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SHORT COMMUNICATION

Influence of tree-fall orientation on canopy gap shape in an Ecuadorian rain forest

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Canopy gaps in tropical rainforests are important drivers of the forest cycle and tree diversity (e.g. Brokaw 1985, Denslow 1987). Increased light and spatial and temporal heterogeneity in gaps are thought to play an important role in the succession, and determination, of species composition in the gap-patch (Poulson & Platt 1989, Raich 1989).

Among the variables that presumably contribute to heterogeneity of gaps are: size, orientation, shape, underlying topography and height of the surrounding canopy. Of these variables, gap shape and its ecological consequences have not yet been assessed objectively.

In this study we analysed the shape of 14 canopy gaps found during June 1997 in a 13.5-ha permanent plot of a virgin *terra firme* forest (Jacobs 1981), at the Tiputini Biodiversity Station (TBS), Napo province, Ecuador (0°40′S, 76°20′W). We focused on a possible relationship between the fall direction of the gap-making elements and the shape pattern of the gaps.

Within the plot, canopy gaps (*sensu* Brokaw 1982, but to a minimal size of 4 m^2) formed between October 1996 and June 1997 were permanently marked at their centre with metallic poles, and, among other variables, the fall direction (ϕ) of the gap-makers (trees, branches or vines) was recorded. If multiple elements were involved in a gap event, the mean fall direction ($\bar{\phi}$) (Batschelet 1981) was used as reference.

Hemispherical pictures (hemiphots) were taken using a CID-100 Digital Plant Canopy Imager (CID 1997). Hemiphots were taken at 2 m above the ground at the marking pole, with the camera oriented toward magnetic north. Images were enhanced for continuity and contrast, and gap area (A_g, in pixel number) and gap perimeter (P_g, in pixel sides) were calculated with a FORTRAN-77 program.

Gap shape was quantified using 17 shape indices. Twelve indices were constructed based on referential geometrical figures (circle, square, rectangle, ellipse, and isosceles and equilateral triangles). Six of those indices were based on the ratio:

$$\frac{A_g}{A_{ref}} = I_k \qquad (k = 1, \cdots 6)$$

and six on the ratio:

$$\frac{P_g}{P_{ref}} = I_k \qquad (k = 7, \cdots 12)$$

where A_{ref} and P_{ref} are the area and perimeter of reference, respectively, calculated for each geometrical figure. Reference area and perimeter are calculated through the known perimeter and area of each gap. We also calculated the fractal dimension (Olsen *et al.* 1993):

$$2\,\frac{\ln(P_g/4)}{\ln(A_g)} = I_{13}$$

and the following indices of compactness:

$$\frac{P_g}{P_{\max}(n)} = I_{14}$$

$$\frac{P_g}{P_{\min}(n)} = I_{15}$$

$$\frac{A_g}{P_g^2} = I_{16}$$

$$\frac{4\sqrt{A_g}}{P_g} = I_{17}$$

$P_{max}(n)$ and $P_{min}(n)$ are the theoretical maximum and minimum perimeter of n pixels. I_{14} and I_{15} are discussed in Bogaert (1996); I_{16} and I_{17} in Bogaert & Impens (1998). After correlation analysis (Spearman's rank correlation, $r_s < 0.90$), three indices were found to quantify the shape of the gaps independently:

$$\frac{A_g}{A_{Isos}} = I_5$$

and indices I_{14} & I_{16}.

A_{Isos} is the area a gap should have if it is considered to be an isosceles triangle, calculating the theoretical isosceles area using P_g:

$$A_{ref} = \frac{1}{2}\left((a)\sqrt{\left(\frac{P_g - a}{2}\right)^2 - \left(\frac{a}{2}\right)^2}\right)$$

where a is the shortest side of the gap-figure's box.

Linear-circular correlation (Batschelet 1981, Mardia 1976) was calculated between the ϕ of the gap-maker elements and the scores of the gap images for each of the independent shape indices. Linear-circular correlation differs from classic linear correlation in that one of the variables is cyclic (values ranging from 0 to 2π). In this case, neither 'positive' nor 'negative' correlation can be addressed. A significant correlation was found between I_5 and the ϕ of the gap-maker elements ($Dn = 0.72$, $P < 0.01$, where Dn is the correlation coefficient). None of the other indices was significantly correlated.

This result suggests that canopy gaps at TBS forests tend to form an isosceles triangular pattern (Figure 1), created by the fall orientation of the gap-making elements (seven gaps were formed by uprooting of trees, four by the fall of branches, one by a snapped tree, one by the fall of vines, and one by a fallen dead stem).

A possible explanation of this pattern is that trees in tropical rainforests tend to have flat, horizontally extended crowns (e.g. Terborgh 1985); when a tree falls, and it leaves an opening in the canopy, the hole will tend to have a triangular shape. This shape can arise from the fact that the falling crown is more likely to drag down other trees or parts of them than does the falling stem, so the base of the triangle is roughly as wide as the elements dragged down by the crown, and the height as long as the fallen stem(s).

Towards the crown of the fallen tree, a 'wall' of standing trees will be present; if the wind blows against that wall, the chance is enhanced that the trees there, insufficiently adapted to direct wind, will fall again in the direction of the first tree. In our case, 78.6% of the trees fell between the range $291° - 52°$ ($\bar{\phi} = 350°$ N–NW) likely due to the wind (no meteorological data is available

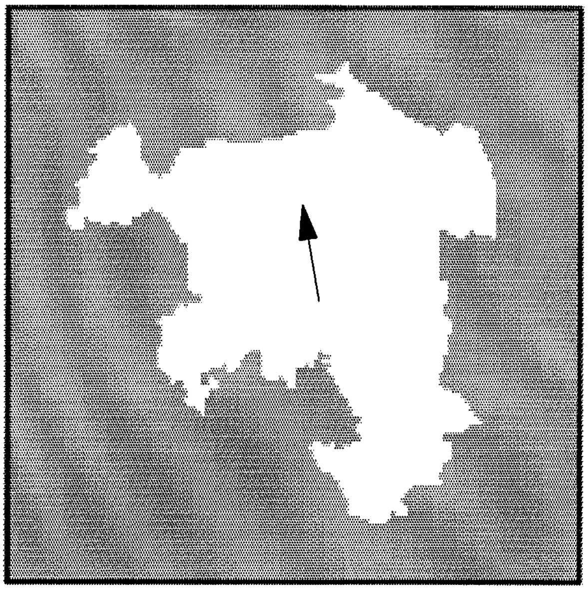

Figure 1. Rasterized hemispherical image of a canopy gap in the study plot at TBS. Arrow shows the mean fall direction ($\bar{\phi} = 350°$).

for TBS, but gap occurrence during storms is common; K. Swing *pers. comm.*), so the most likely place where more falls can occur is northwards, magnifying in this direction the triangular shape pattern (nine of the 14 gaps were created by domino-wise falls).

The amount of light reaching the forest floor and its distribution in gaps has microclimatological effects, which influence forest composition, architecture and tree population dynamics (e.g. Raich 1989). Besides area and orientation, gap shape is a main factor influencing the penetration of light in gaps; therefore, gap shape and its causes should be studied more profoundly, as well as the effects of gap shape on the light regime and the subsequent ecological processes occurring in gaps. In this study, the first step, i.e. shape quantification, is proposed.

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