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CROWN ASYMMETRY, TREEFALLS, AND REPEAT DISTURBANCE OF BROAD-LEAVED FOREST GAPS¹

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Abstract. Gap-edge trees were significantly more likely to fall into pre-existing gaps than in other directions in a moist tropical forest on Barro Colorado Island (BCI), Panama. Trees not at gap edges were more likely to fall away from near neighbors than toward them. We show that gross asymmetries of tree crowns were the rule rather than the exception for all trees. The crowns of most gap-edge trees were strongly asymmetrical into their adjoining gaps, and trees not at gap edges were strongly asymmetrical away from near neighbors. Trees had a strong and significant tendency to fall on these heavy sides. Such treefalls, and related limbfalls, can result in redisturbance of gaps and a retardation of gap regeneration. An analysis of 5 yr of canopy height data from a mapped 50-ha plot on BCI revealed that sites within larger gaps were significantly more likely to be redisturbed by secondary treefalls than were sites in the smallest gaps or nongap quadrats. These results suggest that treefall gaps in tropical forests may be more persistent disturbances than previously thought.

Key words: canopy; crown asymmetry; disturbance; forest dynamics; gaps; tree architecture; treefalls.

INTRODUCTION

Gap dynamics are believed to be fundamental to the community structure of forests, and a major force maintaining tropical diversity (White 1979, Orians 1983, Brokaw 1985*a, b*, 1987, Denslow 1987, Brandani et al. 1988, Levey 1988, Platt and Strong 1989, Schaetzl et al. 1989, Schupp and Frost 1989). However, there is only limited understanding of the forces affecting the likelihood and direction of treefalls, one of the major factors creating gaps.

Although most models of forest community and population structure assume that gaps are random or correlated only with tree age or growth rate (West et al. 1981, Shugart 1984, Busing and Clebsch 1987, Lorimer et al. 1988, Kienast and Kuhn 1989, Vanclay 1989, van Daalen and Shugart 1989), there is evidence that tropical forest gaps are sometimes spatially clumped (Lawton and Putz 1988). Some understory species require multiple disturbance events to reach the canopy, and such redisturbances may not be uncommon (Canham 1985, Runkle and Yetter 1987, Martinez-Ramos et al. 1988).

Gaps created by treefalls are often much larger than the crown size of the fallen tree, due to the destruction of trees and parts of trees in the path of the falling tree (Brokaw 1985*a*). However, the factors that influence the direction of treefalls in natural forests and their consequences have been largely unexamined (van Daa-

len and Shugart 1989). Although treefalls in north temperate conifer forests were mainly in a downwind direction (Henry and Swan 1974, Falinski 1978), this tendency was weak in subtropical (Arriaga 1988) and tropical (Caballe 1984) forests. Canopy asymmetries in gap-edge trees are produced by competition with forest-edge trees (Brunig 1964, Trimble and Tryon 1966, Ranney et al. 1981), but the treefall consequences of asymmetry have not been explored.

We report here that crown asymmetries produced in response to shading neighbors in a wet lowland tropical forest result in the tendency for trees to fall into older forest gaps. This observation affects the way we think about forest dynamics, disturbance regimes, and the ecology of gap plants. The classical model of gap dynamics does not consider the likelihood of secondary treefalls that might retard gap regeneration. If gaps are more predictable in space and time, so may be the biology of gap plants. Redisturbance adds another dimension to the heterogeneity of forest ecosystems, and could therefore contribute to tropical species richness.

STUDY SITE AND METHODS

In January–February 1987, we mapped the crown shapes of all 127 large (> 20 cm dbh [diameter at breast height]) trees in a 0.8-ha subplot within a 50-ha mapped plot of a moist tropical forest on Barro Colorado Island (BCI), Panama. Heights of individual trees were estimated using a range finder. The distance from the bole to the crown edge was measured at each of eight compass points on each tree, with each point determined

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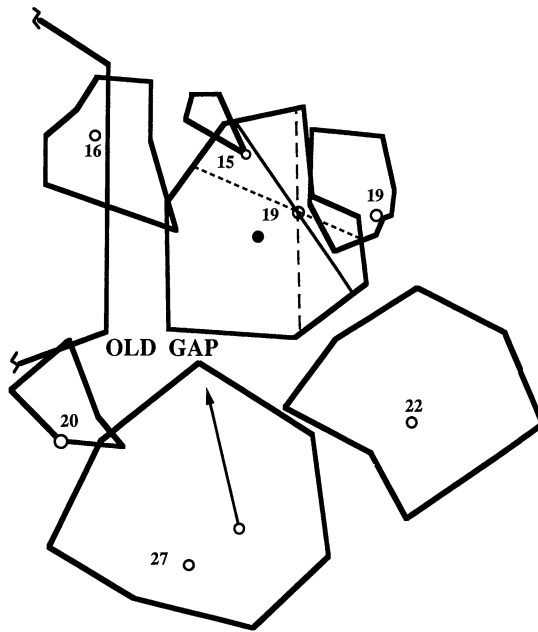


FIG. 1. Seven mapped tree crowns from the 0.8-ha subplot. The open circles (O) indicate the locations of bases of the boles and the numbers are tree heights in metres. For one tree, the following are also illustrated: ● is the center of area of the crown; — is the line of absolute asymmetry; --- is the line of asymmetry relative to the nearest neighbor that was as tall (± 1 m) or taller than the reference tree; is the line of asymmetry relative to the gap. The arrow points in the direction of fall of a recently fallen tree.

from directly below the crown edge. The crowns were drawn on prepared maps that also showed the locations of the bases of the boles of all trees. The center of area of each crown was determined by cutting paper outlines of crowns and suspending each from multiple pivot points (Giancoli 1985:130).

To estimate absolute crown asymmetry, a line was drawn through the bole perpendicular to a line between the center of crown area and the base of the bole (Fig. 1). The areas on either side of this line were calculated with an area meter, and absolute asymmetry calculated as the greater of these two areas divided by the total area.

Using the prepared maps of crown shapes and tree and gap locations, two kinds of relative crown asymmetries were calculated. First, for all trees with a neighbor within 10 m that was as tall (± 1 m) or taller ($n = 113$), crown asymmetry relative to the nearest large neighbor was measured by drawing a straight line through the bole of the reference tree perpendicular to the line between the two boles (Fig. 1). The compass direction from the base of the bole to the center of crown area was plotted relative to the compass direction to the nearest large neighbor. Second, for gap-edge trees ($n = 22$), crown asymmetry into the gap was measured by drawing a line through the bole of the reference tree that was parallel to the tangent of the gap

edge (Fig. 1). In both cases, an area meter was used to calculate the areas on either side of these reference lines. Relative asymmetry was calculated as A/T , where A was the crown area either away from the neighbor or into the gap, and T was the total crown area.

In January–February 1987 and June–July 1990, compass directions of two kinds of fallen trees were recorded, taking a compass bearing from the base of the tree along the bole toward the top of the fallen tree. (1) Gaps evident in 1983 canopy height maps were surveyed for gap-edge trees that had fallen since 1983 ($n = 34$). These pre-existing gaps were also surveyed for recent limbfalls. All fallen limbs ≥ 5 cm diameter that could have fallen from a gap-edge tree were measured and their location noted. (2) Treefalls not at gap edges were surveyed in the 0.8-ha subplot and along the trails running through the 50-ha plot ($n = 42$).

Existing data on canopy heights and treefall gaps collected annually on a 5×5 m sample grid throughout the 50-ha plot on BCI (Hubbell and Foster 1986, Wellden et al. 1991) were analyzed to determine the fate of gap sites over a 5-yr period, 1983–1987. A gap quadrat was defined as a 5×5 m quadrat for which the recorded canopy height in 1983 was ≤ 5 –10 m. Three classes of gaps were analyzed: (1) “Small” gaps were single gap quadrats separated from the next nearest gap quadrat by at least 20 m. All 85 small quadrats were surveyed. (2) “Medium” gaps were areas containing 5–6 contiguous gap quadrats. All 143 quadrats in all 26 medium gaps were surveyed. (3) “Large” gaps were areas containing at least 15 contiguous gap quadrats. These gaps varied in size from 15 to 59 quadrats. All 549 quadrats in all 21 “large” gaps were surveyed. In total, 777 quadrats in 132 gaps were surveyed.

The yearly canopy records for each gap quadrat from 1983 to 1987 were examined and each quadrat put into one of three classes: (1) “up,” a monotonic increase in canopy height, indicating filling of a canopy gap, either from below or by lateral ingrowth; (2) “down,” a decrease in canopy height, whether or not this decrease preceded or followed an episode of canopy height increase (this was an index of repeat disturbance of the pre-existing gap); (3) “same,” canopy height remaining essentially unchanged. This latter class could be due to repeated disturbance and regrowth on a scale to which yearly surveys were not sensitive, or to some suppressing influence, such as lianas or low vegetation (cf. Koop and Hilgen 1987). Therefore we estimated redisturbance rates in two ways, including “same” with “down” (liberal estimate) or omitting “same” from the analysis (conservative estimate).

We also examined the canopy records for 143 non-gap quadrats, which had canopies in the 30-m height class in 1983. These were put into three classes: (1) “undisturbed,” canopies remaining at 30 m throughout the study period; (2) “disturbed,” quadrats with a dramatic loss of canopy height, to the 0, 2, 5, or 10 m height classes; (3) “ambiguous,” quadrats in which can-

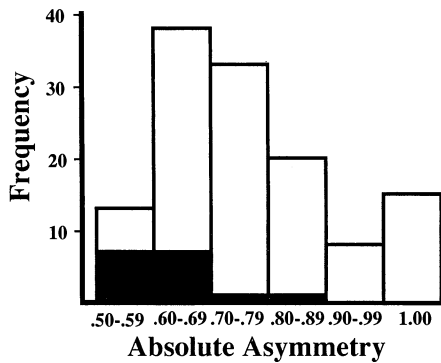


FIG. 2. The frequencies of absolute crown asymmetries for 127 trees. Absolute asymmetry = G/T , where G is the maximum area that can be created on one side of a straight line drawn through the bole (see text, *Study site and methods*, and Fig. 1), and T is the total crown area. Solid bars are for emergent trees.

opy height changed from 30 to 20 m, or in which there was only a temporary decrease in canopy height. These latter could have been due to either canopy loss or to errors in measurement. Therefore disturbance rates were estimated two ways, including "ambiguous" quadrats with either "disturbed" quadrats (liberal estimate), or including "ambiguous" quadrats with "undisturbed" quadrats (conservative estimate).

RESULTS

Tree crowns in this lowland tropical forest were often strongly asymmetrical (Fig. 2). Absolute crown asymmetries averaged 0.743, with nearly three-quarters of their crown area on their heaviest sides. Emergent trees (>1 m taller than all trees within 10 m laterally) were significantly more symmetrical than nonemergent trees (absolute asymmetries: 0.619 ± 0.020 [$\bar{X} \pm \text{SE}$] vs. 0.760 ± 0.012 , $t = 22.9$, $P < .001$). This was associated with a weak but significant negative relationship between tree height and absolute asymmetry ($r = -0.25$, $n = 127$, $P < .05$).

Crown asymmetries were not random relative to nearest large neighbors and gap edges. Tree crowns were strongly asymmetrical away from their nearest large neighbors (Table 1). On average, twice as much vertically projected crown area occurred away from the nearest large neighbor as toward it (proportion away = 0.668 ± 0.017 [$\bar{X} \pm \text{SE}$], $n = 112$). The centers of crown area were usually located on the sides of the trees facing directly away from their near large neighbors (Fig. 3; $\chi^2 = 61.9$, $\text{df} = 3$, $P < .001$). This pattern is particularly striking given that ongoing treefalls are constantly changing the neighborhood relations in the forest. Only 12% of the surveyed trees were asymmetrical with a larger fraction of their crown toward their nearest large neighbor. There was a weak significant negative correlation between the distance to the nearest large neighbor and relative crown asymmetry away from that neighbor ($r = -0.23$, $n = 112$, $P < .05$).

TABLE 1. The distribution of crown asymmetries relative to nearest large neighbor for 110 large (diameter at breast height [dbh] > 20 cm) tropical forest trees.

Asymmetry away from neighbor*	Number of trees	Proportion of trees
≥ 0.50 ($\geq 1:1$)†	97	0.88
≥ 0.67 ($\geq 2:1$)	55	0.50
≥ 0.75 ($\geq 3:1$)	35	0.32
≥ 0.80 ($\geq 4:1$)	19	0.17

* Relative asymmetry = A/T , where A is the crown area away from the line of asymmetry relative to the nearest large neighbor (see text, *Study site and methods*, and Fig. 1), and T is the total crown area.

† Numbers in parentheses represent the ratio of area away from neighbor to area toward neighbor. The dividing line between areas is the line of asymmetry.

Treefall gaps were even more influential than large neighbors in shaping the crown asymmetry of smaller canopy trees at the edges of gaps. Trees taller than 23 m were on average unaffected by nearby gaps, but gap-edge trees < 23 m tall were strongly asymmetrical into their gaps (proportion of canopy into gap = 0.493 ± 0.047 [$\bar{X} \pm \text{SE}$, $n = 7$] for trees > 23 m tall vs. 0.723 ± 0.049 [$n = 15$] for shorter trees, $t = 2.75$, $P < .02$). For shorter gap-edge trees (< 23 m tall), crown asymmetry into the gap was significantly greater than asymmetry away from the nearest large neighbor ($t = 2.09$, $P < .05$).

Asymmetry was of two forms. Most commonly, the bole was vertical and the crown was asymmetrical relative to the upper bole, due to differential branch growth. In some trees ($\approx 12\%$), the bole itself leaned in a particular direction, the crown being asymmetrical or not relative to the upper bole. In these ways, trees produce crowns away from competing neighbors and into pre-existing gaps.

Asymmetrical directly away from nearest large neighbor

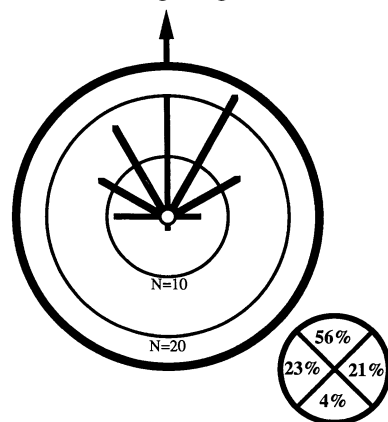


FIG. 3. The distribution of angles between (a) the direction from the bole to the center of crown area for each reference tree, and (b) the direction from the bole of each reference tree to the bole of its nearest large neighbor. The length of each line is proportional to the frequency of records for each angle class.

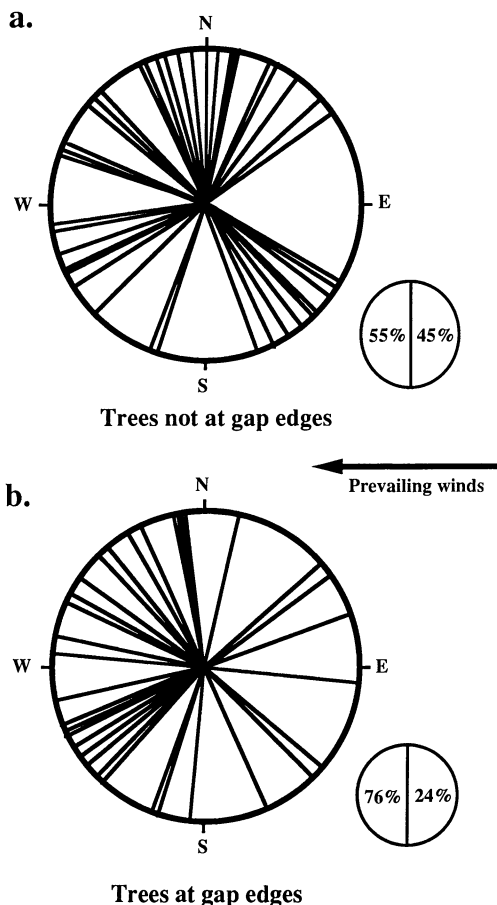


FIG. 4. The directions of treefalls relative to compass direction for (a) trees not at gap edges, and (b) gap-edge trees. Prevailing winds on Barro Colorado Island are mainly from the east.

The pattern of treefall directions paralleled that of crown asymmetry. For trees not at gap edges, there was no obvious pattern of treefall direction relative to compass direction (Fig. 4a; $\chi^2 = 0.39$, $df = 1$, $P > .50$). However, there was a strong and significant ($\chi^2 = 25.0$, $df = 3$, $P < .001$) tendency for trees to fall into the 90° quadrant directly away from their nearest large neighbor (Fig. 5). For gap-edge trees, there was a strong and significant tendency ($\chi^2 = 43.2$, $df = 3$, $P < .001$) to fall into the pre-existing gap (Fig. 6). There was also a lesser tendency for gap-edge trees to fall downwind (Fig. 4b; $\chi^2 = 8.76$, $df = 1$, $P < .01$). Limbfalls from gap-edge trees were significantly more likely to fall into

TABLE 2. The number tree branches from gap-edge trees that either fell into pre-existing gaps or fell outside the gap.

	Branch diameter (cm)				Total	
	5-9	10-14	15-19	≥20	No.	%
Outside gap	3	4	2	0	9	29
Into gap	7	10	1	4	22	71

TABLE 3. Proportion of 5 × 5 m quadrats that showed reductions in canopy heights from 1983 to 1987 for small, medium, and large gaps, and for nongap quadrats. Proportions are means for each gap size. Statistics are from two-tailed *t* test comparisons of small gaps within medium and large gaps, using arcsine-transformed data.

Gap size (no. quadrats included)	Proportion redistributed			
	Liberal estimate		Conservative estimate	
	Proportions	<i>P</i>	Proportions	<i>P</i>
1	.36		.31	
5-6	.59	<.05	.53	<.01
≥15	.57	<.01	.46	<.05
Nongap quadrats	Proportion disturbed			
	.24		.13	

adjacent gaps than into the areas around the outside of the gap (Table 2; $\chi^2 = 5.52$, $df = 1$, $P < .05$). This is a conservative estimate, because some of the limbs scored as falling outside the gaps could have come from trees that were not along the gap edge.

Quadrats in larger gaps were significantly more likely to experience a redistribution that resulted in a reduction in canopy height than were quadrats in very small, isolated gaps (Table 3). The values in Table 3 should not be taken as estimates of absolute redistribution rates. Consecutive measurements of canopies near height category boundaries may have differed because of observer error, leading to overestimates of the rates of canopy height reduction. However, this effect should be independent of gap size, and the greater rates of canopy height loss for large and medium gaps were probably indicative of greater rates of redistribution than in very small gaps. This potential observer error made it inappropriate to statistically compare quadrats with differing initial canopy heights, i.e., gap quadrats vs. nongap quadrats. However, even the liberal estimate of canopy disturbance for nongap quadrats was

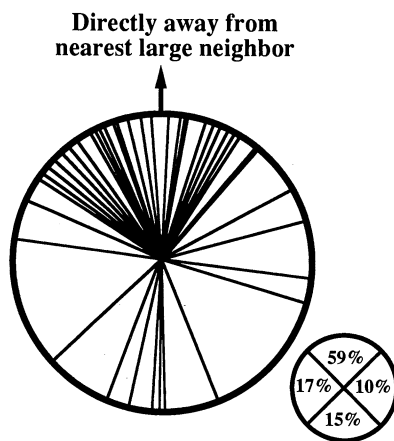


FIG. 5. The directions of treefalls relative to nearest large neighbors for trees not at gap edges.

Directly Into Pre-existing Gap

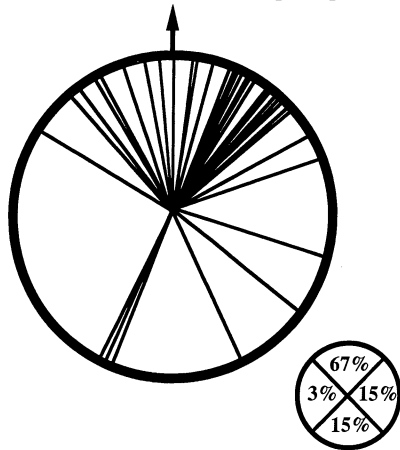


FIG. 6. The directions of treefalls relative to pre-existing gaps for gap-edge trees.

less than the conservative estimates of canopy disturbance for gap quadrats (Table 3).

DISCUSSION

It appears that canopy disturbances in this tropical forest were not random, but tended to occur at the sites of pre-existing gaps (Table 3). There are two possible explanations for this, which are not mutually exclusive. First, trees at gap edges may fall at a higher frequency than trees not at gap edges (cf. Hubbell and Foster 1986, Lawton and Putz 1988). We have not examined this, other than to note that shorter gap-edge trees were significantly more asymmetrical into adjacent gaps than away from near neighbors.

Second, trees at gap edges may be more likely to fall into gaps than in other directions, regardless of treefall rate. We have shown this to be the case (Fig. 6). Most trees were strongly asymmetrical away from shading neighbors and into gaps, and trees were significantly more likely to fall in the direction of their heavy sides. These patterns indicate that crown asymmetry can be an important force in disturbance regimes in tropical forests.

Neighbors can reduce both shoot growth and shoot survivorship, presumably through shading (Jones and Harper 1987a, b), although physical damage may also

play a part. Asymmetry away from near neighbors in herbs (cf. Solangaarachchi and Harper 1989, Novoplansky et al. 1990) is presumably the consequence of such interactions. Asymmetry apparently results in unequal stresses within a tree; any structural compensation (cf. Scurfield 1973, Boyd 1985, Timell 1986) that occurs is apparently insufficient to prevent trees falling on their heavy sides. Most current models of tree architecture and stress do not consider the possibility of crown asymmetry (Halle et al. 1978, King and Loucks 1978, King 1986, Cannell and Morgan 1987, Tomlinson 1987, Cannell et al. 1988, but see Henwood 1973). In addition to the effects of asymmetrical canopies, laterally shaded trees and sheltered trees may be inherently more susceptible to stem failure because they produce architectures that are taller than the critical height for their respective stem diameters (Holbrook and Putz 1989).

It is not surprising that only shorter trees (<23 m) responded to gaps by producing asymmetrical canopies. Light is a critical limiting resource in many forest ecosystems (Wales 1972, Hutchinson and Matt 1977). The taller the tree, the less likely it is that an adjacent tree or gap will affect its light environment.

Although trees at this site and elsewhere fall mostly during windy and wet weather, and during particular windstorms, there was no strong tendency for tropical trees to fall downwind (Caballe 1984, Arriaga 1988, nongap trees in this study). Wind-tossed trees were more likely to fall, but did so on their heavy sides. The greater tendency for conifer trees to fall downwind (Henry and Swan 1974, Falinski 1978) may be due to the fact that, compared to hardwoods, the monopodial growth form of conifers is less likely to produce asymmetrical crowns in response to gaps and near neighbors (S. P. Hubbell and D. Blockstein, *unpublished data*).

The data of Falinski (1978) from a natural forest in Poland allow a test of this difference. Falinski mapped treefall directions for two community types, and these data are re-analyzed here (Table 4). The pattern of treefall directions for the most common tree, the conifer *Picea abies*, departed significantly from random, tending to fall downwind. However, the pattern of treefall directions for the other trees in the same localities, most of which were broad leaved, was not significantly different from random. This forest also provides a demonstration of the strong tendency for broad-leaved

TABLE 4. Chi-square analysis of the treefall data of Falinski (1978), testing the null hypothesis of randomness in treefall directions for different tree types in two forest types. $df = 3$ for all tests. All 254 treefalls were included, with samples ranging from 24 to 84 for each test.

Tree species	Forest type					
	Mixed coniferous			Mixed deciduous		
	% broad-leaved	χ^2	P	% broad-leaved	χ^2	P
<i>Picea abies</i>	0	21.43	<.001	0	79.97	<.001
Other spp.	67	2.23	>.5	100	3.00	>.5

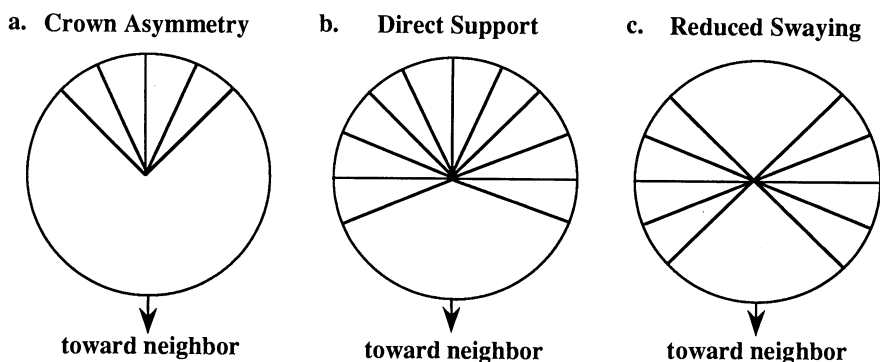


FIG. 7. Different ways in which a neighbor may influence the direction of a falling tree. Shaded areas indicate predicted patterns of treefall when the effect of a neighbor is to (a) produce an asymmetrical crown, (b) directly support a tree, or (c) prevent swaying toward, and therefore away from, the neighbor.

trees to fall away from near neighbors, largely independent of wind direction (Falinski 1986:Fig. 34).

It is not obvious why gap-edge trees in this study did show a tendency to fall downwind, when nongap trees did not (Fig. 6). Data from the 0.8-ha subplot do not indicate that trees on the leeward sides of gaps were more symmetrical than trees on the windward sides. In any case, the tendency for gap-edge trees to fall downwind is much less strong than their tendency to fall into pre-existing gaps.

In addition to influencing treefalls through crown asymmetry, it is possible that a nearby tree may physically prevent a reference tree from falling in certain directions (Fig. 7). By supporting a failing tree, a near neighbor would minimize treefalls directly toward it, but should allow treefalls in all other directions, i.e., lateral falls as well as falls directly away from the neighbor (Fig. 7b). Alternately, a near tree may prevent swaying to and fro, but allow swaying laterally. This would increase lateral treefalls at the expense of treefalls directly toward or away from the near neighbor (Fig. 7c). The observed patterns of treefalls relative to nearest large neighbor (Fig. 5) and gap edge (Fig. 6) suggest that crown asymmetry is the major factor determining treefall direction in this study (Fig. 7a).

Lateral growth of limbs appeared to be much greater on relatively unshaded sides of tree crowns. Lateral growth rates in a temperate forest of up to 60 cm/yr have been reported (Runkle and Yetter 1987). The longest lateral branch in this study extended >13 m out from the bole. Long horizontal branches must be under severe stress. Limbfalls can be an important source of forest disturbance (Aide 1987), and individual limbfalls can be as large as small treefalls. The frequencies and directions of such limbfalls are probably affected by the same neighborhood relations that affect treefalls, increasing the rate of repeat gap disturbance.

It is clear that we must be aware of not only the location of a tree that falls, but also the direction it falls, if we are to fully understand gap dynamics. The

tendency for lowland wet tropical forest trees to fall on their heavy sides away from large neighbors, and particularly to fall into pre-existing gaps, has important consequences for our understanding of forest dynamics.

1) Treefalls and resultant gaps are not random in space, but tend to recur at the same sites repeatedly. This creates the possibility of "hot spots" of forest disturbance. Forest turnover time has traditionally been calculated as the inverse of the fraction of new gap area created each year (Hartshorn 1978, Brokaw 1982, 1985a, Lieberman et al. 1985, Yamamoto 1989), and can be thought of as the mean "waiting time" between disturbance events for a given point in the forest. If gaps are more persistent and nonrandom through redisturbance, the distribution of turnover times would depart significantly from random (Lawton and Putz 1988), with relative over-abundances of very short and very long "waiting times."

2) The biology of gap plants may be more predictable than previously thought. Sites of successful recruitment for short-lived gap plants may be more fixed in space, and occur at more frequent intervals, because the presence of a gap plant would be a nonrandom indicator of the location of a future gap. Also, growth studies have indicated that understory saplings may require multiple gap events to reach the canopy, and that redisturbance may not be uncommon (Canham 1985, Runkle and Yetter 1987, Martinez-Ramos et al. 1988). Conversely, the life-span of individual gap plants may often be limited by redisturbance; subsequent treefalls would undoubtedly kill some gap plants. Some understory *Piper* species may have evolved architectures that can withstand repeated damage from limb- and treefall (Gartner 1989).

3) It is possible that crown asymmetry may affect not only the direction but also the frequency of treefalls, with asymmetrical trees being more likely to fall than trees with symmetrical crowns. This would explain why trees at gap edges are more likely to fall than other trees (Hubbell and Foster 1986, Lawton and Putz 1988).

Putz and Chan (1986) report that gap-edge trees damaged during a treefall have high subsequent mortality rates.

4) The extents of older gaps partly redistributed by new treefalls are likely to be underestimated when gap area is determined by the age or maturity of plants in gaps (Fox 1989) because the gap area attributed to the more recent treefall is not included in the area of the older gap, leading to possible overestimates of gap expansion (cf. Whitmore 1984, Foster and Reiners 1986). Similarly, rates of gap formation based on repeat surveys of gap area (Brokaw 1982) may underestimate true rates of gap formation. This may explain in part the observation that tree mortality rates appeared to be greater than estimated rates of gap formation in a tropical forest (Putz and Milton 1982).

5) Gaps add to the diversity of a forest in several ways. Gap age and size provide two environmental gradients along which plant diversity can occur, as does gap "zone" (Orians 1983, Brandani et al. 1988). We suggest that redistribution regimes may be yet another environmental gradient that provides the opportunity for the occurrence of plants specialized for high or low redistribution rates, further increasing potential species richness.

We do not suggest that crown asymmetry fully explains patterns of forest treefalls, but rather that by incorporating crown asymmetry and the neighborhood relations that cause it, treefalls become more predictable. Treefalls are also influenced by wind direction (Henry and Swan 1975, Falinski 1978, Arriaga 1988), rain (Brokaw 1985a, Lawton and Putz 1988), lianas, landslides (Garwood et al. 1979), lightning (Brunig 1964, Taylor 1971), topography (Caballe 1984, Lawton and Putz 1988, Arriaga 1988), elephants (Pellew 1983, Caughley 1976), and tree age and size (Naka 1982, Kanzaki and Yoda 1986). However, crown asymmetry may be contributing factor in many of these forces. For example, trees on slopes tend to be shaded mainly by crowns upslope (above), creating canopies that are strongly asymmetrical downslope (cf. Koike 1985) and increasing the tendency for trees to fall downhill (Caballe 1984). Whatever the force that proximally causes a tree to fall, crown asymmetry should increase the likelihood of a particular tree succumbing to the force, and affect the direction of fall.

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