

# Repeated disturbances and canopy disturbance regime in a tropical semi-deciduous forest

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**Abstract:** The canopy disturbance regime and the influence of gap methods on the interpretation of forest structure and dynamics were evaluated in a tropical semi-deciduous forest in south-eastern Brazil. We encountered a gap density of 11.2 gaps ha<sup>-1</sup> and an average size which varied from 121 to 333 m<sup>2</sup> depending on the gap delimitation method considered (minimum gap size was 10 m<sup>2</sup>). Although average size was slightly higher, the median value obtained (78 m<sup>2</sup>) was comparable to other tropical forest sites and the gap size-class distribution found supported the pattern described for such forest sites. Among 297 gap makers, snapping and uprooting were the most common modes of disturbance. The number and basal area of gap makers were good predictors of gap size. Almost 25% of all gaps suffered from repeated disturbance events that brought about larger gap sizes. Such processes, along with delimitation methods, strongly influenced the estimation of turnover rate and therefore the interpretation of forest dynamics. These results demonstrated the importance of further studies on repeated disturbances, which is often neglected in forest studies.

**Key Words:** Canopy gaps, complex gaps, gap size, south-eastern Brazil, treefalls, turnover rate

## INTRODUCTION

Disturbances are common to most, if not all, mature forest communities and they represent a crucial component in the maintenance of its pattern and processes (van der Maarel 1993). In tropical forests, disturbance activities are mainly represented by the death of part of a tree, of a whole tree or of several trees. Due to internal (e.g. diseases) and/or external causes (e.g. wind), trees mostly fall by uprooting or stem breakage (Arriaga 2000, Runkle 1982, van der Meer & Bongers 1996a). Yet, trees can still die standing and gradually decompose its crown. Branch-falls and inclined trees can also occur, though they are not related to the death of an individual. Each one of these modes of disturbance has its own consequences on light transmission, understorey vegetation and soil disturbance (Clark 1990). Openings in the canopy may be formed as a consequence of tree death and their influence on forest structure and regeneration are broadly known

(Busing 2005, Denslow 1980, Hubbell & Foster 1986). However, not all events of tree mortality result in canopy gaps (Poore 1968, van der Meer & Bongers 1996a). Lieberman *et al.* (1985) estimated that at least half of the dead trees bigger than 10 cm diameter at breast height (dbh) were not associated with canopy gaps.

The community pattern of tree mortality, known as forest disturbance regime, is regarded as a good descriptor of forest structure and regeneration (Clark 1990). Its description is usually done in two different ways. One is based on tree individual mortality and its consequences (Busing 2005, Lieberman *et al.* 1985) and the other comprises the description of the number, average size, frequency and spatial distribution of canopy gaps (Brokaw 1982b, Grau 2002, Kapos *et al.* 1990). More complete studies involve the association of both approaches (van der Meer & Bongers 1996a) and the recording of gap expansion processes (Runkle 1990, Tanaka & Nakashizuka 1994). An alternative approach in describing the disturbance regime is estimating the forest turnover rate, defined as the mean time between the formation of successive gaps on the same forest spot

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(Poore 1968). The calculation is normally based either on the rate of gap formation (Hartshorn 1978) or on the rate of tree mortality (Lieberman *et al.* 1985).

Although considered a good index in assessing forest dynamics (Denslow 1980), authors point out practical limitations of turnover estimation related to gap delimitation and measurement methods (Lima 2005, van der Meer *et al.* 1994), to the exception of repeated disturbances events (Riera & Alexandre 1988) and to the fact that many treefalls do not create canopy gaps (Lieberman *et al.* 1985, Martini *et al.* 2007). In tropical semi-deciduous forests, where seasonal fluctuations in canopy cover are inherent to forest functioning, the influence of gap processes on forest dynamics may be of less importance (Denslow & Hartshorn 1994). Although seasonal fluctuations in canopy cover overshadow the influence of gap processes on forest dynamics, studies emphasizing the subject are very scarce for this forest formation. In this paper we assess the canopy disturbance regime in a tropical semi-deciduous forest in south-eastern Brazil. By means of an exhaustive recording of canopy gaps, we attempt to evaluate size, age and size-class frequencies of such openings and the gap makers related to them. More specifically, we addressed the following questions: How do gap delimitation methods and repeated disturbances influence the estimation of canopy turnover rate and other disturbance regime descriptors? And what are the main factors controlling gap size?

## SITE DESCRIPTION

This study was carried out in the Estação Ecológica de Caetetus (EEC), a state forest reserve which belongs to Gália county (22°41'S and 49°10'W). It has a total area of 2178 ha covered by an old-growth semi-deciduous seasonal forest, with a canopy height ranging from 20 to 35 m. The terrain is flat, with elevation ranging from 550 to 650 m asl. The soil is red-yellow Acrisols (Ultisols) and red-yellow Ferrasols (Oxisols) but haplic Gleysols (Entisols) can be found on the lowest points of the landscape. Average annual precipitation is around 1400 mm and characterized by the occurrence of a marked dry season. The average annual temperature is 21 °C. Near the centre of the reserve, a permanent plot of 10.24 ha was established in 2002 to study forest composition and dynamics. In the 2005 plot census, 12 039 individuals > 5 cm dbh were sampled, belonging to 148 species, 110 genera and 44 families. Plot basal area was 36.8 m<sup>2</sup> ha<sup>-1</sup>. The richest families were Myrtaceae, Euphorbiaceae, Fabaceae, Mimosaceae and Rutaceae, and the five most abundant species were *Metrodorea nigra*, *Ocotea indecora*, *Trichilia clausenii*, *Aspidosperma polyneuron* and *Trichilia catigua*.

## METHODS

In 2005, 8.96 ha (280 × 320 m) of the permanent plot was completely surveyed for canopy gaps during the dry season. The canopy gap definition used followed Runkle (1992) who defines a gap as formed by the death (absence from the canopy) of at least one-half of a tree. Additionally, we marked and measured canopy openings, defined here as openings in the canopy without past or present evidence of the death of gap makers. Large gaps that exceeded the plot limits were not completely measured and only the area inside the plot was used to estimate the total plot gap area. In contrast, smaller gaps with some portions outside gap limits were measured completely and used in the gap area analyses, as explained below.

Once the canopy gap or opening were located, we used two different methods to set its limits: Brokaw (1982a: the vertical projection of the 'hole in the forest extending through all levels down to an average height of two meters above ground') and Runkle (1982: 'the ground area under a canopy opening extending to the bases of canopy trees surrounding the canopy opening'), referred from now on simply as Brokaw and Runkle methods, respectively. Thus, for each gap, we obtained the area directly above the canopy gap and the expanded gap area. Each method was applied by the same observer to avoid bias. We set 10 m<sup>2</sup> as a minimum gap size and a minimum size of 20 cm dbh to define the surrounding canopy trees. The size of each canopy gap was measured using the method proposed by Lima (2005). Exceptions were made for three large gaps that had part of their area outside the study plot. In these cases, we noted the tag number of all bordering canopy trees and size measurement by Runkle's method was made *a posteriori* based on their coordinates. Gap size inside the plot was then obtained by the area of the polygon, linking all bordering canopy trees sketched using a graphic editor program (*Arc View GIS 3.3*). Hence, Brokaw gap size was estimated based on the regression equation obtained comparing both delimitation methods.

For each gap, we set an arbitrary centre inside Brokaw's limits, from which all measures were taken using a DME 201 (Haglöf Sweden AB). Next, we made a complete survey for gap makers (i.e. all dead trees or branch falls > 20 cm dbh) that were identified (whenever possible) and measured for dbh and mode of disturbance (uprooting, snapping, standing dead, fall of a stem from multi-stemmed trees, branch fall, inclined tree and the association of two or more modes of disturbance, hereafter called 'complex trees'). To define gap makers in this study, the distinction between initiator and domino trees were not made due to difficulty of differentiating between them in the field, especially inside multiple-event gaps. We then made estimates of gap age, based on the presence/absence of tree identification tags on gap maker(s). Since tags were

placed in 2002, we created two broad age classes: recent gaps (gaps newer than 3 y old) when the gap maker was tagged; and old gaps, when the gap maker not tagged and presented more advanced stages of wood decay. Although a 3-y-old gap may not be accurately defined as recent, the presence of tags assured an excellent time parameter because of the information it gave us for the period 2002–2005, aiding in the calculation of the disturbance and turnover rates.

Complex gaps, formed by distinct episodes of tree mortality, received a special approach as suggested by Runkle (1992). When the spatial distinction between tree-and/or branch-fall episodes was structurally unclear, total superposition of the two fall episodes was assumed. Accordingly, the gap was regarded as a single gap with two different age classes, one relative to the first fall episode and one from the second. During analysis, when the age class was required these gaps were excluded, except for estimations of turnover rate. Complex gaps with clear spatial differentiation between fall episodes were then subdivided into two contiguous fractions (partial overlapping), each one with its own age class and area. During the estimation of turnover rate, each fraction of these gaps was used separately. The limit between these contiguous gaps was determined by considering the area of influence of each episode (with one or more gap makers), sapling height and relative decay of surrounding debris.

### Data analysis

Since gap size data did not follow a normal distribution, comparisons among delimitation methods, types of gaps (single and complex gaps) and age classes (old and recent) were made by the inspection of median confidence intervals in notched box-plots. Non-overlapping confidence intervals were considered as an indication of dissimilar distributions (McGill *et al.* 1978). A regression analysis was carried out to investigate the relationship between Brokaw and Runkle methods; a non-linear model was adopted because the inclusion of the quadratic term significantly improved the model fit ( $df=91$ ,  $F=6.99$ ,  $P=0.009$ ). A standard multiple regression was also applied to evaluate the strength of number and size of gap makers on the prediction of canopy gap size. In both regression analyses, the three large canopy gaps not completely measured were not included. The evidence of different size distribution of the gap makers among the different modes of disturbance was evaluated using Analysis of Variance (ANOVA). During some of the analysis, such as regression and average comparison, a number of gaps were excluded due to partial measurement of area and contours. Canopy openings were not included in the gap size versus gap maker analysis either. Therefore, the number of gaps used varied between analyses.

We also made estimates on the gap disturbance rate (i.e. new gaps per hectare per year) to calculate the stand turnover rate, defined according to Poore (1968, p. 178). The mean disturbance rate was obtained by dividing the total gap area of recent gaps by the number of years since tree mortality started being recorded in 2002. The turnover rate was expressed indirectly as the number of years necessary to cover the entire plot area with gaps and calculated following Hartshorn (1978). To assess the effect of including repeated disturbances events on turnover rate, we calculated the turnover rate by adding the area of recent gaps that partly or entirely covered older gaps (complex gaps, as explained above). To compare average gap size and turnover rate to other studies, values were corrected in respect to the method of size measurement adopted, following the linear equations provided in Lima (2005).

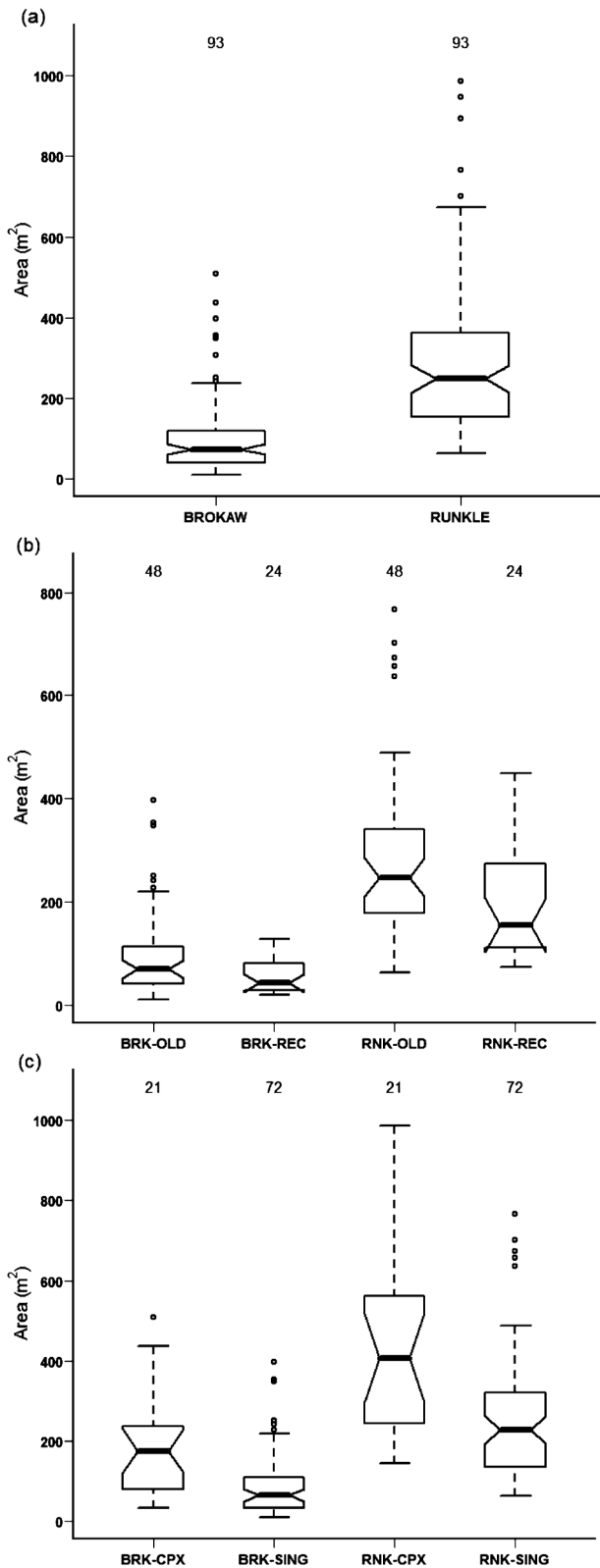
## RESULTS

### Disturbance regime and turnover rate

We found a total of 100 canopy gaps totally or partially inside the studied area ( $11.2 \text{ gaps ha}^{-1}$ ). Among these, canopy openings were uncommon ( $0.8 \text{ gaps ha}^{-1}$ ), presented smaller values than single canopy gaps (inspection of notched box-plots, data not presented) and contributed only 3.0% and 4.3% of Brokaw and Runkle total gap area, respectively. As expected, Brokaw gap areas were significantly lower than Runkle's (Figure 1a) and the quadratic regression applied revealed significant relation between methods ( $\text{Runkle size} = 0.00046 (\text{Brokaw size}^2) + 1.94 \text{ Brokaw size} + 100$ ;  $r^2 = 0.809$ ;  $N = 93$ ;  $P < 0.001$ ). But, there was considerable deviation on individual gap sizes. For example, for a Brokaw gap size of  $78 \text{ m}^2$ , a Runkle gap size of  $249 \text{ m}^2$  is expected. However, observed values varied from  $158$  to  $448 \text{ m}^2$ .

Among all gaps, we encountered 21 complex gaps ( $2.4 \text{ gaps ha}^{-1}$ ) with distinct episodes of complete or partial gap overlap (Table 1). These gaps varied greatly in size from  $32$  and  $145 \text{ m}^2$  to  $507$  and  $1109 \text{ m}^2$  (Brokaw and Runkle sizes, respectively). The biggest of all gaps also corresponded to a complex gap ( $1004$  and  $1619 \text{ m}^2$ , respectively) but since we did not measure its complete area (gap largely exceeded plot limits), it and two other partially measured gaps were not used during analysis. There was strong evidence of complex gaps being bigger than single gaps for both delimitation methods (Figure 1b). Complex gaps corresponded to 21.0% of all canopy gaps found in our study plot and contributed for  $4400$  and  $10\,587 \text{ m}^2$  (37.1 and 33.2%) of total Brokaw and Runkle gap area.

The size class frequencies (Figure 2) revealed that 77% of canopy gaps measured using the Brokaw method were



**Figure 1.** Size distribution of canopy gaps found in a tropical semi-deciduous forest, south-eastern Brazil. Size values measured according to two different delimitation methods and separated as follows: all gaps (a), old and recent gaps (b) and single and complex gaps (i.e. gaps formed by distinct episodes of tree mortality) (c). For all figures, the centre

smaller than 150 m<sup>2</sup> and gaps bigger than 400 m<sup>2</sup> were rare (3%). As expected, gaps smaller than 150 m<sup>2</sup> had a disproportionate contribution of only 42% of total gap area. Correspondingly, 71% of all the gaps were smaller than 350 m<sup>2</sup> but they accounted for no more than 45% of the total Runkle gap area. Moreover, there was evidence of difference in Runkle gap area between age classes but the same was not true for Brokaw method (Figure 1c). Thus, for Runkle method, older gaps were bigger than recent ones (complex gaps and canopy openings excluded from this analysis). The number and the proportionate contribution of gaps in the old age class were respectively about two and three times bigger than recent gaps, a result practically independent of the delimitation method.

We further compared the number of gaps and the contribution to total gap area as if we had not considered repeated disturbance events. Both variables had considerable discrepancies related to the exclusion of repeated disturbances events. As a consequence of differences in total area related to the inclusion of overlapping gap areas, the turnover rates were quite different between the two situations (Table 2). The results between gap delimitation methods were different as well. The mean annual rate of newly formed gaps (i.e. disturbance rate) calculated for the three years of records was 1.1 gaps ha<sup>-1</sup>.

### Canopy gap makers

Related to 93 canopy gaps, we encountered 297 gap makers representing a median and average ( $\pm$  SD) of 2.0 and  $3.2 \pm 2.6$ , respectively. On account of some difficulty in measuring the dbh of some of the old fallen trees, we measured 289 gap makers (Table 3) that ranged from 0.2 (lower limit previously defined) to 1.7 m. The basal area of gap makers per gap was  $0.45 \pm 0.50$  m<sup>2</sup> (average  $\pm$  SD, N = 93) and their total basal area was roughly 4.6 m<sup>2</sup> ha<sup>-1</sup>. Snapping, uprooting and standing dead were the most common mode of disturbance and together accounted for 83.8% (Table 3). Uprooted trees were significantly larger in dbh than branch falls (ANOVA: N = 292, F = 3.20, P = 0.014). The multiple regression indicated that the number of gap makers and the total basal area were good predictors of gap size, for both methods (Table 4). The analysis showed

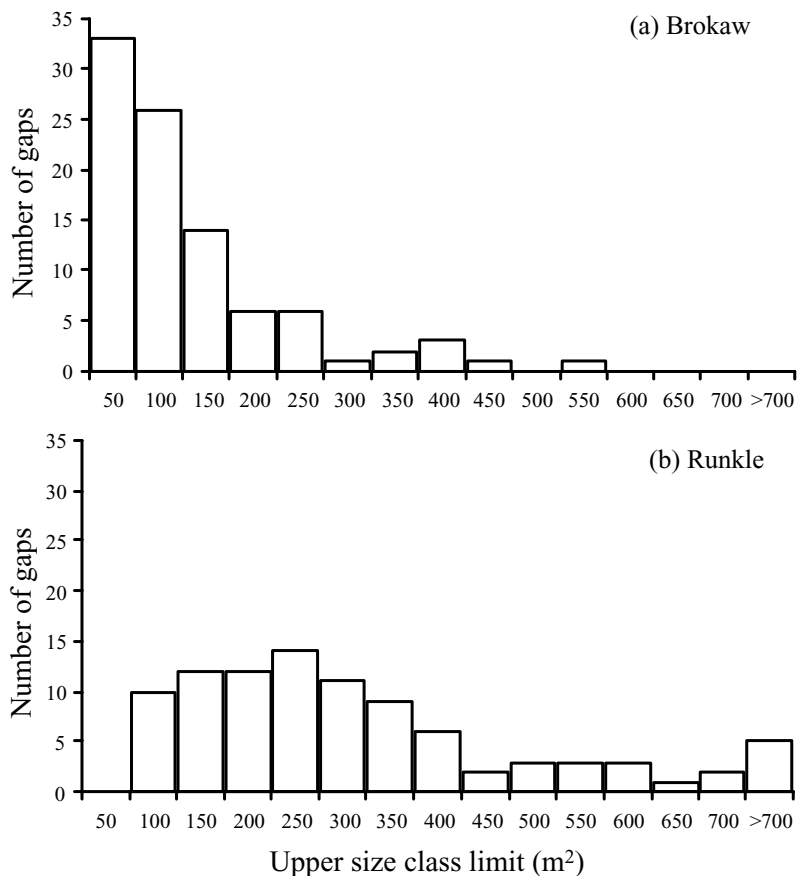
vertical line marks the sample median. Box edges represent the first and third quartiles. Boxes are narrowed at the median and return to full width at the lower and upper confidence interval. Whiskers show the range of values that fall within 1.5 times the length of the box. Outliers are plotted as empty circles. BROKAW (or BRK) = Brokaw gap size; RUNKLE (or RNK) = Runkle gap size; SING = Single gaps; CPX = Complex gaps; OLD = Single gaps formed before 2002; REC = Single gaps formed between 2002 and 2005.

**Table 1.** Number and categories of canopy gaps found inside 8.96-ha of tropical semi-deciduous forest in south-eastern Brazil. Inside = gaps completely measured and inside plot limits; Border = gaps completely measured but partially inside gap limits; Partial = large gaps measured only inside plot limits. Brokaw and Runkle refer to the two methods of gap delimitation employed. Complex gaps = canopy gaps formed by distinct episodes of tree mortality. Canopy openings = canopy gaps without evidence of gap makers. Values of area for all categories are corrected by subtracting gap portions outside plot limits.

Gap category	Number			Total	Gap area (%)	
	Inside	Border	Partial		Brokaw	Runkle
Single gaps	67	3	2	72	7.8	22.4
Complex gaps						
Totally overlapped	9	–	–	9	0.8	2.9
Partially overlapped	11	1	–	12	4.3	8.9
Canopy openings	7	–	–	7	0.4	1.5
All categories	94	4	2	100	13.2	35.7

a significant increase of gap area in respect to total basal area ( $F(1, 86) = 64.3$  and  $48.3$  for Brokaw and Runkle sizes, respectively) but the inclusion of the number of gap makers significantly increases the variance explained by the regression ( $F = 22.5$  and  $22.1$ , respectively). The specific identity of the gap maker was difficult to determine due to decay of the fallen log and especially because

most of them were related to old tree- or branch-fall events (67.0%). Therefore, a large number of gap makers remained with undetermined identification ( $N = 124$ ). Still, the five most common species among the identified gap makers were *Aspidosperma polyneuron* (38), *Ocotea indecora* (29), *Syagrus* spp. (19), *Metrodorea nigra* and *Centrolobium tomentosum* (16).



**Figure 2.** Size class frequencies of canopy gaps measured applying Brokaw (a) and Runkle (b) gap delimitation methods ( $N = 93$ ), in a tropical semi-deciduous forest, south-eastern Brazil. Gaps exceeding the limits of the plot (i.e. not completely measured) are not included.

**Table 2.** Total gap area and forest turnover rate calculated for both delimitation methods and for two different estimations of recent gap area: including and excluding repeated disturbance events. Brokaw and Runkle refer to the gap delimitation methods employed. Recent gap area represented by the mean gap area opened per year, calculated for a 3 years interval. Recent and old age classes are gaps newer and older than 3 y old, respectively.

Repeated disturbance	Variable	Gap delimitation method			
		Brokaw		Runkle	
		Recent	Old	Recent	Old
Excluded	Area (m <sup>2</sup> )	3018	8583	7804	23 754
	Gap area (%)	26.0	74.0	24.7	75.3
	Turnover (y)	97.7		37.8	
Included	Area (m <sup>2</sup> )	3708	7893	10 420	21 138
	Gap area (%)	32.0	68.0	33.0	67.0
	Turnover (y)	79.5		28.3	

## DISCUSSION

### Disturbance regime

The average gap size found in this study (93 m<sup>2</sup>; value corrected to Brokaw (1982a) gap size measuring method) was comparatively larger than several rain-forest sites. This was true for forests at Nouragues (54 m<sup>2</sup>; van der Meer *et al.* 1994), Tai (55 m<sup>2</sup>; Jans *et al.* 1993), Carlos Botelho (56 m<sup>2</sup>; Lima 2005), Christmas Island (around 83 m<sup>2</sup>, Green 1996) and Barro Colorado (86 m<sup>2</sup>; Brokaw 1982b). However, this difference is probably due to the presence of large gaps in the EEC, reinforcing the use of the median to compare asymmetric values such as canopy gap size. Canopy openings were not numerous and predominately small. In our study area, these areas naturally free of trees are probably very old gaps in its final stages of canopy closure. Only three of seven canopy openings had no evidence of gap makers at all and the other four presented gap makers smaller than 20 cm dbh (usually branch falls). However, the distinction of canopy openings is still important because they may resemble canopy gaps in composition and function but not in their dynamics (Runkle 1992).

**Table 4.** Summary of the standard multiple regression results applied to predict gap size based on number and size of gap makers. Canopy openings (i.e. canopy gaps without evidence of gap makers) not included in the analysis. Statistics: Brokaw F (2, 86) = 43.6, P < 0.001, SE of estimate: 0.617; Runkle F (2, 86) = 35.2, P < 0.001, SE: 0.497. \*P < 0.001, ns = not significant. Data log(x + 1)-transformed.

Parameter	Gap delimitation method (N = 89)	
	Brokaw (r <sup>2</sup> = 0.503)	Runkle (r <sup>2</sup> = 0.450)
	b ± SD	b ± SD
Intercept	2.90 ± 0.20*	4.44 ± 0.16*
Basal area	0.65 ± 0.41 <sup>ns</sup>	0.30 ± 0.33 <sup>ns</sup>
Number of falls	1.00 ± 0.21*	0.80 ± 0.17*

As already discussed elsewhere (Popma *et al.* 1988), different gap delimitation methods generate differences of 2.8 times on average in gap size. This result is very alike to the one obtained by van der Meer *et al.* (1994) comparing the same methods. Even though the regression obtained was significant, conversions of individual gap size should be made carefully due to substantial variation between the observed size values of the two delimitation methods. Among the factors that may have contributed to the production of such variation, we can cite understorey vegetation damage

**Table 3.** Diameter at breast height (dbh) and age-class distribution of gap makers in respect to the disturbance mode considered. Different superscript letters designate significant differences between means (Tukey test:  $\alpha = 0.05$ ). The data on dbh were 1/square-root-transformed prior to ANOVA. Branch fall values correspond to the fallen branch and not to the supporting tree. Complex falls (i.e. association of different modes of disturbance) were excluded from the ANOVA.

Disturbance mode	dbh (m) (mean ± SD)	Gap makers		Total
		Recent	Old	
Snapped tree	0.38 ± 0.20 <sup>ab</sup>	37	61	98 (33.0%)
Uprooted tree	0.43 ± 0.18 <sup>a</sup>	18	70	88 (29.6%)
Standing dead tree	0.37 ± 0.17 <sup>ab</sup>	24	39	63 (21.2%)
Stem fall	0.32 ± 0.08 <sup>ab</sup>	7	10	17 (5.7%)
Inclined tree	0.35 ± 0.17 <sup>ab</sup>	9	7	16 (5.4%)
Branch fall	0.29 ± 0.10 <sup>b</sup>	1	9	10 (3.4%)
Complex falls	0.42 ± 0.17	2	3	5 (1.7%)
Total	0.39 ± 0.18	98	199	297

(e.g. number and height of surviving individuals), the presence of inclined canopy trees bordering the gap and lateral extension of tree branches (creating asymmetrical crowns around gaps).

Information on number and area of gaps formed by distinct episodes of tree mortality are still scarce in gap literature, particularly for semi-deciduous forests. Nonetheless, several authors stated that trees around gaps are more susceptible to falling for different reasons (Grau 2002, Hubbell & Foster 1986, Young & Hubbell 1991, but see Runkle 1990). Runkle (1990) found that more than 60% of gaps suffered from repeated disturbances and Riera & Alexandre (1988) found that 14% of total gap area suffered from new treefalls. In our study site such gaps represented approximately 25% of all gaps found and they contributed up to one third of total gap area.

Although repeated gap disturbances are supposed to be common (Lieberman *et al.* 1985, Poore 1968, van der Meer & Bongers 1996b, Yavitt *et al.* 1995), we do not know to what extent researchers have not considered complex gaps or if they simply did not notice their existence. As stated by Runkle (1992), most researchers probably combined the sections of such gaps together into a single entity. Other researchers have consciously excluded complex gaps from their analysis according to their needs (Hartshorn 1978, Runkle 1982, van der Meer *et al.* 1994). However, this sort of treefall gap certainly influences gap regeneration in a different way (Tanaka & Nakashizuka 1994), especially in the time required for gap closure. Therefore, the exclusion of such gaps or the merger of their sectors into one bigger gap, will probably generate limitations of interpretation on gap disturbance regime (Runkle 1992). Despite the practical difficulties in the recognition of complex gap sectors, we strongly recommend their inclusion in future studies aiming to describe the canopy disturbance regime.

The size class distribution was quite similar to many other tropical and non-tropical forest sites (Abe *et al.* 1995, Brokaw 1982b, Runkle 1990, van der Meer & Bongers 1996b), corroborating the pattern of canopy gap formation mainly with sizes smaller than 100 m<sup>2</sup>, median gap size commonly within 50–80 m<sup>2</sup> size class (but see Jans *et al.* 1993, Lertzman & Krebs 1991) and maximum gap size rarely more than 400 m<sup>2</sup> (but see Sanford *et al.* 1986). For instance, Green (1996) and Yavitt *et al.* (1995) found that 90% and 87% of all canopy gaps were smaller than 120 and 125 m<sup>2</sup>, respectively. These results are quite similar to ours if we consider the differences associated to the method of size measurement applied (Lima 2005). In addition, our and Lertzman & Krebs (1991) results for median gap size (both around 78 m<sup>2</sup>) were comparatively greater due to differences on gap size measurement as well.

Although the decrease of gap size over time was expected due to lateral and vertical growth of trees, our

data showed that older gaps tended to be larger than more recent ones for Runkle but not for Brokaw gap limits. One possible explanation would be the rate of repeated disturbances found in our study area that gradually increases gap area (Hubbell & Foster 1986, Lawton & Putz 1988, Runkle 1990, Tanaka & Nakashizuka 1994). Another may be related to the past activity of a catastrophic disturbance agent that generated bigger gaps during a specific period of time (Abe *et al.* 1995). The difference among methods occurred probably because Brokaw limits are more unstable over short periods of time than the Runkle method, which requires a tree to reach a certain dbh (generally 20 cm) to have any change on its limits. Still with respect to gap age, it is difficult to state if the proportion of gaps in the older age class is simply a result of natural accumulation of events or if gaps are somehow failing to regenerate. Many old canopy gaps in the study area were related to small height of internal vegetation and/or to a marked abundance of lianas and woody bamboos (probably *Merostachys* sp.).

### Turnover rate

Values of turnover rate for different forest sites varied (average 129 y: Bongers *et al.* 1988, Chandrashekara & Ramakrishnan 1994, Jans *et al.* 1993, van der Meer *et al.* 1994). The only result found for another seasonal forest (88 y: Brokaw 1982b) was quite close to the one observed here (98 y) suggesting that seasonal forests may be more dynamic than rain forests. No results were found for nearby forests and as far as we know this is the first record of turnover rate for Brazilian forests. However, gap density and the total per cent of gap area were markedly high than all studies reviewed. These and other results discussed above suggest that a catastrophic disturbance event probably occurred in the EEC more than 5 y ago. As we do not have meteorological data previous to the plot establishment in 2002, we can only suppose what possibly happened. Rocha (2003) cited an episode of strong winds that occurred in 2002 at the EEC that could have promoted such intense disturbance episode. In addition, a massive invasion of lianas and bamboo species that probably occurred after this major event may have held back gap regeneration and kept old gaps open for longer periods of time.

Our results reinforced the limitations related to the calculation and interpretation of the turnover rate (*sensu* Hartshorn 1978). The rate varied greatly between delimitation methods, stressing the importance of clearly expressing the gap methods employed (Clark 1990, Lima 2005). The same is valid for the inclusion of repeated disturbance events. Hartshorn (1978), for instance, decided not to include such events in his study. However, we found that turnover estimates were highly influenced

by the inclusion of repeated disturbance events. Other important issues on the interpretation of the rate are the spatial heterogeneity of the disturbance regime (Arriaga 2000, Kapos *et al.* 1990, Lima & Moura 2007, Poorter *et al.* 1994) and the limitation of rates based on one-time gap surveys (van der Meer *et al.* 1994). Moreover, increases of about 14% in canopy openness related to deciduous canopy trees are expected during the dry season (R.A.F. Lima & A.M.Z. Martini, unpubl. data), a phenomenon that may greatly influence species regeneration in our study site, as well as the biological meaning of the estimated rate.

### Canopy gap makers

The proportion of gap makers in each mode of disturbance was quite similar to lowland and montane tropical forests (Arriaga 2000, Brokaw 1982b, Green 1996, Lima & Moura 2007, Martínez-Ramos *et al.* 1988, Putz *et al.* 1983, van der Meer & Bongers 1996a), where snapped and uprooted trees are more common than branch-falls and standing dead trees (but see Carey *et al.* 1994, Lieberman *et al.* 1985). This pattern is quite different from the observed for some temperate forest sites where standing dead trees seem to be more frequent (Lertzman & Krebs 1991, Runkle 1982). We also found that uprooted trees were significantly larger than those subject to other modes of disturbance, as did Arriaga (2000), Martínez-Ramos *et al.* (1988) and Putz *et al.* (1983), though there are authors that found the contrary to be true (Carey *et al.* 1994). For a more detailed assessment of diameter distribution among the modes of disturbance in the EEC, see Martini *et al.* (2007).

We found no evidence that gap maker dbh was a better predictor of gap size in contrast to the suggestion found in the gap literature (Brokaw 1982b, Denslow & Hartshorn 1994, Hubbell & Foster 1986). As observed by van der Meer & Bongers (1996a), our results indicate that the number of gap makers has more to do with gap size. In addition, the mode of disturbance can also have an important effect on gap size, as suggested by Lima & Moura (2007). For instance, Lertzman & Krebs (1991) found small average gap size (41 m<sup>2</sup>) and a big mean number of gap makers (mean  $\pm$  SD: 5.7  $\pm$  3.8 m<sup>2</sup>) in a sub-alpine forest, probably as a result of the high proportion of standing dead trees (55%). Similarly, the mean gap area of 55 m<sup>2</sup> in the Ivory Coast (Jans *et al.* 1993) was probably due to the proportion of gaps formed by branch-falls that generally produce smaller gaps.

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