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CANOPY PERFORATION IN AMAZONIAN ECUADOR

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Abstract: The canopy perforation regime by means of treefall disturbance was monitored for two years in a 13.5 ha of old-growth *terra firme* rainforest at the Tiputini Biodiversity Station, Ecuadorian Amazon. The area of the 48 gaps formed during this time corresponded to ca. 1% of the forest area yearly, and resulted in a gap density of 1.55 - 2.00 gaps ha^{-1} y^{-1}. The size of these gaps was most frequently between 21 and 40 m^2, and the majority of sizes was smaller than 150 m^2, which constitutes a typical gap size distribution for a rainforest. Moreover, the amount of forest area opened by gaps per month was randomly distributed and roughly smaller than 300 m^2 over the two years, except for February with an exceptionally large gap. Of the forest area in gaps, about one half corresponded to interior zones, i.e. the uncovered area projected on the ground. Probably because of soil conditions, the most common gap-maker elements at TBS are uprooted trees, followed by snapped stems and by branch- and vinefalls. These gap-makers fell at random directions, and although uprootings are typical for domino events, most of the gaps were opened by a single gap-maker.

The turnover time at TBS was estimated between 49 and 83 years, but this parameter is strongly dependent on the definition of gap used. Roughly compared, the gap formation regime at TBS is similar to that of other rainforests, with only small variations in the share of the gap-maker elements.

The randomness and variability found among the considered parameters constitute additional sources of spatio-temporal heterogeneity of resources, which are considered as a key factor in stimulating forest diversity. The application of gap theory is therefore promising for forest management practice and conservation policy.

Introduction

Forest canopy dynamics involves two reciprocal spatio-temporal processes: perforation and aggregation (Forman 1997, Farina 2000). Perforation is the process of making holes (gaps) in the canopy, and is probably the most frequent way of beginning land transformation (Forman 1997). Canopy gaps are created by the falling of structural elements of the forest (gap-makers), such as trees, branches and vines, and constitute small time- and space-scale disturbances inherent to the forest system (Pickett & White 1985, Urban et al. 1987, Clark 1990). On the other hand, aggregation starts when disturbance by perforation stops; the vegetation then recovers and fills in the gap horizontally and vertically (Salvador-Van Eysenrode et al. 1998a, Farina 2000).

Canopy gap formation hence affects forest structure and composition, and is considered to be important in driving the forest cycle and in maintaining tree species diversity and coexistence. This occurs by allowing sunlight penetration to the understory, by making free space available for forest regeneration, and by creating resource heterogeneity (Watt 1947, Denslow 1980 and 1987, Brokaw 1982a, Pickett & White 1985, Oldeman 1989, Clark 1990, Hubbell et al. 1999).

Characterization and study of disturbance regimes enable comparison between ecosystems, and are crucial to couple structural, compositional, and developmental responses of species to the limits and dynamics of their environment.

In this paper, we quantify and evaluate aspects of the canopy perforation regime of an Ecuadorian lowland *terra firme* rainforest (Jacobs 1981), such as the number of gaps formed yearly, their size distribution, the presence of gap interior and edge, the type of gap-maker elements, and the gap formation rate and forest turnover time. Other aspects related to the perforation regime of our study location, such as gap shape (the two-dimensional distribution of gap area), and the spatio-temporal dispersion of the number of gaps are discussed elsewhere (see Salvador Van Eysenrode et al. 1998b, 1999 and 2000a). Finally, we compare our study with seven other reported studies on gap formation in Amazonian rainforest locations (Ecuador, French Guiana, Peru and Venezuela), and emphasize the role of gap theory for forest conservation.

Materials and Methods

Study site

We carried out the study at the Tiputini Biodiversity Station (TBS, joint venture between the Universidad San Francisco de Quito - USFQ - and Boston University - BU -). TBS comprises a 650 ha tract of old-growth lowland rainforest located in the province of Orellana, and adjacent to the Yasuní

Biosphere Reserve (0°40'S, 76° 20'W, altitude ca. 300 m). The yearly rainfall of the region, totaling around 3000 mm y^{-1}, follows a bimodal pattern; the yearly mean temperature exceeds 25 °C with a relative air humidity above 80% (Direccion de Aviacion Civil, Coca Airport, 0°27'8''S, 76° 59'2''W). The soils at TBS are alluvial and clayey, and the overall topography is flat (Baldock 1982). We performed the study in a 13.5 permanent sample plot of *terra firme* forest, which we delimited on a platform surrounded by an ox-bow lake and by swamps.

Gap definition

We used two standard definitions to delimit the gaps, namely the definitions of Runkle (1981) and Brokaw (1982a). We considered these definitions to be suitable for our study because of their significance at both the ground and the canopy level, and mainly because of their practical workability (Van der Meer et al. 1994). According to Runkle, a gap is defined as the *ground area under a canopy opening extending to the bases of the canopy trees surrounding the canopy opening*, while Brokaw defines a gap as *a hole in the canopy extending through all levels down to an average height of two m above the ground* (Van der Meer et al. 1994). The gap areas resulting from these definitions are further denoted as A_R and A_B respectively (Figure 1).

To determine gap area according to both definitions, we firstly marked all gaps with a metal stake in their centroid. To estimate A_B, we then traced 8 radii (at 45° intervals starting from the north) between the marking stake and the intersection point with the line of the ground projection of the crowns of the trees surrounding the canopy opening (the thick white dashed line in Figure 1). A_B was consequently calculated by adding the areas of the resulting octants. Likewise, we estimated A_R by tracing radii between the marking stake and the stem bases of the first trees surrounding the gaps, and by adding the areas of the resulting polygons enclosed by the line linking such stems. The first trees surrounding the gap were defined as those whose crowns enclosed the canopy opening, and to be considered as such, the stems of those trees also needed to have a minimum diameter at breast height of 20 cm.

Number of gaps

Within the plot, we located all canopy gaps (but to a minimum size of four m^2 A_B), and recorded their formation date (monthly resolution) as of October 1996 until December 1998. In order to detect annual variation, we divided the study into two time periods of approximately one year each: a first period from October 1996 until October 1997, and a second period from November 1997 until December 1998.

Gap interior and edge

Runkle and Brokaw define a gap as a 2-D polygon under a canopy opening, either at ground level or at two m height; consequently a gap can be considered as a forest *patch* in an early stage of regeneration (Watt 1947, Forman & Godron 1986, Oldeman 1989). A patch is composed of an *interior zone*, of an edge zone peripherical to the interior, and of a *perimeter* line enclosing the *edge zone* (Forman 1997). However, none of these zones can be discriminated by the definitions listed. In order to determine the interior (I) and edge (E) of the gaps, we combined A_R and A_B such that

$$E = A_R - A_B \tag{1}$$

Hereby it follows that $I = A_B$, and the gap edge is equivalent to A_R with the exception of I (Figure 1).

Gap-maker elements

We counted the number of gap-makers per gap, and from these we classified the gap *starter* by mode of falling as uprooted tree, snapped tree stem, fallen branch, or fallen liana (Clark 1990). We also discriminated between gaps opened by a single gap maker and by 'domino' events, i.e. gaps opened by more than one gap-maker. The fall direction

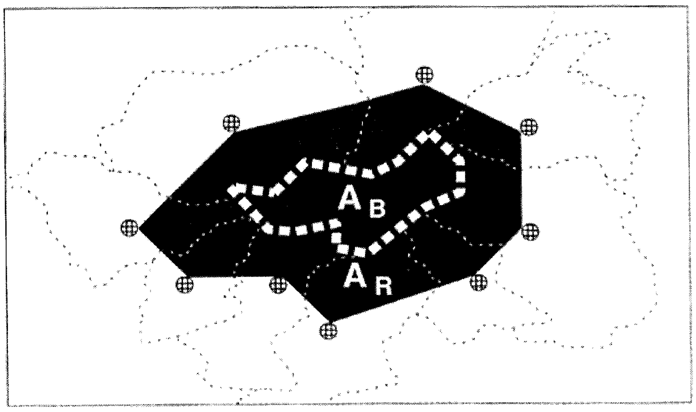

Figure 1. Ground projection of a canopy gap. The thin dotted lines represent the crowns of the trees surrounding the gap. The black area, extending to the stems (discs) of the surrounding trees, represents the gap area as defined by Runkle (A_R). This area contains the gap as defined by Brokaw (A_B, enclosed by the thick white dashed line), which is the vertical projection of the opened canopy.

of the gap *starter* element was also determined. We processed this directional - and also all circular - data using circular statistics (Batschelet 1981).

Gap formation rate and forest turnover

We determined the gap formation rate (a), defined as the cumulative area of forest opened up by gaps yearly as a percentage of the total forest (plot) area, using both A_R and A_B (Van Der Meer & Bongers 1996a). We calculated the forest (or stand) turnover time (t_l), which is the mean time interval between two successive gap formations at a same particular location (Pickett & White 1985). This t_l can be determined in two ways, based upon (1) tree mortality (Van Der Meer & Bongers 1996b), and (2) gap formation (i.e. using the gap formation rate). In this study, we applied the latter method using the following equation:

$$t_l = \frac{1}{a} \qquad (2)$$

This linear model, however, is limited by the assumptions of absence of re-disturbance, and of constancy throughout the years, which is not always the case (Young & Hubbell 1991). In order to avoid these limitations, Riéra and Alexandre (1988) proposed a stochastic model to calculate the *stand half life* ($t_{0.5}$), i.e. the time needed to cover half of the plot area with gaps. This was calculated using:

$$t_{0.5} = -\frac{\ln[0.5]}{a} \qquad (3)$$

Results

Number of gaps, and gap size distribution

Forty-eight gaps were formed in the plot at TBS during the whole study time: 21 in the first period, and 27 in the second. The gap density was 1.55 and 2.00 gap ha^{-1} y^{-1} for each period, respectively.

The gap size distribution for the whole study time, using A_B and A_R, was skewed to the right, i.e. towards the smaller size classes (Figure 2). The size distribution following Brokaw's definition was more skewed because of smaller gap sizes than the distribution based on Runkle's definition, as a consequence of the relationship $A_B < A_R$ (Figure 1). However, for both gap definitions, gap size frequencies were dominant between 21 and 40 m^2, and almost all gap sizes were smaller than 150 m^2. Only a non-significant difference was found in gap size distribution between the first and the second period (Mann-Whitney U-test, $P = 0.59$ for A_B, and $P = 0.56$ for A_R), and the gap size distribution of either of these periods was similar to the distribution of the complete survey (Figure 2).

The (temporal) distribution of the cumulative area (A_B) of monthly formed gaps showed a significant concentration for February, considering the whole study time (Figure 3, Rayleigh test for randomness, grouped data, $P < 0.001$, $\alpha =$ February; confirmation by the V-test for directedness, $P < 0.05$). Except for February, April and May, the total area opened by gaps was less than 300 m^2, and the peak observed

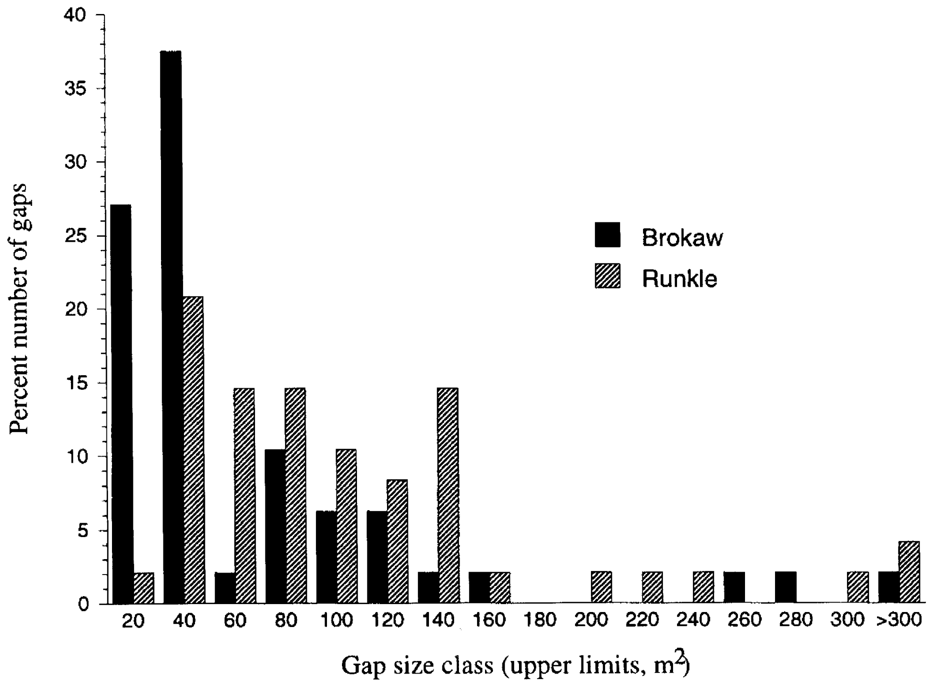

Figure 2. Size class distribution of gaps, sensu Brokaw (A_B) and Runkle (A_R) formed in the 13.5 ha plot in TBS during two years. The most frequent size class of each of the gap definitions is found between 21 and 40 m^2, and the relationship [$A_B < A_R$] is evident.

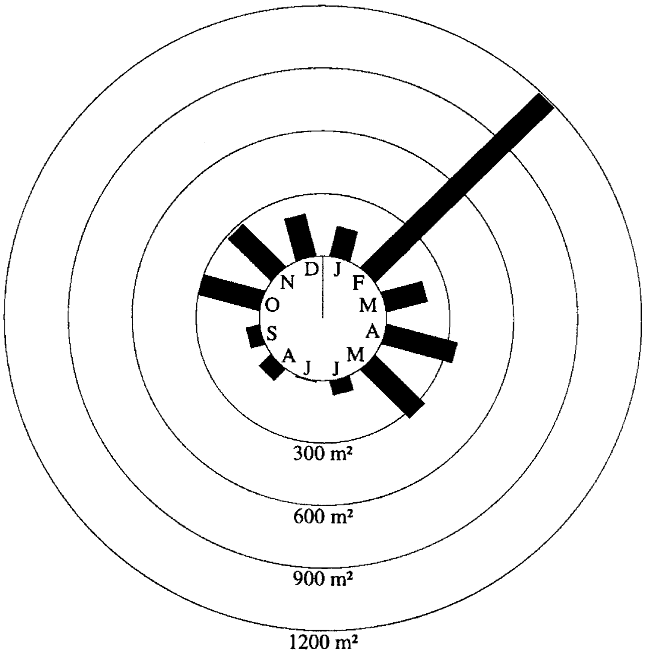

Figure 3. Distribution of forest area (m^2) opened to gaps (Brokaw's definition) by month, from October 1996 to December 1998 at TBS. Roughly less than 300 m^2 of forest area in gaps was observed, and the peak of February resulted from the coincidental occurrence of the largest gap in this month.

for February resulted from the coincidental formation of the largest gap in this month (750 m^2).

Gap interior and gap edge presence

Dividing the total gap area in an interior (I) and an edge (E) zone, we found that 58% of the total forest area opened by gaps (A_R) corresponded to I, while the remaining to E (whole study period considered). I was not found to be correlated with E (Spearman's r = 0.08, P = 0.56), and only a slight non-significant difference in gap edge size distribution was found between the first and the second period (Kolmogorov-Smirnov two sample test, $P > 0.05$).

Gap maker elements

For the whole study, we found the majority of gaps created by the falling of uprooted trees, followed by snapped trees, by branches and by vines (Table 1). Uprooted trees were found to be the common gap starters during both study periods; likewise, vinefalls were the rarest, but the relative contribution of snapped trees and branchfalls was switched between the first and the second study period.

During the complete survey, gaps were opened by a single gap-maker 1.5 times more than by domino events (Table 1). A fallen branch was the most frequent cause of gap formation by a single gap-maker element, equally followed by uprooted and snapped trees, and then by fallen vines. Nevertheless, for gaps started by a single gap-maker, variation was found if both periods were considered separately: during the first, two uprooted trees, three snapped trees, five branches, and one vine started gaps; during the second, the share changed to six uprooted trees, eight snapped trees, five branches, and two vines.

In the case of domino-wise created gaps, uprooted starters were the most common, followed by snapped trees, branches and a vine. Successively, the same order of frequency was also observed for the first study period (six uprootings, two snappings, one branch and one vine) and the second (five uprootings, three snappings, one branchfall and no vines). On average, 3.10 (SE ± 0.35) gap-maker elements were found per domino-wise created gap.

When relating gap starters to the total gap size, we found that about 2/3 (A_R) to 3/4 (A_B) of the cumulative gap area was opened by gaps started by uprooted trees (Table 1). The remaining fraction of the forest area was opened, in this order, by snapped tree stems, branches and vines. Finally, the gap starters in our plot fell at random directions, both for all gap starters together, and separately by type of gap-maker (Rayleigh test, $P > 0.05$ for all cases; vines and branches were pooled).

Gap formation rate and forest turnover

For the first and second study period, we found a gap formation rate of 1.50% and 0.90% for A_B; considering A_R, the gap formation rate for each period respectively was 2.24%

Table 1. Gap-starter data, and gap area opened by different gap starters for the 13.5 ha plot at TBS. I = October 1996 - October 1997, II = November 1997 - December 1998; N = 48.

	I	II	I + II				
Type of starter	gaps (%)	gaps (%)	gaps (%)	single (%)	domino (%)	A_B m² ($\overline{X} \pm$ 1SD)	A_R m² ($\overline{X} \pm$ 1SD)
Uprooted tree	8 (38.1)	11 (40.7)	19 (39.6)	8 (42.1)	11 (57.9)	2 415 (127.1 ± 162.0)	3 567 (192.5 ± 256.8)
Snapped tree	4 (19.0)	9 (33.3)	13 (27.1)	8 (61.5)	5 (38.5)	359 (27.6 ± 27.5)	919 (70.7 ± 50.1)
Branch	7 (33.3)	5 (18.5)	12 (25.0)	10 (83.3)	2 (16.7)	384 (32.0 ± 26.8)	712 (59.3 ± 27.7)
Vine	2 (9.5)	2 (7.4)	4 (8.3)	3 (75.0)	1 (25.0)	70 (17.5 ± 7.4)	276 (69 ± 45.3)
Total:	21	27	48	29 (60.4)	19 (39.6)	3 228 (67.3 ± 114.6)	5 564 (115.9 ± 176.1)

Table 2. Canopy gap surveys in Amazonian lowland rainforests. § = see eq. (3); † = assuming gap persistence of 5 y; ‡ = gap status at survey time; A_B and A_R = Brokaw and Runkle's gap definitions (A_{B4} = minimum gap size of 4 m² when known); gap formation rate: percentage of the plot area in gap phase per year; A = Uhl & Murphy 1981; B = Hartshorn 1990; C = Riéra & Alexandre 1988; D = Durrieu de Madron 1994; E = Van Der Meer & Bongers 1996a; F = Kapos et al. 1990; G = this study.

Study site	Study time (y)	Plot Size (ha)	Gap formation rate (% y^{-1})	Turnover (y)	Half life§ (y)
Venezuela					
San Carlos ^{A}	5	1	0.96†	104	72
Perú					
Palcazú ^{B}	3	9.7	1.09	92	64
French Guiana					
Ste. Elie ^{C}	3	21.3	1.1	100	63
Paracou ^{D}	7	18.75	1.33	75	52
Nouragues ^{E}	3	12	$0.22^{A_{B4}}/2.87^{A_R}$	$455^{A_B}/35^{A_R}$	$315^{A_B}/24^{A_R}$
Ecuador					
Sumino ^{F}	1	0.7	$1.4‡^{A_B}$	71	50
Río Quilla ^{F}	1	0.7	$5.1‡^{A_R}$	20	14
Tiputini ^{G}	2	13.5	$1.2^{A_{B4}}/2.06^{A_R}$	$83^{A_B}/49^{A_R}$	$58^{A_B}/34^{A_R}$

and 1.88% (Table 2). Using the mean gap formation rate of the two years, the stand turnover time (t_1) at TBS was estimated to be 83 years (A_B), and 49 years (A_R). The stand half life ($t_{0.5}$) was estimated to be 58 years, and 34 years, for each definition respectively. A turnover time obtained through the stand half life ($2 \times t_{0.5}$) results in 116 and 68 years respectively.

Discussion

Number of gaps and area

The yearly gap density found at TBS can be considered as typical for a rainforest, although some variation is reported among study sites and periods (e.g. Hartshorn 1978, Kapos et al. 1990, Van Der Meer & Bongers 1996a).

The distribution of gap size for both A_B and A_R was also similar to that found in other rainforest surveys, with a majority of gaps smaller than 150 m^2 (Brokaw 1982b, Denslow 1987, Jans et al. 1993, Durrieu De Madron 1994, Yavitt et al. 1995, Van Der Meer & Bongers 1996b). As in other Amazonian locations (unlike in the Caribbean region where hurricanes are a common disturbance phenomenon), very large gaps are exceptional at TBS, which means that, in general, the impact of the disturbance by perforation is limited with regard to size. Within its typical range, however, gap size varies depending on the definition of gap used, and this variation will influence all calculations of size-related parameters (Van Der Meer et al. 1994); the implications of this problem are further discussed with regard to the turnover rate (see below). To the degree that gap size is a good index of resource availability and microclimatic conditions, the gap size frequency distribution can be a useful basis to compare forest systems (Denslow 1987). Ecologically, gap size is considered as a dominant characteristic because it determines the amount of light reaching the understory, the physical space or area of a forest patch available for regeneration, and plant species composition and growth responses (Denslow 1980, Brokaw 1985, Salvador-Van Eysenrode et al. 1999).

Except for February, the temporal availability of total gap area in our plot was roughly less than 300 m^2, which corresponds to less than 0.002% of the total forest area. The coincidental occurrence of the largest gap in February statistically induced a non-random monthly distribution of forest area in gaps, but if this gap is considered as an outlier, then the distribution is random and no temporal concentration of gap area can be expected. Moreover, in a previous study on the temporal and spatial distribution patterns of the *number* of gaps, we found the spatial gap formation to be clustered and the temporal gap formation to be random. We also found no correlation between monthly rainfall and the total monthly gap area opened by gaps (Salvador-Van Eysenrode et al. 2000a).

In any case, internal, temporal and spatial variation in the number of gaps, the gap density, the gap occurrence, and in gap size constitute additional sources of habitat and resource heterogeneity, which implies more development opportunities and regeneration niches available for plants (Orians 1982). This environmental heterogeneity is considered to be a key factor in species partitioning and maintenance of diversity (Denslow 1980, 1987).

The results show that it is difficult to determine exactly the number of gaps formed yearly, the size of an up-to-come gap, and the exact time and place of gap formation. However, if the density of gaps and the pattern of gap size distribution are typical, then they constitute good models or indicators to monitor the functioning of a forest, useful as reference in forest conservation (Hartshorn 1990).

Gap interior and edge

To our knowledge, studies on gaps in Amazonia have not yet recognized a gap interior and an edge zone as done in Central America (e.g. Barton 1984, Denslow et al. 1990). We justify the way how we characterized these zones based on the difference they show in light intensity, which also matches Brokaw's gap definition in combination with Runkle's definition. Runkle's gap corresponds to the ground area of forest which is affected by light enhancement when a gap is formed, but Brokaw's gap, which is found inside, corresponds clearly to the uncovered zone in the gap where light is at its maximum. Centrifugally from this core or gap interior, light dims out until it reaches the general level of the closed forest, which occurs roughly at the perimeter of the Runkle-zone. This shaded zone corresponds to the edge in the definition (Forman 1997). These definitions were tested at another location, by linking the gap zones to light totals using a Gap Estimation System (Salvador-Van Eysenrode et al. 2000b); based on the match we found between gap zones and light totals, the combined use of the two gap definitions can consequently be considered as a suitable alternative for light measurements. The critical importance of light for plant life, and the correlation with other microclimatological variables, justified in turn the use of light as the discriminating para- meter to define the gap's interior and edge (Jones 1992, Whitmore et al. 1993).

From the total area of forest in gap phase, we found that about one half corresponded to interior. However, the width of the edge zone varies among gaps and since we did not find correlation between both zones, it is not possible to determine the amount of edge that will go together with any given interior area. Differences in the amount of edge result from a combination of factors such as crown shapes and sizes of the surrounding trees, of the size and shape of the gap itself, and damage of the branches of the trees surrounding the gap. The different habitat conditions, and hence niches found in these two gap zones, together with their variability constitute heterogeneity of resources. Plants from different regeneration guilds can allocate these resources differentially, though still be present in the same gap, and so influence plant presence, and diversity (Grubb 1977, Denslow 1980, Barton 1984, Swaine & Whitmore 1988). Note that plants both resident to the place before the gap is opened and colonizers will be affected by the availability of particular resources in a gap. For instance, enhanced sunlight (visible or UV-B, Flint &

Caldwell 1998) in the gap interior could have severe consequences for many plant species not adapted to such conditions, or positive effects for others, e.g. pioneer species (Oldeman & Van Dijk 1991).

Not only the heterogeneity of resources in gaps is important, but also the structural vegetation differences between the gap interior and edge zones. Some seedlings and saplings resident to the place before a gap is opened will be crushed by the gap-maker elements, and this is expected to occur roughly in the area that corresponds to the interior. In the edges, however, plants may marginally, or not, be affected in this way, which also leads to differences in vegetative and growth responses between gap interiors and edges (Denslow et al. 1990, Chen 1991). All of this may shape compositional and structural patterns of gap closure, issues to be investigated in detail and over a longer time span.

Gap maker elements

Most, but not all falling trees or parts of them create gaps. Different types of gap starters result in different gap zones and environments, independent of the interior and edge zones; for example, uprooted trees create a root zone, a bole zone and a crown zone, but root zones are absent in gaps opened by other type of gap makers (Brandani et al. 1988). The environmental conditions particular to each of these zones constitute additional niches available in gaps (Grubb 1977, Jacobs 1981). Brandani et al. (1988) found that soil mounds at the root zones are privileged places for plant regeneration, so their lack or presence may influence plant regeneration patterns, and species composition in gaps (Orians 1982, Putz 1983, Riéra 1985).

Uprooted trees are common in some locations (e.g. Durrieu de Madron 1994, this study), while other gap-makers such as snapped stems are more common in other sites (e.g. Martínez Ramos et al. 1988, Rankin de Merona et al. 1990, Van Der Meer & Bongers 1996a). The variability in the share of types of gap starters among forests is presumably dependent of a combination of local factors such as soil type, atmospheric conditions, topography, age, and mechanical features of the structural elements of the forest (Putz et al. 1983, Pickett & White 1985, Clark 1990, Kapos et al. 1990). We speculate that the commonness of uprooted trees at TBS is due to soil-related factors which affect root anchorage (Kapos et al. 1990). Consequently the soils at TBS are, in turn, more mechanically disturbed by means of gaps than soils in locations where uprootings are less common (Richards 1996). Another consequence of uprootings is that gaps created by them can be expected to be larger, not only because uprooted trees are typically the largest gap-maker elements (Salvador-Van Eysenrode et al. 1999), but also because uprooted starters are the most common initiators of domino events which create the largest gaps.

The random fall direction of the gap-starters indicates that there is no determinant directional factor influencing treefalls. This, together with the variability in the type and number of gap-makers and the availability of particular gap zones, contribute to environmental heterogeneity, and detailed predictions with regard to patterns are therefore difficult.

Gap formation rate and forest turnover time

The annual gap formation rate (a) at TBS is roughly similar to that of other Amazonian rainforests, despite inconsistency in the use of gap definitions among studies, and sometimes the lack of knowledge of a minimum gap size (Van Der Meer et al. 1994; Table 2). From the gap formation rate, it can be expected that a complete forest cycle at TBS will take between 48 (for A_R) and 83 years (for A_B).

It is evident that depending on the measurement method and definition of gap used, gap area can easily vary by a factor of two or more (Brokaw 1985, Van Der Meer et al. 1994). Consequently, this will cause variation in gap formation rate and forest turnover time, frustrating the interpretation of the data and making difficult the comparison of these valuable indicators between study sites. This highlights the importance to explicitly and consistently use a suitable, and accurate definition of canopy gap, and as long as a standard is sought, we suggest the use of both Runkle's and Brokaw's definitions.

Variation in gap formation rate can also be the result of anthropogenic gap creation (e.g. by logging). Natural and anthropogenic gap formation together in the same forest will cause its 'normal' gap formation rate to increase, speeding up the turnover time, and influencing the forest cycle.

Finally, studies on gap formation in tropical rainforests should always incorporate data on the type of gap starters, not only to assess if they cause differences in forest regeneration (e.g. successional pathways, composition, Brandani et al. 1988), but also in order to better evaluate the differences in gap formation rates. For example, if uprooted trees are the most common gap starters in a given forest, and consequently larger gaps are present, then the gap formation rate may be higher and its turnover time shorter as compared to forests where other of gap-makers are dominant.

Although the estimation of the turnover can also be done through tree mortality, exceptionally some trees may live longer than predicted by the turnover time. Unfortunately, dating tree age in tropical rainforests is complicated, and despite the use of ingenious dating methods (e.g. Martínez Ramos et al. 1988), the only solution to exactly date tree and forest age is tracking the complete forest cycle from gap to mature forest patch, i.e. the aggregation process (Forman 1997).

Concluding remarks

Of the estimated 406 million ha of lowland tropical rainforest in South America (estimated in 1990, Whitmore 1997), 77.65 ha have been surveyed for gaps during only short study periods compared to the estimated turnover times (Table 2). From this studied area, our plot at TBS represents 17.38% (which is 90.6% for Ecuador), and our study time is relatively short (mean = 1.13 years, SE ± 0.48, Table 2).

Studies on forest dynamics have contributed much to the understanding of the importance of gaps in tree mortality, forest regeneration, stand turnover and diversity. However, little attention has been given to the potential application of this knowledge to rainforest conservation and management (Hartshorn 1990). Considering anthropogenic activities also causing canopy perforation, the application of gap theory constitutes a promising conservation tool for tropical rainforests.

Although less than ten studies have been reported so far (Table 2), the way how gaps are formed is relatively well studied compared to the way how gaps close in Amazonian rainforests (Uhl & Murphy 1981, Brokaw 1985, Van Der Meer & Young & Hubbell 1991, Bongers 1996b). This makes the compositional and structural patterns of gap closure a main issue for further theoretical and applied research. Despite the growing body of information on Amazonian rainforest canopies (Nadkarni & Parker 1994), more research on canopy gaps is needed for a better understanding of rainforest dynamics, tree mortality and regeneration, and species assemblages and diversity in these forests (Hartshorn 1990).

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