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Article

Tree damage, growth and phenology after a hurricane in a tropical dry forest in Veracruz Árboles dañados, crecimiento y fenología después de un huracán en una selva seca en Veracruz

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Abstract

As a major disturbance, hurricanes affect growth and phenology of trees. Tree diameters were annually measured for three years, and the phenology of 16 tree species monthly recorded in a seasonally dry tropical forest in Veracruz, Mexico, when on September 2010, Hurricane Karl struck the region. One month later, tree damage was recorded and phenological observations resumed for 12 more months, and diameter measurement for two more years. Tree damage due to the hurricane was high: 10 % were uprooted, 7 % broken and 2 % bent. All trees uprooted died, but some broken or bent trunk trees resprouted (15 % of tagged trees died). Overall, mean diameter growth of trees that survive the hurricane (0.79 cm yr^{-1}) was greater than pre-hurricane growth rate (0.68 cm yr^{-1}). For all the studied species together, leaf fall, leafing, and flowering phenology did not differ between pre- and post-hurricane whereas fruiting was lower for the post-hurricane year. At species level, most species displayed differences in reproductive phenology between pre-hurricane and post-hurricane years. Most species did not flower, lower flowering and fruiting (*Calyptanthes schiedeana*), or did not fruit (*Luehea candida*, *Maclura tinctoria*, *Tabebuia chrysantha*) the year following the hurricane. In conclusion, due to hurricane damage, tree mortality was high but many trees recovered from damage, and that the hurricane negatively influenced intensity in reproductive phenology, and in turn may alter forest structure, shift species composition, and affect the trophic relationships and functioning of the whole forest community.

Key words: Uprooted trees, flowering, fruiting, Hurricane Karl, tree mortality, sprouting.

Resumen

Los huracanes son disturbios importantes que afectan el crecimiento y la fenología de los árboles. Durante tres años se registró el crecimiento anual y la fenología mensual de 16 especies arbóreas en una selva seca en Veracruz. En septiembre del 2010, el huracán Karl azotó la región, y un mes después se registró el daño en árboles y se reanudaron las observaciones fenológicas. El daño en árboles fue elevado: 10 % desenraizados, 7 % quebrados, y 2 % doblados. Todos los árboles desenraizados murieron, pero algunos quebrados o doblados rebrotaron (15 % de los árboles etiquetados murieron). El crecimiento diamétrico promedio de árboles sobrevivientes (0.79 cm año^{-1}) fue mayor que el crecimiento pre-huracán (0.68 cm año^{-1}). Para todas las especies juntas, la caída de hojas y producción de hojas y flores no fueron estadísticamente diferentes entre pre- y post-huracán, pero la fructificación fue menor en el año post-huracán. A nivel de especie hubo diferencias en fenología reproductiva entre años. En el año siguiente al huracán, la mayoría no produjeron flores, disminuyeron floración y fructificación (*Calyptanthes schiedeana*) o no fructificaron (*Luehea candida*, *Maclura tinctoria*, *Tabebuia chrysantha*). Se concluye que debido al daño por el huracán, la mortalidad en árboles fue alta pero muchos árboles se recuperaron; el huracán influyó negativamente en la intensidad de la fenología reproductiva, lo que a su vez puede alterar la estructura de la vegetación, cambiar la composición de especies y afectar las relaciones tróficas y el funcionamiento de toda la comunidad forestal.

Palabras clave: Árboles desenraizados, floración, fructificación, huracán Karl, mortalidad de árboles, rebrotes.

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Introduction

For many seasonally dry tropical forests (SDTF) in the Neotropics, hurricanes are important disturbance events. It has been documented how hurricanes affect forest structure, environmental conditions, and biotic interactions (Whigham *et al.*, 1991; Zimmerman *et al.*, 1994; Koptur *et al.*, 2002; Van Bloem *et al.*, 2003; Angulo-Sandoval *et al.*, 2004; Bonilla-Moheno, 2012; Jimenez-Rodríguez *et al.*, 2018; Stan and Sánchez-Azofeifa, 2019). Several authors have reported that tree growth rates of surviving trees increase following hurricanes (Whigham *et al.*, 1991; Tanner and Bellingham, 2006; Tanner *et al.*, 2014). This boost in plant growth likely occurs due to the extra and a seasonal precipitation that comes with hurricanes, which is especially important in water-limited ecosystems (Parker *et al.*, 2018). In Jamaica, Tanner and Bellingham (2006) described that stem diameter growth rates increased during the Hurricane Gilbert decade, and that double growth rate occurred in the post-Gilbert decade. In *Yucatán*, Whigham *et al.* (1991) also recorded that, for the first year after Gilbert, relative diameter growth for most species was greater than average growth for pre-hurricane years. Hurricanes also change phenology in the forests and it has been reported that their damages increase leaf production, and decrease both herbivory (Koptur *et al.*, 2002; Angulo-Sandoval *et al.*, 2004) and food availability for vertebrates (Wunderle, 1999; Schaffner *et al.*, 2012; Renton *et al.*, 2018). Furthermore, fruiting patterns lag behind, diminish or even are completely suppressed after hurricanes in Puerto Rico (Wunderle, 1999) and in Mexico, in the *Yucatán* Peninsula (Schaffner *et al.*, 2012) and in the *Chamela Cuixmala* Biosphere Reserve in the coast of *Jalisco* (Renton *et al.*, 2018).

Tropical regions where hurricane landfalls used to be rare are experiencing an increment in extreme events. Global warming will likely decrease the frequency of all storms but the frequency of the most intense storms (hurricanes) is projected to increase in the Gulf of Mexico (Biasutti *et al.*, 2012). On September 14th-18th 2010, the SDTF of central *Veracruz*, Mexico was struck by Hurricane Karl (category 3)

causing major disasters throughout the region (Stewart, 2011). However, before Karl, the last recorded event was in 1932, when an unnamed hurricane, category 3 struck this region (Gómez, 2006).

The aims of this study were to examine the impact of Hurricane Karl on tree mortality and the way trees died, and compare diameter growth, and the phenological patterns observed in this SDTF before and after the hurricane event.

Materials and Methods

The study was conducted in a SDTF in central *Veracruz*, Mexico (19°16' N, 96°29' W, elevation: 97-117 m asl, area: 21 ha). Mean total annual precipitation is 932 mm and most rain falls between June and October; mean annual temperature is 25 °C. Dominant tree species are *Bursera cinerea* Engl., *B. fagaroides* (Kunth) Engl., *B. simaruba* (L.) Sarg., *Calyptrocalyx schiedeana* O. Berg, *Heliocarpus donnellsmithii* Rose, *Stemmadenia pubescens* Benth. and *Tabebuia chrysantha* (Jacq.) G. Nicholson (Williams-Linera and Lorea, 2009). Monthly precipitation and temperatures were obtained from the nearest meteorological station located at 7 km from the study site.

Along a < 1 m-width trail crossing the forest fragment, at 30 m from the forest edge, one tree near the trail was randomly chosen, and then the nearest neighbor of each consecutive tree was tagged until 165 trees belonging to 16 common species with 3-19 individuals per species were tagged (Table 1).

The status of each phenological phase was observed in each tree from the ground with the aid of binoculars (Swift, SeaHawk 7x50 No. 753). The percentage of the crown that was leafless or producing leaves, flowers or fruits was visually estimated, considering the following categories: 0 (0 %) 1 (1-25 %), 2 (26-50 %), 3 (51-75 %) and 4 (76-100 %). These values were averaged over individuals for each species by month and were used as a phenological index of intensity. Monthly phenological observations were made from October 2007 until September 2010 just a few days before Hurricane Karl struck (Williams-Linera and Álvarez-Aquino, 2016). In early

November 2010, the monthly phenological observations were resumed for one more year (until October 2011).

Table 1. Tree species and families in the tropical dry forest in *Veracruz*, Mexico.

Species	Acr	WD	No.	UR	BE	BR	Dead
Bignoniaceae							
<i>Tabebuia chrysantha</i> (Jacq.) G. Nicholson	Tab	0.33	19	0	0	1**	0
Bixaceae							
<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	Coc	0.48	14	0	2	0	2
Burseraceae							
<i>Bursera cinerea</i> Engl.	Buc	0.35	11	0	1	0	1
<i>Bursera simaruba</i> (L.) Sarg.	Bus	0.78	9	0	1	0	1
Convolvulaceae							
<i>Ipomoea wolcottiana</i> Rose	Ipo	0.22	11	1	2	1**	3
Fabaceae							
<i>Gliricidia sepium</i> (Jacq.) Kunth ex Walp.	Gli	0.58	3	1	0	0	1
<i>Leucaena lanceolata</i> S. Watson	Leu	0.53	7	0	0	0	0
<i>Senna atomaria</i> (L.) H. S. Irwin & Barneby	Sen	0.28	4	2	0	0	2
Hernandiaceae							
<i>Gyrocarpus jatrophiifolius</i> Domin	Gyr	0.16	7	0	0	0	0
Malvaceae							
<i>Ceiba aesculifolia</i> (Kunth) Britt. & Baker f.	Cei	0.44	10	0	0	0	0
<i>Guazuma ulmifolia</i> Lam.	Gua	0.94	10	0	0	0	0
<i>Heliocarpus donnellsmithii</i> Rose	Hel	0.91	16	7	3*	1**	8
<i>Luehea candida</i> (DC.) Mart.	Lue	0.76	15	1	1**	0	1
Meliaceae							
<i>Trichilia trifolia</i> L.	Tri	0.80	8	0	0	0	0
Moraceae							
<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	Mac	1.04	10	4	1**	1	5
Myrtaceae							
<i>Calypttranthes schiedeana</i> O. Berg	Cal	0.80	11	1	0	0	1
Total			165	17	11	4	
Dead within a year				17	7	1	25

*Two survived; **One survived; Acr = Acronym; WD = Wood density (g cm^{-3} ;

Chave *et al.*, 2006); No. = Number of tagged trees before Hurricane Karl, and number of trees that were uprooted (UR), bent (BE), broken (BR), and dead within the year following the hurricane.

Tree diameter was measured using a DBH tape (Forestry Suppliers, Inc.) in June-July 2007 to 2009, and then just after Hurricane Karl in 2010, June 2011 and October 2013. A month later, in October, all the trees that had been tagged for the phenological observations were surveyed, and classified as undamaged, uprooted, and bent or broken trunk.

Data analysis

The response variables (climate, diameter increment and phenology) were tested with analysis of deviance (ANODE) to determine if they differed among years. ANODE is similar to analysis of variance, but the test does not assume normal distribution. Differences in diameter increment before and after the hurricane, and differences in annual precipitation and maximum and minimum temperatures among years were analyzed using generalized linear models (GLM) with normal distribution and log link function. Differences among years for each phenophase intensity for all species together were tested using GLM; phenophase proportions were fitted assuming binomial distribution for the response variable and the logit link function. The model used for diameter increment included species, year (pre- and post-hurricane) and the interaction term. The model for climate and phenology included year only. When significant differences were detected orthogonal planned contrasts were used to determine whether the post-hurricane year was different from each of the three previous years. Data were analyzed using JMP v10.0.0 (SAS Institute, 2012).



Results

Climate

For the hurricane year, rainfall was higher (1 440 mm) than the average (932 mm) for the region (Figure 1). However, precipitation ($X^2 = 1.84$, $P = 0.60$), maximum temperature ($X^2 = 1.81$, $P = 0.61$) and minimum temperature ($X^2 = 0.23$, $P = 0.97$) for the hurricane year (2010) did not differ statistically from the climate variables recorded during pre-hurricane (2007-2009) and the post-hurricane (2011) year (Figure 1).

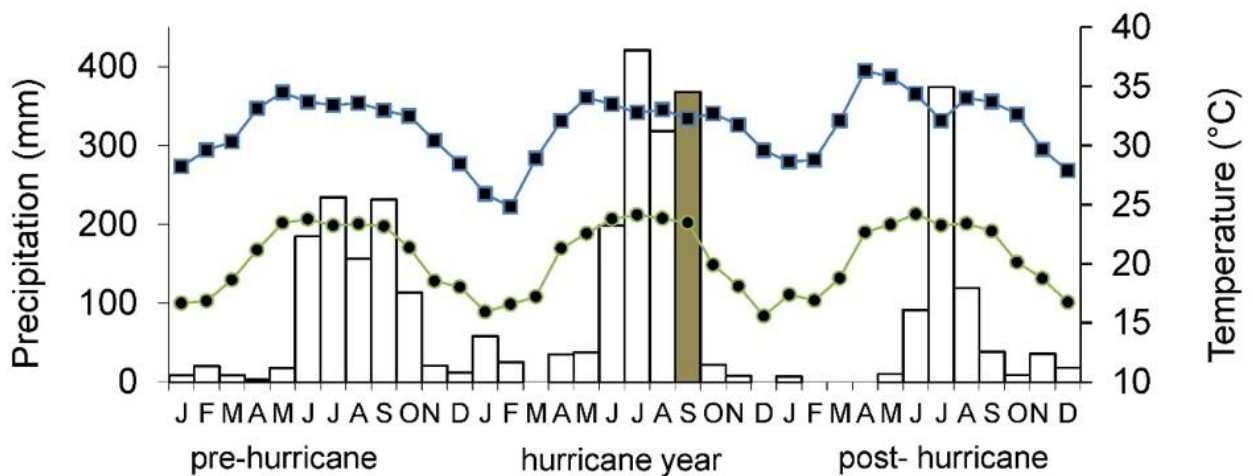


Figure 1. Monthly precipitation (bars) and maximum (blue line and squares) and minimum (green line and circles) temperature for pre-hurricane (average of 3 years), hurricane year (2010) and post hurricane year. Data from the nearest meteorological station located at 7 km from the study site.



Tree damage and mortality

Hurricane Karl defoliated all the trees, but damage varied among species. Thirty-two tagged individuals were damaged, however, some of these died while others resprouted after three to twelve months following the hurricane (Table 1). More trees died uprooted (17), than from being bent (7) or broken (1). Five species with bent and broken trunks sprouted, whereas all uprooted trees died (Table 1). The highest mortality occurred in tree species with relatively high wood density (*Heliocarpus donnellsmithii*, *Maclura tinctoria* (L.) D. Don ex Steud.) (Table 1), but other species with low wood density also showed intermediate number of damaged trees (e.g, *Ipomea wolcottiana* Rose, *Senna atomaria* (L.) H.S. Irwin & Barneby). Other late successional species with high wood density that were partially damaged survived to the hurricane impact, such as *Leucaena lanceolata* S. Watson and *Trichilia trifolia* L., or *Tabebuia chrysantha* that had one individual with a broken trunk that sprouted (Table 1).

Diameter growth

Overall, there were significant differences between pre- (0.68 ± 0.09 cm yr⁻¹) and post-hurricane (0.79 ± 0.10 cm yr⁻¹) growth rate ($X^2 = 5.12$, $P = 0.024$) and among species ($X^2 = 66.36$, $P < 0.0001$, Figure 2). However, the interaction between species and hurricane effect was not significant ($X^2 = 17.16$, $P = 0.25$). The studied species diameter growth rates before and after the hurricane varied from 0.33 to 1.63 cm yr⁻¹ and 0.30 to 1.89 cm yr⁻¹, respectively (Figure 2). The species with the highest diametric growth was *Luehea candida* (DC.) Mart., followed by *Guazuma ulmifolia* Lam. and *Senna atomaria*.

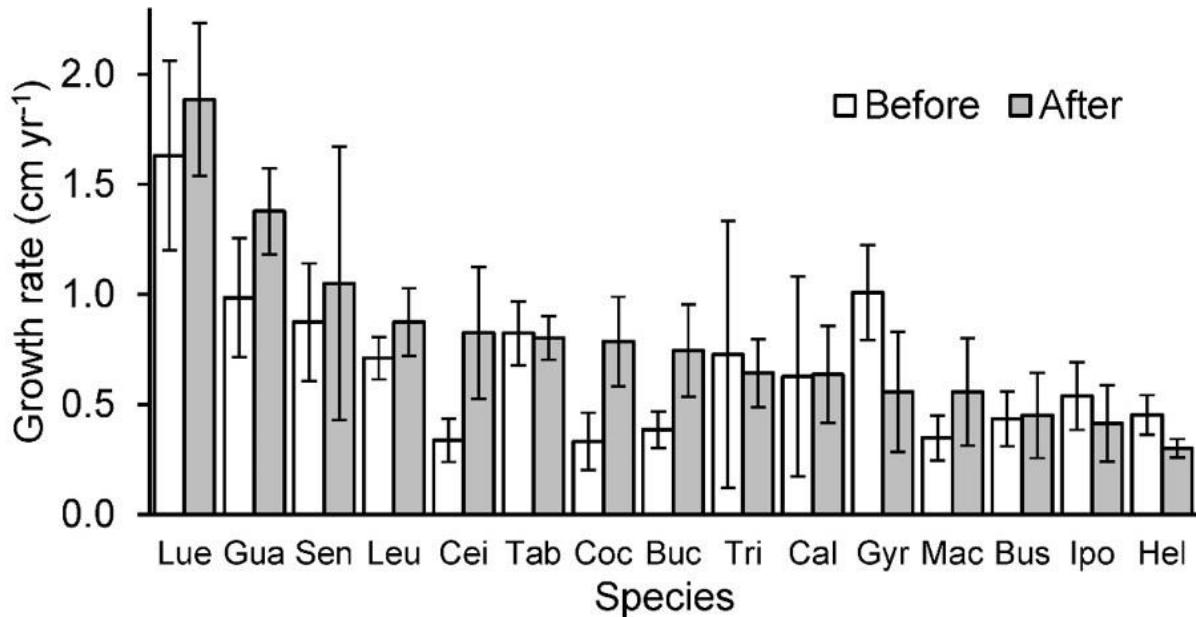


Figure 2. Mean diametric growth rate recorded annually during three years before and two years after hurricane Karl. Species acronyms are in Table 1.

Phenology

At the community level, leafless status, leafing, and flowering display cyclic annual patterns (Figure 3a, b, c). Phenology within the 3 pre-hurricane years is presented to give an idea of the variation without hurricane disturbance (Figure 3), so it can be observed if the post-hurricane data fall within the year-to-year variation. The forest was leafless during the dry season, and all trees were with leaves in July-September (Figure 3a, b). Leaf fall, leafing and flowering were statistically similar between the pre- and post-hurricane years, but the peak of flowering shifted after the hurricane to April-May (Figure 3c). Fruit production was much lower during the post-hurricane year (Figure 3d).

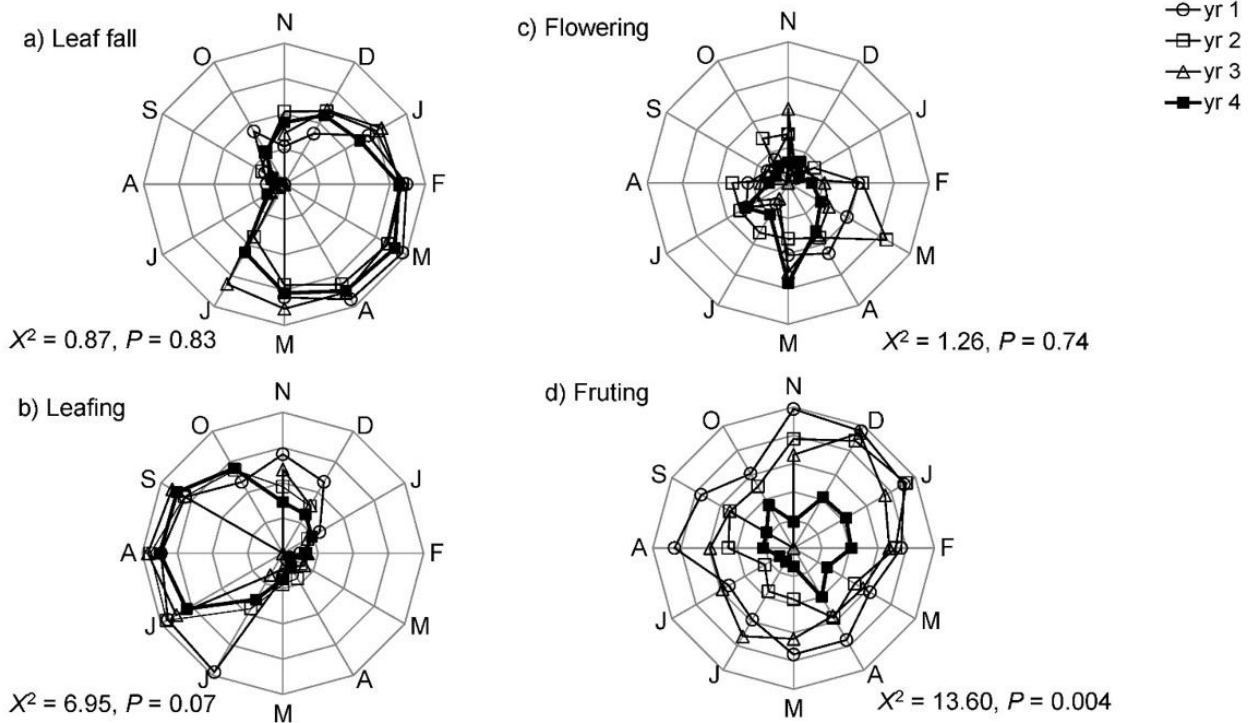


Figure 3. Phenological activity recorded at community level during three years before the hurricane (yr1 = Nov 2007- Oct 2008; yr 2= Nov 2008-Oct 2009, yr 3= Nov 2009- Sep 2010); year 4 starts in November 2010 just after the hurricane stroke central Veracruz, Mexico. a) Leaf fall, b) leaf production, c) flowering, and d) fruiting.

At the species level, the vegetative phenological patterns remained similar before and after the hurricane. In contrast, intensity of the reproductive phenophases was affected by the hurricane (figures 3 and 4). For most species (12), flowering intensity decreased in the post-hurricane year, and three species did not flower at all (*Calyptanthes schiedeana*, *Luehea candida* and *Tabebuia chrysantha*), while for two others (*Bursera simaruba* and *Guazuma ulmifolia*) (Figure 4a) flowering intensity was higher after the hurricane. Fruiting during the year following the hurricane was null in four species, and lower for most of the species, or the fruiting peak was shifted

(*Leucaena lanceolata* and *Senna atomaria*); only one species (*Gliricidia sepium* (Jacq.) Kunth ex Walp.) showed higher fruiting after the hurricane (Figure 4b).

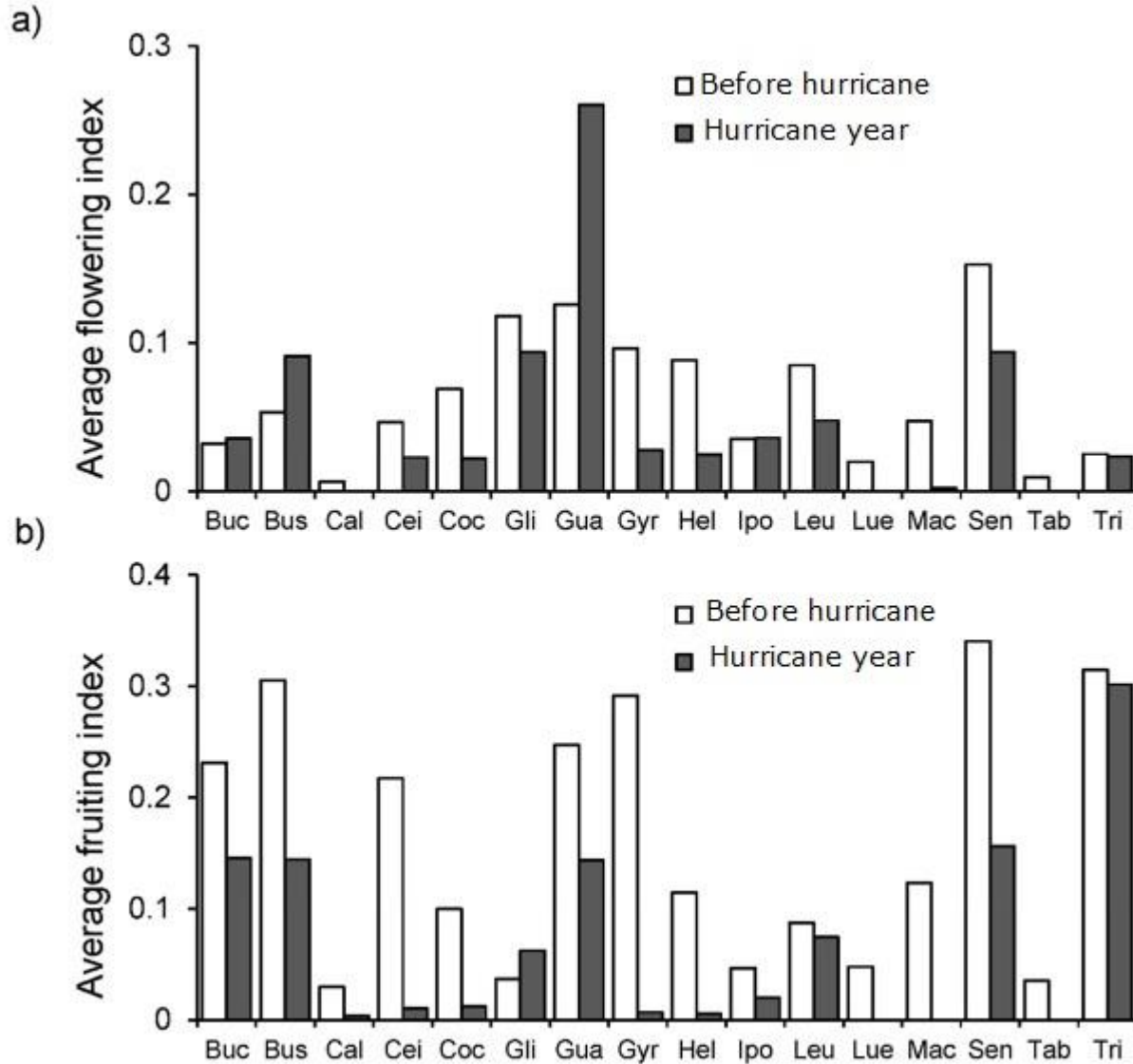


Figure 4. Monthly average flowering (a) and fruiting (b) phenology recorded in a tropical dry forest for three years pre- and a year post-hurricane Karl. Species acronyms are in Table 1.



Discussion

Fifteen percent of the trees (25 out of the 165 in %) died within the post-hurricane year; a value at the upper level of the 7-14 % range of values reported after hurricanes at stand level for Neotropical forests (e.g., Brokaw and Walker, 1991; Zimmermann *et al.*, 1994; Bonilla-Moheno, 2012; Stan and Sánchez-Azofeifa, 2019). In the studied forest, most trees died uprooted, followed by bent and broken trunks, but tree species mortality was not related to wood density. In other dry forests where hurricanes are frequent, few trees died uprooted but broken trees experienced the highest mortality (Whigham *et al.*, 1991; Zimmerman *et al.*, 1994; Bonilla-Moheno, 2012). Some authors have reported that early successional species are more susceptible to stem breakage than late successional species (Zimmermann *et al.*, 1994; Ross *et al.*, 2001). In general, tree damage occurs in taller trees as they could be more vulnerable to mechanical damage (Jiménez-Rodríguez *et al.*, 2018), thus larger trees suffered more uprooting and snapping than small ones (Bonilla-Moheno, 2012; García and Siliceo-Cantero, 2019).

The high mortality and degree of uprooting might be related to the fact that Karl was the first hurricane that arrived to this region in more than 60 years (Gómez, 2006). It is possible that this first hurricane in a long time struck the most vulnerable or exposed trees. Bonilla-Moheno (2012) has reported that the impacts of subsequent hurricanes were minor compared to the first one, suggesting that dry forests may have a high degree of recovery depending on the level of subsequent hurricanes.

Tree diameter growth after hurricane Karl was higher than the average growth recorded before the hurricane. Several authors have reported increased diameter growth following hurricanes (Tanner and Bellingham, 2006; Tanner *et al.*, 2014). However, in this study, the high precipitation during the two months preceding the hurricane could also had a positive effect on tree diameter growth. Apparently, change in growth rate depends on the tree species; significant differences among tree species were found. Tanner *et al.* (2014) also indicated a variation among species, and that the increase was much greater in some light-demanding species (e.g., *Alchornea latifolia* Sw.) than in others. Whigham *et al.* (1991) stated

that high relative growth rates may reflect the greater availability of nutrients, as large amounts of P, K, Ca, Mg, and Mn were deposited on the forest floor by the storm.

The phenology of the forest was studied for three years before the hurricane (Williams-Linera and Álvarez-Aquino, 2016). Leafing patterns remained similar before and after the hurricane, but at community level, the defoliation caused by Hurricane Karl affected the seasonality timing of leaf fall and the community remained leafless for a month. Flowering was particularly affected because, before the hurricane, significant peaks were apparent at all levels, but after the hurricane there was not seasonality. Shifts in flowering peaks have been documented in Southern Florida where Hurricane Andrew delayed flowering in a tropical shrub for two months, although heavy defoliation might also be related to high flowering (Pascarella, 1998).

Fruit phenology was most affected the year following the hurricane. In *Puerto Rico*, Wunderle (1999) reported the effect of Hurricane *Hugo* on fruiting phenology as the lowest fruit production and asynchrony, with trees taking four months for the number of fruiting species to reach a level equivalent to the normal yearly low. Fruit production in the *Yucatán Peninsula*, was four times higher during the dry season before than after hurricanes (Schaffner *et al.*, 2012). In the *Chamela-Cuixmala* Biosphere Reserve flowers and fruits were reduced during the first-year after hurricanes *Jova* and *Patricia*, forest recovered phenological cycles by the second-year post-Hurricane (Renton *et al.*, 2018).

The impact of hurricanes on phenology may have a strong effect on trophic relationships. Some studies have reported that the forest compensates for damage by increasing leaf production and there are lower levels of herbivory, likely because the disturbance eliminates herbivore insect populations allowing plants to recover (Koptur *et al.*, 2002; Angulo-Sandoval *et al.*, 2004). Also, the shortage of fruits affects the behavior of other herbivores, such as spider monkeys (Schaffner *et al.*, 2012) and other threatened species like parrots (Wunderle, 1999; Renton *et al.*, 2018). Long-term effects of hurricanes can cause shifts in species composition (Tanner *et al.*, 2014); in the studied forest composition can be particularly affected since two species that did not flower or fruited are *Calyptanthes schiedeana* and *Tabebuia chrysantha*, the first is endemic to Veracruz; and the second is threatened, according to the Mexican red list (NOM-059-SEMARNAT) (Semarnat, 2010).

Conclusions

Due to hurricane damage, tree mortality was high, but many trees recovered from damage, likely because this forest has not been greatly affected by recent hurricanes and due to the high resilience of this forest type. More research is needed to better understand how the predicted increase in intense hurricanes could influence forest structure and phenology in SDTF in the region. The results suggest that although pre- and post-hurricane vegetative phenological patterns were similar, hurricane Karl clearly had a negative effect on the intensity of the reproductive phenology, which in turn, may shift species composition and have an impact on the trophic relationships and functioning of the forest community.

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Conflict of interest

The authors declare no conflict of interest.

Contribution by author

Guadalupe Williams Linera: research design, data analysis and writing the manuscript; Claudia Álvarez Aquino and Javier Tolome: collection of the field data and reviewing the manuscript.



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