
UNDERSTANDING SMALL-SCALE DISTURBANCES IN GUAYANA'S MONTANE FORESTS: GAP CHARACTERIZATION IN THE SIERRA DE LEMA, VENEZUELA

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SUMMARY

This case study describes the structure of gaps in a montane forest in Sierra de Lema, Bolívar State, Venezuela. The sizes of the gaps were measured in the forest canopy (canopy gaps) and at ground level (extended gaps), and the corresponding microhabitats assessed. The trees involved in the formation of gaps were recorded, and their basal areas and volumes calculated. A distinction was made between gap makers and those trees that were brought down by gap makers. The mode of fall was recorded for all fallen trees. The main gap formation mode was the uprooting of trees, bringing about multiple tree-falls. The gap sizes observed (canopy gaps: 31-896m², extended gaps: 83-1235m²) were 30-90% larger than those reported for most tropical forests.

Gap formation resulted in a loss to the basal area and volume of the stand of ~5.8 and ~0.5%, respectively. Canopy gaps occupied 1.4% of the forest area, which is in the range reported for tropical forests. The microhabitat 'undisturbed ground' accounted for the largest area within the gaps. The predominance of uprooting as a cause of gap formation in the forests of the Sierra de Lema was probably due to the superficial rooting of the trees. The larger gap area is explained by the frequent occurrence of multiple tree-falls. From the large gap sizes and the high proportion of undisturbed ground in the gaps, high survival rates of advanced regeneration, and of numerous new maidens of pioneer species, might reasonably be expected.

The Guayana forests represent ~90% of the Venezuelan forest area and are part of the Guayana Shield. About 60% of the plant species present in Venezuela (15500 species) can be found in the Guayana Shield (Llamoza *et al.*, 2003). Around 22% of the vascular plants are endemic (native to a geographic region) to Venezuelan Guayana (Berry *et al.*, 1995). In addition to the huge biodiversity of the region, these forests are also important because of the environmental services they provide, specially logging and the generation of hydroelectricity, meeting ~70% of the country's electricity demand (Belvilacqua *et al.*, 2002).

The forests of the Sierra de Lema, a mountain range located in the eastern part of Venezuelan Guayana and in the upper Caroní river basin, are relatively unknown from either a botanical or an ecological perspective (Huber, 1995; Hernández and Ortíz, 2004). To date there have been several botanical expeditions to the area (Sanoja, 2009), but there are many areas within these forests that have not been visited thus far and it is likely that there are numerous plant species that have not yet been reported, some of which might not yet have been described at all. The ecology of the Sierra de Lema forests has only been studied over the last decade, through the monitor-

ing of permanent plots established in the forests as part of a long-term study of tropical forest dynamics. At present, this is the only ecological research being carried out in the montane forest area of the Guayana Shield (Hernández and Castellanos, 2006). The study of the structure of forest gaps (openings in the canopy extending down through the forest understory) presented in this paper was carried out within the framework of this research project.

The forests of the Sierra de Lema have not been cleared and are almost intact ecosystems (Duellman, 1997; Huber *et al.*, 2000; Blanco, 2001). The forests of the study area have been classified as

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'very humid submontane forest' (Ewel and Madriz, 1968; Holdridge *et al.*, 1971). The main canopy of the stands reaches 20-25m, with emergent trees over 40m in height. These forests are characterized by moss-covered tree trunks, abundant epiphytic and semi-epiphytic plants, fern trees (Cyatheaceae) and palms of the species *Geonoma interrupta* and *Prestoea tenuiramosa*. The most diverse tree families are Lauraceae, Clusiaceae, Rubiaceae, Sapotaceae, Melastomataceae, Myrtaceae, Moraceae, Burseraceae, Chrysobalanaceae and Euphorbiaceae (Sanoja, 2009). The most frequent tree species are *Licania intrapetiolaris*, *Sextonia rubra*, *Micropholis spectabilis*, *Eschweilera* sp. and *Protium* spp. (Durán, 2001; Hernández and Castellanos, 2006). These forests have a large proportion of endemic plants (Picón, 1994), with ~13% endemic tree species (Sanoja, 2009).

The high diversity levels present in tropical forests have been partially explained by the regeneration niche hypothesis (Grubb, 1977), which states that plant species coexist by occupying different habitats (Denslow, 1987; Brokaw and Busing, 2000). However, the hypothesis of functional equivalence (Hubbell, 2005) states that, specially in the case of species-rich tropical vegetation, many species overlap in terms of their functions within the ecosystem, and the species that are present and those that are regenerating relate to their dispersal and recruitment limitations. Natural forests can be regarded as being a mosaic of structural patches (Whitmore, 1989) of developing, developed and decaying phases. This successional process is initiated after damage occurs to a part of the stand, creating a forest patch (Hallé *et al.*, 1978; Oldeman, 1983; Whitmore, 1988). Gaps, which correspond to the first years of the developing phase, are created in natural forests by small scale disturbances; e.g., the fall of branches, crowns, or single or multiple trees (Brandani *et al.*, 1988). Gaps in tropical forests create a variety of microclimatic niches and microhabitats for species (Brown, 1993).

The environmental conditions in the stand after gap formation differ considerably to those present in the understory of areas where the cano-

py remains closed. Gaps create mosaics and gradients of light (Sanford *et al.*, 1986), and change forest microclimate and structure (van Dam, 2001). Differences in gap sizes, gap shapes and modes of gap formation result in gap heterogeneity and microclimate variability (van der Meer and Bongers, 1996a; van Eysenrode *et al.*, 1998; Brokaw and Busing, 2000; Carvalho *et al.*, 2000). Light, temperature, radiation and wind speed all increase in gaps, and relative humidity decreases (Swaine and Whitmore, 1988; van Dam, 2001). Nutrient cycling processes are altered (van Dam, 2001). The size of a gap influences the extent of the change of the spatial mosaic and, therefore, the floristic composition of the next successional phase (Whitmore, 1989). Gap shape influences the penetration of light into gaps (van Eysenrode *et al.*, 1998). Long gaps have a lower overall area exposed to direct sunshine than round gaps. Finally, information about total gap areas and their size distribution is useful for comparing ecosystems (Denslow, 1987). A knowledge of these structural characteristics of gaps is needed (Kapos *et al.*, 1990) for many ecosystems. These gap characteristics have not yet been researched in the forests of the Sierra de Lema or of the Caroní basin. Forest gap studies and forest dynamics research and monitoring will contribute to the understanding of hydrological cycles in the Caroní basin.

The structure of gaps present in a 53.5ha site in the high Sierra de Lema forests was characterized in this case study; the aim was to provide a description of the patterns of gap formation, gap structure and changes in the structure of these forests caused by the formation of gaps. The questions specifically asked were: How are gaps created? In which direction do the gap maker trees (those trees that fall and so create the

opening in the canopy) fall? Do secondary gap trees (non-gap maker trees that also become involved in gap formation) fall in the same direction? Do thinner trees tend to snap, whereas larger diameter trees are uprooted? Are gap maker trees larger in diameter than secondary gap trees? Are gap sizes correlated with the dimensions (diameter and height) of the fallen trees? What are the spatial proportions of the different microhabitats occurring in gaps? What is the range of variation in gap sizes? What gap shapes occur? To what degree are the basal area and volume of the forest stand reduced by gap formation? What proportion of the study area is covered by gaps?

Methods

Study area

The forests of the Sierra de Lema cover a continuous area of more than 1000km², and have an altitudinal distribution ranging from 150 to 1490masl (Hernández and Castellanos, 2006; Sanoja, 2009; Figure 1). The Sierra de Lema comprises an igneous-metamorphic basement, sedimentary rocks of the Roraima Group of the Precambrian Age, and diabase intrusions of the Mesozoic (Huber, 1995). The study area (53.5ha) is situated on a plateau that is deeply rived by small gullies.

The soils are characterized by a low nutrient content, low pH in KCl of 4.6-5.3 and low cation exchange capacity (Durán, 2001) and are deeply weathered. Most derive from sedimentary rocks, and a few from diabase outcrops. The latter soils are more fertile (Dezseo and Foelster, 1994; Huber, 1995). The rooting of the vegetation of the region is only superficial, down to just 30cm in the mineral soil (Foelster *et al.*, 2001).

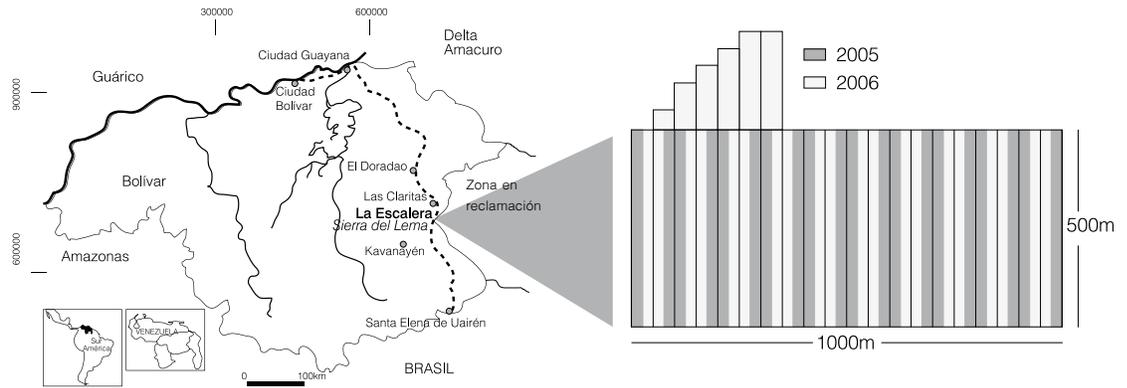


Figure 1. The location of the study area, the Sierra de Lema forests of La Escalera, Bolívar State, Venezuela, is depicted on the left. The inventoried area is shown to the right. Dark grey bars correspond to transects inventoried in 2005 and the light grey bars the transects inventoried in 2006.

A very humid premon-tane climate predominates across the study area (Ewel and Madriz, 1968; Holdridge *et al.*, 1971), with a mean annual temperature ranging 18-24°C (Hernández and Castellanos, 2006). Mean annual precipitation is ~4800mm (data for 1988-2004, from CVG-EDELCA climate station, at 1412masl, ~20km from the study area).

Structural characterization of the gaps

The study was carried out at ~1430masl, in the ‘very humid submontane’ (Holdridge *et al.*, 1971) forests of the Sierra de Lema. A total of 50 gaps met the gap definition criteria (see below) and were inventoried over an area of 53.5ha over the course of two field campaigns. In 2005, an area of 25ha was delimited in eleven transects separated by a distance of 50m (nine transects of 50×500m and two transects 25×500m; Figure 1), and all of the gaps found there were inventoried. As most of the gaps were located on plateaux, for the purposes of a subsequent tree regeneration study only those gaps on a plateau were considered in the next field campaign. In 2006, the areas between the transects (25ha) and an adjacent area (3.5ha) were inventoried. Gaps were defined and measured (Figure 2) at the canopy level (canopy gap) and the ground level (extended gap). A canopy gap was defined using the gap definition developed by Brokaw (1982), namely as “a hole in the forest extending through all levels down to an average height of two meters above ground.” The extended gap was defined as “the ground area under a canopy opening that extends to the bases of the canopy trees surrounding the canopy opening” (Runkle, 1981). For both gap definitions three criteria were applied: 70% of the ground vegetation had to be <2m in height; the gap area had to be >16m² and the gap diameter had to be >4m. As the formation of a gap might not disturb all of the existing vegetation completely (some trees may remain standing), the first criterion ensured the consideration of several gaps that might not have been comprised solely of vegetation <2m in height. The last two criteria were applied in order to avoid the inclusion of overly small forest gaps that are partially closed by the branches of adjacent trees. The extended gaps were only measured in 2006 after refinements were made to the gap definition used on the basis of field observations from the first year of data collection.

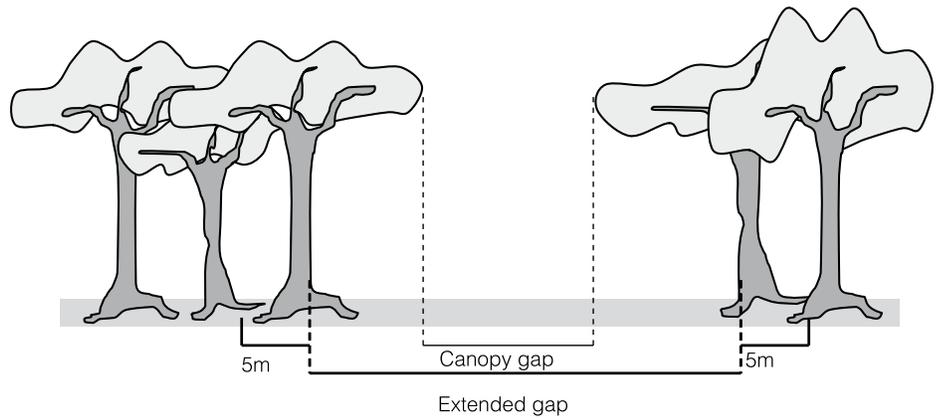


Figure 2. Illustration of the canopy and extended gap measurements, and of the 5m border zone.

Gap maker trees and secondary gap trees with a diameter >10cm (measured at 1.3m from the base of the broken trunk of fallen trees) were considered. Each was classified according to one of the following categories: uprooted tree, tree snapped at the base, tree snapped above the base, crown fall, and branch fall (van der Meer and Bongers, 1996b). The fall direction of the gap maker and any secondary trees were measured (azimuth in degrees). The diameters of all fallen trees were recorded and their basal areas calculated. The length and width of fallen crowns were measured and, using the formula to calculate the area of an ellipse, the area of the crown projection onto the ground (referred to subsequently as the crown area) was calculated.

The perimeter of each gap (canopy and extended gap) was identified on the ground, drawn in a scaled sketch and digitized. Gap area was calculated using ArcGIS 9.1 (ESRI Inc., 1999-2005). An index was developed and applied to characterize the breadth of each gap:

$$B_i = L / ((wc + w1 + w2) / 3),$$

where B_i : gap breadth index; L : longest axis through the gap; wc : width of the gap, measured perpendicular to the main axis at the midpoint; $w1$ and $w2$: widths measured perpendicular to the main axis midway between the midpoint and the two ends of the main axis. $B_i = 0$ means that the breadth of the gap is similar in each direction; i.e., an almost circular shape. The narrower the gap, the higher the index value.

As the ground level environment of a gap is heterogeneous (Ricklefs, 1977; Brown, 1996), which was suggested to be a reason for the huge species diversity in the tropics (Ricklefs, 1977), in each gap the following microhabitats (ab-

brevisions in parentheses) were distinguished at ground level: fallen crown (crown), fallen large branch with diameter <20cm (branches), lying large trunk with diameter ≥20cm (trunk), and undisturbed ground (undisturbed). The undisturbed forest floor area of the closed forest adjacent to the gap (border) was classified as a non-gap microhabitat. The border was defined as a 5m wide zone stretching from the edge of the extended gap into the adjacent forest (Figure 2). Although the border zone does not belong to the actual gap, it is influenced by the physical and climatic conditions within the gap. Several environmental factors influencing the establishment and growth of tree regeneration (Poorter, 2002) may differ between the various gap zones (Núñez-Farfán and Dirzo, 1988). For instance, plant growth in forest gaps on *tierra firme* near San Carlos de Río Negro, Venezuelan Amazon, was found to be influenced by microhabitats (Uhl *et al.*, 1988). The microhabitats were illustrated in the sketch and their areas were calculated.

Proportion of the gap area

The magnitude of gap disturbances on the forest stand was assessed using three indicators: the basal area of the fallen trees in gaps, their deadwood volume, and the proportion of the study area covered by gaps as a percentage. The total volume of a downed stem, which comprised the stem section from the base to the crown onset, was calculated by the following regression formula developed for trees of Venezuelan forests (Konrad, 1990):

$$v = d^2 \times (0.39682 + 0.46013 \times h)$$

where v : volumen of the fallen tree stem (m³), d : diameter (m), and h : length of the tree stem (m). The results for all of the measured stems were then added for each gap.

The proportion of the study area that was occupied by canopy gaps was

calculated only for the first field campaign (25ha), where all of the gaps occurring were inventoried. The areas of all of the canopy gaps present within the 25ha were added up, and their proportion relative to the total area of 25ha was calculated. As the extended gap area was not measured for gaps during the first field campaign, these areas were calculated by means of a regression equation derived using the areas of the canopy gaps and their corresponding extended gaps measured in the second campaign in 2006. The relative proportion of the 25ha occupied by extended gaps was then calculated also.

Statistical analysis

The normality of the distributions of the variables studied was checked using the Shapiro-Wilk test. As the values

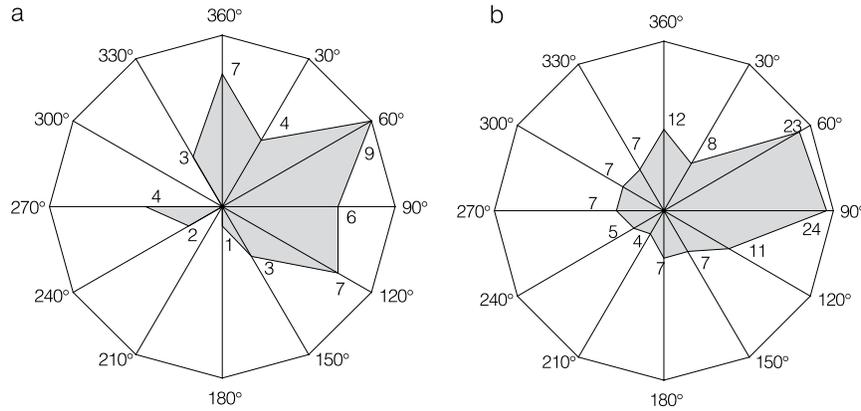


Figure 3. Orientation of the fallen trees (diameter >10cm). Numbers next to the shaded areas indicate the number of trees with a fall-orientation corresponding to the particular azimuth section (e.g., 30-60°). a: gap maker trees, b: secondary gap trees.

were not normally distributed, further analysis of the data relied on non-parametric tests. The Wilcoxon rank sum test was applied to determine whether the medians of the data sets stemmed from similar populations. Spearman's rank correlation was used to analyze the relationships between variables (Hartung *et al.*, 1986).

Core Team, 2008).

Results

Gap formation

The main mode of gap formation was the fall of uprooted trees (51%), followed by the snapping of trees at the base (29%). Only 9% of the gap maker trees snapped above the base, and crown and branch fall caused 2% and 9% of the gaps, respectively. In most gaps several trees were pulled down by an adjacent gap maker, to which they were frequently connected by lianas, an example of the so called 'domino effect' (van der Meer and Bongers, 1996b). Most of the fallen trees present in the gaps lay in a north-easterly direction (Figure 3). The majority of the gap maker and secondary trees were oriented in the range 0-120° and 30-120° azimuth, respectively.

No significant difference in the diameter of fallen trees was found in relation to the mode of tree fall (Table I). The diameters of uprooted and snapped trees did not differ significantly. A total of 186 fallen trees were measured, 18% of which were gap maker trees and 82% were secondary gap trees. The diameters of

TABLE I
RANGE, MEAN, MEDIAN AND STANDARD DEVIATION OF SEVERAL PARAMETERS MEASURED IN THE GAPS IN THE SIERRA DE LEMA

	Range	Mean	Median	sd	Shapiro test
Diameter of uprooted trees (cm)	10 - 110	30.95	25	19.92	W= 0.84*** a
Diameter of snapped trees (cm)	10 - 120	31.87	24.5	20.98	W= 0.81 ***a
Diameter of gap maker trees (cm)	11.59 - 120	58.80	58.57	21.92	W= 0.95 ns b
Diameter of secondary gap trees (cm)	10 - 56.34	24.21	22.92	10.05	W= 0.92 ***c
Correlation of canopy gap sizes with total number of trees (m ²)	-	-	-	-	W= 0.76 ***
Total number of trees ^{&}	-	-	-	-	W= 0.82 ***
Correlation of canopy gap area with total basal area ^{&} (m ²)	-	-	-	-	W= 0.77 ***
Total basal area ^{&} (m ²)	-	-	-	-	W= 0.93 ns
Correlation of canopy gap sizes with total crown areas ^{&} (m ²)	-	-	-	-	W= 0.96 ns
Total crown area ^{&} (m ²)	-	-	-	-	W= 0.80 *
Canopy gap sizes (m ²)	31 - 896	207.12	179.5	146.65	-
Correlation of total canopy gap sizes with extended canopy sizes (m ²)	31 - 896	235.23	184	186.16	W= 0.77 ***
Extended canopy gap sizes (m ²)	83 - 1235	422	377	268	W= 0.87 *
Gap shape index	1.51 - 5.62	2.93	2.86	1.13	-
Correlation of square root of total canopy gap sizes with extended gap sizes (m ²)	-	-	-	-	W= 0.93 ns
Square root of extended gap areas (m ²)	-	-	-	-	W= 0.96 ns
Number of secondary gap trees in the Sierra de Lema	1 - 16	6.72	5	4.7	W= 0.91 ns d
Number of secondary gap trees in Carlos Botelho National Park	1 - 4	1.67	1	0.90	W= 0.74 ***e

[&]: per gap; sd: standard deviation; ns: p>0.05, *: p<0.05, **: p<0.01, ***: p<0.001. Different letters indicate significant differences between rank sums. Wilcoxon rank sums were a: W= 2512; ns, b and c: W= 4697.5***; d and e: W= 239***.

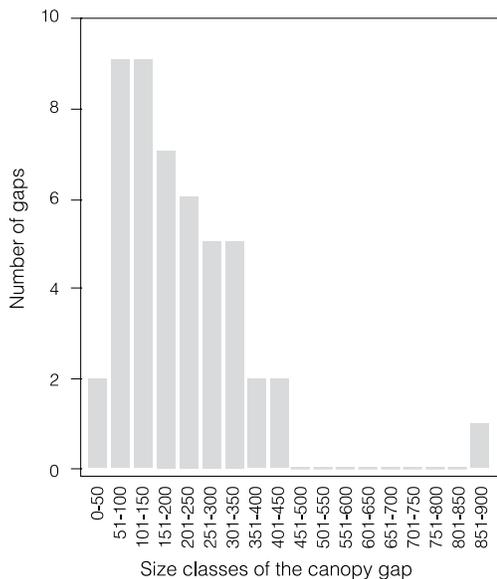


Figure 4. Frequency of canopy gaps per gap size class (areas in m²).

gap maker trees and secondary gap trees did differ significantly, however. Those trees causing gaps had significantly larger diameters than those that were either pushed or pulled down by the gap maker. Gap makers with larger diameters also created bigger gaps; and the more fallen trees, the greater the gap size. Gap size was positively, but only weakly, correlated with the total number of fallen trees (Spearman's rank correlation $S = 1847.163$, $p = 0.002$, $\rho = 0.5$) and their total basal area ($S = 1374.693$, $p = 4.375e-06$, $\rho = 0.7$), but was not correlated with their total crown area ($n = 10$, $S = 76$, $p = 0.1133$, $\rho = 0.5$).

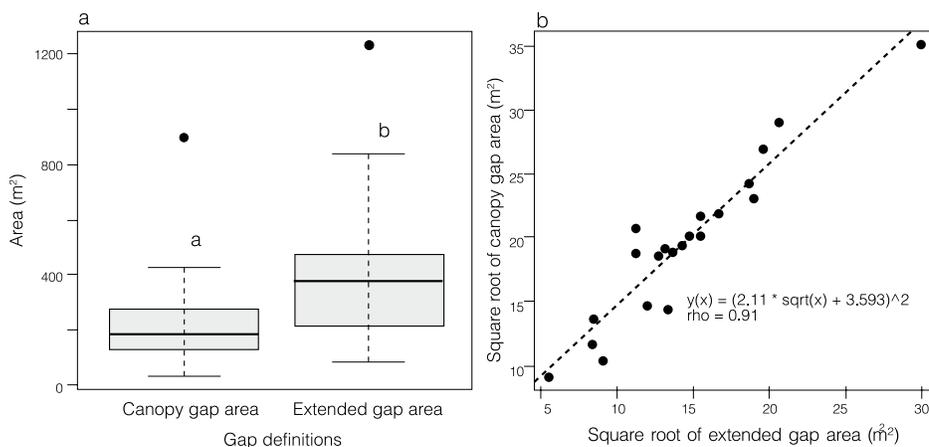


Figure 5. a: sizes of canopy and extended gaps ($n=21$). Each box contains 50% of the respective gap areas. Horizontal line: median value, whiskers: maximum und minimum gap area values, unless outliers (black dots) are present, different letters indicate significant differences between gap areas. b: relationship between canopy and extended gap areas. Spearman's rank correlation $S = 127.0825$, $p < 0.001$, ρ : coefficient. In the formula y : extended gap area, and x : canopy gap area ($n = 21$).

Gap structure

The sizes of the canopy gaps ranged from 31 to 89 m². About 85% of the gaps were 50 to 350m² in size (Figure 4, Table I). The extended gap areas ranged from 83 to 1235m². The canopy gaps were 15-70% smaller than their corresponding extended gaps (Figure 5a), and their areas were highly correlated (Figure 5b). The gaps varied in breadth, from broad to narrow. The majority of the gaps were broad ($B_f = 0.2-3.5$).

The proportions of the various microhabitat areas within a gap varied greatly between gaps. Undisturbed ground covered the largest combined area (4442.71m²), whereas fallen crowns, large trunks and large branches exhibited smaller total areas (1601.77, 2435.28 and 1610.99m², respectively). The border area, identified as a non-gap microhabitat, covered about twice the area classed as undisturbed ground (12008.74m²).

Magnitude of gap disturbances

The loss of tree basal area in the forests of the Sierra de Lema due to gap formation ranged between 2.4 and 2.7m²·ha⁻¹, corresponding to a trunk deadwood volume of between nearly 0 and 19.75m³·ha⁻¹ (mean = 4.86m³·ha⁻¹). The area of the 25ha subplot covered by the canopy and extended gaps amounted to 3558 and 7550.75m², respectively, corresponding 1.4 and 3.7% of the subplot area.

Discussion

Modes of gap formation

The observation of uprooting as the main mode of gap formation in the study area coincided with the findings for Counami (Colson *et al.*, 2006) and Nouragues (van der Meer and Bongers, 1996b) in French Guiana, for La Selva (Brandani *et al.*, 1988) and Cordillera de Tilarán (Lawton and Putz, 1988) in Costa Rica, and Christmas Island in the Indian Ocean (Green, 1996).

The predominance of uprooting as a cause of gap formation in the forests of the Sierra de Lema was probably due to the superficial rooting. The soils of the study region have a humus layer with a dense root mat and high humus content. The fine root (<2mm diameter) systems in the soils of the region are superficial due to the acidity combined with a Ca deficiency and high Al³⁺ concentration (Dezseo *et al.*, 2004; Dezseo and Foelster, 1994; Foelster, 1986; Foelster *et al.*, 2001). There are as yet no estimates for thicker roots (>2mm diameter) and their depths in the region, but shallow rooting (Priess and Foelster, 1994) and shallow soils (<50cm depth; Dezseo *et al.*, 2004) have been reported. Similar relationships between soil infertility, superficial rooting and gap creation caused by the uprooting of trees have also been reported for other tropical forests (Jans *et al.*, 1993; van der Meer and Bongers, 1996b; Gale and Barfod, 1999).

The most plausible explanation for the direction of tree fall is the wind direction. The prevailing wind direction recorded at the nearest meteorological station (EDELCA, at Parupa) coincides roughly (70-130°) with the direction of the fall of gap maker and secondary gap trees.

Modes of tree fall in gaps in the Sierra de Lema

The gap maker trees were found to be thicker than the secondary gap trees. The high proportion of secondary gap trees that were smaller than the neighboring gap maker indicates that these are not strong enough to withstand the downward push of the larger gap makers, or the downward pull in the case of secondary trees attached to a gap maker by lianas (domino effect). The shallow root systems of the trees may also play a role.

Around 80% of the fallen trees in the gaps of the Sierra de Lema were pushed down by a single large gap maker tree. Each gap maker often pulled down several adjacent smaller trees. This underlines the importance of shallow tree rooting and lianas in the context of disturbance patterns in the region. The results of a study carried out in Nouragues, French Guiana, also showed that the diameters of the trees initiating forest disturbances were significantly larger than those of secondary gap trees (van der Meer and Bongers, 1996b) and consequently it could be assumed for these forests that tree size is a determinant of canopy disturbance (Jansen *et al.*, 2008). The positive relationship between the number of trees involved in gap formation with gap sizes also agrees with the pattern found in other tropical forests (Lawton and Putz, 1988; Jans *et al.*, 1993; Arévalo and Fernández-Palacios, 1998; Ferreira de Lima and Cunha de Moura, 2008; Jansen *et al.*, 2008).

Gap size, breadth and regeneration potential

The average gap size indicated that gaps in the Sierra de Lema are amongst the largest natural gaps recorded in tropical forests (Table II), exhibiting sizes similar to those recorded in Nouragues, French Guiana (van der Meer and Bongers, 1996b), Rio Hoja Blanca, Ecuador (Gale, 2000) and on Christmas Island (Green, 1996).

These large gap areas in the forests of the Sierra de Lema may be explained by the large number of trees that fall during a gap creation event (domino effect, Table II) and also by the occasional occurrence of heavy windstorms (Foster and Terborgh, 1998; Nelson *et al.*, 1994). Unfortunately, there is no meteorological information for wind speeds in the Sierra de Lema, but wind speed tends to increase at higher altitudes (Esteban Perdomo, personal communication). The frequency of the domino effect documented for tropical forests cited in the relevant literature (Table II) was in all cases <30%, with an exception being the Carlos Botelho State Park, Brazil, at 63% (Ferreira de Lima and Cunha de Moura, 2008). Even though the frequency of the domino effect in the Sierra de Lema was only slightly higher (70%), the number of secondary trees involved in each gap event was significantly high-

er (Table I) than in gaps in the latter National Park. This highlights the role played by the domino effect in gap formation in the forests of the Sierra de Lema.

The large gap sizes were not explained by tree height. The literature consulted (see Table II) revealed that the canopies of other forests studied have heights similar to those of the fallen trees in the gaps in the Sierra de Lema, but often the emergent trees found elsewhere are much taller than those in Sierra de Lema (the longest fallen tree measured in a gap had a length of 38.5m, whereas examples from the literature refer to emergent trees with lengths >50m). In spite of this, most gaps in the study area were larger than the average gap sizes observed in tropical forests with similar canopy heights and taller emergent trees.

From the large gap sizes and their broad shapes, characteristics allowing for the high availability of direct light within the gaps, the potential for the abundant regeneration of pioneer species exists, and also that of species characteristic of the subsequent successional phase. However, this potential for the regeneration of pioneer woody species is suppressed in part by the presence of considerable quantities of advanced regeneration in the gaps. Around 44% of the total gap area was categorized as undisturbed ground. Here the vegetation was not damaged in the process of gap formation, meaning that the advanced regeneration remained intact (Uhl *et al.*, 1988; van der Meer *et al.*, 1998; Poorter, 2002; Ferreira de Lima and Cunha de Moura, 2008).

Also, if it is assumed that microhabitats in gaps differ with respect to the prevailing environmental conditions and, therefore, in how they determine patterns of tree regeneration, as a function of the adaptation of different species to these microhabitats (Ricklefs, 1977), then a distinctive tree species regeneration or even species assemblages in the different microhabitats within gaps would be expected.

Effects of gap disturbances on forest stands

The loss of tree volume caused by gap formation in the study area was equivalent to a mean 0.5% of the stand volume per ha, calculated on the basis of the gap frequency derived in this study (Table II)

and the tree volume determined for a forest stand located close to the study area, at about the same altitude (97m³ per 0.1ha, trees with diameters ≥10cm; Hans Georg, Karsten Heyn and Lionel Hernández, personal communication). Gap formation resulted in a loss of ~5.7% of the basal area per ha. This finding was based on basal areas ascertained for two 1ha reference plots within the study area and the gap frequency value obtained (basal areas: 41 and 46m²·ha⁻¹ for trees with diameter ≥10cm; basal area data provided by Litzinia Aguirre, Carolina González and Elio Sanoja, personal communication). It is, therefore, important that these gap creation events be considered when studying changes to forest structure.

It was expected that the area of canopy gaps relative to the entire forest area would be larger, the reason for this being that the gaps in the study area are large compared to those found in other tropical forests (considering that all used the same gap definition). Nevertheless, the total gap area derived for the study area in the Sierra de Lema is in the range (0.2-6.3%) reported for tropical forests (Table II). An explanation for this could be the low frequency of gaps in the Sierra de Lema (1.1 gaps/ha) compared to other areas (Table II), such as the Ivory Coast (16.9 gaps/ha), which has the highest reported frequency. In order to better compare different forests, larger study areas are necessary. Some of the sites studied to date were too small (1.2 and 5ha; Lang and Knight, 1983; Lawton and Putz, 1988; Jans *et al.*, 1993). Replications are also required within each region studied, as it has been shown that gap frequency is not consistent even within a particular region (Kapos *et al.*, 1990).

Conclusions

This study represents the first recording of gaps across a large forest area in either Venezuela or the mountain areas of the Guayana Shield. Some of the characteristics of gap formation observed in the Sierra de Lema, such as the large gap sizes and the high frequency of multiple tree falls, were clearly distinct from the patterns of gap formation documented for other tropical forests situated on fertile soils, such as Barro Colorado Island in Panama, La Selva in Costa Rica and in Ecuador (soils of volcanic origin). Further studies of

TABLE II
GAP SIZES AND FREQUENCIES IN TROPICAL FORESTS

Location of research area, country (reference)	Measr. h (m)	Range gap size (m ²)	Mean gap size (m ²)	Gap area in forest (%)	Freq. (gaps/ha)	Canopy h (m)	Emergent tree h (m)	Domino effect
La Selva, Costa Rica (Brandani <i>et al.</i> , 1988)		25 - 1273	144					“few”
La Selva, Costa Rica (Ostertag 1998)	2	9 - 154	65					
La Selva, Costa Rica (Sanford <i>et al.</i> , 1986)	5	40 - 781	161	6.3	2.1	30 - 40	55	“few”
Monte Verde, Costa Rica (Lawton and Putz, 1988)	3	4 - 135		1.4		5 - 23		
Barro Colorado Island, Panama (Dalling <i>et al.</i> , 1998)	5	25 - 125	33					11%
Barro Colorado Island, Panama (Hubbell <i>et al.</i> , 1999)	5	25 - 1550						
Barro Colorado Island, Panama (Brokaw, 1982)	2		85					
Barro Colorado Island, Panama (Lang and Knight, 1983)	2			3.8	8.7	20 - 25	35	
Carlos Botelho State Park, Brazil (Ferreira de Lima and Cunha de Moura, 2008)	2	6 - 227	56					63%
Santa Genebra County Reserve (Venâncio Martins and Ribeiro Rodrigues, 2002)	2	20 - 468	126					20%
Río Sumino, Ecuador (Kapos <i>et al.</i> , 1990)	2		10	1.4				
Río Quilla Pacay, Ecuador (Kapos <i>et al.</i> , 1990)	2		15	5.1				
Río Hoja Blanca, Ecuador (Gale, 2000)	2	50 - 1100	206	0.2	5.3	31	55	3%
Counami, French Guiana (Colson <i>et al.</i> , 2006)	2	56 - 991	359			30	55	
Nouragues, French Guiana (van der Meer and Bongers, 1996a)	2	4 - 100	26	0.2	8.5	24	60	25%
Four tropical forests: La Selva, Barro Colorado Island, Cocha Caschu, Peru, and km 41 close to Manaus, Brazil (Poorter, 2002)	2	20 - 490	140					
Anaga Natural Park, Tenerife, Canary Islands (Arévalo and Fernández-Palacios, 1998)	2	17 - 125	41			10 - 20		
Christmas Island, Indian Ocean (Green, 1996)	3	17 - 700	169			40		“few”
Täi, Täi National Park, Ivory Coast (Poorter <i>et al.</i> , 1994)	2	11 - 204	42	0.8	16.9		55	25%
Para, Täi National Park, Ivory Coast (Poorter <i>et al.</i> , 1994)	2	11 - 244	44	0.8	16.9		55	30%
Zagné, Täi National Park, Ivory Coast (Poorter <i>et al.</i> , 1994)	2	11 - 231	36	0.8	16.9		55	33%
Sierra de Lema, Venezuela (this study)	2	31 - 896	296+	1.4	1.1	22 §	39 §	70%

The gap areas referred to the canopy level. h: height; Measr. h: height above the ground (m) at which the gap area was measured; Domino effect: frequency of gap events with a corresponding occurrence of the domino effect (“few” is a qualitative estimation of this frequency cited in the literature), elsewhere the proportion (%) is given; +: mean gap size (excluding a very large gap of 896m² it is 192m²; §: mean length of fallen trees in the gaps; §: length of the largest fallen tree in the gaps.

gap structure in the montane forest ecosystems of the Guayana Shield are necessary in order to draw firm conclusions about the gap structures occurring in these forests. Gaps should be deemed to be a structural feature of forests when studying forest function and process.

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DISTURBIOS A PEQUEÑA ESCALA EN UN BOSQUE TROPICAL MONTANO DE GUAYANA: CARACTERIZACIÓN DE CLAROS EN LA SIERRA DE LEMA, VENEZUELA

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RESUMEN

El presente estudio describe la estructura de claros en el bosque tropical montano de Sierra de Lema, Estado Bolívar, Venezuela. Para ello se determinaron las superficies del claro a nivel del dosel (CAN) y del suelo (EXT), así como las superficies de los microhábitats. Se calcularon también las áreas basales y los volúmenes de madera de los fustes de los árboles que formaron los claros. Para cada claro se diferenciaron entre los árboles que iniciaron la formación del claro y los árboles secundarios, determinándose para ambos el modo de caída. Los claros fueron formados principalmente por árboles desraizados, y la caída múltiple de árboles fue un evento frecuente. Los claros tienen superficies (CAN= 31-896m²; EXT= 83-1235m²) que superan entre 30 a 90% a aquellas reportadas para la mayo-

ría de los bosques tropicales. La reducción del área basal y volumen de fustes generada por los claros fue de 5,8 y 0,5% respectivamente. Los claros configuran cerca del 1,4% de la superficie de los bosques. El microhábitat más importante en los claros es el suelo no perturbado. El predominio de árboles desraizados como formadores de claros estaría relacionado con un enraizamiento superficial de los mismos. Las grandes superficies de los claros en Sierra de Lema se explican por el alto número de árboles involucrados en los eventos. La regeneración remanente del suelo no perturbado puede ser un componente importante en la regeneración del claro, aunque el gran tamaño de los mismos harían posible una abundante regeneración de especies pioneras.

DISTURBIOS A PEQUENA ESCALA DO BOSQUE TROPICAL MONTANO DE GUAYANA: CARACTERIZAÇÃO DAS CLAREIRAS NA SIERRA DE LEMA, VENEZUELA

Cristabel Durán Rangel, Albert Reif e Lionel Hernández

RESUMO

O presente estudo descreve a estrutura de clareiras no bosque tropical montano de Sierra de Lema, Estado Bolívar, Venezuela. Para isto foram determinadas as superfícies das clareiras a nível do dossel (CAN) e do solo (EXT), assim como as superfícies dos microhábitats. Calcularam-se também as áreas basais e os volumes de madeira dos troncos das árvores que formaram as clareiras. Para cada clareira foram diferenciados os grupos de árvores que iniciaram a formação da clareira e o das árvores secundárias, determinando-se para ambos o tipo de queda. As clareiras foram formadas principalmente por árvores desraizadas, e a queda múltipla de árvores foi um evento frequente. As clareiras têm superfícies (CAN=31-896m²; EXT=83-1235m²) que superam entre 30 a 90% a aquelas relata-

das para a maioria dos bosques tropicais. A redução da área basal e volume de troncos gerada pelas clareiras foi de 5,8 e 0,5% respectivamente. As clareiras configuram cerca de 1,4% da superfície dos bosques. O microhábitat mais importante nas clareiras é o solo não perturbado. O predominio de árvores desraizadas como formadores de clareiras estaria relacionado com um enraizamento superficial das mesmas. As grandes superfícies das clareiras na Sierra de Lema se explicam pelo alto número de árvores envolvidas nos eventos. A regeneração em remanescente de solo não perturbado pode ser um componente importante na regeneração em clareira, ainda que o grande tamanho dos mesmos fariam possível uma abundante regeneração de espécies pioneiras.