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Structure in Tropical Forest Fragments

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## Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments<sup>1</sup>

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### ABSTRACT

Edge structure is one of the principal determinants of the extent and magnitude of edge effects in forest fragments. In central Amazonia, natural succession at forest edges typically produces a dense wall of vegetation dominated by *Cecropia* spp. that buffers the forest interior. Fire encroachment into forest edges, however, eliminates the soil seed bank, enhances plant mortality, and promotes succession to an open, *Vismia*-dominated edge that does not buffer the forest interior. Contrasting open, fire-encroached forest edges and closed, non-fire-encroached edges were examined in central Amazonia to assess the effects of edge structure on microclimate and vegetation structure in tropical forest fragments. Edge penetration distances for most microclimate and vegetation structure variables were as much as two to five times greater at open edges than at closed edges. The magnitude of these differences suggests that edge structure is one of the main determinants of microclimate and vegetation structure within tropical forest fragments.

Edge effects also varied systematically with fragment area. For a given edge type, 100-ha fragments had consistently lower canopy height, higher foliage density, higher temperature, a higher rate of evaporative drying, lower leaf litter moisture content, and lower litter depth than continuous forest, at all distances from the forest edge. These differences, however, were relatively minor compared to the striking differences in edge penetration between open and closed forest edges. For organisms in small fragments, the difference between open and closed edges may be the difference between total edge encroachment on one hand and an effective nature reserve on the other, relatively independent of absolute fragment area.

**Key words:** *Cecropia*; central Amazonia; edge effects; fire; forest fragmentation; microclimate; succession; vegetation structure; *Vismia*.

TWO PRINCIPAL SETS OF FACTORS DETERMINE the extent and magnitude of edge effects in forest fragments. First, climate influences “edge penetration distance” (the distance to which edge effects can be detected into the forest), both spatially through variation in such factors as aspect and latitude (Wales 1972; Ranney *et al.* 1981; Williams-Linera 1990a, 1993; Brothers & Spingarn 1992; Matlack 1993; Fraver 1994; Young & Mitchell 1994; Chen *et al.* 1995; Murcia 1995) and temporally, through variation in such factors as time of day and season (Young & Mitchell 1994, Chen *et al.* 1995). Second, edge structure has a further spatiotemporal influence on edge penetration distance. In some forest types, dense second growth always develops

at the forest edge and buffers the forest interior (Gysel 1951; Wales 1972; Ranney *et al.* 1981; Palik & Murphy 1990; Williams-Linera 1990a, b, 1993; Brothers & Spingarn 1992; Kapos *et al.* 1993; Fraver 1994; Young & Mitchell 1994; Camargo & Kapos 1995), while this does not occur in other forest types (Chen *et al.* 1990, 1992, 1993a, b, 1995). In addition, edge structure often, but not always, becomes more dense with time (Williams-Linera 1990a, Matlack 1993, Camargo & Kapos 1995). The traditional focus of edge effect studies has been on climatic factors, and relatively little consideration has been given to the importance of edge structure as a determinant of edge penetration distance.

Forest regeneration in natural gaps and at edges is a lottery between competing “weedy” species, such as *Cecropia* spp. in central Amazonia and dormant forest seeds and seedlings (Barton 1984, Brokaw 1985, Garwood 1989). Williams-Linera (1990b) showed that established seedlings and seeds in the soil seed bank are more important than dispersing pioneers in the closure of newly formed

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edges. As the edge ages and secondary vegetation becomes more dense, edge penetration declines from as high as 50–100 m down to 0–20 m after 5–10 years (Kapos 1989, Williams-Linera 1990a, Matlack 1993, Camargo & Kapos 1995). Some forest types, particularly at higher latitudes, regenerate much more slowly of course, and edge penetration may not decline significantly for 20 years or more (Williams-Linera 1990a). Some other forest types essentially do not regenerate at edges in the short to midterm, and edge penetration distances are maintained indefinitely at 137–240 m or more (Chen *et al.* 1990, 1992, 1993a,b, 1995).

There is a further, generally unrecognized modification of edge structure that greatly enhances the severity of edge effects in fragmented forests, one resulting from fire encroachment. Fire encroachment, as a direct result of land management practices, modifies edge structure and inhibits the normal increase in vegetation density with edge age. Consequently, the forest interior remains unbuffered from external influence. Here, we present an extreme example of the impact of edge structure on microclimate and vegetation structure in fragmented forest in central Amazonia to illustrate the marked difference in edge penetration between dense, closed edges and (fire-encroached) open edges.

## EDGE STRUCTURE IN CENTRAL AMAZONIA

At many forest edges in central Amazonia fire encroachment into the forest causes marked changes in edge structure, due to plant mortality (Lovejoy *et al.* 1986), the elimination of the soil seed bank (Fearnside 1990, Maury-Lechon 1991), changes in soil structure (Buschbacher 1986, Fearnside 1990), and the dominance of hardy secondary growth species of the genus *Vismia* (for a general discussion of fire ecology, see Whelan 1995). *Vismia* spp. are low-growing (5–8 m) tree species well adapted to xeric environments, and dominate the early stages of succession after fire by inhibiting other seedlings (Uhl & Jordan 1984, Maury-Lechon 1991). At fire-encroached, open edges, ten years after their creation, *Vismia* spp. still dominate in a hot, dry environment that shows no sign of succession. In marked contrast, regeneration at closed, non-fire-encroached edges is more similar to regeneration in treefall gaps where a dense, secondary-growth plant community develops from the intact soil seed bank (and via dispersal inputs). *Cecropia* spp., in particular, grow rapidly to 15–20 m and form a relatively

dense canopy. Lower vegetation strata are similarly dense and the edge effectively becomes a closed wall of vegetation, buffering the interior from external microclimatic influences. There is, therefore, a stark dichotomy in edge type between closed edges dominated by *Cecropia* spp. and open (fire-induced) edges dominated by *Vismia* spp.

The lack of a dense regrowth zone at open edges results in a greater likelihood of edge effects penetrating deep within the forest interior, profoundly affecting the size of the undisturbed core area in forest fragments (Laurance & Yensen 1991). Fire-induced changes in edge structure appear to be stable, at least on the order of several decades. Qualitatively then, these two edge types vary greatly in microclimate and vegetation structure. The quantitative importance of edge structure in modifying the interior environment of forest fragments is the focus of this study.

## METHODS

**STUDY SITE.**—The study was carried out January–August 1994 at the Biological Dynamics of Forest Fragments Project (BDFFP), 80 km north of Manaus, central Amazonia Brazil (2°25'S, 59°50'W). The Instituto Nacional de Pesquisas da Amazônia (INPA) and Smithsonian Institution-administered experimental forest fragmentation area offers an unparalleled opportunity to examine edge effects at sites of known age and history. The forest is a uniform upland dry (terra firme) forest on yellow alic latosol soils of high clay content (Chauvel 1983). The climate in central Amazonia is highly seasonal with a pronounced dry season June–October at the BDFFP. Rainfall during the study period increased steadily from 230 mm/mo in January to 400 mm/mo in April, and then decreased to 100 mm/mo in July and August (Didham 1997). Forest disturbance in the area is due principally to cattle ranching, with pastures created and maintained by fire. For further description of the study area see Lovejoy *et al.* (1986), Bierregaard *et al.* (1992), and Bierregaard and Stouffer (1997).

Four edges, all created 10–12 years ago, were selected for study; there were two open edges and two closed edges. To determine the relative importance of edge structure over fragment area, edge effects were measured in two 100-ha fragments (one open, one closed) and in two continuous forest edges (open and closed). All edges were adjacent to well maintained pasture and all were west-facing, except the open-edged 100-ha where the only edge adjacent to well maintained pasture was north-fac-

ing. Pasture was maintained by grazing and localized burning (although there was no evidence that fire encroached upon edges after initial edge formation). Edges were up to 30 km apart, and while this degree of separation could affect environmental measurements on a given day (*e.g.*, localized rainfall patterns), overall variation in edge effects among transects should not be dependent on site location at this scale. Two continuous forest transects located 10 km from the nearest clearcut edge and >2 km apart acted as controls.

**SAMPLING FOR EDGE EFFECTS.**—Transects were sampled repeatedly at seven distances from the forest edge (0, 13, 26, 52, 105, 210, and 420 m), reflecting the assumption that environmental conditions would change most rapidly with distance immediately adjacent to the forest edge. Samples were taken at an identical series of distances along the two deep forest control transects.

Sampling was designed to quantitatively describe forest edges in three ways: (1) vegetational structure of open versus closed edges, using measures of canopy height and canopy density; (2) microclimatic changes in response to edge structure, quantified by air temperature and evaporative drying rate; and (3) changes in the ground layer, quantified by leaf litter moisture content, litter depth, and standing litter biomass.

**VEGETATION STRUCTURE.** In the early dry season, June 1994, ten 5 × 5 m quadrats were randomly located perpendicular to the transect at each site, and sampled for canopy height and density using modifications of the methods of Hubbell and Foster (1988).

**Canopy height.** All measurements were made by the same observer (RKD) and are a relative measure of canopy height, estimated against the height of a 3-m sighting pole. These measurements tended to underestimate actual canopy height by *ca* 3–5 m when compared to measures made with a range finder along one of the same transects (Camargo 1992). Five measurements of canopy height (and canopy density, see below) were taken in each of the ten 5 × 5 m quadrats at each site and the resulting mean values used in subsequent analyses. The data were not normally distributed; therefore, canopy height is expressed as the mean ± 95 percent confidence limits after back-transformation from cubic-transformed variates. At the 100-ha closed edge transect, variates could not be normalized and data are presented as median ± quartile values. Average continuous forest canopy height is the mean ± 95 percent confidence limits of *N* =

140 measurements from the 14 sampling points along the two continuous forest control transects. More than other variables, canopy height may vary as a function of pre-fragmentation conditions, as well as subsequent modification due to fragmentation.

**Canopy density.** A 3-m pole was used as a vertical sighting instrument to estimate canopy (>5 m) foliage density, scored on an arbitrary scale of 0 to 3 (0 = no foliage intercepting the line of sight; 1 = trace–33% foliage in line of sight; 2 = 33–66% foliage in line of sight; and 3 = 66–100% foliage in line of sight). The data were not normally distributed and are presented as median ± quartile ranges. Continuous forest background foliage density is the median ± quartile range of *N* = 140 measurements at the 14 sites along the two continuous forest control transects.

**MICROCLIMATE.** During the dry season, from mid-July to mid-August 1994, air temperature and evaporative drying rates were measured simultaneously between 1000–1500 h on three consecutive days by continuously walking back and forth along transects and taking readings at each sampling distance. These data characterize early to mid dry season daytime gradients.

**Temperature.** Air temperature was measured 1.8 m above ground level with an electronic temperature probe (Atkins K thermocouple thermometer, model 39565-K; accurate to 0.1°C). In an attempt to overcome variation in air temperature among different transects sampled on different days, a standard daily (1000–1500 h) temperature cycle was constructed from six days' measurements at the 14 sites along the two continuous forest control transects (Fig. 1). Air temperatures along edge transects were then expressed as the difference between observed air temperature and "expected" continuous forest air temperature at the same time of day. Temperature differentials at each of the seven sampling distances are the mean (±SE) of *N* = 33 (100-ha closed edge), *N* = 27 (100-ha open edge), *N* = 23 (continuous forest closed edge) or *N* = 30 (continuous forest open edge) measurements. For comparison, continuous forest "background" temperatures are presented as the mean ± 95 percent confidence limits of residuals around the fitted temperature profile in Figure 1 (*N* = 740).

**Evaporative drying rate.** Evaporative drying rate was measured using the simple apparatus illustrated in Figure 2. The apparatus uses readily available materials: a test tube, wooden spatula, and filter paper wick, to increase evaporative surface area.

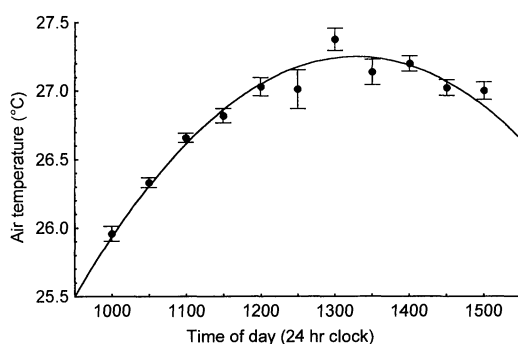


FIGURE 1. Daily (1000–1500 h) air temperature profile for deep continuous forest in central Amazonia. Plotted values are mean ( $\pm 1$  SE) air temperature ( $^{\circ}\text{C}$ ) in 30-min time classes, pooled across six days' measurements at 14 sites. The quadratic function  $y = 5.65 + 3.25x - 0.12x^2$  describes the temperature profile during this time interval ( $R^2 = 0.329$ ,  $N = 740$ ).

Rate of water loss (calculated in ml/hour) can be altered to suit the experimental situation (and ease of measurement) by changing the surface area of the wick. Evaporative drying measures are thus comparative and are a product of ambient temperature, relative humidity, and wind speed—factors of greater combined biological importance for organisms than measures of relative humidity alone. Measurements were made at ground level using five tubes located randomly at each site. Approximately hourly measurements were taken at each sampling distance along transects for three consecutive days, in conjunction with air temperature measurements. Because tubes were placed in the same locations each day, hourly rates and differences among the five tubes at each site were not independent. Therefore, a mean daily rate of evaporative water loss was calculated across all hourly measurements from all tubes. Evaporative drying rate at each sampling distance is thus the mean ( $\pm \text{SE}$ ) of  $N = 3$  daily rates. Continuous forest “background” evaporative drying rate is the mean ( $\pm 95\%$  confidence limits) of three days' measurements at the 14 sites along continuous forest control transects ( $N = 42$ ).

**GROUND LAYER.** Three leaf-litter variables were measured during the rainy season from January to May 1994: litter depth, biomass, and moisture content. Twenty  $25 \times 25$  cm quadrats were randomly located at each sampling point and all fine litter (*i.e.*, excluding woody debris  $> 2$  cm diameter) was collected down to the compact soil layer. Daily sampling was randomly allocated among different transects and sites from January to May to prevent bias arising from daily and monthly vari-

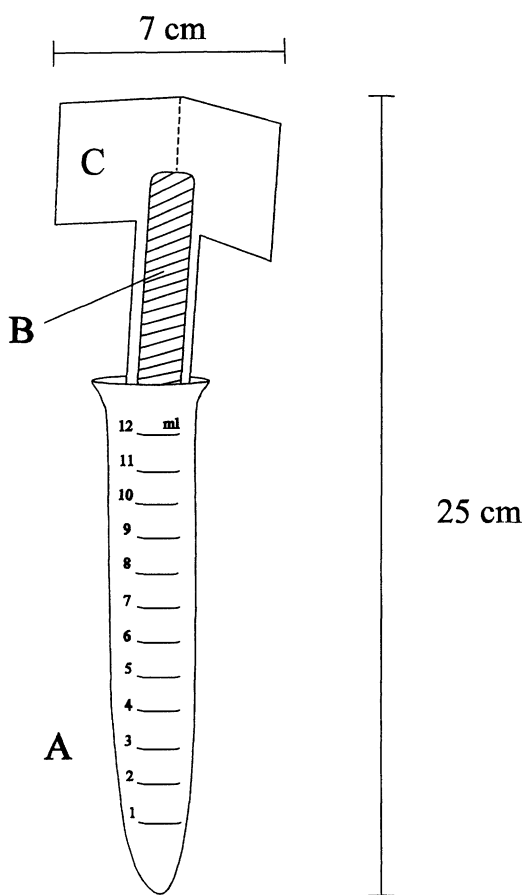


FIGURE 2. A simple apparatus for measuring relative evaporative drying rates. The apparatus consists of a graduated tube filled with water (A) and a wooden spatula (B) supporting a filter paper wick (C). The wick changes the evaporative surface area to increase or decrease the rate of water loss, depending on the frequency of measurement. In this study the wooden spatula was  $1 \times 25$  cm, and the wick was 14-cm long and had a total exposed surface area of  $35 \text{ cm}^2$ .

ation in leaf litter variables. The litter was weighed, and then oven-dried and weighed again; moisture content was calculated as  $1 - \text{dry weight/wet weight}$ . Five litter depth measurements were made with a ruler in undisturbed litter immediately adjacent to the litter quadrats and the mean of these used as a single variate in subsequent analyses. Continuous forest “background” values are the mean ( $\pm 95\%$  confidence limits) of measurements at the 14 sites along the two continuous forest control transects ( $N = 280$ ). Means ( $\pm 95\%$  confidence limits) for litter biomass are presented as back-transformed values from  $\ln$ -transformed vari-

ates, and means ( $\pm 95\%$  confidence limits) for litter moisture content are back-transformed from arcsine square root transformed percentages.

**ANALYSIS.**—Because environmental variables were sampled repeatedly at discrete distances from the forest edge, we tested for significant trends in the data using ANOVA with (Type I) regression approach (Sokal & Rohlf 1995: 476). Coincidentally, three of the four edge transects had unusually high air temperature (and other variable) measurements at the 420-m distance as a result of close proximity to treefall gaps or windward-facing ridges. These data are treated as outliers and all regression calculations exclude 420-m sites.

For each environmental variable, we tested the significance of deviations from a linear regression and the equality of regression slopes among the four edge transects; however, none of the data met the assumptions of ANCOVA and so direct comparisons among regressions was not possible. When the data could not be normalized (*i.e.*, canopy height at the 100-ha closed edge and canopy density at all edges), we used the nonparametric Kendall's rank correlation coefficient to test for significant trends in the data as a function of log distance from forest edge (Sokal & Rohlf 1995: 539). This method does not tell us the slope of the relationship, only that it is significantly different from zero. This is sufficient for our purposes since we are primarily interested in edge penetration distance, which we calculate by a different method (see below).

**MEASURING EDGE PENETRATION DISTANCE.**—Edge effects generally attenuate curvilinearly with distance from forest edge as they approach the background primary forest level (*e.g.*, Kapos 1989; Williams-Linera 1990a; Chen *et al.* 1992, 1993a, 1995, 1996). To estimate the rate of attenuation, we regressed each environmental variable ( $y$ ) against discrete log-transformed distances ( $x$ ) using ANOVA with (Type I) regression, but fitting *only* those sites that differed significantly (at the 95% confidence level) from the forest interior. We used the Spjøtvoll/Stoline post hoc comparison of means test (the  $T'$ -method, an extension of Tukey's honestly significant difference [HSD] test for unequal sample sizes [Spjøtvoll & Stoline 1973]) to establish which sites differed significantly from conditions along the continuous forest control transects ("edge" sites), and which sites did not ("core" sites). This procedure is conservative, and will generally

underestimate the full extent of edge penetration into the forest interior.

When only one or two sampling distances closest to the forest edge (0–13 m) were significantly different from continuous forest background levels, it was not possible to fit a regression. In these cases, edge penetration distances were estimated as the midpoint distance between the last sampling distance that was significantly different from continuous forest and the adjacent interior sampling distance.

## RESULTS

**CANOPY HEIGHT AND DENSITY.**—Canopy height (Fig. 3a) declined significantly from the interior to the edge of both open and closed forest edges (continuous forest closed edge:  $F_{(1,4)} = 56.73$ ,  $P < 0.002$ ; 100-ha closed edge: Kendall's  $\tau = 0.453$ ,  $N = 60$ ,  $P < 0.0001$ ; continuous forest open edge:  $F_{(1,4)} = 13.19$ ,  $P < 0.025$ ; 100-ha open edge:  $F_{(1,4)} = 13.48$ ,  $P < 0.025$ ). The forest rapidly approached full canopy height within 10–20 m of the edge, although there was a more extensive low-canopy zone at the 100-ha closed edge.

As expected, canopy density (Fig. 3b) differed markedly between open and closed edges. Foliage density declined sharply in the low-canopy *Vismia* zone (0–13 m) at open edges (continuous forest open edge: Kendall's  $\tau = 0.338$ ,  $N = 60$ ,  $P < 0.0002$ ; 100-ha open edge:  $\tau = 0.205$ ,  $N = 60$ ,  $P < 0.025$ ), but remained high (or increased) at the boundary of closed edges (continuous forest closed edge:  $\tau = -0.249$ ,  $N = 60$ ,  $P < 0.005$ ; 100-ha open edge:  $\tau = 0.003$ ,  $N = 60$ , NS). Consequently, canopy foliage density was strongly correlated with canopy height at open edges (Spearman's  $r = 0.687$ ,  $P < 0.0001$ , and  $r = 0.641$ ,  $P < 0.0001$ ; both  $N = 70$  for 100-ha and continuous forest edges, respectively), but more weakly, or not at all, at closed edges ( $r = 0.312$ ,  $P < 0.009$ , and  $r = -0.042$ ,  $P < 0.730$ ; both  $N = 70$  for 100-ha and continuous forest edges, respectively). At both open and closed edges, 100-ha forest fragments had consistently lower canopy height and consistently higher foliage density than continuous forest edges.

**AIR TEMPERATURE AND EVAPORATIVE DRYING RATE.**—Air temperature (Fig. 3c) increased significantly from the interior to the edge of all edge transects (continuous forest closed edge:  $F_{(1,4)} = 17.74$ ,  $P < 0.02$ ; 100-ha closed edge:  $F_{(1,4)} = 35.75$ ,  $P < 0.005$ ; continuous forest open edge:  $F_{(1,4)} = 230.43$ ,  $P < 0.0001$ ; 100-ha open edge:  $F_{(1,4)} =$

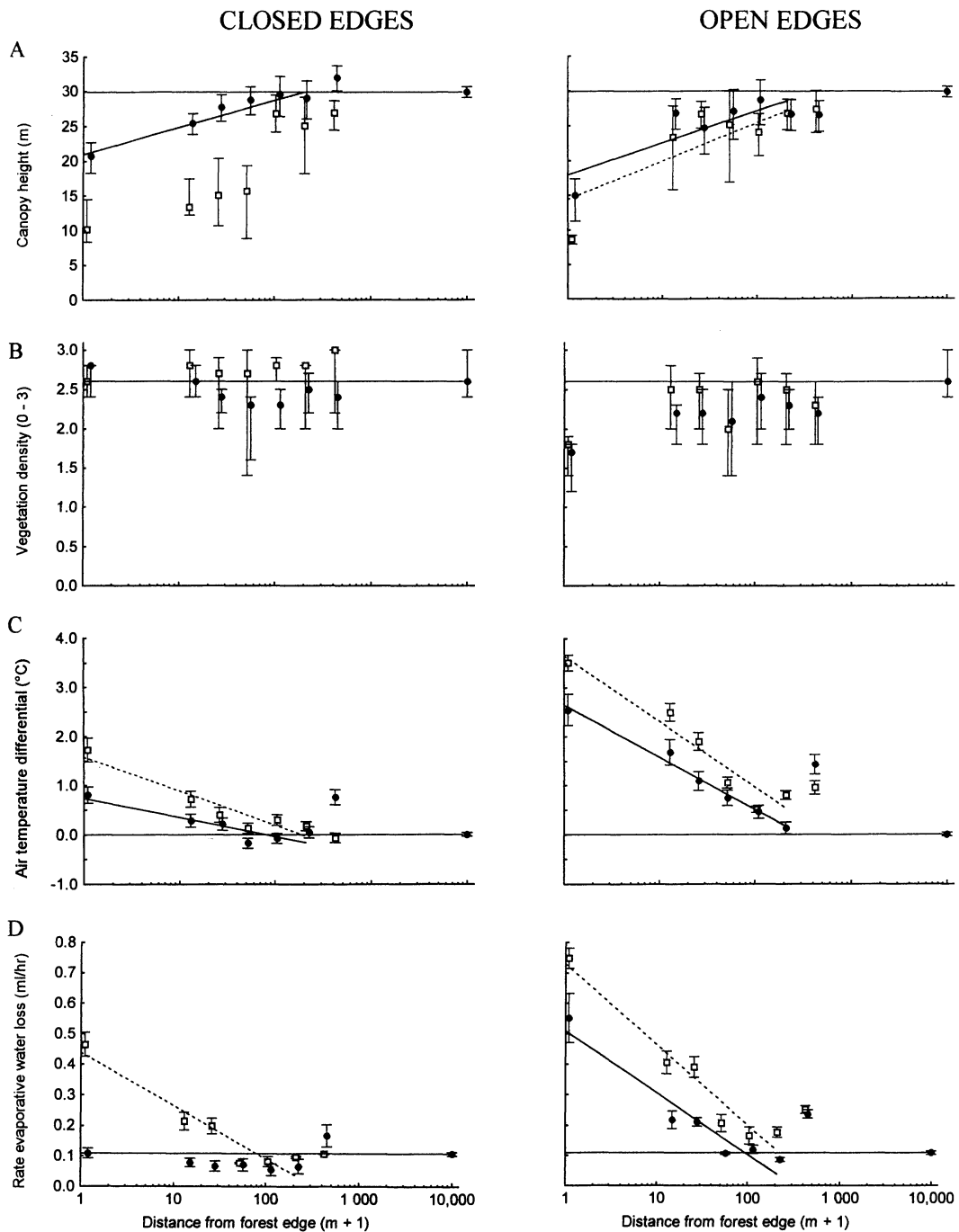
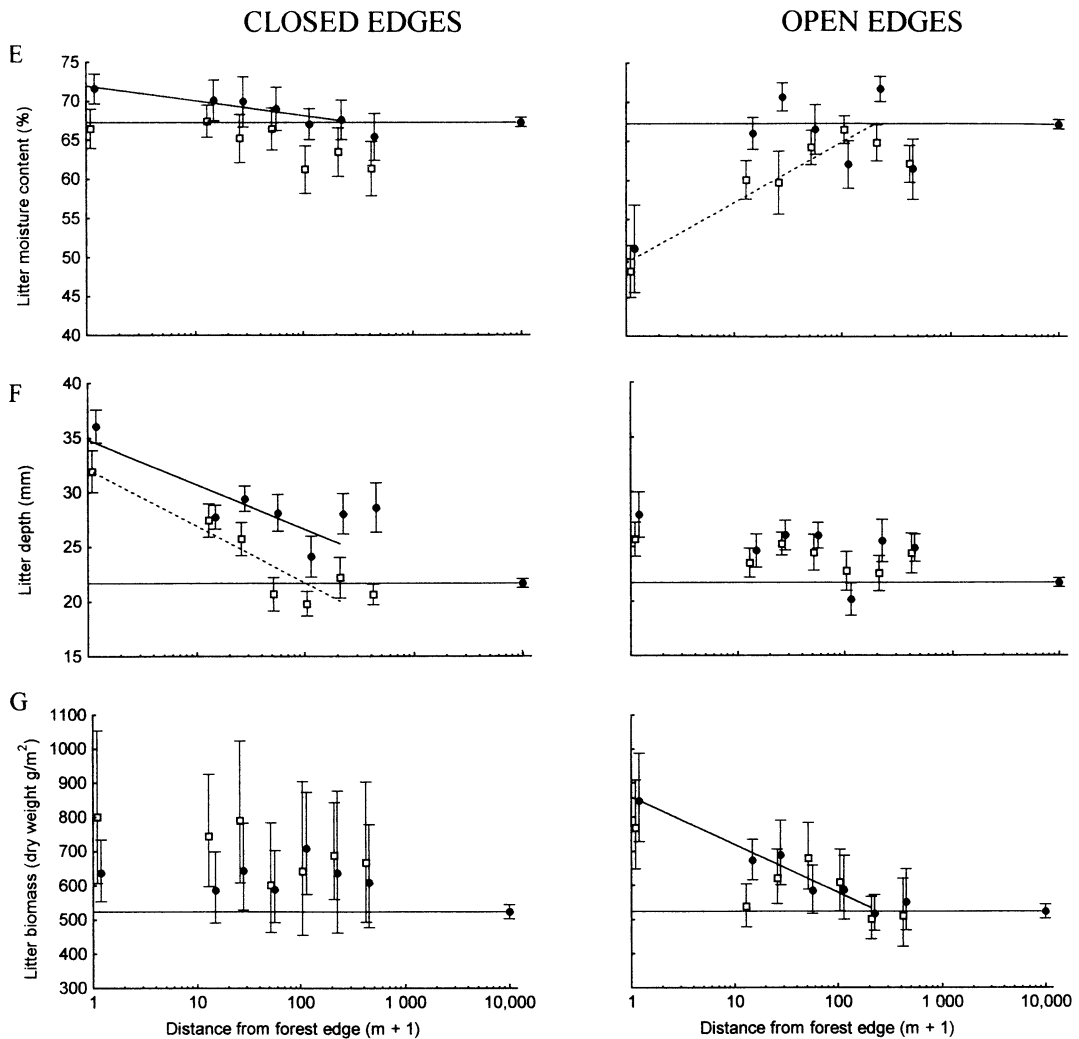


FIGURE 3. Variation in microclimate and vegetation structure between closed edges and open edges in central Amazonia. Filled circles and solid fitted regression lines = continuous forest edges; open squares and dashed fitted regression lines = 100-ha fragment edges. Regressions were calculated for 0–210 m sites only. Solid horizontal lines indicate “background” levels measured at the 14 sites along the two continuous forest control transects. Note that distance from forest edge is on a log scale. (a) transformed mean ( $\pm 95\%$  CL) canopy height, except the closed 100-ha edge where data are median ( $\pm$  quartile values [continuous forest closed edge:  $y^3 = 9211.18 + 3264.90 \log(x + 1)$ ; continuous forest open edge:  $y^3 = 5764.12 + 3254.75 \log(x + 1)$ ; 100-ha open edge:  $y^3 = 2978.95 + 3154.63 \log(x + 1)$ ]; (b) median ( $\pm$  quartile) canopy density; (c) mean ( $\pm$  SE) air temperature [continuous forest closed edge:  $y =$

FIGURE 3. *Continued.*

46.99,  $P < 0.005$ ). Figure 3c provides the most striking example of differing environmental gradients between open and closed forest edges. Regression slopes varied significantly among edges ( $F_{(3,16)}$

$= 9.60$ ,  $P < 0.001$ ), with open edges having significantly higher slopes than closed edges (post hoc multiple comparison of slopes test). In addition, within each edge type, 100-ha forest fragments

0.74–0.17  $\log(x + 1)$ ; 100-ha closed edge:  $y = 1.58 - 0.30 \log(x + 1)$ ; continuous forest open edge:  $y = 2.64 - 0.46 \log(x + 1)$ ; 100-ha open edge:  $y = 3.65 - 0.58 \log(x + 1)$ ]; (d) mean ( $\pm$ SE) daily rate evaporative water loss from an experimental apparatus [100-ha closed edge:  $y = 0.44 - 0.08 \log(x + 1)$ ; continuous forest open edge:  $y = 0.51 - 0.09 \log(x + 1)$ ; 100-ha open edge:  $y = 0.73 - 0.12 \log(x + 1)$ ]; (e) transformed mean ( $\pm$ 95% CL) litter moisture content [continuous forest closed edge:  $\arcsin \sqrt{y/100} = 58.01 - 0.52 \log(x + 1)$ ; 100-ha open edge:  $\arcsin \sqrt{y/100} = 44.566 + 1.95 \log(x + 1)$ ]; (f) mean ( $\pm$ SE) litter depth [continuous forest closed edge:  $y = 34.80 - 1.78 \log(x + 1)$ ; 100-ha closed edge:  $y = 32.12 - 2.26 \log(x + 1)$ ]; and (g) transformed mean ( $\pm$ 95% CL) litter biomass [continuous forest open edge:  $\log(y) = 6.76 - 0.09 \log(x + 1)$ ]. See Methods for units of measure and sample sizes. See Results for statistical significance.



were hotter than continuous forest at all distances <420 m from the forest edge (Fig. 3c).

Mean evaporative drying rates (Fig. 3d) were strongly positively correlated with mean air temperatures across all edge sites ( $r = 0.916$ ,  $P < 0.0001$ ,  $N = 28$ ). Consequently, results were similar to those obtained for air temperature differentials along the same edges (continuous forest closed edge:  $F_{(1,4)} = 4.00$ , NS; 100-ha closed edge:  $F_{(1,4)} = 42.71$ ,  $P < 0.005$ ; continuous forest open edge:  $F_{(1,4)} = 50.79$ ,  $P < 0.005$ ; 100-ha open edge:  $F_{(1,4)} = 80.57$ ,  $P < 0.001$ ). Regression slopes varied significantly ( $F_{(3,16)} = 18.08$ ,  $P < 0.0001$ ), with the regression slope for the 100-ha closed edge differing significantly from slopes of the other three edges.

**LITTER MOISTURE CONTENT, LITTER DEPTH, AND LITTER BIOMASS.**—There were marked differences in leaf litter moisture content between open and closed forest edges (Fig. 3e). Open edges, with high air temperatures and high evaporative drying rates, had correspondingly lower litter moisture contents near the forest edge. For the 100-ha open edge, there was a linear decrease in litter moisture content with decreasing log distance from forest edge ( $F_{(1,4)} = 51.15$ ,  $P < 0.002$ ); for the continuous forest open edge, litter moisture content varied significantly among sites ( $F_{(5,114)} = 24.05$ ,  $P < 0.001$ ), but not as a linear function of distance from edge ( $F_{(1,4)} = 6.38$ , NS; Fig. 3e).

In contrast, litter moisture content was not significantly affected by proximity to the forest edge at the 100-ha closed edge ( $F_{(1,4)} = 2.61$ , NS), and increased from the interior to the edge of the continuous forest closed edge ( $F_{(1,4)} = 25.42$ ,  $P < 0.01$ ; Fig. 3e).

Corresponding to the higher air temperatures and higher evaporative drying rates in 100-ha forest fragments, fragment edges had consistently lower litter moisture content than continuous forest edges (of the same edge type) at all distances from the forest edge. Across all edges, mean litter moisture content was strongly negatively correlated with mean air temperatures and mean evaporative drying rates ( $r = -0.488$ ,  $P < 0.009$  and  $r = -0.579$ ,  $P < 0.002$ , respectively; both  $N = 28$ ).

Leaf litter depth (Fig. 3f) did not vary significantly with log distance from forest edge at open edges (continuous forest open edge:  $F_{(1,4)} = 1.97$ , NS; 100-ha open edge:  $F_{(1,4)} = 6.29$ , NS), but did increase significantly from the interior to the edge of closed edges (continuous forest closed edge:  $F_{(1,4)} = 10.80$ ,  $P < 0.03$ ; 100-ha closed edge:  $F_{(1,4)}$

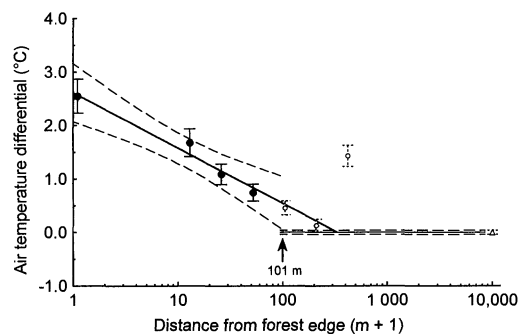


FIGURE 4. Sample calculation of edge penetration distance for mean ( $\pm$ SE) air temperature at the continuous forest open edge. ANOVA with (Type I) regression was used to calculate a log-linear function of air temperature versus distance from forest edge,  $y = 2.61 - 1.03 \log(x + 1)$ ,  $R^2 = 0.212$ ,  $N = 120$ . Only those sites significantly different from continuous forest air temperature (solid circles) were included in the regression (ignoring the aberrant 420-m site; see text). The intersection of 95% confidence limits for the regression and the 95 percent confidence interval for continuous forest air temperature (dashed lines) identifies the edge penetration distance,  $d = 101$  m.

$= 21.72$ ,  $P < 0.01$ ). For both edge types, continuous forest edges had marginally greater litter depth than 100-ha forest fragments at all distances from the forest edge. Interestingly, these patterns were largely reversed for leaf litter biomass (continuous forest open edge:  $F_{(1,4)} = 3.72$ , NS; 100-ha open edge:  $F_{(1,4)} = 64.62$ ,  $P < 0.005$ ; continuous forest closed edge:  $F_{(1,4)} = 0.21$ , NS; 100-ha closed edge:  $F_{(1,4)} = 3.44$ , NS; Fig. 3g). Surprisingly, litter depth and litter biomass were either relatively weakly, or not correlated at any edge (continuous forest open edge:  $r = -0.037$ ,  $P > 0.663$ ; 100-ha open edge:  $r = 0.238$ ,  $P < 0.005$ ; 100-ha closed edge:  $r = -0.014$ ,  $P > 0.865$ ; continuous forest closed edge:  $r = 0.042$ ,  $P > 0.626$ ; all  $N = 140$ ) or at control sites ( $r = 0.021$ ,  $P > 0.724$ ,  $N = 280$ ). Litter biomass also was considerably more variable at closed edges (Fig. 3g). Across all edges, mean litter biomass correlated strongly (and negatively) with mean canopy height ( $r = -0.433$ ,  $P < 0.02$ ,  $N = 28$ ).

**EDGE PENETRATION DISTANCE,  $d$ .**—The aberrant nature of some 420-m sites (see above) significantly overinflated measurements of edge penetration distance; thus 420-m sites were removed from all calculations of  $d$ . Figure 4 shows a sample calculation of edge penetration distance for air temperature at the continuous forest open edge. In this example,

TABLE 1. Variation in edge penetration distances (m) of seven microclimate and vegetation variables across edges of differing structure (open vs. closed) and forests of differing area (continuous forest vs. 100-ha forest fragments) in central Amazonia.

	Closed edges		Open edges	
	Contin- uous forest	100-ha frag- ment	Contin- uous forest	100-ha frag- ment
Canopy height	6.5	78.0	6.5	6.5
Canopy density	0.0	0.0	6.5	6.5
Air temperature	6.5	19.5	101.0	184.0
Evaporative drying rate	0.0	19.5	6.5	49.0
Litter moisture content	0.0	0.0	6.5	37.0
Litter depth	154.0	6.5	0.0	0.0
Litter biomass	0.0	39.0	6.5	6.5

only mean air temperatures at 0–52 m sites were significantly higher than in continuous forest (Spjøtvoll/Stoline test, all  $P < 0.0001$ ). Consequently, we fitted regressions using data from the 0–52 m sites only ( $F_{(1,2)} = 57.154$ ,  $P < 0.018$ ,  $N = 120$ ; *i.e.*, four sites of  $N = 30$  temperature measurements each). Edge penetration,  $d$ , was calculated from the intersection of 95 percent confidence bounds for the regression and the 95 percent confidence interval for variation in mean temperatures on the control transects (see Methods); by this method,  $d = 101$  m (Fig. 4).

Similar calculations (and midpoint distance estimates in cases in which regressions could not be fitted) produced widely varying edge penetration distances for different variables (Table 1). Nineteen of the 28 edge penetration distances were  $< 13$  m and for these measures the midpoint distance estimate was used (Table 1). The main relationships between edge penetration distances and edge type are depicted in Figure 5. Closed continuous forest edges were most similar to primary forest and had the lowest edge penetration distances for most variables; edge penetration distances thereafter increased in the sequence: 100-ha closed edge  $<$  continuous forest open edge  $<$  100-ha open edge. A significant increase in air temperature was detectable up to a remarkable 100–184 m from the forest edge at open edges. Edge penetration distances for evaporative drying rate were less extreme than those for air temperature, and edge penetration distances for litter moisture content were lower again (Fig. 5). Litter depth was an exception to this general ranking, with edge penetration distance being

greatest at the continuous forest closed edge. Canopy height and litter biomass showed no clear trends in edge penetration distances among edge types, although both had very high edge penetration at the 100-ha closed edge (Table 1).

## DISCUSSION

There were marked differences in edge effects between open edges and closed edges in central Amazonian forest. Edge penetration distances for most microclimate and vegetation structure variables were as much as two to five times greater at open edges than closed edges, irrespective of whether they were 100-ha fragment edges or continuous forest edges. These extreme differences between fire-encroached and non-fire-encroached edges are analogous to other components of spatial and temporal variation in edge structure that have been identified (Table 2). Studies of edge effects in forests with closed edges (*e.g.*, Gysel 1951, Wales 1972, Ranney *et al.* 1981, Miller & Lin 1985, Palik & Murphy 1990, Brothers & Spingarn 1992, Williams-Linera 1993, Fraver 1994, Young & Mitchell 1994) typically report markedly lower edge penetration distances than the few studies of forests with naturally open edge structure (*e.g.*, Chen *et al.* 1992, 1995; Table 2). This generalization holds for numerous biotic, as well as abiotic, variables. Temporally, the rapid increase in edge vegetation density as an edge ages produces a comparable decrease in edge penetration distance (Williams-Linera 1990a, Matlack 1993, Camargo & Kapos 1995; Table 2). Clearly, open versus closed edge structure and analogies such as young versus old or fire-encroached versus non-fire-encroached edges, have a major influence on edge penetration distances.

In addition to variation between open and closed edges, edge effects varied systematically with fragment area (although further data are required to rigorously test the statistical significance of these observations). For a given edge type, 100-ha fragments had consistently lower canopy height, higher foliage density, higher temperature, higher evaporative drying rate, lower leaf litter moisture content, and lower litter depth than continuous forest, at all distances from the forest edge. This indicates an unexpectedly strong effect of forest area on microclimate and forest structure. These variables are unlikely to respond in this manner to area reduction, *per se*; rather they appear to be responding to the shift from a single edge to multiple edges in isolated fragments. This conclusion is supported by

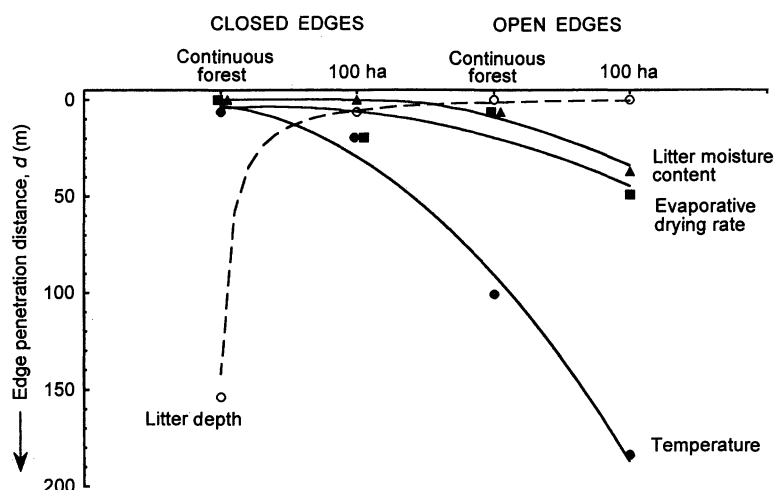


FIGURE 5. Graphical representation of the main trends in edge penetration distance with variation in edge structure. Edge penetration distances for air temperature, evaporative drying rate, and litter moisture content all increased with edge openness, while the opposite was true for litter depth. Lines were fitted by eye and simply serve to illustrate general trends.

recent additive models of edge effects (Malcolm 1994). The environment in forest fragments is thus more severe than expected from simple edge effect models.

The observed differences in edge effects between open and closed, and 100-ha and continuous forest edges produced a characteristic ranking of edge penetration: closed continuous forest edge < closed 100-ha fragment edge < open continuous forest edge < open 100-ha fragment edge. Abiotic factors, such as air temperature, rate of evaporative drying, and litter moisture content, showed the simplest (curvi-)linear functions of distance from forest edge. Edge penetration distances for these variables were highly intercorrelated; edge penetration for air temperature was detectable to 184 m at open edges, but to a lesser distance for evaporative drying rate and to an even lesser distance for litter moisture content, reflecting the dependence of the latter variables on air temperature in a form of "damped" measurable response. Air temperature itself is partially dependent on wind penetration; thus wind penetration should be detectable to still greater distances than air temperature. This is in accordance with the three to six tree height rule that forest meteorologists predict from heat and momentum flux (e.g., Raynor 1971, Miller 1980).

The utility of edge penetration measurements is in their application to fragmentation models (such as the core area model of Laurance & Yensen 1991) that predict the impact of edge effects on

biotic and abiotic processes in forest fragments of varying size and shape (Skole & Tucker 1993). As such, widely varying estimates of edge penetration for different variables at different forest edges have led to difficulties in determining "average" edge penetration. In this study, for example, edge penetration distances for most variables were <13 m, whereas air temperature was significantly elevated at 184 m into the open-edged 100-ha fragment. We have shown that much of this variation is due to varying edge structure. Rather than simply averaging measured edge penetration distances, a more useful approach would be to incorporate a measure of edge openness into fragmentation models. No agreed upon method exists to quantify "openness," but the most obvious candidate would be light levels at a standard point at the forest edge relative to external light levels. Air temperature would seem to be the simplest (as well as the most conservative) surrogate variable to develop models of edge penetration as a function of edge openness.

Research has yet to establish the biological importance of this degree of change in microclimate and vegetation structure for organisms living in forest fragments. There are also problems in extrapolating from the edge responses of abiotic variables to the edge responses of biotic variables (Murcia 1995). Vegetation structure does not appear to respond consistently to direct gradients in abiotic edge effects. Edge penetration distances for canopy height, canopy density, litter biomass, and litter

TABLE 2. *The impact of spatial and temporal variation in edge structure on edge penetration distances, m, of various biotic and abiotic variables. The range of values given for each variable incorporates aspect and other variation as presented by the original author. Measurements were arbitrarily calculated by a wide variety of methods, and hence are only broadly comparable. PAR = photosynthetically active radiation; VPD = vapor pressure deficit.*

	Closed edges	Open edges	Source
Spatial variation in edge structure:			
Canopy leaf density	15		Miller and Lin (1985)
Tree and sapling basal area	15–30		Ranney <i>et al.</i> (1981)
Plant stem density	15–30		Ranney <i>et al.</i> (1981)
Plant stem density	2–11		Gysel (1951)
Plant species composition	5–45		Palik and Murphy (1990)
Plant species richness	20–40		Fraver (1994)
Relative cover of exotic plants	10–60		Fraver (1994)
Density of saplings	0–10		Fraver (1994)
Plant species composition	10–50		Fraver (1994)
Plant species composition	0–15		Williams-Linera (1993)
Vegetation structure	0–20		Wales (1972)
Exotic plant invasions	0–10		Brothers and Spingarn (1992)
PAR, VPD, and temperature	10–50		Young and Mitchell (1994)
Canopy cover		44	Chen <i>et al.</i> (1992)
Plant stem density		43–85	Chen <i>et al.</i> (1992)
Plant growth		26–53	Chen <i>et al.</i> (1992)
Dead trees		125	Chen <i>et al.</i> (1992)
Plant regeneration		16–137	Chen <i>et al.</i> (1992)
Air temperature		180–240	Chen <i>et al.</i> (1995)
Soil temperature		60–120	Chen <i>et al.</i> (1995)
Humidity		240	Chen <i>et al.</i> (1995)
Shortwave radiation		15–60	Chen <i>et al.</i> (1995)
Wind speed		240	Chen <i>et al.</i> (1995)
Soil moisture		0–90	Chen <i>et al.</i> (1995)
Temporal variation in edge structure:			
	Old edges (>5 yr)	Young edges (0–1 yr)	
Canopy openness	5–6	10	Williams-Linera (1990a)
Dead trees	6–10	13	Williams-Linera (1990a)
VPD	0	40	Camargo and Kapos (1995)
Air temperature and humidity	0–10	40	Camargo and Kapos (1995)
PAR		40	Kapos (1989)
Soil moisture content	0–20	20	Camargo and Kapos (1995)
Light, VPD, shrub cover, temperature	0	0–50	Matlack (1993)
Litter moisture content	0–39	0–50	Matlack (1993)
Litter depth	15–40	0–23	Matlack (1993)

depth varied in a complex manner that may have more to do with biological processes than abiotic edge effects. For example, unlike other variables, leaf litter depth showed an inverse response to edge openness, with greatest edge penetration at closed continuous forest edges. *Cecropia* spp. abscise relatively few, very large leaves to the leaf litter at closed edges, while *Vismia* spp. abscise numerous small leaves at open edges, leading to marked differences in litter structure. Therefore, litterfall rates (Sizer 1992) and litter decomposition rates (Didham 1998) are likely to vary among edges. Leaf litter is significantly deeper at closed edges, al-

though litter biomass is similar. Differences in leaf size and fall rate also account for the lack of correlation between litter depth and litter biomass and the high variability of litter biomass at closed edges. A similar response for litter depth was found by Matlack (1993) in the eastern United States (Table 2).

We draw a simple, but important, message from these observations. While many abiotic factors decay as a simple function of distance from the forest edge, biotic systems may not necessarily respond in the same fashion (Murcia 1995). For example, an organism balancing optimal tempera-

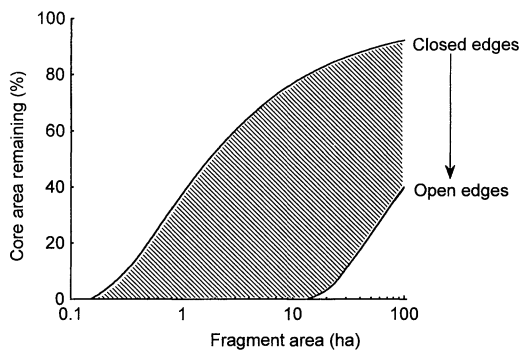


FIGURE 6. Illustrative example of percent remaining undisturbed core area in forest fragments of different sizes, based on air temperature edge penetration distances of 19.5 and 184 m for closed and open 100-ha edges, respectively. Remaining core area in a fragment of a given size varies enormously (shaded region) depending on the structure of the forest edge (e.g., for a 10-ha fragment, percent core area remaining can vary from 0–75% depending on edge openness).

ture and litter depth requirements may have a pattern of distribution apparently unrelated to either individual variable. Nevertheless, all other factors being equal, open edges should give rise to more adverse conditions for organisms within forest fragments, so that fragments with unbuffered, open edges will have a smaller unaffected core area than fragments with closed edges (e.g., Fig. 6). For organisms in small fragments, the difference between open and closed edges may be the difference between total edge encroachment on one hand and an effective nature reserve on the other. At the magnitude of edge penetration we measured (Table

1 and Fig. 5), edge structure will be of greater importance for many organisms in small forest fragments than the absolute area of the fragment (Fig. 6).

These results provide opportunities for conservation managers. The majority, but not all, forest edges respond rapidly to edge formation by forming a dense buffer zone around forest fragments (Gysel 1951; Wales 1972; Ranney *et al.* 1981; Palik & Murphy 1990; Williams-Linera 1990a, b, 1993; Brothers & Spingarn 1992; Kapos *et al.* 1993; Fraver 1994; Young & Mitchell 1994; Camargo & Kapos 1995). We have shown that unbuffered, open-edged fragments will be more severely impacted than fragments with closed edges. Hence, any form of nonintrusive buffering at open edges, including windbreak planting, will cause a marked two- to fivefold reduction in edge penetration, providing a ready management solution to the protection and enhancement of surviving forest fragments.

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