterfall and decrease in standing biomass, it is also possible that premature loss of leaves causes some trees to die.

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