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# Treefall Gap Dynamics in a Tropical Rain Forest in Papua New Guinea<sup>1</sup>

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**Abstract:** Treefall gaps play important roles in tropical rain-forest ecology. But studies rely increasingly on models, remote sensing, and a few intensively studied research sites, mostly in the neotropics. We studied the basic parameters of gap dynamics (size, causes, and frequency) of treefall gaps in a lower montane primary forest on the southern flank of the central range of Papua New Guinea. We found 40 treefall gaps formed on 10.4 km of transect sampled annually over 3 yr. Mean proportion of forest under new gaps was 0.015/yr. Mean area of treefall gaps  $\leq 1$  yr old was 312 m<sup>2</sup>, and gap area was positively correlated with diameter of the fallen tree. Mostly only large trees (diameter at breast height [DBH]  $\bar{x}$  = 53 cm) fell as snapped ( $n = 23$ ) or uprooted ( $n = 17$ ), creating both single ( $n = 34$ ) and multiple ( $n = 6$ ) treefall gaps. There was no strong directionality in the bearings of treefalls. This study provides some of the first information on gap dynamics in Papua New Guinea, where such data can be used to inform sustainable forestry harvesting practices.

THE CLOSED CANOPY of tropical rain forests blocks most light from reaching the forest interior. In such forests, treefalls are fairly frequent but unpredictable in time and space (Hubbell et al. 1999, Brokaw and Busing 2000). Treefalls produce gaps, allowing sunlight to penetrate the interior (Denslow 1987, Marthews et al. 2008b). This pulse of increased light is important in the life histories of rain forest tree species; most “shade tolerant” species rarely reach the canopy without periods of enhanced growth beneath gaps (Denslow 1995, Wright et al. 2003, Brienen and Zuidema 2006). Gaps create variation in microclimates (Marthews et al. 2008a) and diversify niches (Denslow 1995, Schnitzer and Carson 2001, Sanchez et al. 2009), they

alter competition for sun (Ruger et al. 2009), they affect nutrient and carbon cycles (Arunachalam and Arunachalam 2000, Feeley et al. 2007), and they affect animal movements and demography (Fredericksen et al. 1999, Beck et al. 2004). Gap dynamics and disturbance regimes also may influence global carbon cycles (Vieira et al. 2004, Feeley et al. 2007).

Gaps may play an important role in the maintenance of high sympatric species diversity of tropical plants (Brokaw 1985a, Denslow 1995, Schnitzer and Carson 2001) and animals (Laurance and Laurance 1996, Owionji and Plumptre 1998). However, this role alone is not enough to explain the high diversity of tropical forests (Hubbell et al. 1999, Brokaw and Busing 2000).

A better understanding of natural disturbance regimes and gap dynamics is important for forest management. Heliophilic invasive plants often establish in gaps (Baret et al. 2008). Management of reduced-impact or certified forestry projects could be improved through better understanding of gap dynamics (Babaasa et al. 2004, Felton et al. 2006, Kukkonen et al. 2008). Baseline data on past and current natural gap formation rates can help assess and predict potential anthropogenic environmental changes, including climate change (Malhi and Phillips 2004, Enquist and Enquist 2010).

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Numerous studies in both temperate and tropical forests show that there is considerable heterogeneity in the rates, causes, and sizes of naturally occurring gaps (Runkle 1981, Brokaw 1982*a,b*). Consistent differences in causes, sizes, and formation rates of treefall gaps could lead to substantial differences in the overall ecology of forests (Denslow 1980). Gap size is predicted to vary according to the size of the tree that falls (Brokaw 1982*b*, Zang and Wang 2002) or if multiple treefalls create a single opening (Chao et al. 2009, Sapkota and Oden 2009). Thus differences in tree stature and wind velocities among forests could lead to different gap dynamics. Whether trees snap, uproot, or die standing, along with direction relative to ground slope could affect gap size and shape (Denslow 1987, Ogden et al. 1991, Runkle 1998). Understanding of gap formation rates and gap sizes are prerequisites to measuring forest turnover rates and long-term floristic changes (Runkle 1982, Denslow 1987, Clark and Clark 2011).

One of the largest remaining rain forests is found on the island of New Guinea (Mittermeier et al. 1998). These forests are botanically unique, with generally 60%–90% species endemism (Johns 1993), but no quantitative studies of gap dynamics have been undertaken there. Anecdotal evidence suggests that the New Guinea forests are particularly dynamic (Paijmans 1976, Johns 1986) in part due to the relative youth and instability of its mountains.

We undertook this study to provide the first quantitative assessments of gap dynamics in the Papuan rain-forest biome. We examined the following four questions in a 3 yr study in lower montane forest: (1) What is the distribution of gap size? (2) Is there a relationship between gap area and the diameter of the falling tree? (3) Does the type, cause, and direction of treefall affect variation in gap size? and (4) What are the gap formation rates of the forest?

#### MATERIALS AND METHODS

##### *Study Site*

We conducted this study at the Crater Mountain Biological Research Station on the south

flank of the central range of Papua New Guinea (6° 43' S, 145° 05' E). The 400 ha study area lies in rugged terrain 850–1,350 m above sea level. The site experiences aseasonal rainfall ( $\bar{x}$  = 6.4 m/yr), with monthly rainfall between 18 and 96 cm (Wright et al. 1997). The forest is typical lower montane primary forest (Paijmans 1976) with natural disturbances, such as treefalls, landslides, and falling debris (Wright et al. 1997, Mack 1998). Census of permanent plant plots showed that this is a mature forest where tree mortality is approximately equal to recruitment (16–18 trees/ha/yr) for trees  $\geq 10$  cm diameter at breast height (DBH) (1.3 m above ground) (D. D. Wright and M. Supuma, unpubl. data). No human disturbance had occurred in at least the last 30 yr based on information obtained from local informants.

##### *Sampling Transects*

We established 116 transects, each 100 m long, in June–July of 2003 to find treefall gaps that had formed in the previous 12 months, consistent with methods used in other studies (Runkle 1982, Murray 1986, Battles et al. 1996). Forty-two pairs of these transects were established parallel to the longest sides of 42 randomly located plant plots (20 m  $\times$  50 m) previously established by Wright (Wright 2005). The remaining transects were begun from random points from the 400 ha study area grid system and followed random compass bearings. Portions of the transects (1.5 km) that were inaccessible due to cliffs or that traversed streams were excluded, yielding a total of 10.1 km of transects searched annually for intersecting canopy treefall gaps. A minimum 40 m interval was set between transects to ensure that no gap was sampled twice because the tallest trees in the study area are usually <40 m (Wright et al. 1997). No gaps were intersected by >1 transect. Subsequent surveys were carried out on the same 10.1 km of transects in June–July of 2004 and 2005. Gaps were marked and mapped to ensure that they were not recounted.

Gaps located on the first survey (2003) were classified as either recent gaps ( $\leq 1$  yr old)

or older gaps (>1 yr old). Criteria used to determine age of gaps on the first census followed Runkle (1992): (1) condition of the decaying treefall bole and branches; (2) freshness and/or intactness of treefall bole and branches; (3) freshness of twigs and leaves, and the regeneration of seedlings and saplings in the gap; (4) stage of regeneration and release of saplings from bud scars of standing and broken saplings and trees in gaps. We had to estimate age only on our initial sampling, because we were sure of the age of newly formed gaps (<1 yr old) that were encountered in the following 2 yr. In this forest heliophilic pioneer species often do not sprout in gaps and are not a good indicator of gap age (unpubl. data).

### *Gap Definition*

Gaps were initially identified following Brokaw's (1982a:159) definition of a gap: "a vertical opening in the canopy extending through all levels at least down to an average height of 2 m above the forest floor." Vertical openings were treated as gaps if the canopy opening was  $\geq 36 \text{ m}^2$ . We then delineated the boundaries of the gap by the standing trees  $\geq 10 \text{ cm}$  DBH that had crowns in contact with the contiguous forest: the "expanded gap" (Runkle 1992).

### *Gap Size*

The expanded gap boundary was mapped using compass bearings and tape measure. The gap length (L) was set as the longest dimension from gap edge to gap edge, and the width (W) as the longest distance perpendicular to L. The shape of the gaps was approximated as ellipsoidal; gap area was calculated using the formula:  $\text{area} = \pi LW/4$  (Runkle 1981, Battles et al. 1996). For all gaps, the gap maker (or initiator), the tree that knocked down any "domino" trees (Ferreira de Lima et al. 2008), was readily determined. We measured DBH, merchantable height (base of tree to the first branch; log form), and total length (base of tree to tip of crown).

### *Types, Causes, Direction, and Formation Rate of Treefalls*

The type of treefall was classed as single (one tree only) or multiple (two or more trees fallen in one gap). The number of trees  $\geq 20 \text{ cm}$  DBH fallen in each multiple gap was recorded. Each gap maker was recorded as uprooted or snapped (cause), and direction of the fall was determined as either upslope, downslope, or across-slope. We recorded the compass bearing of the downed gap maker and the ground slope where it had stood. The total length of transects under new canopy treefall gaps each year was divided by the total length of transects to determine the annual gap formation rate (Runkle 1982, Murray 1986, Battles et al. 1996).

### *Data Analysis*

Only recent treefall gaps,  $\leq 1$  yr old, sampled over the 3 yr were used in the analyses. No landslide gaps were encountered, but they are an important component of the overall disturbance regime in montane New Guinea (Johns 1986).

Tests for skewness and kurtosis showed that the gap sizes and DBH of gap makers were normally distributed. Means are reported with one standard deviation. Statistical tests followed Sokal and Rohlf (1997) and Zar (1999).

## RESULTS

### *Treefall Gap Size*

Mean gap size was  $312 \text{ m}^2$  (SD = 115, range = 71–530  $\text{m}^2$ ,  $n = 40$ ) (Figure 1). Two branch falls and one large windfall gap were excluded from analyses to focus on treefall parameters. Very large gaps from storm downbursts or very small gaps from branch falls are different phenomena (but ecologically important); their inclusion would create statistical outliers. Only 15% of gaps were less than 200  $\text{m}^2$ , with a similar proportion being large gaps > 450  $\text{m}^2$ ; 30% of gaps were < 250  $\text{m}^2$  (Figure 1).

Gap area (for single treefalls) was positively correlated with the DBH of the gap

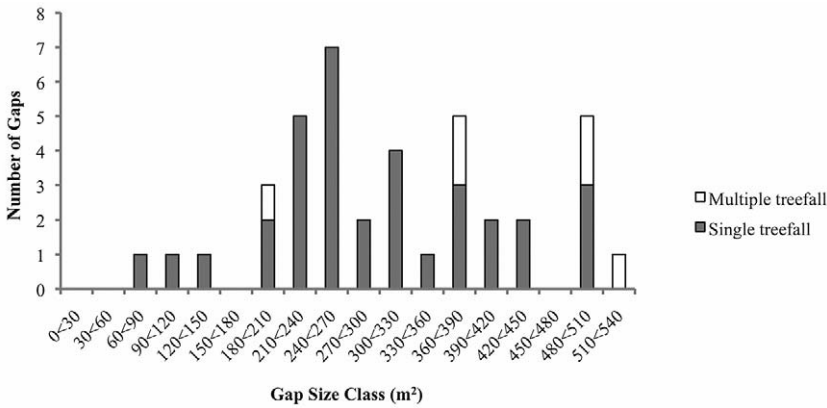


FIGURE 1. Size class distribution of canopy treefall gaps ( $n = 40$ ) in New Guinea montane forest sampled over a 3 yr period. Gaps, as defined by Brokaw (1982a), were  $\leq 1$  yr in age sampled on random transects and measured using the “expanded gap” method of Runkle (1992).

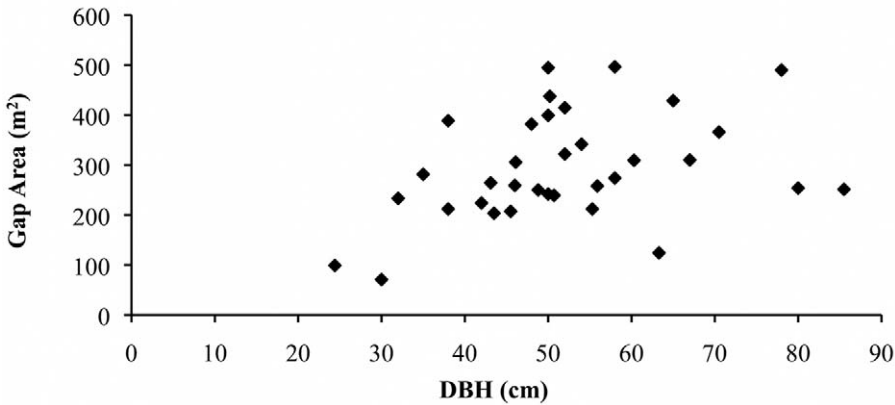


FIGURE 2. Relationship between size of the gap maker and area of the resulting gap for new ( $\leq 1$  yr old) single treefall gaps ( $n = 33$ ) in a New Guinea montane forest sampled over a 3 yr period. Gap area measured according to Runkle (1992).

maker ( $r_s = 0.395$ ,  $P < .02$ ,  $n = 33$ ) and merchantable log length ( $r_s = 0.55$ ,  $P < .001$ ,  $n = 33$ ) (Figure 2). The mean size (DBH) for gap makers was  $53.2 \text{ cm} \pm 13.9$  (range =  $24.4\text{--}85.5 \text{ cm}$ ,  $n = 40$ ) (Figure 3). Multiple treefall gaps were not formed by larger trees ( $60.1 \pm 13.2 \text{ cm}$ , range =  $24.4\text{--}85.5 \text{ cm}$ ,  $n = 6$ ) than single treefall gaps ( $51.9 \pm 13.9 \text{ cm}$ , range =  $44.9\text{--}83.2 \text{ cm}$ ,  $n = 34$ ;  $t = -1.34$ ,  $df = 38$ ,  $P \geq .19$ ).

*Gap Types*

Out of 43 gaps ( $\leq 1$  yr old), 79% occurred as single treefalls, 14% resulted from multiple treefalls (0, 2, 4 in 2003, 2004, 2005, respectively), 5% occurred from branches falling, and one (2%) was caused by a large windfall that appeared to be the result of a downburst. Gap makers were not a random subset of trees in this forest (Figure 3). Gap makers were

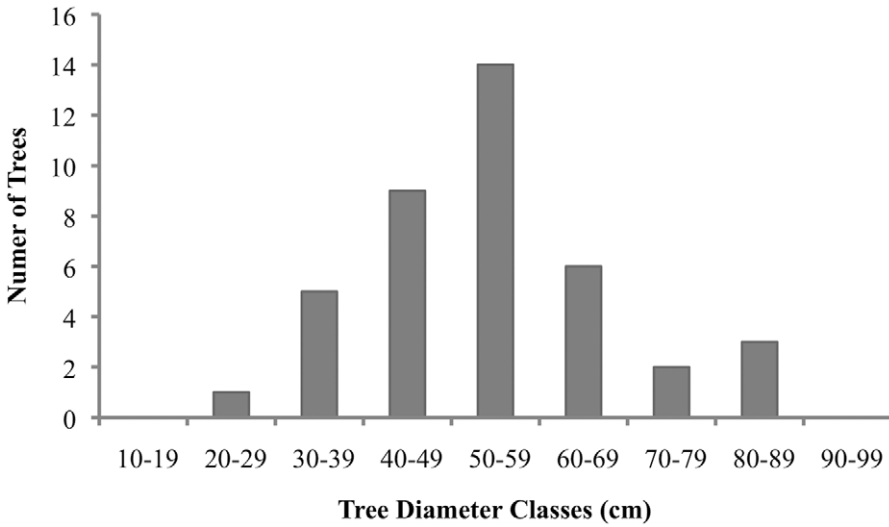


FIGURE 3. Size class distribution of diameter (DBH) of trees ( $n = 40$ ) that fell and formed gaps in a New Guinea montane forest. New gaps ( $\leq 1$  yr old) that intersected 10.1 km of random transects were sampled annually over a 3 yr period.

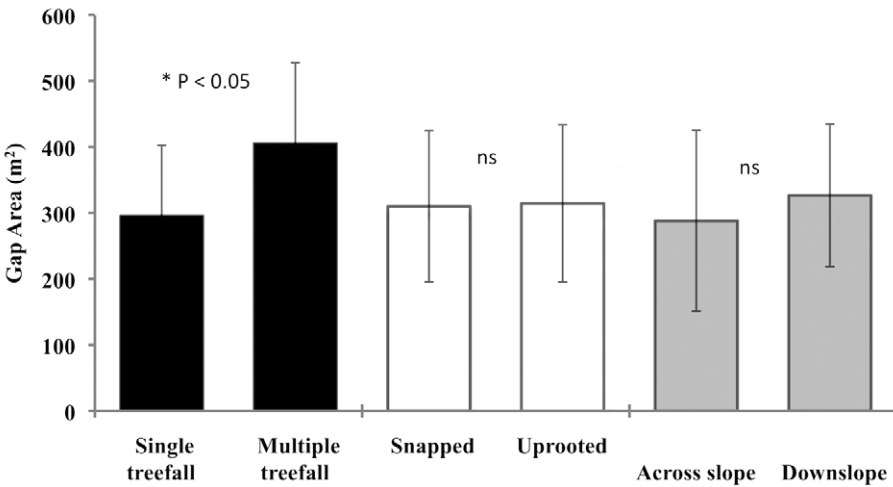


FIGURE 4. Effects of single versus multiple treefalls, uprooted versus snapped, and across-slope versus downslope directionality on treefall gap area. Gaps were sampled over a 3 yr period in a lower montane forest in New Guinea along 10.1 km of random transects ( $n = 40$  gaps).

larger (Kolmogorov Smirnov test,  $n_1 = 40$ ,  $n_2 = 272$ ,  $P < .01$ ) than the average tree size on a 1 ha plot in the study area (Wright et al. 1997). Single treefalls created significantly smaller

gaps ( $295 \pm 107$  m<sup>2</sup>, range = 71–496 m<sup>2</sup>,  $n = 34$ ) than multiple treefalls ( $405 \pm 122$  m<sup>2</sup>, range = 191–530 m<sup>2</sup>,  $n = 6$ ;  $t = 2.27$ ,  $df = 38$ ,  $P < .03$ ) (Figure 4).

### Gap Causes

Treefalls caused by snapped boles were not significantly more numerous than uproots ( $\chi^2 = 0.9$ ,  $df = 1$ ,  $P > .25$ ). The mean area of gaps created by snapped treefalls ( $310 \pm 115 \text{ m}^2$ , range = 99–530  $\text{m}^2$ ,  $n = 23$ ) did not differ significantly from that created by uprooted treefalls ( $314 \pm 119 \text{ m}^2$ , range = 71–495  $\text{m}^2$ ,  $n = 17$ ;  $t = -0.11$ ,  $df = 34$ ,  $P > .8$ ) (Figure 4).

### Gap Direction

Direction of treefalls relative to ground slope differed significantly; most fell downhill (27) versus across slope (11), and only two fell uphill ( $\chi^2 = 6.74$ ,  $df = 1$ ,  $P < .01$ ,  $n = 38$ ). The mean gap size created by trees falling across slope ( $288 \pm 136 \text{ m}^2$ , range = 71–496  $\text{m}^2$ ,  $n = 11$ ) did not differ significantly from that caused by trees falling downslope ( $327 \pm 108 \text{ m}^2$ , range = 124–530  $\text{m}^2$ ,  $n = 27$ ;  $t = -0.92$ ,  $df = 36$ ,  $P > .36$ ) (Figure 4). There was no strong directionality of treefalls (Rayleigh test,  $z = 0.37$ ,  $n = 40$ ,  $P > .5$ ).

### Gap Formation Rate

The number of gaps intersecting 10.1 km of transects in this forest was relatively uniform, with 14, 13, and 13 new gaps in 2003, 2004, and 2005, respectively. The total length of transects covered by gaps in all 3 yr was 447 m, making the mean proportion of forest under gaps 0.015/yr.

## DISCUSSION

Despite the interest in gaps and their importance to forest ecology, synthetic studies are hampered due to the variety of methods and definitions employed and the relatively few sites with multiannual surveys (Ferreira de Lima 2005). Comparative studies will be strengthened by including sites with evolutionarily distinct histories (e.g., Papuan), rather than by including sites within a region with a shared evolutionary history (Westoby 1988). This study reports some of the first details of natural treefall dynamics from the third most expansive tract of rain forest in the

world—the island of New Guinea (Mittermeier et al. 1998).

### Gap Size

The size and frequency of gaps are important parameters that vary by location and differences in methodology. Ferreira de Lima (2005) compared the same gap data using two standard gap definitions and found that mean gap size was 121  $\text{m}^2$  using the definition of Brokaw (1982a) and 333  $\text{m}^2$  using the “expanded gap” definition of Runkle (1992). We found the Brokaw (1982a) definition useful for determining gap from nongap and the Runkle (1992) definition superior for nonsubjective measurement of gap size.

The sizes of treefall gaps in our study showed a normal distribution, with the mean (312  $\text{m}^2$ ) similar to that of other tropical forests (218  $\text{m}^2$ , range 86–628  $\text{m}^2$ ) (Brokaw 1985b). Variation among different studies can also be strongly affected by the definition of minimum gap size used. For example, some studies show that size distributions of all gaps (including branch falls) are skewed to the left, with most (70%–90%) of the gaps < 200  $\text{m}^2$  (Brokaw 1982a,b, Sanford et al. 1986, Arriaga 1988), but our sample of treefalls showed the opposite, with 85% of the gaps > 200  $\text{m}^2$ . The second smallest gap maker (30 cm DBH) fell to create the smallest gap, of 70  $\text{m}^2$  (Figure 2), nearly twice the size of our minimum size criterion for a gap. Gap size was positively correlated with the size of the gap maker (Figure 2), consistent with other studies (Sapkota and Oden 2009).

### Gap Type

We found single treefall gaps much more numerous than multiple treefall gaps at this site, and numerous other studies in tropical forests yielded similar results (Sapkota and Oden 2009). Mean gap size of multiple treefalls was greater than that of single treefalls, and our study did not encounter the very large gaps occasionally formed by landslides or “downbursts” (Garstang et al. 1998) that do occur in the area infrequently (A.L.M., unpubl. data). The ecological implications of many, small,

single tree gaps versus few, large, multiple tree gaps are substantial. The larger gaps are drier and sunnier (Barton 1984, Barik et al. 1992) and recover differently than small gaps. Lateral ingrowth contributes to rapid closure of single tree gaps (Runkle 1985, Valverde and Silvertown 1997, Mack et al. 1999), meaning that there is little change in local species composition relative to succession in large gaps (Whitmore 1990).

### Gap Cause

The cause of treefalls can have important consequences. Snapped trees might resprout (Paciorek et al. 2000). Uprooted trees create additional habitats in the root zone that different species utilize. In our study, more treefall gaps formed due to boles snapping than to uprooting. Although not significantly

more, the high frequency of snapped boles indicates, at this site, that uprooting is not the main source of gap formation. Major storms with strong winds are rare at this site. The downburst windthrows more typical of lowland tropical rain forest weather rarely occur at this elevation (Garstang et al. 1998). The rare occurrence of such openings can be ecologically important because of their size but is not part of the typical annual cycle we studied.

Our results from New Guinea fall in the middle of reported results for the relative frequency of treefall gaps resulting from snapped boles relative to uprooted trees in other tropical forests (Table 1). Most studies have found that gaps are caused by tree snaps more often than by uprooting, and by a larger margin than the studies where uprooting was more frequent. The substantial heterogeneity

TABLE 1

Comparison of Gap Parameters among Different Studies in the Tropics in Contrast to a New Guinea Montane Forest

Location	Ratio of Snapped to Uprooted	Mean Gap Size (range) (m <sup>2</sup> )	Citation
Tai, Ivory Coast	1:0.19	61 (13–244) <sup>a</sup>	Jans et al. (1993)
Barro Colorado Island, Panama	1:0.33		Putz and Milton (1983)
Monteverde, Costa Rica	1:0.36	n.a.	Matelson et al. (1995)
Western Ghats, India	1:0.36	n.a.	Ayyappan and Parthasarathy (2004)
Northwestern Amazonia	1:0.59	n.a.	Chao et al. (2009)
Zagne, Ivory Coast	1:0.61	59 (11–204) <sup>a</sup>	Jans et al. (1993)
Danum, Borneo	1:0.64	n.a.	Gale and Hall (2001)
Papua New Guinea	1:0.74	98 <sup>a,c</sup> 295 <sup>b</sup> (71–496) <sup>b</sup>	This study
Para, Ivory Coast	1:0.77	44 (11–231) <sup>a</sup>	Jans et al. (1993)
Belalong, Borneo	1:0.81	n.a.	Gale and Hall (2001)
French Guiana	1:0.83	371 <sup>b</sup> (4–>1,000) <sup>d</sup>	VanderMeer and Bongers (1996)
Southeastern Brazil	1:0.90	93 (~30–150) <sup>a</sup>	Ferreira de Lima et al. (2008)
Western Ecuador	1:0.97	n.a.	Gale and Barfod (1999)
São Paulo, Brazil	1:1.25	n.a.	Martini et al. (2008)
Andalau, Borneo	1:1.27	n.a.	Gale and Hall (2001)
Tamaulipas, Mexico	1:1.28	n.a.	Arriaga (2000)
Northeastern Amazonia	1:1.74		Chao et al. (2009)
Veracruz, Mexico	n.a.	66 (19–219) <sup>a</sup>	Lara-Gonzalez et al. (2009)

*Note:* Results are expressed as a ratio of snapped to uprooted because different studies included different categories of gap makers (e.g., branch falls, standing dead, leaning). Gap sizes were measured in various ways, but most approximated either Brokaw (1982a) or Runkle (1992); however, different studies had different minimum gap size criteria for inclusion, which can shift the mean size relative to other studies. Studies including anthropogenic gaps and gaps older than 1 yr were excluded.

<sup>a</sup> Gap definition closer to that of Brokaw (1982a).

<sup>b</sup> Gap definition (“expanded gap”) closer to that of Runkle (1981).

<sup>c</sup> Estimated Brokaw area using quadratic relationship (Ferreira de Lima et al. 2008).

<sup>d</sup> Includes gaps from multiple treefalls.



among studies due to methodological differences and real ecological differences (Table 1) indicates that it is not safe to generalize about the causes of treefall gaps in tropical forests.

#### *Gap Formation Rate*

The annual gap fraction of transects was 1.5%; any point in the forest has roughly a 0.015 probability per year that a gap will form over it. Reviews and meta analysis show an average gap fraction around 0.3%–2% per annum for both temperate and tropical forests (Brokaw 1982*b*, Runkle 1982, 1985, Murray 1986, Denslow 1987). The gap formation rate calculated for our study is consistent with rates estimated for both temperate and tropical rain forests of the world, but direct comparisons are difficult because observed rates may vary with methods (Fraver et al. 1998).

Our results are consistent with other research in the same study area. In a study monitoring canopy closure and seedling growth, 2.5% of points on the forest floor had canopy gap openings form above them each year (Mack et al. 1999). In a study of tree survivorship in the same study area over a 9 yr period, 2.8% of trees over 10 cm DBH on 5.2 ha died (mostly uprooted or snapped) per year (M. Supuma and D. D. Wright, unpubl. data). Trees that die standing are uncommon at this study site. Thus three different methods in independent studies of gap dynamics and tree mortality (transect-intercept, hemispherical canopy photographs, and tree plot monitoring) in the same study area all yielded roughly consistent measures of mortality and gap formation rates of 1.5%–2.8% per year.

#### *Gap Makers*

Gap makers were not identified to species when leaves were no longer present. For those gap makers that still had intact leaves, most were recognized as long-lived pioneer species (Whitmore 1991), despite these being fairly uncommon at the site (Wright et al. 1997). It is possible that a higher than expected proportion of gap makers in this forest are long-lived pioneer species.

#### *Forest Management Implications*

Understanding gap dynamics and the associated characteristics of gaps can guide better forest management practices and ensure that timber resources are harvested more sustainably. Different forestry practices create different-sized gaps due to variation of felling intensities (Johns et al. 1996, Pinard and Putz 1996, Sist et al. 1998), and this can have negative effects on regeneration and growth of native species. Large logging gaps are hotter and drier than smaller natural gaps (Webb 1997, Ediriweera et al. 2008). Such gaps are often better locations for the establishment of invasive plants like *Piper aduncum*, which is an aggressive colonizer of disturbed habitats in Papua New Guinea (Rogers and Hartemink 2000).

Papua New Guinea still has extensive unlogged forests, but these are under considerable pressure from logging operations (Shearman et al. 2009). Mimicking the size and frequency of natural gaps rather than creating larger, multiple tree openings as occurs in many forestry operations is considered a more sustainable way forward for logging in tropical rain forests (Johns et al. 1996, Webb 1997, Sist et al. 1998). Portable sawmills (“*wokabaut*” sawmills in Papua New Guinea) have been promoted as a low-impact alternative to industrial, large-scale operations (Lindemalm and Rogers 2001).

Given the results of our study, we recommend that trees with DBH of 45–65 cm be felled because these would produce typical gap openings. Directional felling to avoid creating multiple treefall openings would further help keep disturbance closer to natural in terms of gap size. In terms of gap frequency, any logging presents an increase because natural gap formation mechanisms do not stop during a forestry project. But knowledge of natural formation rates presents a useful baseline metric for monitoring. An overall harvesting plan aimed at clearing around 1.5% of the concession area per year would roughly double the gap formation rate. By selecting the larger trees that might be prone to form gaps naturally, the overall gap formation rate from selective logging might be somewhat less than double the natural rate.

Understanding the underlying natural gap formation rate in a forest may provide a useful metric for assessing the potential impact of logging protocols and setting regionally relevant standards for certifying sustainable practices. Until there are data from New Guinea evaluating impacts of increased canopy openness on regeneration, we feel it safest to design protocols that strive to keep gap size within typical bounds and no more than double natural gap formation rates. We recommend studies where natural annual gap formation rates and regeneration are measured and compared with regeneration where gap formation rates are inflated by logging.

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#### Literature Cited

- Arriaga, L. 1988. Gap dynamics of a tropical cloud forest in northeastern Mexico. *Biotropica* 20:178–184.
- . 2000. Types and causes of tree mortality in a tropical montane cloud forest of Tamaulipas, Mexico. *J. Trop. Ecol.* 16:623–636.
- Arunachalam, A., and K. Arunachalam. 2000. Influence of gap size and soil properties on microbial biomass in a subtropical humid forest of North-east India. *Plant Soil* 223:185–193.
- Ayyappan, N., and N. Parthasarathy. 2004. Short-term changes in tree populations in a tropical evergreen forest at Varagalaiar, Western Ghats, India. *Biodivers. Conserv.* 13:1843–1851.
- Babaasa, D., G. Eilu, A. Kasangaki, R. Bitariho, and A. McNeilage. 2004. Gap characteristics and regeneration in Bwindi Impenetrable National Park, Uganda. *Afr. J. Ecol.* 42:217–224.
- Baret, S., L. Cournac, C. Thebaud, P. Edwards, and D. Strasberg. 2008. Effects of canopy gap size on recruitment and invasion of the non-indigenous *Rubus alceifolius* in lowland tropical rain forest on Reunion. *J. Trop. Ecol.* 24:337–345.
- Barik, S. K., H. N. Pandey, R. S. Tripathi, and P. Rao. 1992. Microenvironmental variability and species diversity in treefall gaps in a sub-tropical broadleaved forest. *Vegetatio* 103:31–40.
- Barton, A. M. 1984. Neotropical pioneer and shade-tolerant tree species: Do they partition treefall gaps? *Trop. Ecol.* 25:196–202.
- Battles, J. J., J. G. Dushoff, and T. J. Fahey. 1996. Line intersect sampling of forest canopy gaps. *For. Sci.* 42:131–138.
- Beck, H., M. S. Gaines, J. E. Hines, and J. D. Nichols. 2004. Comparative dynamics of small mammal populations in treefall gaps and surrounding understorey within Amazonian rainforest. *Oikos* 106:27–38.
- Brienen, R. J. W., and P. A. Zuidema. 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *J. Ecol.* 94:481–493.
- Brokaw, N. V. L. 1982a. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160.
- . 1982b. Treefalls: Frequency, timing, and consequences. Pages 101–108 in E. G. Leigh Jr., A. S. Rand, and D. M. Windsor, eds. *The ecology of a tropical forest: Seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- . 1985a. Gap-phase regeneration in a tropical forest. *Ecology* 66:682–687.
- . 1985b. Treefalls, regrowth and community structure in tropical forests. Pages 53–71 in S. T. A. Pickett, and P. S. White, eds. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.

- Brokaw, N., and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. *Trends Ecol. Evol.* 15:183–188.
- Chao, K. J., O. L. Phillips, A. Monteagudo, A. Torres-Lezama, and R. V. Martinez. 2009. How do trees die? Mode of death in northern Amazonia. *J. Veg. Sci.* 20:260–268.
- Clark, D. A., and D. B. Clark. 2011. Assessing tropical forests' climatic sensitivities with long-term data. *Biotropica* 43:31–40.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12:47–55.
- . 1987. Tropical rain-forest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18:431–451.
- . 1995. Disturbance and diversity in tropical rain forests: The density effect. *Ecol. Appl.* 5:962–968.
- Ediriweera, S., B. M. P. Singhakumara, and M. S. Ashton. 2008. Variation in canopy structure, light and soil nutrition across elevation of a Sri Lankan tropical rain forest. *For. Ecol. Manage.* 256:1339–1349.
- Enquist, B. J., and C. A. F. Enquist. 2010. Long-term change within a Neotropical forest: Assessing differential functional and floristic responses to disturbance and drought. *Glob. Change Biol.* 17:1408–1424.
- Feeley, K. J., S. J. Davies, P. S. Ashton, S. Bunyavejchewin, M. N. N. Supardi, A. R. Kassim, S. Tan, and J. Chave. 2007. The role of gap phase processes in the biomass dynamics of tropical forests. *Proc. R. Soc. Lond. B Biol. Sci.* 274:2857–2864.
- Felton, A., A. M. Felton, J. Wood, and D. B. Lindenmayer. 2006. Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. *For. Ecol. Manage.* 235:186–193.
- Ferreira de Lima, R. A. 2005. Gap size measurement: The proposal of a new field method. *For. Ecol. Manage.* 214:413–419.
- Ferreira de Lima, R. A., A. M. Z. Martini, S. Gandolfi, and R. R. Rodrigues. 2008. Repeated disturbances and canopy disturbance regime in a tropical semi-deciduous forest. *J. Trop. Ecol.* 24:85–93.
- Fraver, S., N. V. L. Brokaw, and A. P. Smith. 1998. Delimiting the gap phase in the growth of a Panamanian forest. *J. Trop. Ecol.* 14:673–681.
- Fredericksen, N. J., T. S. Fredericksen, B. Flores, and D. Rumiz. 1999. Wildlife use of different-sized logging gaps in a tropical dry forest. *Trop. Ecol.* 40:167–175.
- Gale, N., and A. S. Barfod. 1999. Canopy tree mode of death in a western Ecuadorian rain forest. *J. Trop. Ecol.* 15:415–436.
- Gale, N., and P. Hall. 2001. Factors determining the modes of tree death in three Bornean rain forests. *J. Veg. Sci.* 12:337–346.
- Garstang, M., S. White, H. H. Shugart, and J. Halverson. 1998. Convective cloud downdrafts as the cause of large blowdowns in the Amazon rainforest. *Meteorol. Atmos. Phys.* 67:199–212.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science (Washington, D.C.)* 283:554–557.
- Jans, L., L. Poorter, R. Vanrompaey, and F. Bongers. 1993. Gaps and forest zones in tropical moist forest in Ivory Coast. *Biotropica* 25:258–269.
- Johns, J. S., P. Barreto, and C. Uhl. 1996. Logging damage during planned and unplanned logging operation in the eastern Amazon. *For. Ecol. Manage.* 89:59–77.
- Johns, R. J. 1986. The instability of the tropical ecosystem in New Guinea. *Blumea* 31:341–371.
- . 1993. Biodiversity and conservation of the native flora of Papua New Guinea. Pages 15–75 *in* B. M. Beehler, ed. *Papua New Guinea conservation needs assessment*. Department of Environment and Conservation, Waigani, Papua New Guinea.
- Kukkonen, M., H. Rita, S. Hohnwald, and A. Nygren. 2008. Treefall gaps of certified, conventionally managed and natural forests as regeneration sites for Neotropical timber trees in northern Honduras. *For. Ecol. Manage.* 255:2163–2176.
- Lara-Gonzalez, R., L. R. Sanchez-Velasquez, and J. Corral-Aguirre. 2009. Regeneration

- of *Abies religiosa* in canopy gaps versus understory, Cofre de Perote National Park, Mexico. *Agrociencia* 43:739–747.
- Laurance, W. F., and S. G. W. Laurance. 1996. Responses of five arboreal marsupials to recent selective logging in tropical Australia. *Biotropica* 28:310–322.
- Lindemalm, F., and H. M. Rogers. 2001. Impacts of conventional logging and portable sawmill logging operations on tree diversity in East New Britain, Papua New Guinea. *Aust. For.* 64:26–31.
- Mack, A. L. 1998. The potential impact of small-scale physical disturbance on seedlings in a Papuan rainforest. *Biotropica* 30:547–552.
- Mack, A. L., K. Ickes, J. H. Jessen, B. Kennedy, and J. R. Sinclair. 1999. Ecology of *Aglaia mackiana* (Meliaceae) seedlings in a New Guinea rain forest. *Biotropica* 31:111–120.
- Malhi, Y., and O. L. Phillips. 2004. Tropical forests and global atmospheric change: A synthesis. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 359:549–555.
- Marthews, T. R., D. Burslem, S. R. Paton, F. Yanyuez, and C. E. Mullins. 2008a. Soil drying in a tropical forest: Three distinct environments controlled by gap size. *Ecol. Modell.* 216:369–384.
- Marthews, T. R., D. Burslem, R. T. Phillips, and C. E. Mullins. 2008b. Modeling direct radiation and canopy gap regimes in tropical forests. *Biotropica* 40:676–685.
- Martini, A. M. Z., R. A. F. Lima, G. Franco, and R. R. Rodrigues. 2008. The need for full inventories of tree modes of disturbance to improve forest dynamics comprehension: An example from a semideciduous forest in Brazil. *For. Ecol. Manage.* 255:1479–1488.
- Matelson, T. J., N. M. Nadkarni, and R. Solano. 1995. Tree damage and annual mortality in a montane forest in Monteverde, Costa Rica. *Biotropica* 27:441–447.
- Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. D. Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: Approaches to setting conservation priorities. *Conserv. Biol.* 12:516–520.
- Murray, K. G. 1986. Consequences of seed dispersal for gap-dependent plants: Relationships between seed shadows, germination requirements, and forest dynamic processes. Pages 187–198 in A. Estrada and T. H. Fleming, eds. *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht, The Netherlands.
- Ogden, J., R. A. Fordham, S. Pilkington, and R. G. Serra. 1991. Forest gap formation and closure along an altitudinal gradient in Tongariro National Park, New Zealand. *J. Veg. Sci.* 2:165–172.
- Owiunji, I., and A. J. Plumptre. 1998. Bird communities in logged and unlogged compartments in Budongo Forest, Uganda. *For. Ecol. Manage.* 108:115–126.
- Paciorek, C. J., R. Condit, S. P. Hubbell, and R. B. Foster. 2000. The demographics of resprouting in tree and shrub species of a moist tropical forest. *J. Ecol.* 88:765–777.
- Pajmians, K. 1976. Vegetation. Pages 23–104 in K. Pajmians, ed. *New Guinea vegetation*. Commonwealth Scientific and Industrial Research Organisation in association with the Australian National University Press, Canberra.
- Pinard, M. A., and F. E. Putz. 1996. Retaining forest biomass by reducing logging damage. *Biotropica* 28:278–295.
- Putz, F. E., and K. Milton. 1983. Tree mortality rates on Barro Colorado Island. Pages 95–108 in E. G. Leigh Jr, A. S. Rand, and D. M. Windsor, eds. *The ecology of a tropical forest: Seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- Rogers, H. M., and A. E. Hartemink. 2000. Soil seed bank and growth rates of an invasive species, *Piper aduncum*, in the lowlands of Papua New Guinea. *J. Trop. Ecol.* 16:243–251.
- Ruger, N., A. Huth, S. P. Hubbell, and R. Condit. 2009. Response of recruitment to light availability across a tropical lowland rain forest community. *J. Ecol.* 97:1360–1368.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041–1051.

- . 1982. Patterns of disturbance in some old growth mesic forests of eastern North America. *Ecology* 63:1533–1546.
- . 1985. Disturbance regimes in temperate forests. Pages 17–33 in S. T. A. Pickett and P. S. White, eds. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.
- . 1992. Guidelines and sample protocol for sampling forest gaps. PNW-GTR-283, U.S. Department of Agriculture Forest Service.
- . 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. *Ecology* 79:1768–1780.
- Sanchez, E., R. Gallery, and J. W. Dalling. 2009. Importance of nurse logs as a substrate for the regeneration of pioneer tree species on Barro Colorado Island, Panama. *J. Trop. Ecol.* 25:429–437.
- Sanford, R. I. J., H. E. Braker, and G. S. Hartshorn. 1986. Canopy openings in a primary Neotropical lowland forest. *J. Trop. Ecol.* 2:277–282.
- Sapkota, I. P., and P. C. Oden. 2009. Gap characteristics and their effects on regeneration, dominance and early growth of woody species. *J. Plant Ecol.* 2:21–29.
- Schnitzer, S. A., and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913–919.
- Shearman, P. L., J. Ash, B. Mackey, J. E. Bryan, and B. Lokes. 2009. Forest conversion and degradation in Papua New Guinea 1972–2002. *Biotropica* 3:379–390.
- Sist, P., T. Nolan, J. G. Bertault, and D. Dykstra. 1998. Harvesting intensity versus sustainability in Indonesia. *For. Ecol. Manage.* 108:251–260.
- Sokal, R. R., and F. J. Rohlf. 1997. *Biometry*. W. H. Freeman and Company, New York.
- Valverde, T., and J. Silvertown. 1997. Canopy closure rate and forest structure. *Ecology* 78:1555–1562.
- VanderMeer, P. J., and F. Bongers. 1996. Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. *J. Ecol.* 84:19–29.
- Vieira, S., P. B. de Camargo, D. Selhorst, R. da Silva, L. Hutryra, J. Q. Chambers, I. F. Brown, N. Higuchi, J. dos Santos, S. C. Wofsy, S. E. Trumbore, and L. A. Martinielli. 2004. Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia (Berl.)* 140:468–479.
- Webb, E. L. 1997. Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of Northeast Costa Rica. *For. Ecol. Manage.* 95:117–129.
- Westoby, M. 1988. Comparing Australian ecosystems to those elsewhere. *BioScience* 38:549–556.
- Whitmore, T. C. 1990. *An introduction to tropical rain forests*. Oxford University Press, Oxford.
- . 1991. *Tropical rain forest dynamics and its implications for management*. Pages 67–89 in A. Gomez-Pompa, T. C. Whitmore, and M. Hadley, eds. *Rain forest regeneration and management*. Parthenon Publishing Group, Park Ridge.
- Wright, D. D. 2005. Diet, keystone resources, and altitudinal movement of dwarf cassowaries in relation to fruiting phenology in a Papua New Guinean rainforest. Pages 204–235 in J. L. Dew and J. P. Boubli, eds. *Tropical fruits and frugivores: The search for strong interactors*. Springer, Dordrecht, The Netherlands.
- Wright, D. D., J. H. Jessen, P. Burke, and H. G. D. Garza. 1997. Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. *Biotropica* 29:250–260.
- Wright, S. J., H. C. Muller-Landau, R. Condit, and S. P. Hubbell. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84:3174–3185.
- Zang, R. G., and B. S. Wang. 2002. Study on canopy disturbance regime and mechanism of tree species diversity maintenance in the lower subtropical evergreen broad-leaved forest, South China. *Plant Biosyst.* 136:241–250.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.