Journal of Tropical Ecology (2001) 17:895–902. With 1 figure

SHORT COMMUNICATION

Low rates of background canopy-gap disturbance in a seasonally dry forest in the Yucatan Peninsula with a history of fires and hurricanes

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(Accepted 3rd April 2001)

KEY WORDS: basal rot, modes of gap formation, snapping, standing mortality, uprooting

Isolated canopy gaps involving one to several trees occur continuously and frequently in many moist and wet neotropical forests (*sensu* Holdridge *et al*. 1971), shaping tree community structure through a shifting mosaic of patches of high resource availability for small and young trees (Denslow 1980). Though there are few relevant data (Jans *et al*. 1993), forests with significant seasonal drought are expected to have lower rates of canopy-gap formation (gaps ha^{-1} y^{-1}), smaller gap sizes, and, thus, lower rates of canopy disturbance (% y^{-1}, see review in Whigham *et al*. 1999). At the extreme, very dry tropical forests do not appear to fit the gap-phase dynamics concept (Swaine *et al*. 1990).

A syndrome of factors is expected to cause low rates of background canopy-gap disturbance in seasonally dry forests (Figure 1). Background canopy gaps

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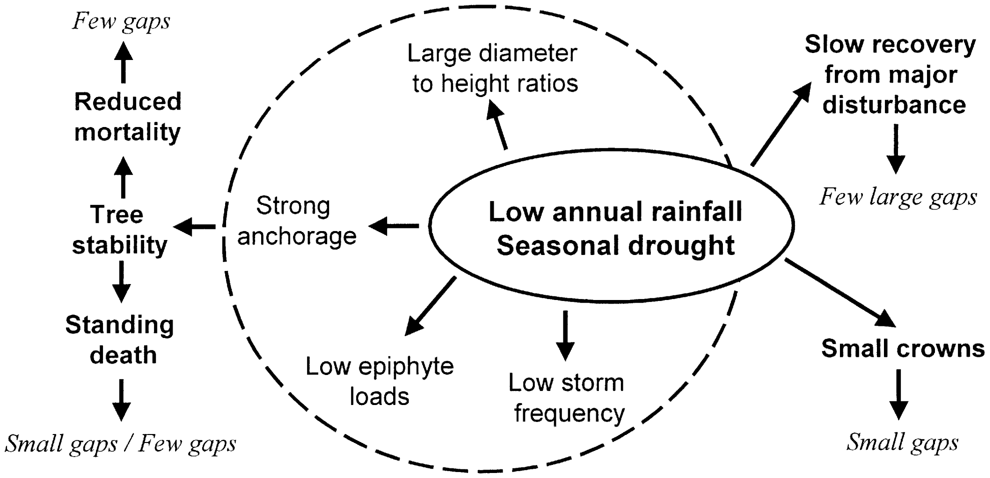

Figure 1. The syndrome of factors associated with low annual rainfall and seasonal drought that are expected to cause low gap formation rates, small canopy gap sizes and thus low rates of canopy disturbance between major disturbance events.

are here defined as gaps caused by one to several trees between major disturbance events (see Whigham *et al.* 1999). Increased tree stability is expected for four reasons. First, trees become shorter for a given trunk diameter as annual rainfall decreases and seasonality increases (Kira 1978). Such trees should be less subject to snapping (Putz *et al.* 1983) and, because of a shorter moment arm, less subject to uprooting. Second, root-to-shoot ratios are high in seasonally dry forests (Richards 1996), providing strong anchorage and, thereby, reducing rates of uprooting. Third, drier forests have lower epiphyte loads (Holdridge *et al.* 1971) and would experience less rain-loading and, thus, lower rates of gap formation (Strong 1977). Finally, seasonally dry forests have a shortened wet season, and, thus, storms that cause structural failure may occur less frequently than in wet forests.

Increased tree stability may have two consequences in seasonally dry forests: lower gap formation rates through reduced tree mortality rates (see Phillips *et al.* 1994) and increases in the proportion of trees that die standing. A tree that dies standing may often leave no gap or a small gap (Putz & Appanah 1987), thereby reducing average gap size and frequency. Small crown size in forests with seasonal drought (Holdridge *et al.* 1971) would also result in smaller canopy gaps than in wet forests.

The effects of seasonal drought on background canopy-gap disturbance in the tropics are expected to be substantially compounded by the effects of major disturbances. Because large trees typically cause large gaps (Brokaw 1982b), high mortality rates of large trees during major disturbances, for example, during hurricanes (Everham & Brokaw 1996), lead to small average gap sizes after these events (Shugart 1984) and, thus, low rates of canopy disturbance (Scatena & Lugo 1995). Lower productivity in seasonally dry forests may translate into lower rates of recovery of forest structure after major disturbances

(Phillips *et al*. 1994) and, thus, more protracted periods with few large gaps and lower rates of canopy disturbance relative to forests that experience little or no seasonal drought.

In this paper, we present data on background canopy-gap disturbance rates and the ways gaps were created in a seasonally dry forest with a history of major natural disturbances (fire and hurricanes) and selective logging. The forest is a 20 000-ha extractive reserve on the mid-eastern side of the Yucatan Peninsula (Quintana Roo, Mexico, 19° 7′ N, 88° 20′ W) and is part of the ejido Noh Bec (a communal land ownership). On average, there have been six consecutive months per year (November to April) with < 100 mm of rainfall and total yearly rainfall is 1500 mm (Snook 1993). The forest has been classified as medium-stature, semi-evergreen forest because it is composed of both dry-season deciduous and evergreen trees and canopy heights range from 20 to 30 m (Dickinson 1998, Pennington & Sarukhan 1968, Snook 1993). Heavy clay soils in the upland study sites were derived from limestone parent material and are often rocky (Furley & Newey 1979). Topographic relief was minimal in the study sites.

Though poorly documented, forests in the region have a long history of natural and anthropogenic disturbances. The frequency and scale of hurricane and fire disturbance can only be inferred from recent records. During the period from 1886–1968, tropical cyclonic storms (including hurricanes) ranged in frequency from approximately 0.24 y^{-1} along the southeastern coast to 0.73 y^{-1} along the northeastern coast of the Yucatan Peninsula (Alaka 1976). The highest frequency of such storms in the Caribbean and adjacent western Atlantic is about 0.85 y^{-1}. Hurricanes in the region's forests typically cause major crown damage and, to a lesser extent, snapping and uprooting (Snook 1993, Whigham *et al*. 1991). The last hurricane to damage forests in Noh Bec was in 1955 (Snook 1993). Fires in the Yucatan Peninsula have been less well documented than hurricanes but the vast majority have been ignited by people (Perez-Villegas 1980). Lower densities of large trees in Noh Bec survived 20th century fires than the 1955 hurricane (Snook 1993). Fires that occur after hurricanes may cause higher mortality than either disturbance alone (Snook 1993). Forest structure and interviews suggest that there have been no fires in our study sites during the past 60 y. No Maya settlements were present in the study forest when the ejido Noh Bec was established in the 1930s and settlement was not likely to have occurred in the several preceding centuries (Edwards 1986). Selective logging has occurred throughout the region's forests since the mid-1900s (Arguelles 1991, Snook 1993) and only small patches of forest have not been logged. As an approximation, logging in Noh Bec has typically removed 1–3 m^3 ha^{-1} of timber on a 25-y cutting cycle.

We described background canopy-gap disturbance in one logged (El Remate) and two unlogged sites (El Limon and El Huasteco). The unlogged sites were the largest blocks of unlogged upland forest that remain in Noh Bec and were selected based on interviews with long-term participants in logging operations, the presence of mahogany trees > 1.2 m dbh, the lack of evidence of skid trails, and the absence of mahogany stumps from felled trees that often persist for decades in this forest (*pers. obs.*; Snook 1993). The species composition of the unlogged sites was similar to much of the rest of the upland portion of the forest (*pers. obs.*). A single 10-ha, 200 × 500-m rectangular plot was sampled in each unlogged site.

The logged site was selectively logged, primarily for mahogany (*Swietenia macrophylla* King), approximately 20 y prior to our study (Arguelles 1991). Gaps were sampled in 40-m-wide transects established for forest inventory purposes over an approximately 400-ha block of forest (see Table 1 for sample areas and dates). The north–south transects were 0.25–1 km apart and ranged from 0.9 to 3.5 km in length; the lengths variable in order to avoid roads and log-concentrating yards. Two transects were sampled in 1993 and three more were added in 1994.

We estimated gap area with a scale drawing based on four measured radii and freehand drawing of irregularities (see gap definition in Table 2). A canopy gap was included in the sample if the base of the gap-making tree (see below) was more than half-way inside the transect or plot (Brokaw 1982b). Gaps were classified as being < 1 y old (new gaps) or $\geq$ 1 y old in the first sample in the logged area and in the single sample in the unlogged forest plots (see Table 1) based on informal comparison with regrowth in gaps of known age. All gaps were marked in the logged forest, making subsequent identification of new gaps unambiguous. In the logged site, we combined data for all transects to estimate the rate of gap formation and the rate of canopy disturbance for each sample year (1993–1995) and then averaged the three estimates, weighting by the area sampled in a given year. Gaps of all ages were sampled in 1993 (the logged site) and 1994 (the unlogged sites) in order to estimate the percentage of the forest in new and old gaps (standing gap fraction).

Gap-making trees were classified by how they caused a gap (see Table 3 for criteria). A gap-making tree was the first tree to fall and cause others to fall (see van der Meer & Bongers 1996) and was usually the largest tree involved.

Table 1. Area sampled, sample year and number of gaps sampled in the logged and unlogged sites.

	Logged	Unlogged	
	Remate	Limón	Huasteco
Total area sampled (ha)			
1993	18.4	—	—
1994	48.4	10	10
1995	48.4	—	—
Sample year(s)			
New gaps	1993–1995	1994	1994
Old gaps	1993	1994	1994
Sample size (number of gaps $\geq$ 10 m^2)			
New gaps	24	0	0
Old gaps	16	5	5

Table 2. Background canopy-gap disturbance statistics from Noh Bec and other sites. Gap-formation rate, mean and maximum size of new gaps, the percentage of the canopy opened to gaps each year (canopy disturbance rate), the gap cycle (the time required to open 100% of the canopy) and the percentage of the forest in both new and old gaps (standing gap fraction) are reported for Noh Bec (rainfall 1500 mm), three forests in the Taï National Park, Ivory Coast (rainfall 1650 to 1875 mm; Jans *et al*. 1993), and seven moist and wet forests sites (rainfall > 2000 mm, from reviews in Hartshorn 1990, Jans *et al*. 1993 and Yavitt *et al*. 1995). All studies used the Brokaw gap definition (Brokaw 1982a)[a], with, at most, minor modifications and made direct measurements of gap sizes and rates of occurrence. Median gap sizes (30.4 m^2 in Noh Bec) were often not reported and are not included in the table.

	Noh Bec			Other forests		
	Logged	Unlogged		Dry site	Moist/wet sites	
	Remate	Limón	Huasteco	Taï	Min	Max
Gap formation rate (gaps ha^{-1} y^{-1})	0.18	0[b]	0[b]	0.7	0.5	1.3
Mean size of new gaps (m^2)	46	—	—	55	54	120
Maximum size of new gaps (m^2)	146	—	—	244	232	781
Canopy disturbance rate (% y^{-1})	0.10	0	0	0.4	0.6	1.6
Gap cycle (y)	1000	—	—	250	167	62
Standing gap fraction (%)	0.06	0.24	0.22	0.8	1.4	7.5

[a] Brokaw definition: a vertically projected hole in the canopy that extended down to an average height of approximately 2 m above the forest floor (Brokaw 1982a, van der Meer *et al*. 1994). Minimum gap size in Noh Bec: 10 m^2. Minimum gap size in other forests: 10–25 m^2.

[b] No gaps < 1 y old were present at the sites when gaps were sampled preventing the calculation of certain statistics.

Table 3. Modes of gap formation in the logged and unlogged sites. Numbers (and percentages) of gap making trees are reported.

Mode of formation	Logged	Unlogged	
	Remate	Limón	Huasteco
Rotten base[a]	15(40.5%)	4	1
Dead standing[b]	11(29.7)	0	0
Snapped bole[c]	7(18.9)	1	0
Uproot[d]	3(8.1)	0	1
Branch fall[e]	1(2.7)	0	3

[a] Gap-making tree failed near ground level because of extensive rot causing minimal soil disturbance.

[b] Gap maker was dead and upright or there was evidence that the tree died before it fell (e.g. large fallen branches around the base or no small branches within the crown).

[c] Gap maker snapped below the first major branch and above the base.

[d] At least a portion of the gap-maker's root system was pulled from the soil and no basal rot was apparent.

[e] Gaps created by the fall of one or more limbs from a live tree.

Tree diameter distributions were characterized in regular arrays of 500-m^2 circular plots in each site. Plots in the logged site (n = 126) were sampled for forest inventory purposes by the Sociedad Civil de Productores Forestales and were at 100-m intervals along each transect noted above (unpubl. data). Twenty plots were sampled in a regular array at each unlogged site.

Rates of background canopy-gap formation, rates of canopy disturbance and standing gap fraction in the logged site in this seasonally dry forest were exceedingly low and gap sizes were small compared with the most similar dry forest and a sample of wet and moist forests reported in the tropical literature (Table 2). Standing gap fractions in the unlogged sites were comparable to those in the logged site. The canopy disturbance rate in the logged site in Noh Bec corresponds, approximately, to an order of magnitude increase in the gap cycle over the moist and wet forests.

Logged and unlogged sites in Noh Bec appear to be very similar in their canopy gap disturbance regime but no statistical comparison is possible because of a lack of replication in logged forest. To date, logging in this forest has been highly selective relative to species and, thus, low volumes of timber are removed in any given logging area. Low logging intensity is reflected in the lack of a difference in tree diameter distributions among the logged and unlogged sites (Table 4). Our sample in the logged site did not include revegetated logging roads and log landings; if they had, differences in the background canopy gap disturbance regime might reasonably be expected.

Evidence suggests that sound trees were stable in this seasonally dry forest. In the logged site, relatively few sound trees created gaps (i.e. only 30% of gaps were caused by uproots, snapped boles or branch falls) while 40% of gap-making trees fell because of basal rot and 30% died standing (Table 4). In the unlogged sites, one half of gap makers fell because of basal rot. *Manilkara zapota* (L.) Royen trees are much more likely to fall from a rotten base than other species (79 vs. 14% of gap making trees in the logged site, n = 36, Pearson χ^2 = 9.8, df = 1, P = 0.002), perhaps because of rot that develops from wounds caused by tapping the trees for latex that is processed into natural chewing gum. *Manilkara zapota* accounts for the majority of the forest's basal area and the majority of gaps, but does not account for more gaps than would be expected from its abundance (Dickinson 1998).

A low occurrence of uprooting in the logged site (8% of gaps) is consistent with the expectation that strong anchorage in this seasonally dry site contributes to tree stability. In a similar forest on the northeast coast of Quintana Roo, Whigham *et al*. (1991) found low rates of uprooting during Hurricane Gilbert, a storm with one of the lowest core atmospheric pressures on record. Anchorage may be improved in the Yucatan Peninsula beyond that expected

Table 4. Diameter (dbh) distributions (percentages and numbers of stems), maximum diameters, basal areas (trees $\geq$ 10 cm dbh), and stem densities (trees $\geq$ 10 cm dbh) in the logged and unlogged sites. Diameter distributions include only trees of a size that formed gaps (the minimum dbh of a gap maker was 28 cm). The diameter distributions are not different (Pearson χ^2 = 1.07, df = 4, P = 0.89).

	Logged	Unlogged	
	Remate	Limón	Huasteco
DBH range (cm)			
30–49.9	81.4%(434)	82.4(89)	79.2(76)
50–69.9	15.2(81)	15.7(17)	17.7(17)
$\geq$ 70	3.4(18)	1.8(2)	3.1(3)
Maximum dbh	91	80	91
Basal area (m^2 ha^{-1})	23.0	27.5	26.1
Stem density (ha^{-1})	572	690	584

in seasonally dry forests in general because of extensive root penetration into cracks in the limestone parent material (see Wadsworth & Englerth 1959).

Forty-seven per cent of trees $\geq$ 10 cm dbh died standing in a multi-year growth and mortality study in the logged site (unpubl. data) while 10–84% of trees died standing in other tropical forests (see review in Whigham *et al*. 1999). This moderate rate of dead-standing mortality is not inconsistent with our expectation that tree structural stability leads to increased rates of dead-standing mortality. More data are required on the effects of dead-standing mortality, including consideration of the proportion of trees that die standing without creating a gap.

Given the magnitude of the difference between background canopy-gap disturbance rates in Noh Bec and other sites (Table 2), we speculate that much of the difference is attributable to mortality of canopy trees in past fires and hurricanes in Noh Bec. The effects of major disturbances are expected to be persistent in sites that experience significant seasonal drought because of relatively low rates of forest regrowth (Phillips *et al*. 1994). Because of fire and extensive disturbance by various human activities (Murphy & Lugo 1995), it may be difficult to find a seasonally dry forest where the background canopy-gap disturbance regime is not affected by the lingering effects of major disturbance.

Opportunities for gap-phase germination, survival, and growth in this seasonally dry forest are concentrated during periods after sporadic major natural disturbances and selective logging events. Between these events, gap-formation rates, rates of canopy disturbance and the total area in new and old gaps are exceedingly low. We speculate that the reduced importance of background canopy-gap disturbance results primarily from the persistent effects of past major disturbances. Evidence also suggests that sound trees are stable, which may reduce overall rates of tree mortality between major disturbance events and, thereby, contribute to low rates of background canopy-gap formation.

ACKNOWLEDGEMENTS

Thanks to P. J. van der Meer, N. Brokaw, an anonymous reviewer, and J. C. Dickinson, for commenting on earlier drafts of the manuscript and to J. D. and J. Matias Martinez for help in the field and the community of Noh Bec for permission to work in their forest. Thanks to the Acuerdo Mexico-Alemania, particularly H. Flachsenberg and A. Arguelles, and the Sociedad Civil de Productores Forestales de Quitana Roo for logistical support. This study was supported by grants from the Smithsonian Environmental Sciences Program, Tropical Research and Development, Tropical Forest Management Trust, the International Hardwood Products Association, Sigma Xi, Florida State University, and the Hardwood Plywood Manufacturers Association.

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