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Recommended Citation

Garrido-Pérez, Edgardo I.; Dupuy, Juan Manuel; Durán-García, Rafael; Ucan-May, Mario; Schnitzer, Stefan A.; and Gerold, Gerhard, "Effects of lianas and Hurricane Wilma on tree damage in the Yucatan Peninsula, Mexico" (2018). *Biological Sciences Faculty Research and Publications*. 733.

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Biological Sciences Faculty Research and Publications/College of Arts and Sciences

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Effects of lianas and Hurricane Wilma on tree damage in the Yucatan Peninsula, Mexico

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Key Words:

canopy stability, liana cutting, secondary succession, tree-fall gaps, tropical dry forest, tropical storms

Abstract

Climate change may increase the intensity of hurricanes (Emanuel 1987, 2003), and thus the size of disturbance in tropical forests. As a consequence, disturbance-specialist plants, such as lianas, may increase in abundance there (Phillips & Gentry 1994). Putz (1984) hypothesized that lianas create larger treefall gaps by connecting trees together and pulling down multiple trees during storms. This positive-feedback cycle may increase the prevalence of lianas in disturbed tropical forests (Schnitzer & Bongers 2002, Schnitzer & Carson 2001).

Alternatively, Putz (1984) proposed that lianas tie and stabilize canopies together, resulting in less disturbance. Forest age may determine the role of lianas during disturbance because liana abundance and composition vary through secondary succession (De Walt *et al.* 2000, Schnitzer *et al.* 2000). To test the two hypotheses of Putz (1984), we evaluated the effect of liana cutting between forests of different successional ages on tree damage by hurricane Wilma.

Studied areas are around the village of Solferino, north-east Yucatan Peninsula, Mexico, (21°26'N, 87°28'W; 10 m asl; INEGI 1993). Soils are poorly developed Luvisols, Rendzines and Vertisols upon a calcareous base that emerged after the Pleistocene (Bautista-Zúñiga *et al.* 2003, Olmsted *et al.* 2000). Topography is flat, annual rainfall averages 1250 mm, most precipitation occurs from May to November, including large storms and occasional hurricanes (Orellana *et al.* 2003). Vegetation is seasonally dry semi-evergreen tropical forest (Tropical Dry Forest *sensu* Holdridge *et al.* 1971). Between November 2003 and March 2004, twelve 20 × 20-m plots were established in areas with high density of lianas in forests of different ages of abandonment after shifting agriculture (Table 1). Plots were paired in order to establish the experimental treatments (liana cutting and control). Distance between paired plots was > or = 20 m; no branches of lianas in a plot entered any other plot. Within each plot, all trees > or = 10 cm girth (3.16 cm diameter) 1.3 m above ground were tagged and their diameters were measured as well as all climbers > or = 1 cm diameter at ground level. Lianas rooted inside a plot but climbing on trees outside were excluded; lianas rooted outside and climbing on trees inside a plot were included.

Table 1. Mean characteristics (\pm 1 SE) of trees > or = 3.16 cm diameter at breast height and lianas > or = 1 cm diameter at ground level in 12 experimental 20 m × 20-m plots in secondary tropical dry forest stands exposed to Hurricane Wilma in north-east Yucatan Peninsula, Mexico (n = 3).

Age (y) and treatment	Density (indiv. ha ⁻¹)		Basal area (m ² ha ⁻¹)		Mean basal area (m ²)		Liana/tree ratios of		Percentage of Trees	
	Trees	Lianas	Trees	Lianas	Density	Basal area	hosting lianas	felled by hurricane		
≥55 cut	3375 ± 527	4483 ± 129	24.9 ± 2.9	0.17 ± 0.03	0.01 ± 0.005	1.2 ± 0.06	0.5 ± 0.2	61.0 ± 2.4	4.5 ± 0.06	
≥55 uncut	3375 ± 435	3433 ± 621	26.4 ± 6.3	0.19 ± 0.03	0.01 ± 0.001	1.03 ± 0.2	0.2 ± 0.2	61.7 ± 7.8	10.9 ± 2.2	
10–18 cut	3408 ± 621	2617 ± 530	13.5 ± 1.6	0.10 ± 0.006	0.02 ± 0.006	0.8 ± 0.2	0.2 ± 0.1	78.2 ± 13.8	11.9 ± 4.0	
10–18 uncut	4275 ± 354	3517 ± 720.6	16.9 ± 3.9	0.10 ± 0.02	0.02 ± 0.005	0.8 ± 0.2	0.2 ± 0.06	85.9 ± 6.8	4.5 ± 2.7	

On 22-23 May 2004 all climbers were cut in one of each of the paired of plots without removing cut lianas to avoid damaging trees. On 21 August 2005 all trees were re-visited to confirm that hurricane Emily (18 July 2005) did not affect tree mortality. On 23 October 2005 (17 mo after the initial census) hurricane Wilma, the most powerful registered to date in the Caribbean (minimum central pressure = 882 hPa; maximum winds = 295 km h⁻¹), struck our plots. On 16-25 January 2006, all plots were re-visited and all substantially damaged (snapped or uprooted) trees quantified, to calculate the percentage of hurricane-felled trees per plot (%HFT; 100% = all trees that were alive and undamaged 2 mo before the hurricane). The effects of liana treatment (cutting vs control) and forest age (10-18 y old vs > or = 55 y old) on plot-level parameters, including %HFT were evaluated using generalized linear models (factorial ANOVA). Among-plot differences in density, total and mean basal area of trees and lianas can influence damages to trees, so they were included as covariables (ANCOVA). General regression was used to explore relationships among the following variables: density, basal area and mean basal area (basal area/number of individuals) of trees and lianas, liana/tree ratios of density and basal area, and percentage of trees hosting lianas. When necessary, variables were transformed to meet normality and homoscedasticity.

Total and mean basal area of trees were significantly higher in > or = 55-y-old forest stands compared to 10-18-y-old stands (Table 1; $F_{1,8} = 6.7$, $P < 0.05$, $F_{1,8} = 11.4$, $P < 0.01$, respectively). In contrast, mean liana basal area, liana-to-tree basal area ratio, and the percentage of trees hosting lianas were all greater in young than in old forest ($F_{1,8} = 21.8$, $P < 0.005$, $F_{1,8} = 5.3$, $P < 0.05$, $F_{1,8} = 5.6$, $P < 0.05$, respectively). The frequency distribution pattern for the number of hosted lianas per tree also differed between forest ages (Figure 1). In young forest, 82% of trees hosted 1-9 liana individuals, while few trees hosted either no lianas (17%) or > or = 10 lianas (1%). In contrast, older forest had comparatively fewer trees hosting 1-9 lianas (56%), and more trees hosting either no lianas (38%) or > or = 10 lianas (6%; Figure 1).

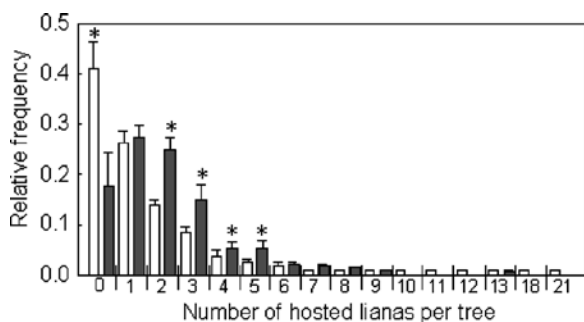


Figure 1. Frequency distribution of number of hosted lianas > or = 1cm diameter at ground level per tree for trees > or = 3.16 cm dbh in >55-y-old (white bars) and 10-18-y-old (dark bars) stands of secondary tropical dry forests in the Yucatan Peninsula (1 SE of the mean; n = six plots 20 × 20 m in both cases). Asterisks denote significant differences between forest successional ages ($P < 0.05$).

Interestingly, we found a significant interaction between liana cutting and forest age on %HFT ($F_{1,8} = 6.5$, $P < 0.05$). The percentage of hurricane-felled trees was reduced by cutting lianas in > or = 55-y-old forest, but enhanced in 10-18-y-old forest (Table 1). Lianas thus appear to increase tree-fall gap formation in old forest stands (consistent with hypothesis 1), but reduce gap formation in young stands (consistent with hypothesis 2). When we included either tree density, liana density, or mean liana basal area as a covariable, the interacting effect of liana cutting and forest age was no longer significant ($F_{1,7} > or = 3.6$, $P > 0.1$ in all cases), suggesting that this interaction is related to among-plot differences in these covariables. The percentage of hurricane-felled trees was overall negatively dependent on tree density ($R^2 = 0.52$, $P < 0.01$).

The latter finding suggests that high densities of trees may help reduce tree felling by acting as a buffer against strong hurricane winds, regardless of forest age and liana size and distribution. Differences in total and mean

tree basal area between young and old forests were consistent with the pattern reported in studies reviewed by Guariguata & Ostertag (2001). The greater ratio of liana-to-tree basal area, and percentage of trees hosting lianas in young than in old stands is also consistent with the greater abundance of lianas found in young compared with old forest (DeWalt *et al.* 2000). But contrary to the findings of DeWalt *et al.* (2000), mean liana basal area was higher in our young than in older stands. This result may be related to differences in land-use and liana species composition between our stands. According to local inhabitants, *Dalbergia glabra* Standl. is resistant to and proliferates after forest fires (Ermilio Rosado, pers. comm.). Slash-and-burn agriculture, which is common to the study region, may thus help explain the high relative abundance and size of *D. glabra*, by far the dominant liana species in our young stands. In contrast, our old forest was used for selective logging and latex extraction from *Manilkara zapota* (L.) P. Royen for chewing gum. Farmers cut lianas around these valuable trees (Garrido-Pérez & Gerold unpubl. data), which may explain the unexpected lower mean size of lianas in our older stands.

The interacting effect of forest age and liana-cutting treatment on %HFT supports both hypotheses of Putz (1984), and suggests that the impact of lianas on tree damage and forest disturbance depends on forest successional age. Differences in mean liana size, mechanical properties, and per-tree liana load distribution between young and older forest may help interpret these seemingly contradictory results. The 10-18-y-old stands had a high ratio of liana-to-tree basal area, and were dominated by comparatively large, heavy-wooded lianas representing on average (\pm SE) 79.3% (\pm 6.8%; $n = 6$) of the total basal area of lianas. These young stands were dominated by *Dalbergia glabra* (Leguminosae - Papilionoideae), but also by species of the genera: *Celtis* (Ulmaceae), *Tournefortia* (Boraginaceae) and *Otopappus* (Asteraceae). These lianas were fairly evenly distributed over trees (Figure 1), and could have formed a strong network binding canopies together (E. I. Garrido-Pérez, pers. obs.), thereby reducing tree uprooting and trunk snapping (hypothesis 2). Under these circumstances, the silvicultural practice of cutting large, heavy-wooded lianas without removing them can result in greater damage to trees during a hurricane compared with non-cutting, since the force exerted by large, heavy (and now loosely connected) lianas could exacerbate the force exerted by strong wind gusts. Cutting and removing such lianas may also be impractical and expensive (Parren & Bongers 2001, Pérez-Salicrup *et al.* 2001). In contrast, the ≥ 55 -y-old stands had a relatively low liana-to-tree basal area ratio, and were dominated by small, light-wooded lianas representing on average 79.9% (\pm 7.6%; $n = 6$) of the total basal area of lianas. They included species of *Cydista*, *Arrabidaea*, *Melloa* (Bignoniaceae), *Serjania* (Sapindaceae) and *Cissus* (Vitaceae). These lianas were patchily distributed over tree canopies (Figure 1, E. I. Garrido-Pérez, pers. obs.), were thereby less likely to form a stabilizing network, and could even contribute to treefall-gap formation, as predicted by hypothesis 1 (Putz 1984). In this case, liana cutting is recommended because it can reduce tree-felling during a hurricane.

Whigham *et al.* (1991) proposed that forests in hurricane zones do not reach successional maturity due to high levels of disturbance. Our results suggest that lianas may reduce hurricane-induced disturbance in young secondary forests. But in our older stands, this reduction is no longer present and lianas may increase gap dynamics, potentially increasing the relative abundance of both lianas and pioneer tree species (Schnitzer & Carson 2001, Schnitzer *et al.* 2000). Thus, the increasing frequency of secondary forests (Cramer *et al.* 2008), increasing abundance and size of lianas (Phillips *et al.* 2002), and increasing intensity of large storms (Emanuel 2003) may affect tropical forest disturbance, dynamics and species turnover in a number of different ways, each of which may depend on local factors, such as liana composition, their mechanical properties, and their spatial distribution, making it difficult to generalize predictions to all forest types.

ACKNOWLEDGEMENTS

Land owners are Mario Ucan, Rosendo Can, Saúl Ancona, José 'Pepe' Quintal and Roberto Antonio Lara. Luz María Calvo and José Luis Hernández made helpful suggestions on statistical analyses. Sponsors were the Organization of American States (OAS), the Mexican Council for Science and Technology (CONACYT), the German Service for Academic Exchange (DAAD), and Mrs Kathrin Pahl. E. Garrido-Pérez also thanks Balbina Ancona de Ucan and his Maya friends Chak Mool and Alux Ob for their crucial help in the field.

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