

CANOPY GAP MORPHOLOGY DETERMINANTS IN AN AMAZONIAN RAIN FOREST

DAVID SALVADOR-VAN EYSENRODE,* JAN BOGAERT AND IVAN IMPENS

Laboratory of Plant Ecology, Department of Biology, University of Antwerp. Universiteitsplein 1, 2610—Antwerpen, Belgium

ABSTRACT. Some features of forest elements making up canopy gaps, and their effects on gap size, shape, and orientation are analyzed. These characteristics, relevant for gap light regime and for ecological processes in gaps, are studied both at the field level and with the aid of digital hemispherical pictures. We found that the length of the gap starter element plays a crucial role in determining gap size. Gap shape-compactness and orientation are rather random results in gap creation. We suggest that gap size will vary among forests at different states of maturity and/or with different canopy heights, which may lead to differences in gap species composition and structure, and so affect their regrowth patterns.

Key words: canopy gaps, shape analysis, tropical rain forest

INTRODUCTION

The fall of major structural elements composing the forest matrix, i.e., trees, branches and vines, usually leads to the formation of gaps by a process of perforation of the canopy layer, allowing light penetration to the forest ground (Bazzaz 1984, Brokaw 1985, Van Der Meer & Bongers 1996a). In tropical rain forests, these small-scale disturbances that alter the heterogeneity of resources through space and time, play an important role in the maintenance of the forest structure and composition (e.g., Brokaw 1982a, Orians 1982, Riéra 1982, Denslow 1987, Clark 1990, Hartshorn 1990). A forest can be considered as a composite of patches in different stages of regeneration, i.e., gaps and forest patches in building and mature phases (Watt 1947, Whitmore 1978, Richards 1996). It has been suggested that gap morphological features, besides other internal sources of heterogeneity, can influence the persistence of plant populations and species coexistence (e.g., Ricklefs 1976, Denslow 1980, Orians 1982, Brandani et al. 1988, Runkle 1989).

Considering gaps as the result of the fall of a volume of forest (Van Der Meer et al. 1994), it is reasonable to hypothesize that some characteristics of such a volume determine the resulting morphological characteristics of gaps. Gap geometry is composed by a core or interior, enclosed by an edge and perimeter (Forman 1997). However, the third-dimensional component of the forest is also relevant to the ecological processes in gaps since it controls light penetration to the understory (e.g., Reifsnnyder & Lull 1965, Terborgh 1985). Gap light regime, which de-

pends on gap size, shape, orientation and height of the surrounding forest, drives microclimatic conditions (e.g., soil moisture, temperature) and subsequently ecological effects such as seed germination, plant growth, mortality, and development (Popma & Bongers 1988, Poulson & Platt 1989, Raich 1989, Raich & Gong 1990, Ostertag 1998).

Gap features are not static through time. Repeated disturbance can occur (Young & Hubbell 1991), leading to an expansion of the core, edge and perimeter. Also, ingrowth of neighboring branches can affect the surrounding canopy height and influence the gap zones, and the vertical plant growth will also contribute to morphologic, structural and microclimatic changes in gaps.

In most of the studies on canopy gaps, gap size (accumulation of area) has been considered the main morphological feature with ecological relevance (e.g., Hartshorn 1978, Brokaw 1985, Denslow 1987). Little attention has been paid to the shape, i.e., spatial distribution of area (Salvador-Van Eysenrode et al. 1998), and orientation, i.e., the spatial distribution of area in relation to a coordinate system.

In this paper, we focus on some features of the gap starter elements and the modes of gap opening, and discuss the possible implications of differences in type and features among gap starters.

STUDY SITE

Data were obtained from a permanent sample plot of 13.5 ha on a tract of virgin *terra firme* forest (Kricher 1989) at the Tiputini Biodiversity Station (TBS, Universidad San Francisco de Quito—Boston University), 0°40'S, 76°20'W, and altitude ca. 300 m, in the new province of

* Corresponding author.

Orellana, Ecuador. The plot was demarcated in June 1997 and consists of two flat terraces surrounded by swamps and an oxbow lake. Soils at TBS are alluvial and clayey (Baldock 1982); yearly mean temperatures are above 25°C, and yearly rainfall totals some 3000 mm per year, following a bimodal pattern (source: Dirección de Aviación Civil, Coca airport, 0°27'S, 76°59'W).

MATERIALS AND METHODS

Within the plot, we searched for all vertical canopy gaps (>4 m²) formed between October 1996 and March 1998. Age of most of the gaps was known; the remaining were dated using referential gaps with known age, comparing the state of vitality of the gap-maker element(s), the freshness of the snap(s), or uprooting(s), and the state of the damaged and grown vegetation in the gap. As soon as possible after their formation, we marked gaps at their center with a numbered metallic pole and recorded the following data.

Gap Makers

Based on Clark's (1990) classification, we noted whether a gap was started by an uprooted tree, snapped tree (stem), branchfall, or vinefall. We recorded the number of gap makers per gap event and measured the height (length) of the gap starter and its diameter at breast height (DBH). In the case of branchfalls, the diameter was measured at the place of the snapping. The diameter of one of the vinefalls was measured as a branchfall. For a second vinefall, its largest diameter was used, and the length of the longest gap diameter within the projected gap area was considered its length. Finally, we determined the fall direction (ϕ) of the gap maker elements. In the case of a second vinefall, we used the direction of the diameter line considered as its length.

Gap Features

Gap sizes were measured according to the definitions of gap of Brokaw (1982b) and Runkle (1981). For Brokaw's gap area (A_B), the distances from the center to the gap edge (projection of the first vegetation over 2 m) were measured along eight radii at intervals of 45°; we obtained gap size adding the areas of the resulting octants. To measure Runkle's area (A_R), we followed the same procedure, but measured the distances from the center towards the stems of the surrounding canopy trees; we considered stems with DBH > 20 cm. Tree-height limits were not considered in this definition (above 10 m). Be-

cause the height of the forest surrounding a gap is variable, we used the mean surrounding canopy height (MSCH) as an estimate of the forest height. We obtained this value measuring the height at each of the eight points used in the measurement of A_B , using a telescopic metric pole and/or a Suunto PM-5/360 PC clinometer.

Hemispherical Imagery

At each gap center, we took a hemispherical picture (hemiphot) with a CID-100 Digital Plant Canopy Imager (CID 1997), at two m above the ground with the camera probe oriented towards magnetic north. Pictures were taken under cloudy sky conditions at dawn.

We enhanced the hemiphotos for contrast and continuity and calculated the area of the gap image (A_g = number of pixels) and the perimeter (P_g = number of pixel side lengths) with a FORTRAN-77 program. Gap shape was quantified with the compactness index (Bogaert & Impens 1998):

$$\frac{P_{\max}(n) - P_g}{P_{\max}(n) - P_{\min}(n)} = \Psi$$

where $P_{\max}(n)$ and $P_{\min}(n)$ are the theoretical maximum and minimum perimeter of n pixels, and $\Psi \rightarrow 1$ for compact patches.

This highly sensitive index is used since we have found that the amount of light reaching the gap floor not only depends on the size of the canopy opening, but also on the gap shape *compactness*. The latter is observed independently of the shape features gaps can have in relation to known geometrical figures (Salvador-Van Eysenrode et al. unpubl. data).

The orientation of A_g with reference to the cardinal points was measured independently of shape as follows: the relativized cumulative sums (ΣR) of pixels in each column and row (area distributions N-S and W-E, respectively) of the gap image were plotted in a bar histogram, each with bar widths relative to the number of columns or rows (FIGURE 1); the area of each bar was calculated (bar height \times width), both for $\Sigma R_{(NS)}$ and $\Sigma R_{(WE)}$ added. Then, the area (A) under the 'curve' of each distribution was calculated and used in an orientation index, i.e.:

$$\frac{A_{NS}}{A_{WE}} = \Theta$$

Finally, gap openness (OPN), the percentage of uncovered sky hemisphere, was calculated using the Winphot-5 software (Ter Steege 1996).

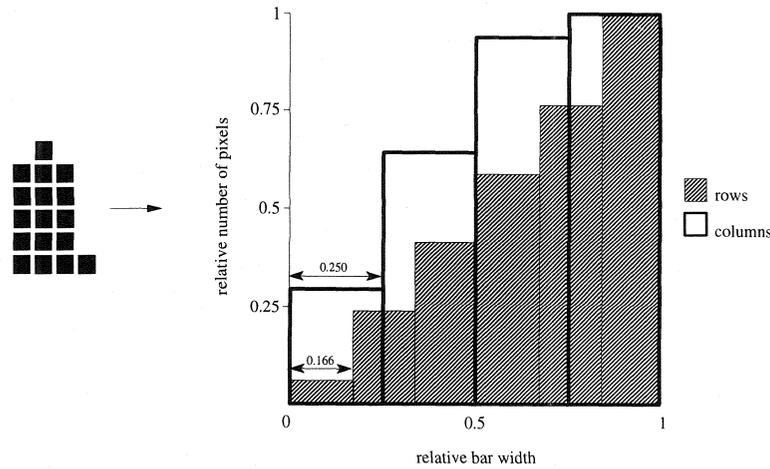


FIGURE 1. Representation of the measurement of the orientation of gap area. The four columns and six rows of the figure at the left (area = 17 pixels) are cumulatively represented in the histogram with relative scales. The total area of the figure is relatively more N-S oriented than W-E (north atop). See text for further explanation.

RESULTS AND DISCUSSION

The number of gap maker elements involved per gap event ($N = 31$) influences A_g , OPN, A_B and A_R (TABLE 1). OPN not only depends on gap size (Ter Steege 1996), but also on the height of the surrounding canopy; this partial dependence is confirmed here by a moderate correlation with the number of gap makers and the length of the gap starter (both partially responsible for gap size). MSCH is also significantly correlated with the number of gap makers, but the first is rather a cause than an effect, i.e., high trees that fall are more likely to produce the fall of more trees. This suggests differences in gap size between single and domino gap events. In tropical rain forests, the relatively common domino-treefalls (e.g., Brokaw 1985) may occur mainly due to the spatial distribution of trees, their interconnection by lianas and their degree of branching. In our study, 41.9% of the gaps formed by more than one element accounted for 72% and 72.5% (gaps sensu Brokaw and Runkle, respectively) of the total plot area in gap phase.

P_g is also positively influenced by the number

of gap makers. Because P_g partly depends on A_g , large gap perimeters are partially a result of large gap areas. This suggests that not only the interior of the gap can be affected by light enhancement, but also that there could be an edge effect around such interior whose behavior may be influenced by its size (Canham et al. 1990). The length of the gap starter elements showed high positive correlations with A_g and MSCH, but mainly with A_B , A_R and OPN, and, although less significantly, with P_g (TABLE 1). This suggests that the length of the gap starter is a crucial feature in gap formation, from which area (size) is mainly dependent. Also, the influence of the gap starter length on gap area is indirect: longer gap starters are more likely to drag down more trees per gap event (correlation, $r_s = 0.72$, $P < 0.01$), and more trees fallen down (domino effects) open more forest area to gaps. In ideal conditions of even gap starter lengths, i.e., even MSCH, the correlation between both may be almost perfect, assuming uprooting as the sole tree-fall mode. However, variation in modes of tree fall (branches, vines, and snapped stems) and canopy heights reduces their correlation.

TABLE 1. Spearman's rank (r) and circular-linear (Dn , Batschelet 1981) correlation coefficient between gap and gap makers' features at TBS. ^A = $P < 0.1$; ^B = $P < 0.05$, ^C = $P < 0.01$. Correlation between ϕ and θ not shown.

	A_g	P_g	Ψ	OPN	A_B	A_R	MSCH
No. gap makers (r)	0.40 ^B	0.30 ^A	0.29	0.50 ^C	0.55 ^C	0.57 ^C	0.46 ^C
Length gap starter (r)	0.56 ^C	0.44 ^B	0.25	0.63 ^C	0.66 ^C	0.66 ^C	0.58 ^C
DBH gap starter (r)	0.28	0.25	0.07	0.28	0.37 ^B	0.44 ^B	0.44 ^B
ϕ (Dn)	0.01	0.00	0.11	0.01	0.06	0.06	0.21 ^B

TABLE 2. Mean and standard deviations (between parentheses) of the features of gap makers and features of gaps at TBS, grouped by types of starter. ^A = $P < 0.1$, ^B = $P < 0.05$, and ^C = $P < 0.01$ in the marked feature between the types of gap makers for the Kruskal-Wallis H-test ($\chi^2_{[\alpha=0.05], 3 \text{ DF}}$).

	Length ^C	DBH ^A	No. gap makers	A_B^B	A_R^B	Ψ	Θ	MSCH
Uprooted tree ($N = 15$)	22.05 (9.50)	39.00 (12.11)	2.73 (2.01)	146.86 (182.90)	204.60 (297.60)	0.94 (0.02)	0.91 (0.25)	18.24 (7.18)
Snapped tree ($N = 6$)	13.37 (6.46)	35.63 (8.73)	1.50 (0.83)	35.16 (39.34)	50.16 (41.06)	0.93 (0.02)	1.05 (0.14)	13.50 (4.11)
Branchfall ($N = 8$)	8.87 (4.76)	26.50 (7.01)	1.12 (0.35)	41.87 (33.17)	56.87 (34.14)	0.93 (0.03)	1.04 (0.17)	15.40 (2.65)
Vinefall ($N = 2$)	9.00 (7.50)	25.50 (28.90)	1.50 (0.70)	21.00 (9.90)	76.50 (75.60)	0.95 (0.01)	1.02 (0.01)	20.06 (15.02)

Gap maker length and DBH together could indicate, in general, the age of the gap maker, which, considered in the context of the forest zone where a gap is formed, can give an idea of the state of maturity of such a zone, regardless of the considerable variation existing among trees in their ratio length-DBH. DBH is, however, less variable than the gap maker length, and shows low correlations with A_B , A_R and MSCH only (TABLE 1). This suggests that gap sizes will differ between zones of forest in different stages of maturity and/or height (reflected in the MSCH), with consequent differences in light regime and microclimate, and maybe regrowth, potential general species composition and structure, and development (e.g., Popma & Bongers 1988, Whitmore et al. 1993). This also means, in general, that a larger gap represents a drastic reset of the completed forest cycle, while small gaps are more likely to be only redisturbances of the building phase during the forest cycle. Other studies have pointed out that gap size and light environment are a function of forest height (Denslow 1987, Clark 1990). Fall direction (ϕ) does not seem to be a determinant for gap features, since there is only a low correlation with MSCH.

Neither significant nor high correlations were found between the features of gap makers and Θ and Ψ , suggesting that the both orientation, and shape-compactness of gap area do not depend on the features of the gap makers. We found that the gap starter's length, A_B and A_R , differ significantly between gaps created by different types of starters (TABLE 2). Although less significantly, DBH also differed.

In this study, uprooting of the trees is the most common cause of gap formation (48.4% of the events). This suggests that the most common gap size would be found among gaps started by uprooted trees. However, high variation should be expected, since uprooted trees are also the most common cause of domino effects (66.6%

of the uprooted trees were domino events, while only 33.3% of the snapped trees and 12.5% of the branchfalls). In other studies, snapping (Putz et al. 1983, Milton et al. 1994, Van Der Meer & Bongers 1996b), and uprooting (Durrieu De Madron 1994) were listed as major causes of tree mortality causing gaps. Of course, not all deaths lead to an opening in the canopy. These differences in modes of tree mortality, presumably caused by contrasting soil conditions (Kapos et al. 1990), and wood and root systems (Putz et al. 1983), affect gap formation (Clark 1990).

Barton (1984) used 300 m² of extended gap area as a breakpoint to divide gaps into small and large; Brokaw (1982a) found 150 m² as a critical area for successful colonization of pioneer species. Based upon the highest modal A_R of our dataset, being near to 150 m², we considered large and small gaps above and under 130 m² respectively. We found that the length and DBH of the gap starters, the number of gap makers and the MSCH differ significantly between large and small gaps ($P < 0.05$, Mann Whitney U -test, two tailed), while Θ and Ψ did not, confirming our previous findings.

Gaps oriented parallel or transversal to the sun will show differences in light conditions (e.g., Denslow 1987). If the largest axis of a gap is determined totally or partially by the length of the starter element, it can be suggested that orientation of the gap area depends upon the ϕ of the starter. Salvador-Van Eysenrode et al. (1998) found that the longest axis of the gap is correlated with the ϕ of the starter. Interestingly, we could not observe a correlation between Θ and ϕ . Moreover, a Rayleigh test (Batschelet 1981) confirmed that ϕ is uniformly distributed, i.e., gap makers at TBS fall at random directions (FIGURE 2).

Not only the types of gap makers and the characteristics of the gap starters are important. Other interplaying factors are also involved in

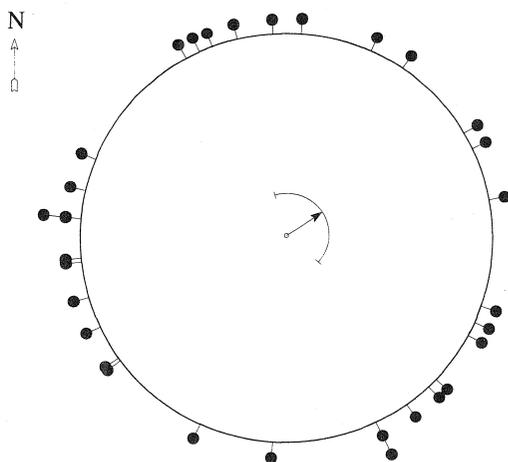


FIGURE 2. Original ϕ of the 31 gap starters at TBS (dots). The central arrow represents the mean $\phi = 56.3^\circ$; mean vector length = 0.2; angular deviation $\pm 72.2^\circ$. The mean vector length falls within the 95% confidence limit (Rayleigh test for randomness).

the differential creation of canopy gaps, such as age of the trees, diseases, mechanical features of the wood, soil characteristics and rooting systems, windblows and canopy shape, and rainfall (Putz et al. 1983, Milton et al. 1994). We have confirmed that the size of gap is the main feature affected by the number of gap starters and their length; gap shape-compactness and orientation of gap area are rather a random result, contributing in this way to habitat heterogeneity within and among gaps. The understanding of gap size distributions and the modes of gap formation among different forest types should be considered in the assessment of logging techniques, forest management, and forest conservation policy.

ACKNOWLEDGMENTS

We thank Fred Kockelbergh and Joris Gansemans for technical support, Kelly Swing and the Universidad San Francisco de Quito for permission to stay at TBS, and the station's staff for assistance. Dr. Piet Van Hecke kindly reviewed and commented on this manuscript. Jan Bogaert is research assistant of the Fund for Scientific Research (F.W.O., Flanders, Belgium).

LITERATURE CITED

Baldock, J.W. 1982. Geología del Ecuador. Boletín de explicación del mapa geológico de la República del Ecuador. Ministerio de Recursos Naturales y Energéticos, Dirección General de Geología y Minas, Quito.

- Barton, A.M. 1984. Neotropical pioneer and shade-tolerant tree species: do they partition treefall gaps? *Trop. Ecol.* 25: 196–202.
- Batschelet, E. 1981. *Circular Statistics in Biology*. Academic Press, London.
- Bazzaz, F.A. 1984. Dynamics of wet tropical forests and their species strategies. Pp. 233–243 in E. Medina, H.A. Mooney and C. Vasques-Yanes, eds. *Physiological Ecology of Plants of the Wet Tropics*. Dr. Junk Publishers, The Hague.
- Bogaert, J. and I. Impens. 1998. An improvement on area-perimeter ratios for interior-edge evaluation of habitats. Pp. 55–61 in F. Muge, R. Caldas Pinto and M. Piedade, eds. *Proceedings of the 10th Portuguese Conference on Pattern Recognition (RECPAD '98, March 26–27 1998)*. Instituto Superior Técnico, Universidade Técnica de Lisboa, Lisbon.
- Brandani A., G.S. Hartshorn and G.H. Orians. 1988. Internal heterogeneity of gaps and species richness in a Costa Rican tropical wet forest. *J. Trop. Ecol.* 4: 99–119.
- Brokaw, N.V.L. 1982a. Treefalls: frequency, timing and consequences. Pp. 101–107 in E.G. Leigh, Jr., A. Stanley Rand and D.M. Windsor, eds. *The Ecology of a Tropical Forest: Seasonal Rhythms & Long Term Changes*. Smithsonian Institution Press, Washington D.C.
- . 1982b. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14: 158–160.
- . 1985. Treefalls, regrowth, and community structure in tropical forests. Pp. 53–69 in S.T.A. and P.S. White, eds. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, London.
- Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T. Spies and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canad. J. Forest Res.* 20: 620–631.
- Clark, D.B. 1990. The role of disturbance in the regeneration of neotropical moist forests. Pp. 291–315 in K.S. Bawa and M. Hadley, eds. *Reproductive Ecology of Tropical Forest Plants*. MAB-UNESCO series, 7. Paris.
- CID. 1997. CID-100 Digital Plant Canopy Imager, instruction manual, CID Inc, Vancouver.
- Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12: 47–55.
- . 1987. Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst.* 18: 431–451.
- Durrieu De Madron, L. 1994. Mortalité des arbres en forêt primaire de Guyane Française. *Bois Forêts Trop.* 239: 43–57.
- Forman, R.T.T. 1997. *Land mosaics. The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge.
- Hartshorn, G.S. 1978. Tree falls and tropical forest dynamics. Pp. 617–638 in P.B. Tomlinson and M.H. Zimmerman, eds. *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge.
- . 1990. An overview of neotropical forest dynamics. Pp. 585–599 in A. Gentry, ed. *Four Neotropical Rainforests*. Yale University Press, New Haven.

- Kapos, V., E. Pallant, A. Bien and S. Freskos. 1990. Gap frequencies in lowland rain forest sites on contrasting soils in Amazonian Ecuador. *Biotropica* 22: 218–225.
- Kricher, J.C. 1989. *A Neotropical Companion: An Introduction to the Animals, Plants, and Ecosystems of the New World Tropics*. Princeton University Press, New Jersey.
- Milton, K., E.A. Laca and M.W. Demment. 1994. Successional patterns of mortality and growth of large trees in a Panamanian lowland forest. *J. Ecol.* 82: 79–87.
- Ostertag, R. 1998. Below ground effects of canopy gaps in a tropical wet forest. *Ecology* 79: 1294–1304.
- Orians, G.H. 1982. The influence of tree-falls in tropical forests in tree species richness. *Trop. Ecol.* 23: 255–279.
- Popma, J. and F. Bongers. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625–632.
- Poulson, T.L. and W.J. Platt. 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70: 553–555.
- Putz, F.E., P.D. Coley, K. Lu, A. Montalvo and A. Iello. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. *Canad. J. Forest Res.* 13: 1011–1020.
- Raich, J.W. 1989. Seasonal and spatial variation in light environment in a tropical dipterocarp forest and gaps. *Biotropica* 21: 299–302.
- Raich, J.W. and W.K. Gong. 1990. Effects of canopy gaps on tree seed germination in a Malaysian dipterocarp forest. *J. Trop. Ecol.* 6: 203–217.
- Reifsnnyder, W.E. and H.W. Lull. 1965. *Radiant Energy in Relation to Forests*. Technical Bulletin 1344, U.S. Department of Agriculture-Forest Service, Washington D.C.
- Richards, P.W. 1996. *The Tropical Rainforest*. Cambridge University Press, Cambridge.
- Ricklefs, R.E. 1976. Environmental heterogeneity and plant species diversity: a hypothesis. *Amer. Nat.* 111: 376–381.
- Riera, B. 1982. Importance des buttes de déracinement dans la régénération forestière en Guyane Française. *Rev. Ecol. (Terre & Vie)* 40: 321–329.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041–1051.
- . 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70: 546–547.
- Salvador-Van Eysenrode, D., J. Bogaert, P. Van Hecke and I. Impens. 1998. Influence of tree-fall orientation on canopy gap shape in an Ecuadorian rainforest. *J. Trop. Ecol.* 14: 865–869.
- Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. *Amer. Nat.* 126: 760–776.
- Ter Steege, H. 1996. Winphot-5. A program to analyze vegetation indices, light and light quality from hemispherical photographs. *Tropenbos-Guyana Reports 1995-2*, Tropenbos-Guyana Programme, Georgetown.
- Van Der Meer, P.J., F. Bongers, L. Chatrou and B. Riera. 1994. Defining canopy gaps in a tropical rain forest: effects on gap size and turnover rates. *Acta Oecol.* 15: 701–714.
- Van Der Meer, P.J. and F. Bongers. 1996a. Patterns of treefalls and branchfalls in a neotropical rain forest in French Guiana. *J. Ecol.* 84: 19–29.
- . 1996b. Formation and closure of canopy gaps in the rainforest at Nouragues, French Guiana. *Vegetatio* 126: 167–179.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1–22.
- Whitmore, T.C. 1978. Gaps in the forest canopy. Pp. 639–655 in P.B. Tomlinson and M.H. Zimmerman, eds. *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge.
- Whitmore, T.C., N.D. Brown, M.D. Swaine, D. Kennedy, C.I. Goodwin-Bailey and W.K. Gong. 1993. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. *J. Trop. Ecol.* 9: 131–151.
- Young, T.P. and S.P. Hubbell. 1991. Crown asymmetry, treefalls, and repeat disturbance of broad leaved forest gaps. *Ecology* 72: 1464–1471.