Damage and recovery of forest structure and composition after two subsequent hurricanes in the Yucatan Peninsula

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Abstract.—Hurricanes are important disturbances shaping tropical forest structure. In the last 35 years the frequency and intensity of these events have changed, and it is predicted that intense hurricanes will become even more frequent with continued ocean surface warming. In 2005, the northeastern region of the Yucatan peninsula was hit by two subsequent category-5 hurricanes (3 months apart), Emily and Wilma. I conducted vegetation surveys to evaluate forest structure and composition soon after each disturbance and after one year, determining number of species, number of stems, basal area, and type of impact presented (defoliated, snapped, or uprooted), for all stems ≥ 5 cm DBH in two different forest stand ages (8-15 yr and > 30 yr). Number of species and basal area varied by forest stand age and survey; stem density decreased after the hurricanes. The highest percentage of damaged individuals was after the second hurricane (60%), but one year later this percentage was greatly reduced (13%). In all surveys, defoliation was the most common damage and uprooting the least common. In general, larger trees suffered more uprooting and snapping than did smaller ones. The importance value of most common species remained similar over time but increased for a few late successional species by the final survey. This forest showed a high degree of recovery to multiple disturbances, reflecting a long history of adaptation to these events.

Keywords.—Disturbance; Forest structure; Hurricane Emily; Hurricane Wilma; Seasonal forest

Introduction

Hurricanes are one of the principal sources of disturbance in some tropical forests (Tanner et al. 1991, Everham and Brokaw 1996, Lugo et al. 2000, Turton and Siegenthaler 2004, Bellingham 2008, Laurence and Curran 2008). In the Caribbean, hurricanes have varied in frequency and intensity over several centuries (Reading 1990); however, the intensity of these events has increased over the last 35 years (Smith 1999, Webster et al. 2005). With the predicted increase in ocean surface temperature, intense hurricanes are expected to become even more frequent (Trenberth 2005, Webster et al. 2005, Hoyos et al. 2006, but see Nyberg et al. 2007).

Since hurricanes are single and sudden events, their effects differ greatly from those caused by constant disturbances, such as those linked to human activities. For example, a study conducted in Nicaragua, showed that post-hurricane forests sites were more similar in species composition to pre-hurricane sites than they were to young post-agricultural fields (five years old) (Boucher et al. 2001). Similarly, a study in Puerto Rico suggested land-use changes were the main determinant of forest composition, and hurricanes had only a small effect on successional trajectories (Pascarella et al. 2004). Hurricanes can shape forest function, structure, and composition through changes in microclimate, tree recruitment and survival (Tanner et al. 1991, Everham and Brokaw 1996). For example, the resulting litterfall deposition after the storm can alter ecosystem processes, such as nutrient cycling (Lodge and McDowell 1992) and the abrupt canopy opening can lead to environmental changes in the understory, such as the increase in temperature and solar radiation (Turton and Siegenthaler

2004), which in some cases hurricanes can promotes the invasion of no-native species (Horvitz et al. 1998, Laurence and Curran 2008). Tree size can also determined the type and severity of the impact an individual will suffer (Tanner et al. 1991), although there is not a clear trend of whether larger or smaller stems suffer more damage (Brokaw and Walker 1991, Whigham et al. 1991, Zimmerman et al. 1994, Sánchez-Sánchez and Islebe 1999, Van Bloem et al. 2006, Canham et al. 2010).

Several functional traits influence trees resistance and recovery from wind disturbances (Laurence and Curran 2008). One important mechanisms to compensate for the damage is by flushing leaves and increasing the number of stems after the disturbance (Van Bloem et al. 2006). In fact, diverse studies have suggested that forest recovery after hurricanes tends to occur more through the release of pre-established seedlings and sprouting species than by the establishment of pioneer species (Brokaw and Walker 1991, Yih et al. 1991, Bellingham et al. 1994, Vandermeer et al. 1997, Boucher et al. 2001, Lomascolo and Aide 2001, Mascaro et al. 2005, Van Bloem et al. 2006, Curran et al. 2008b); consequently species composition is largely unaffected. The intensity of the impact, however, can affect tree mortality rates (Whigham et al. 1991, Elmqvist et al. 1994), and therefore the relative proportions of species, which will locally affect dominance and diversity patterns (Brokaw and Walker 1991, Yih et al. 1991, Whigham et al. 2003). In addition, stronger impacts, such as uprooting, snapping, or high defoliation, may have a direct effect in individuals' survival (Dittus 1985).

Whereas there have been many studies describing forest damage and vegetation recovery following single hurricanes, the impact of multiple hurricanes within a short period of time (less than 6 months apart), has not been well studied. It has been suggested that a first wind disturbance will remove vulnerable individuals from the system and therefore subsequent ones will have less severe repercussions on remaining vegetation (Everham and Brokaw 1996). If this is the case, then changes in number of species, stems, and basal area would not be affected by the subsequent disturbances. On the other hand, if trees weakened by the first storm are more susceptible (Everham and Brokaw 1996), then subsequent hurricanes may have additional impacts on vegetation.

In 2005, two major hurricanes Emily and Wilma, only three months apart, hit the northeastern region of the Yucatan Peninsula. These events gave me the opportunity to study damage and short-term recovery (1-yr) of forests after subsequent hurricanes in the Yucatan peninsula, addressing the following questions: (1) How does hurricane disturbance affect the number of species, stems, basal area, and species composition, in different forest stand ages immediately following the event and one year later?; (2) Is stem size (DBH) associated with the type and severity of the damage that a tree suffers?; and (3) Do a second hurricane of equal intensity as the first one, causes additive impacts on vegetation?

Materials and Methods

Study Site

This study was conducted in the "Otoch Ma'ax Yetel Kooh" reserve located in the northeastern region of the Yucatan Peninsula (20° 38' N, 87° 37' W; mean alt. 14 m) (CONANP 2006). Mean annual temperature is 26.6°C, and mean annual precipitation is between 1000 and 1200 mm. The wet season is from May to November and the dry season is from December to April. Soils in the region, as in most of the Peninsula, are generally very shallow (<10 cm in depth) and underlain by limestone (CONANP 2006). The dominant vegetation is seasonally-dry tropical forest in different successional stages. Like most of the Yucatan Peninsula, this region has historically been under rotational slash-and-burn, or swidden, agricultural practices, where maize is the main crop, which has promoted a landscape of vegetation in different successional stages. For detailed information on vegetation and land-use in the area see Garcia-Frapolli et al. (2007).

In 2005, two hurricanes both classified as category-5 (the highest on the Saffir-Simpson scale) affected this region. Hurricane Emily hit in July with a minimum atmospheric

pressure of 955 hPa (Unzón and Bravo 2005a), while Hurricane Wilma struck in October, lasted for three days, and had the lowest atmospheric pressure ever recorded for that Atlantic ocean (882 hPa) (Unzón and Bravo 2005b). The eye of both hurricanes passed over the study site. Although the Yucatan Peninsula has been under the influence of hurricanes for centuries; in the last 150 years, more than 100 hurricanes have impacted the region (Boose et al. 2003). However, the study region had not experienced a strong hurricane since Hurricane Gilbert in 1988.

I conducted three surveys to study the effect of hurricanes on forest structure and species composition. The first two were within a month after each hurricane (August 2005 and November 2005, respectively) and the third in June 2006, eleven months after hurricane Emily and nine months after hurricane Wilma (hereafter referred to as the 1-year-after survey); I did not have pre-hurricane information on the forest. I established 22 belt transects (2 × 100 m) to sample woody vegetation in all three surveys. Vegetation age since last human agricultural disturbance ranged from 8 to > 50 yr. Transects were spread randomly in N - S direction, in two forest stand ages: 8-30 and > 30 yr old. Age of the forest stands was determined in previous studies using satellite images, ground verification, and local knowledge about land-use history (Espadas-Manrique and González-Iturbe 2003, Garcia-Frapolli et al. 2007). Within each transect, all stems ≥5 cm in Diameter at Breast Height (DBH) at 130 cm above the ground were counted, identified to species, visually inspected and classified using one of four impact categories: (1) no visual damage; (2) defoliated (≥50% canopy loss); (3) snapped trunk; or (4) uprooted. Stems were classified in three DBH categories: 5-10, 11-25, and >25 cm for comparative analyses.

I did repeated measures ANOVAs (rmANOVA) (JMP 7.0.1) to analyze variations in number of stem, number of species, and basal area across sampling events (Emily, Wilma, 1 Yr.) in both forest stand age -FA- (< 30 yr and > 30 yr). To evaluate relationships between tree size (DBH) categories, type of impact, and sampling event,

I did a Chi-square (χ^2) test and examined the standardized deviates (SYSTAT 2007). To evaluate if a subsequent disturbance, equal in intensity to the first one, would cause additive effects on vegetation, I estimated the expected number of stems that would show damage after Wilma if this hurricane had caused the same proportional damage as Emily did or the "Expected number of stems impacted after Wilma"(EIW). For this, I first calculated the proportion of damaged individuals after Emily as the ratio of the number of stems after Emily that showed some kind of impact (IE) to the total number of stems after Emily (TE): IE/TE. I then used the number of undamaged individuals after Emily, obtained as the difference between TE and IE (TE–IE), to calculated the number of stems that could potentially be damaged by Wilma (EIW = [(TE–IE)*(IE/TE)]), and added the resulting number to the observed number of impacted stems after Emily (EIW+IE). Based on the resulting number, I calculate the percentage of expected impacted stems after Wilma (EPIW): EPIW = (EIW+IE)/ TW*100; where TW is the total number of stems after Wilma. I calculated this for each category (defoliation, snapping or uprooting) and compared the expected to the observed results. To evaluate species change from Emily to the next surveys I calculated the importance values (IVs) for all species after each event. IVs were calculated as the sum of the relative frequency (number of transects where species were observed), relative density (number of individuals per species), and relative abundance (basal area) of each species in the survey.

RESULTS

The number of stem was similar by the forest stand age and decreased after each survey (i.e., Emily, Wilma and 1 Yr) (Fig. 1A). Basal area differed by forest stand and survey but not by their interaction (Fig. 1B). Defoliation was the most prevalent impact and uprooting the least common impact after all surveys (Fig. 2). After Emily 38% of the stems were damaged: 27% were defoliated, 8% snapped, and 3% uprooted (Table 1, Fig. 2). After Wilma hit three
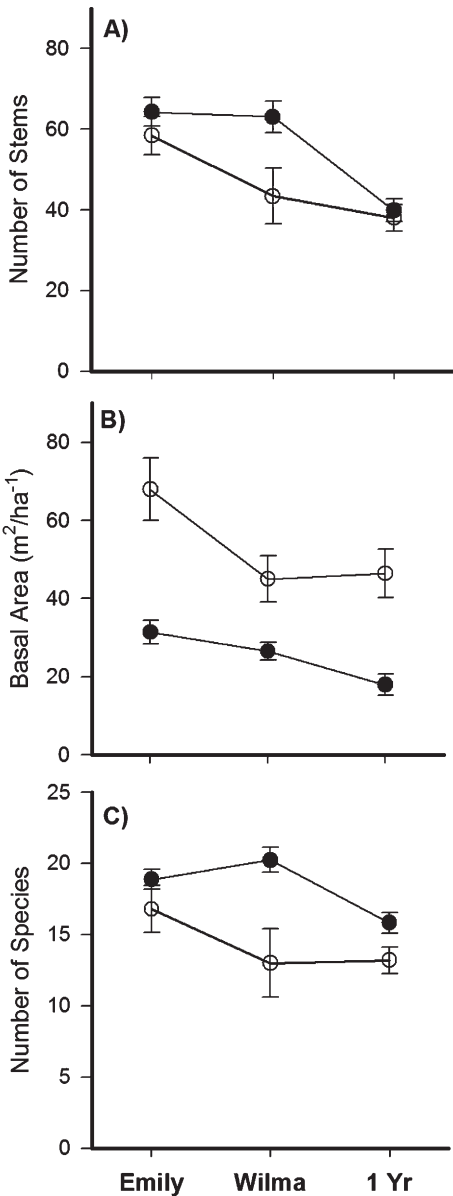
Fig. 1. Number of Stems (A); Basal Area (B); and Number of Species (C) after each survey. Filled circles represent forest of 8-30yrs; open circles forest > 30 yrs. Values are means ± 1 SD. FA = Forest Age. rmANOVA-Number of Stems (Survey: F = 28.3, df = 2, P < 0.0001; FA: F = 3.6, df = 1, P = 0.0706; Survey × FA: 3.6, df = 2, P = 0.0448); Basal Area (Survey: F = 9.3, df = 2, P < 0.0015; FA: F = 51, df = 1, P < 0.0001; Survey × FA: 1.9, df = 2, P = 0.1713); Number of Species (Survey: F = 6.06 df = 2, P = 0.0092; FA: F = 12.8, df = 1, P = 0.0018; Survey × FA: 3.4, df = 2, P = 0.0528).
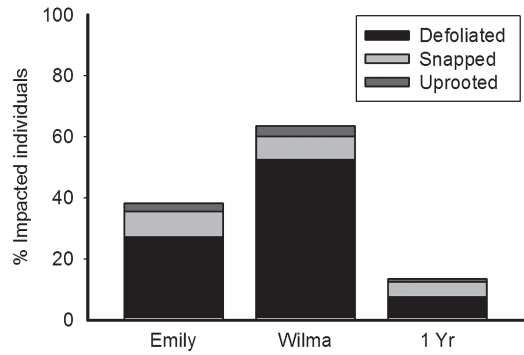

Fig. 2. Percentages of impact type across surveys.

months later, more than 60% of the stems showed some kind of damage. Despite the intensity and duration of the second disturbance, the extra impacts caused by Wilma were primarily through defoliation: ~25% more trees were defoliated beyond those affected by Emily, which was only 2% more than expected if the impacts of the two hurricanes were strictly additive (Table 1, Fig. 2). The proportion of snapped and uprooted stems did not increase beyond those killed after Emily, which is lower than the expected under a model of additive impacts (Table 1). The forest recovered quickly and after a year only 13% of stems showed some kind of impact: 7% were defoliated, 5% were snapped, and 1% uprooted, but the total number of stems reduced considerably presumably due to mortality; from 1382 in the first survey to 868 in the last one (Table 2, Fig. 2).

There were strong interactions between tree size categories and type of damage in all surveys (Emily - χ^2 = 20.1, df = 6, P = 0.003; Wilma - χ^2 = 48.7, df = 6, P < 0.001; 1-yr after - χ^2 = 26.2, df = 6, P < 0.001). The standardized deviates showed that for all

Table 1. Expected vs. observed impacted individuals and percentages (in parentheses) after the second disturbance based on the proportional impact of the first one.

	Emily	Expected Wilma	Observed Wilma
Defoliated	375 (27)	648 (50)	676 (52)
Snapped	117 (8)	224 (17)	100 (8)
Uprooted	36 (3)	71 (6)	43 (3)

TABLE 2. Frequencies and percentages (in parentheses) of stem size categories (cm) and type of impact stems showed at each survey. E=Emily; W=Wilma; Yr=1 Year after.

Impact/cm	No impact			Defoliated			Snapped			Uprooted			Total		
	E	W	Yr	E	W	Yr	E	W	Yr	E	W	Yr	E	W	Yr
5-10	627	322	545	250	546	36	67	60	19	24	32	5	968	960	605
	(65)	(34)	(90)	(26)	(57)	(6)	(7)	(6)	(3)	(2)	(3)	(1)			
11-25	206	139	185	106	119	25	42	32	21	10	8	3	364	298	234
	(57)	(47)	(79)	(29)	(40)	(11)	(11)	(11)	(9)	(3)	(3)	(1)			
>25	21	9	21	19	11	4	8	8	4	2	3	0	50	31	29
	(42)	(29)	(72)	(38)	(35)	(14)	(16)	(26)	(14)	(4)	(10)	(0)			
Total	854	470	751	375	676	65	117	100	44	36	43	8	1382	1289	868
	(62)	(36)	(87)	(27)	(52)	(7)	(8)	(8)	(5)	(3)	(3)	(1)			

surveys, small stems were less likely to be snapped than intermediate and larger stems. In addition, after Wilma, small stems were more likely to be defoliated, and larger stems were more likely to be uprooted (Table 2).

The number of species differed by forest stand age and hurricane but not by the interaction of these two (Fig. 1C). Similarly, after Hurricane Emily and Wilma the total number of species was similar (81 and 80 respectively), but a year later only 70 species were present. In general, IVs for most species remained similar across surveys, but there were notable shifts in the ranking of some species in the three surveys (Table 3). In all cases, *Bursera simaruba* had the highest IV. Among the species that greatly reduced their IV from one survey to the next were *Cochlospermum vitifolium, Hampea trilobata, Spondias mombin,* and *Thevetia gaumeri* (Table 3). On the other hand, there were also

TABLE 3. Importance values and ranks (in parentheses) for the 15 most common species for each survey. Species are in descending IV rank for Emily.

SPECIES	FAMILY	Emily	Wilma	1 Yr
Bursera simaruba	Burseraceae	23.3 (1)	35.9 (1)	35.5 (1)
Piscidia piscipula	Fabaceae	14.0 (2)	12.8 (4)	15.0 (4)
Lysiloma latisiliquum	Fabaceae	12.5 (3)	22.9 (2)	24.7 (3)
Hampea trilobata	Malvaceae	11.4 (4)	9.0 (8)	4.3 (21)
Diospyros cuneata	Ebanaceae	8.3 (5)	11.8 (5)	9.4 (8)
Spondias mombin	Anacardiaceae	7.7 (6)	2.6 (33)	2.8 (32)
Vitex gaumeri	Verbenaceae	7.2 (7)	9.9 (6)	12.2 (5)
Swartzia cubensis	Fabaceae	7.1 (8)	4.2 (22)	5.4 (13)
Brosimum alicastrum	Moraceae	7.1 (9)	18.9 (3)	26.3 (2)
Caesalpinia gaumeri	Fabaceae	7.0 (10)	8.7 (9)	10.3 (6)
Luehea speciosa	Tiliaceae	6.6 (11)	2.9 (31)	2.4 (35)
Cochlospermum vitifolium	Bixaceae	6.4 (12)	6.2 (14)	4.5 (19)
Metopium brownei	Anacardiaceae	5.6 (13)	9.2 (7)	9.6 (7)
Lonchocarpus rugosus	Fabaceae	5.6 (14)	1.0 (52)	1.7 (43)
Pouteria campechiana	Sapotaceae	5.4 (15)	1.9 (40)	2.9 (31)
Gymnopodium floribondum	Polygonaceae	5.3 (16)	6.7 (12)	5.2 (15)
Thouinia paucidentata	Sapindaceae	5.3 (17)	7.2 (10)	6.7 (12)
Neea sp.	Nyctaginaceae	4.9 (21)	4.3 (21)	5.2 (14)
Thevetia gaumeri	Apocynaceae	4.8 (22)	5.4 (15)	2.7 (33)
Lonchocarpus sp.	Fabaceae	4.3 (29)	6.3 (13)	7.0 (10)
Eugenia yucatanensis	Myrtaceae	4.3 (30)	6.8 (11)	4.3 (20)
Manilkara zapota	Sapotaceae	3.6 (33)	4.5 (19)	8.5 (9)
Malmea depressa	Annonaceae	3.4 (35)	5.0 (16)	6.9 (11)

species such as *Malmea depressa, Brosimum alicastrum* and *Manilkara zapota* that tripled or double respectively, in IV after each hurricane (Table 3).

Discussion

The literature on vegetation impacts from short-term subsequent hurricanes is scarce and this study contributes to it. As expected, the highest proportion of affected individuals was after the second disturbance. Ideally, it would be necessary to have pre-hurricane data to make conclusions about the recovery of forests; however, it is possible to infer forest structure and composition from the first sampling. The first hurricane had an important effect on forest structure, but the addition of a second disturbance significantly increased the rate of damaged trees (respectively, 38 and 64% of sampled individuals suffered some type of impact). In the present study, defoliation was the most common impact across all surveys, and uprooting the least common, which coincide with previous studies including in the Yucatan (Brokaw and Walker 1991, Whigham et al. 1991, Vester and Olmsted 2000, Dickinson et al. 2001, Franklin et al. 2004, Curran et al. 2008a, Metcalfe et al. 2008). Although defoliation may be the least strong damage compared to snapping or uprooting, it may have indirect long-term effects for community composition (Lugo 2008), and changes in phenological patterns may affect future recruitment since it is a factor influencing the heterogeneity of the landscape and may redirect succession.

The significant reduction of number of stem, species, and basal area a year after the hurricanes suggests that effects at the community level are more likely to be noticed some time after the event. This has been also suggested for other Caribbean forests (Bellingham et al. 1995); for example in seasonally dry forest on Guadeloupe where forest structure had yet to returned to pre-hurricane conditions after nine years of hurricane disturbance (Imbert and Portecop 2008), or in Jamaican forests where after 16 years, forests became even more dissimilar to the pre-hurricane state (Tanner and Bellingham 2006). In fact, although hurri-

canes have been suggested as one of the most important causes of sudden tree mortality (Lugo and Scatena 1996), it has been suggested that sites impacted by hurricanes should be followed up to a decade to infer real catastrophic damage by mortality (Everham and Brokaw 1996). In this study, hurricane surveys were carried out just few weeks after the disturbances. If trees suffered mechanical damage this was noted immediately, but it was probably not enough time to detect overall mortality of individuals. The great reduction of stems from the first to the last survey, however, could suggest that while less than 10% of individuals died from the first to the second hurricane, an extra 30% a year after the surveys.

Results from damage by tree diameter categories supports the idea that larger classes were more likely to suffer the strongest impacts (those that presumably would kill them such as uprooting or snapping), which has also been noticed in other studies (Brokaw and Walker 1991, Zimmerman et al. 1994, Vester and Olmsted 2000, Franklin et al. 2004, Metcalfe et al. 2008; but see Curran et al. 2008a). One possible reason for this difference could be that smaller trees have their crown less exposed to the strongest winds. This pattern was observed after a cyclone in Sri Lanka where more exposed individual suffered the greater impacts (Dittus 1985), and could also explain the increased defoliation in small stems during Wilma, since presumably larger stems damaged after Emily, would not have provided protection to remaining vegetation.

After the second hurricane trees recover rapidly, as evidenced by the increased in the frequency and percentage of undamaged individuals from Wilma to the next survey. This quick recovery was likely due to the fast flushing of leaves, a characteristic noted in previous studies as an important recovery method (Brokaw and Walker 1991, Yih et al. 1991, Vester and Olmsted 2000), and to the ability of some species to re-sprout (Bellingham et al. 1994); for these species, snapping may not be fatal. In fact, re-sprouting may be higher in stems that have suffered defoliation caused by strong winds (Van Bloem et al. 2006) and has been suggested as a compensatory mechanism

of weak-wooded trees (Putz et al. 1983, Bellingham et al. 1994, Whigham et al. 2003, Curran et al. 2008b). In fact, the overall percentage of snapped and uprooted individuals remained equal from the first to the second survey and actually decreased for the final survey. These results coincide with previous results after two hurricanes (~ 22 months apart) in Samoa where percentage of uprooted individuals did not increased after the second disturbance (Elmqvist et al. 1994). Two important characteristic could possibly explain the generally low uprooting this study: one the high investment in root systems individuals have in seasonal forests to survive drought periods (Holbrook et al. 1995, Kennard 2002, Allen et al. 2003), and two the presence of limestone soil which has been suggested as an important factor that can improve root anchorage (Dickinson et al. 2001, Franklin et al. 2004).

The low rate of uprooting (the impact that could potentially kill individuals) across surveys and high percentage of tree recovery by the final survey, would suggest that the addition of a strong disturbance (Wilma) does not affect species composition. Changes in IVs, however, showed that whereas the most abundant species after Emily were always present, their numbers dropped considerably across surveys. Variations in these values are due to the decrease of particular species, rather than to the recruitment of others (i.e, 1-yr is not enough to detect a significant recruitment from most species into the adult stage). Results showed these disturbances caused differential damage and mortality among species; the most susceptible species decreased in relative abundance, while the most resistant species increased in relative abundance. A very interesting aspect of our results was that some mature-forest species resisted the disturbances better than others, and in fact, their IVs increased across surveys. Examples of this were *Brosimum alicastrum* and *Mailkara zapota*, which are typically considered mature forest species in the region, and had been reported as having high mortality after Hurricane Gilbert in a site approximately 50 km away from the present study site (Whigham et al. 1991). This

trend had also been noted in Puerto Rican rain forests where mature forest species affected by a hurricane had lower mortality and stem damage than pioneer trees (Zimmerman et al. 1994), but significantly greater crown damage (Canham et al. 2010). Another interesting case was *Bursera simaruba*, an abundant species in the Yucatan that has shown high resilience to these disturbances (Vester and Olmsted 2000) and not only remained as the most important species, but also greatly increased its IV. In general, species that were impacted by both events were fast-growers, such as *Cochlospermum vitifolium* or *Hampea trilobata* which suffered high levels of damage due to their likely low wood density; though this trait may also facilitate their rapid recovery (Curran et al. 2008b).

While hurricanes are important disturbances in the forests of the Yucatan Peninsula, these forests have also been under human influence for centuries. Results obtained in this study cannot be dissociated from the land-use history of the region. Although vegetation recovery in the area is influenced by the high re-sprouting and trees left aside when preparing agricultural plots, most of the large trees were found in the >50 yr forest sites and the high density of small stems was likely result of high sampling in young successional forest. Other studies have found greater canopy openness (due to greater damages in trees) in old-growth forest compared to sites of selective logging (Grove et al. 2000) or younger successional stages (Lomascolo and Aide 2001). Interestingly, younger forests decreased in the number of stem and species from the first to the second disturbance, while effects on older forest were more evident a year after the events.

Results from this study concur with other comparative studies (Whigham et al. 1991, Sánchez-Sánchez and Islebe 1999), suggesting that dry forests, particularly in the Yucatan Peninsula, show a high degree of recovery and re-sprouting from subsequent hurricanes, which is likely due to their long history of exposure to such disturbances. Although single hurricanes can cause close to 100% defoliation (Whigham et al. 1991, Sánchez-Sánchez and Islebe 1999), results

from this study suggest a second hurricane within a few months of the first one can cause additional defoliation on forest.

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