Chapter 10

Impacts of Hurricanes on the Forests of Quintana Roo, Yucatán Peninsula, Mexico

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INTRODUCTION

Hurricanes are common throughout the Caribbean (Alaka 1976; Vega and Binkley 1993), and they often cause extensive disturbance to forests (Walker et al. 1991; Yih et al. 1991; Smith et al. 1994; Zimmerman et al. 1994; Bellingham, Tanner, and Healley 1995; Bellingham et al. 1996; Foster, Fluet, and Bosse 1999; Stoddart 1963). Within the Caribbean, the Maya zone (southeastern Mexico, Belize, and portions of Guatemala) is an area that has been impacted by many hurricanes (López 1983; Konrad 1996). In fact, the most severe hurricane ever recorded in the Caribbean (Hurricane Gilbert) occurred in the Maya zone (Whigham et al. 1991).

Several recent studies have focused on the impacts of hurricanes in the Caribbean as well as the short-term and long-term recovery of forests

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following hurricane damage. A special issue of *Biotropica* (Walker et al. 1991) was devoted to impacts of hurricanes in the Caribbean, and several papers in a second special issue (Walker et al. 1996) dealt with recovery of forests from hurricane damage (e.g., Scatena et al. 1996; Vandermeer et al. 1996). Other investigators have also focused on the recovery of Caribbean and Central American forests from hurricane damage (Dallmeier, Comiskey, and Scatena 1998; Granzow de la Cerda et al. 1997; Reilly 1998; Rogers and Reilly 1998; Weaver 1998a; Whigham and Lynch 1998; Vandermeer, Granzow de la Cerda, and Boucher 1997; Vandermeer, Brenner, and Granzow de la Cerda 1998).

A general consensus seems to be that the species composition of hurricane-damaged forests changes little (Bellingham, Tanner, and Healley 1995; Walker, Zimmerman et al. 1996b; Harrington et al. 1997; Frangi and Lugo 1998; Reilly 1998; Whigham and Lynch 1998), even though severely damaged areas are often invaded by herbs, vines, *Carica papaya*, and *Cecropia* sp. (Dallmeier, Comiskey, and Scatena 1998). Vandermeer et al. (1996) suggested that hurricanes maintain species diversity by decreasing competition in a density-independent manner. Ecological processes (e.g., rates of tree growth and annual litter production) also appear to return to pre-disturbance levels within relatively few years following hurricane damage (see Scatena et al. 1996; Vandermeer, Granzow de la Cerda, and Boucher 1997; Reilly 1998; Whigham and Lynch 1998).

In this chapter, short-term and long-term studies of forests damaged by Hurricane Gilbert (1988) and Hurricane Roxanne (1995) will be summarized. Both hurricanes impacted forests on the Caribbean coast of the northern Yucatán Peninsula, an area that is part of the Maya zone. One objectives is to demonstrate that the primary long-term impact of Hurricane Gilbert was a decrease in the basal area of live trees, which will take decades to reach pre-hurricane levels because of slow rates of tree growth. Additionally, data from a long-term study of marked trees in permanent plots are used to demonstrate that the recovery of ecological processes was relatively fast. Long-term mortality appeared to be independent of the degree of hurricane damage, and changes in species composition were minimal. We discuss similarities and possible differences between hurricane damage to forests in Quintana Roo, Mexico, compared to other forests in the Caribbean region and in Central America will be discussed. Finally, we suggest that the direct impacts of hurricanes are potentially less important than the effects of subsequent fires—a phenomenon that may be especially important in dry tropical forests.

HURRICANES ON THE YUCÁTAN PENINSULA

The Yucatán Peninsula is impacted primarily by hurricanes that originate in the Atlantic Ocean, the Caribbean, and the southern Gulf of Mexico. Hurricanes that have their origin in the Pacific Ocean impact portions of southeastern Mexico, but rarely cause significant damage in the Yucatán Peninsula (hereafter called "the peninsula"). Between 1871 and 1999, 52 hurricanes struck the peninsula; most impacted the northern portion of the peninsula and the Caribbean coast (Konrad 1996; Pereira and Vester 2000). Most hurricanes that had their origin in the Caribbean have traversed the peninsula and continued into the Gulf of Mexico.

Figure 10.1 we show the trajectories of the two hurricanes that impacted forested areas studied: Hurricane Gilbert in September 1988, and Hurricane Roxanne in October 1995. Table 10.1 we compare the characteristics of Gilbert and Roxanne with the 18 hurricanes that hit the peninsula since 1886 within a 100-kilometer (km) radius of Puerto Morelos (Jordan-Dahlgren and Rodríguez-Martinez in press), a coastal village near our primary study site. All category H3-H5 hurricanes have hit the peninsula after 1950.

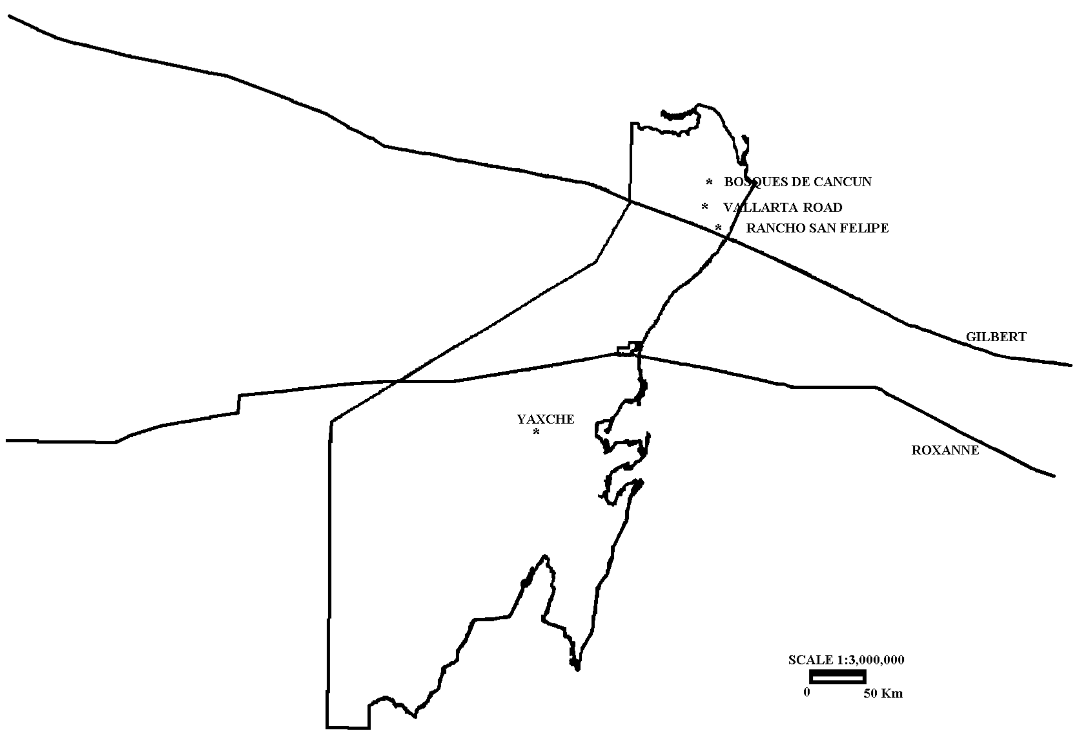

FIGURE 10.1. Outline map of Quintana Roo, Mexico, showing the tracks of Hurricane Gilbert (1988) and Hurricane Roxanne (1995). The location of the study sites described in the paper are also shown (modified from Vester & Olmsted 2000).

TABLE 1. Summary data for Hurricane Gilbert, Hurricane Roxanne, and 18 other hurricanes that impacted the northern part of the Yucatán Peninsula since 1886

Variable	Gilbert	Roxanne	Others
Category	H5	H3	(6) H1, (10) H2, (2) H3
Maximum wind speed (km hr^{-1})	300–340	186	156
Lowest eye pressure (mb)	892	958	970
Diameter of eye (km)	20	27	No data

Source: From Jordan-Dahlgren and Rodriguez-Martinez in press.

Gilbert was the only hurricane to reach category 5, and it impacted the northern part of the peninsula. Hurricane Gilbert had, by far, the highest recorded wind speeds and the lowest barometric pressure in the eye of the hurricane (Table 10.1). Wind speeds associated with Hurricane Roxanne were also higher than average, and the barometric pressure in the eye of the hurricane was slightly lower than the average values for the other 18 hurricanes.

METHODS

Study sites damaged by Hurricane Gilbert

The impacts of Hurricane Gilbert have been monitored at Rancho San Felipe, located on the Caribbean coast approximately 10 km south of Puerto Morelos (Quintana Roo). This study site is located about 2 km from the coast; based on annual precipitation, the forest would be classified as medium-statured semievergreen (Miranda 1958), or dry or very dry in the Holdridge system (Whigham et al. 1990). Twelve plots, each 40 m by 40 m, were established in 1984, and all stems ≥ 10 cm dbh (i.e., diameter at breast height) at a height of 1.5 meters (m) were marked and identified. All marked trees have been measured annually since 1984 during the months of January and February. We used the yearly census data to determine annual mortality. Mortality reported for any one year (e.g., 1989) represents trees dying during the preceding 12 months (e.g., between the 1988 and 1989 census). In-growth in 1993 and 2000 was determined by marking and identifying all new stems ≥ 10 cm dbh. In addition to tree growth and mortality, annual litter production was measured between 1984 and 1991 (Whigham et al. 1991; Whigham and Lynch 1998).

The immediate impacts of Hurricane Gilbert (September 1988) were evaluated within two weeks by scoring the amount of damage incurred by each marked tree in the 12 plots. We assigned each tree to one of six damage classes: (1) crown completely removed but the trunk not snapped; (2) only larger branches remaining; (3) most large branches remaining; (4) only twigs and small branches remaining; (5) trunk snapped; and (6) tree uprooted. At the time of the first census, we could not locate a few tagged trees; eventually, all trees were found and damage was categorized during subsequent sampling periods. In February 1989, the amount of coarse woody debris in the plots was measured for comparison between pre-hurricane and post-hurricane conditions (Harmon et al. 1994).

Beginning in March 1989, extensive fires (135,000 hectares [ha.] in northern Quintana Roo) occurred throughout much of the area impacted by Hurricane Gilbert. Some fires were contained locally, and all remaining fires were extinguished by rain in August 1989. At Rancho San Felipe, the site was protect the site except for small areas of two plots that were burned when fire jumped the fire lane. In 1990, we sampled all live trees $\geq$ 10 cm dbh in four plots, each 40 m x 40 m, in a burned area within 500 m of our study plots.

In January 1990, six additional plots (each with a total area of 1,600 m^2) were established in other areas impacted by Hurricane Gilbert. One set of three plots was about 8 km west of Rancho San Felipe along the Vallarta Road. Two of these plots were in a burned area, and the third was a control plot in an adjacent unburned area. The other three plots were established at a site known as Bosques de Cancun, about 25 km inland from the Cancun Airport and 40 km northwest from Rancho San Felipe. Two plots at Bosques de Cancun were established in an area where some trees survived the fire, and the third plot was in an unburned area. In each plot, all living and dead trees $\geq$ 10 cm dbh were identified, and dbh and height were measured.

Study site damaged by Hurricane Roxanne

In October 1995, the semievergreen forest near Felipe Carrillo Puerto was hit by strong winds just outside the eye of Hurricane Roxanne. Felipe Carrillo Puerto is located in Quintana Roo, about 200 km south of Puerto Morelos. Five years after the hurricane, an area—locally known as Yaxche—that was about 40 km from the coast (see Figure 10.1). The forest at Yaxche was younger than the forest at Rancho San Felipe, based on the abundance or absence of some species as well as the lower basal area of trees $\geq$ 10 cm dbh (approximately 20 m^2 $ha.^{-1}$). *Bursera simaruba*, a common species of early successional sites was very abundant at Yaxche, while a species typical of older forests (*Brosimum alicastrum*) was absent. In addition, there was only one stem $\geq$ 10 cm dbh of *Manilkara zapota*, a species that is also common in older forests. Four species (*B. simaruba*, *Coccoloba spicata*, *Gymnanthes lucida*, *Thouinia paucidentata*) were among the ten most abundant species at the Rancho San Felipe and Yaxche sites, and a Sorenson Index of Similarity (45 percent) indicates that the two forests had many similar characteristics. The Sorenson Index would have been greater had more plots been samples at Yaxche. In March 2000, five years after Hurricane Roxanne occurred, 25 plots, each 10 m by 10 m, were sampled and identified and the diameter of all trees that had a dbh $\geq$ 10 cm. were measured. The amount of damage that had been done to each tree was recorded using the categories applied at Rancho San Felipe.

RESULTS

Hurricane Gilbert

Hurricane impact

The immediate impacts of Hurricane Gilbert at Rancho San Felipe on birds (Lynch 1991) and plants have been previously documented (Whigham et al. 1991; Harmon et al. 1994) and are summarized here. First, it is important to note that the Rancho San Felipe site is located within 2 km of the coast and was impacted by the full force of the most intense storm ever recorded in the region (see Table 10.1). The impacts of Gilbert on the forest at Rancho San Felipe should thus be considered to be at the upper end of the range of disturbances associated with hurricanes (Whigham, Dickinson, and Brokaw 1999).

The forest canopy was completely defoliated, and all marked trees were damaged. The majority of trees sustained structural damage, and approximately 30 percent of the trees were uprooted, had snapped trunks, or had most of the major branches removed (Whigham et al. 1991). Seventeen months after the hurricane, 155 (10.7 percent) of the marked trees had died, including 15 (9.3 percent) that were killed by fire that burned parts of two plots. Trees not killed by fire (90.7 percent) occurred in all damage categories, but most (54.6 percent) were in only the three damage categories listed previously (Whigham et al. 1991). Mortality also occurred in all sizes of trees (data not shown). Mortality resulted in a decrease of the basal area of trees in the 12 plots from 26.9 $\pm$ 0.9 (1 standard error, SE) m^2 $ha.^{-1}$ in 1988 to 24.1 $\pm$ 0.7 m^2 $ha.^{-1}$ in 1989 and 22.4 $\pm$ 0.8 m^2 $ha.^{-1}$ in 1990 (Figure 10.2).

Two species were eliminated from the population of marked trees by the hurricane, and both had only one marked individual in the plots. The trunk of the single 23.5 cm dbh *Senna racemosa* snapped in the hurricane, and a 12 cm dbh *Amyris elemiflora* was uprooted.

Defoliation of the forest canopy resulted in the transfer of more than 800 g m^{-2} of litterfall, mostly green leaves, to the forest floor—an amount approximately twice the annual litterfall measured in the four prehurricane years (Whigham et al. 1991). Because most of the litterfall consisted of green leaves, the concentrations of nutrients in litterfall and the total amounts of nutrients transferred to the forest floor were higher than any of the previous pre-hurricane years (Whigham et al. 1991). The biomass of coarse wood transferred to the ground was also massive (> 4000 g m^{-2}) and represented almost a doubling of the coarse woody debris that was present prior to the hurricane (Harmon et al. 1994).

Initial recovery

Some aspects of recovery have been reported (Whigham and Lynch 1998), and other data are presented in this paper. Compared to other tropical

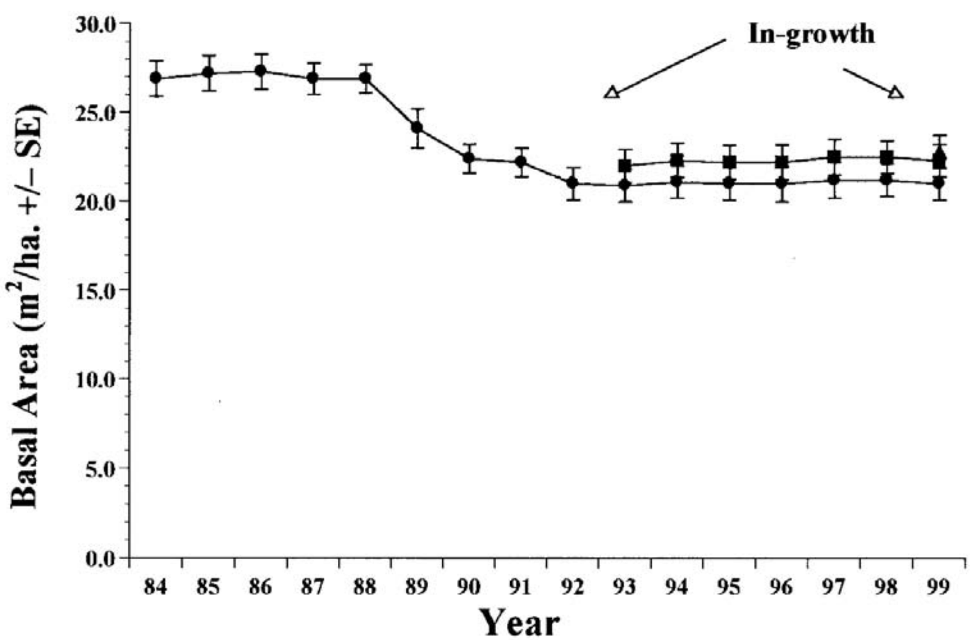

FIGURE 10.2. Total basal area ($m^2ha.^{-1}$) for 12 plots at Rancho San Felipe. Values are means ± 1 standard error (SE). Data are separated into the original group of trees that were marked in 1984 and in-growth measured in 1993 and 2000.

forests, mortality rates of canopy trees in Yucatán forests are very low (Whigham et al. 1990; Dickinson, Whigham, and Hermann 2000). Thirty-nine (2.6 percent) of the marked trees died in the four years prior to Hurricane Gilbert, and mortality appeared to be inversely related to the total annual precipitation (Whigham et al. 1990). Mortality associated with Hurricane Gilbert was greater, especially within the first five years of the disturbance, and the mortality pattern was consistent among the damage classes (Figure 10.3). Mortality was low in 1989 for all damage classes except trees that were uprooted. Mortality of uprooted trees decreased after 1989 and reached prehurricane rates by 1993. Mortality rates were also higher in the "crowns removed" and "trunk snapped" damage categories and—similar to other damage categories—varied from year to year, with the highest rates measured in 1990 and 1993.

Mortality resulted in the loss of seven more species of marked trees between 1989 and 1992. All but one species (*Daphnopsis americana*) had a single marked stem. Two species were eliminated in 1989 (*Coccoloba swartzii*, *Bunchosia swartziana*), one species in 1991 (*Platymiscium yucatanensis*),

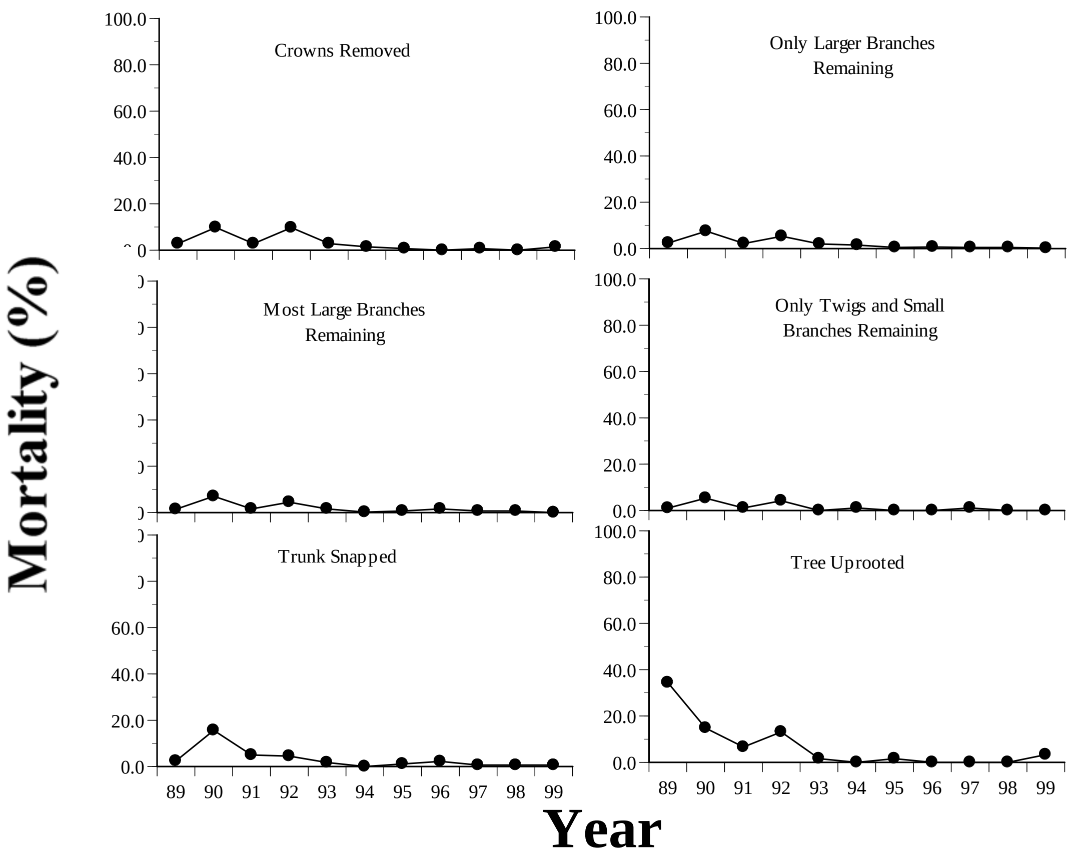

FIGURE 10.3. Mortality of trees in six damage categories described in the Methods section. Mortality for each damage category was calculated as follows: Number of trees that died each year = Number of trees in the damage category in 1998 x 100.

and three species in 1992 (*Protium copal*, *Coccoloba* sp., *Casearia nitida*). One individual of *D. americana* died in 1989, and the second in 1991. Stems of the seven species ranged in size from 10 to 24.4 cm, and they were in damage classes 2, 3, 5, and 6. An unexpected result was the elimination from the permanent plots of 98 percent of all tree-sized individuals of *Brosimum alicastrum*, a widespread and common species (Whigham and Lynch 1998).

Based on prehurricane data, a significant negative relationship was found between annual litterfall and annual precipitation, demonstrating that more leaves were shed during years with lower precipitation (Whigham et al. 1990). Following the hurricane, annual litterfall was less than pre-hurricane levels, but we continued to find a significant negative relationship between litterfall and annual precipitation (Whigham and Lynch 1998). This result suggests that there was little impact of the hurricane on annual litterfall, even though there must have been less total leaf biomass in the forest canopy during the first few posthurricane years. Total phosphorus in the leaf litter reached prehurricane levels within two years of the hurricane because the concentration of phosphorus in leaf litter was higher compared to pre-hurricane years (Whigham and Lynch 1998).

Relative basal area growth one year after the hurricane (1989) was greater than the rates that had been measured in all but two of the five pre-hurricane years (Figure 10.4). Relative growth rates were slightly lower in 1990 and 1991 and increased in 1992 and 1993. The characteristic low rates of tree growth at Rancho San Felipe (Whigham et al. 1990) resulted in no noticeable increase in the basal area of live trees during the first five years following the hurricane, even when in-growth was included in 1993 and 2000 (see Figure 10.2.)

Ten years and beyond

After 1993, our study at Rancho San Felipe was limited to measurements of the marked trees. Tree mortality returned to pre-hurricane levels by 1994, and they have not changed measurably since then (see Figure 10.3). Because of low tree growth rates, the total basal area of live trees also has changed little since 1994 (see Figure 10.2).

Three additional species were eliminated after 1993 as tree-sized individuals. Similar to previous years, species that were eliminated (*Bauhinia divericata*, *Hampea trilobata*, *Lonchocarpus rugosus*) had very few marked individuals (n = 2–3) and represented a range of sizes (10.4–21.9 cm) and damage classes (1–6). One of the marked trees belonging to *B. divericata* died in 1990, and the last remaining tree from this species died in 1993. Three individuals of *H. trilobata* died between 1988 and 1993, while three individuals of *L. rugosus* died between 1994 and 1996.

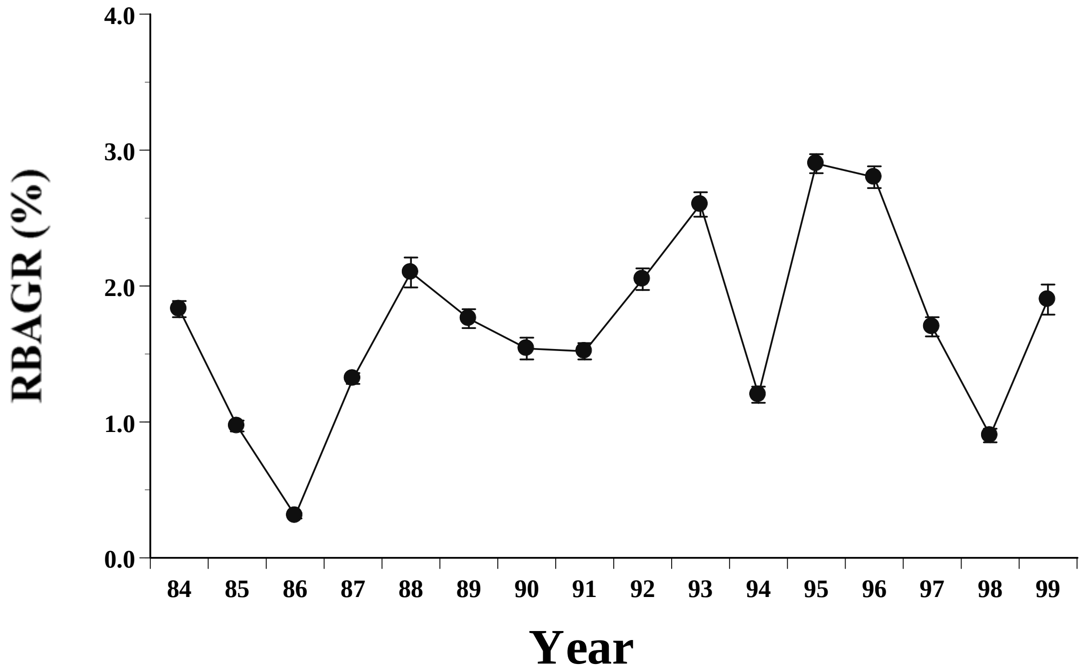

FIGURE 10.4. Relative basal area growth (RBAGR) for all trees in the 12 plots at Rancho San Felipe. Values are means ± 1 standard error (SE). RBAGR/ $(BA_{t+1} - BA_t) = BA_t \times 100$

Seven new species were identified and marked as part of the in-growth measurements in 1993, and another genus (*Agonandra* sp.) was added in 2000. Species added in 1993 were *Ardisia escallonioides*, *Cecropia peltata*, *Jatropha gaumeri*, *Malpighia glabra*, *Neomillspaughia emarginata*, *Pithecellobium dulce*, and *Pouteria campechiana*. All new species were present as single individuals except for *C. peltata*, which was almost completely restricted to portions of two plots that had burned. *Cecropia* and a few other short-lived species that did not reach tree size (e.g., *Carica papaya*, *Cnidoscolus aconitifolius*) also invaded non-burned plots, but the number of individuals was small and they all were short-lived.

Fire impacts

The fires that followed Hurricane Gilbert were extensive and resulted in widespread damage to the forests. The damage ranged from the death of all trees in some areas to no fire-related death in areas where fires had been suppressed. At Rancho San Felipe, attempted were made to keep fire from entering the plots by cutting fire lanes around the site and by actively suppressing the fire with water. Fire jumped the fire lane at two locations, resulting in the death of 15 trees in two of the study plots. There were between 15 and 57.5 trees ha.$^{-1}$ (average = 42) in the four plots that we sampled in a burned area within 500 m of the Rancho San Felipe plots. By comparison, the density of trees $ha.^{-1}$ in the 12 plots at Rancho San Felipe was 768 $\pm$ 23 (SE). The basal area of live trees in the four burned plots was 2.6 $\pm$ 0.9 m^2 $ha.^{-1}$, approximately 10% of the values measured in the 12 unburned plots (see Figure 10.2).

Most of the burned plots had a dense growth of bracken fern (*Pteridium aquilinum*) as well as a few short-lived shrub species that are common in abandoned milpas and other disturbed habitats (e.g., *Solanum erianthum*, *Pluchea odorata*). A few seedlings of short-lived successional trees (e.g., *Cecropia peltata*, *Carica papaya*) were also present. Most of the fire damage sustained by the trees was restricted to the base of the stems and the roots. Most of the soil in the plots had completely burned.

In January 1990, we measured two forested areas further inland from Rancho San Felipe (Olmsted et al. 1991). At the Vallarta Road site, the unburned control plot had a basal area of 27.3 m^2 $ha.^{-1}$, a value similar to the basal area of the Rancho San Felipe plots (see previous discussion and Figure 10.2). In contrast, the basal area of live trees in two burned plots was much less, 2.4 and 6.7 m^2 $ha.^{-1}$. The total basal area of dead standing trees in the burned plots was 24.0 m^2 $ha.^{-1}$. The impact of the fire was less severe at the Bosques de Cancun site (Olmsted et al. 1991). Total basal area of live and dead trees in the unburned plot was 24.8 and 2.9 m^2 $ha.^{-1}$, respectively. In the two burned plots, the basal area of live trees was 11.2 and 8.3 m^2 $ha.^{-1}$; the basal area of dead trees was 14.2 and 10.7 m^2 $ha.^{-1}$.

Hurricane Roxanne

Hurricane impact

Hurricane Roxanne had lower maximum wind speed and higher barometric pressure than Hurricane Gilbert (Table 10.1). The impacts of Roxanne would, therefore, be expected to be less damaging than those associated with Gilbert. The Yaxche site impacted by Roxanne was sampled five years after the hurricane (Vester and Olmsted 2000). There were 294 live and dead trees in the 25 plots, and hurricane-related damage could still be recognized on 132 (44.9 percent) trees.

Most of the trees that could not be placed into damage categories (162; 55.1 percent) were in the lowest damage category used at Rancho San Felipe (i.e., “only twigs and small branches remaining”). By comparison, trees in the lowest damage category at Rancho San Felipe only accounted for 7.3 percent of the damaged trees (Whigham et al. 1991). For the 132 damaged trees at Yaxche that could be categorized, three damage categories (“tree uprooted [n = 19; 14 percent],” “trunk snapped” [n = 21; 16 percent], “crown removed” [n = 33; 25%]) accounted for 55 percent of the trees. The same damage categories at Rancho San Felipe accounted for 27.6 percent of the damaged trees (Whigham et al. 1991). Two intermediate damage categories (“only larger branches remaining,” “most large branches remaining”) accounted for

45 percent of the trees at Yaxche compared to approximately 70 percent at Rancho San Felipe (Whigham et al. 1991).

At Yaxche, 18.2 percent of the trees in the "crown removed" category, 52 percent of the trees in the "trunk snapped" category, and 58 percent of the trees in the "tree uprooted" category were dead after five years. A smaller percentage of trees (9.7 percent) were in two intermediate damage categories ("only larger branches remaining," "most large branches remaining"). In comparison with Rancho San Felipe, a higher percentage of trees at Yaxche were in the lowest damage category, but a higher percentage of trees died in the highest damage categories.

DISCUSSION

Permanent plots at Rancho San Felipe have been monitored for four prehurricane and 11 posthurricane years and three other areas have been sampled in northern Quintana Roo that were damaged by hurricanes. Sánchez Sánchez and Islebe (1999) also sampled an area near Rancho San Felipe that was damaged by Hurricane Gilbert. The immediate impacts of Hurricane Gilbert were clearly detectable, but the long-term impacts have been minimal.

There have been few short-term or long-term studies of hurricane impacts on the peninsula, but comparisons can be made among the few studies that have been conducted. It also seems appropriate to compare results from studies on the peninsula with those conducted elsewhere in the Maya zone, along with studies in a range of forest types that have been conducted elsewhere in the region (e.g., Caribbean islands, Florida, and Nicaragua). An obvious similarity between forests on the peninsula and elsewhere is that there are many similar short-term impacts. There has been an increase in litter, coarse woody debris, and increased tree mortality everywhere that hurricane impacts have been measured (e.g., Whigham et al. 1991; Harmon et al. 1994; Scatena et al. 1996; Rogers and Reilly 1998; Weaver 1998b).

Similar to other forests, hurricane damage to forests in northern Quintana Roo (Olmsted et al. 1991; Snook 1993; Sánchez and Islebe 1999; Vester and Olmsted 2000) and elsewhere in the Maya zone (Stoddart 1963) is spatially variable. The forest at Rancho San Felipe suffered severe damage. However, given the intensity of Hurricane Gilbert, it would be expected that the damage would have been even greater. Even as far inland as Yaxche (see Figure 10.1), Roxanne, a less intense hurricane than Gilbert, caused sufficient damage to be noted five years after its occurrence. In fact, the percentage of trees in the highest damage classes (i.e., crown removed, trunk snapped, and tree uprooted) was higher in Yaxche than at Rancho San Felipe. The percentage of trees that died during the first five years after the hurricane in the three highest damage classes was also higher at Yaxche. Elsewhere in the Caribbean, portions of forests in Jamaica (Bellingham 1991), Nicaragua (Vandermeer et al. 1996), and St. John Island (Weaver 1998a) were more severely damaged by hurricanes that were less intense than Hurricane Gilbert. Several factors could possibly contribute to lower levels of hurricane damage to forests on the northern Yucatán Peninsula. First, hurricanes are very common on the peninsula (Konrad 1996). Forests that experience repeated hurricane disturbance might be expected to have lower average canopy heights; the lower the canopy, the less severe the impacts of a hurricane. Second, the peninsula is a very flat landscape, and forests would not experience the extreme levels of damage associated with topographically complex areas (e.g., Caribbean islands and mountainous areas further south in Central America). Forests appear to be most heavily damaged when they are located on elevated ridge crests, topographically exposed areas, and in valleys where hurricane winds are funneled (Bellingham 1991; Reilly 1998).

Other factors may also be partially responsible for lower-than-expected levels of hurricane damage following Hurricane Gilbert. Soils in the northern part of the peninsula are typically very shallow. Soil depth in the permanent plots at Rancho San Felipe averaged less than 20 cm (Whigham and Cabrera 1991), and most soil occurred in depressions between exposed limestone rocks. Therefore, trees have very shallow root systems that are interwoven and anchored to the fissured limestone. The percentage of trees that were uprooted at the Rancho San Felipe site (4.5 percent) was low compared to the percentage of trees with snapped trunks (12.4 percent). Dallmeier, Comiskey, and Scatena (1998), as well as Everham and Brokaw (1996), also found that uprooting in other forests was less likely to occur when there was root grafting and anchorage to rocks in areas with shallow soils. Low rates of tree uprooting have also been reported for hurricane and fire impacted forests in southern Quintana Roo (Dickinson, Hermann, and Whigham in press).

Within the Maya zone—the Caribbean and Nicaragua—hurricanes appear to have little long-term impact on species composition, unless the forests are burned following the hurricane. Short-term and intermediate-term changes in species composition can, however, be significant in topographically complex landscapes where some portions of the forest are heavily impacted (Lugo et al. 1983; Vandermeer et al. 1996; Dallmeier, Comiskey, and Scatena 1998; Reilly 1998; Rogers and Reilly 1998). At Rancho San Felipe, for example, mortality resulted in the loss of a few species of marked trees, but individuals of other species have reached tree size since the hurricane, resulting in no significant change in species composition. All eliminated species had few individuals, which is a pattern similar to the one found by Reilly (1998) on St. John Island following Hurricane Hugo.

Few, if any, future changes are anticipated in species composition at the Rancho San Felipe site because mortality rates have returned to prehurricane levels (see Figure 10.3). In addition, there was almost no recruitment of new species as seedlings (Whigham personal observation). One interesting impact of Hurricane Gilbert was the complete death of all tree-sized individuals of *Brosimum alicastrum* (Whigham and Lynch 1998). This response was completely unanticipated because trees survived the impact of the hurricane at the Vallarta Road and Bosques de Cancun sites, and *B. alicastrum* is one of the most widespread species in the region (White and Darwin 1995). Perhaps trees at Rancho San Felipe were physiologically impacted by the hurricane (perhaps by desiccation), which, when compared to other hurricanes, had less associated precipitation. The trees died slowly (Whigham and Lynch 1998), and they all regularly produced unsuccessful sprouts between the time of Hurricane Gilbert and their death. The death of the trees that were originally tagged will not, however, eliminate the species from the plots as seedlings and saplings were common, and one individual reached tree-size by the time of the 2000 in-growth census.

With the possible exception of mangroves and palms, a common feature of many hurricane-damaged forests is the ability of surviving trees to produce sprouts on stems and roots (Bellingham 1991; Walker 1991; Scatena et al. 1996). All of the surviving trees in our plots produced stem sprouts, but few species produced root sprouts. Root sprouting may be more common in forests with higher rainfall and a shorter dry season. Reilly (1998), for example, made no mention of root sprouts following Hurricane Hugo in the St. John Island, an area with annual precipitation that is similar to this study's site. Root sprouts were found, in contrast, in wetter hurricane-damaged forests in Nicaragua (Vandermeer, Granzow, and Boucher 1997) and Puerto Rico (Walker 1991). Root sprouts were also common in taller forests in southern Quintana Roo that are impacted by logging activities (Dickinson, Whigham, and Hermann 2000). The amount of sprouting may also be positively related to the amount of damage. *Gymnanthes lucida*, for example, did not sprout at Rancho San Felipe, but sprouts were abundant in the Vallarta Road plots that had been damaged by both Hurricane Gilbert and subsequent fires (Olmsted personal observation).

Following Hurricane Gilbert, herbaceous vines (e.g., *Cionocissus excisus*, *Momordica charantia*) and the short-lived tree *Carica papaya* germinated in the study plots. Overall, however, the plots were invaded by few early successional species—a pattern that differed from many other hurricane-damaged forests that have been studied in the region (Walker 1991; Vandermeer, Granzow, and Boucher 1997; Dallmeier, Comiskey, and Scatena 1998). The presence of a dense layer of leaf litter and branches probably inhibited seed germination (Guzmán-Grajales and Walker 1991), but we found that almost no long-lived tree species emerged from soils that were collected from the plots and watered regularly in a common garden (data not shown).

Why there were so few tree species in the buried seed bank at Rancho San Felipe; to our knowledge, there have not been any studies of soil seed banks in forests that are similar to those that we have studied (Garwood 1989). Based on Garwood's review, however, several factors might have contributed to low levels of viable tree seeds in the soil. First, Garwood suggested that seed production is low in forests with low production. This factor does not seem to be important at Rancho San Felipe, even though tree growth rates are very low compared to other tropical forests (Whigham et al. 1990). We have noted seed production of many of the tree species at Rancho San Felipe, and seedlings were often abundant for such common species as *Manilkara zapota*, *Myrcianthes fragrans* (Whigham and Cabrera 1991), *Drypetes lateriflora*, and *Brosimum alicastrum*. Many of the species, however, may not produce seeds that remain viable in the soil for long periods of time. Soils also seem to contain more tree species in forests where treefall gaps are commonly produced and where the average gap size is large (Garwood 1989). Both factors are not important at Rancho San Felipe. The rates of treefall creation in Quintana Roo forests appear to be among the lowest reported for tropical forests, and the average gap size is small (Dickinson, Whigham, and Hermann 2000). The dynamics of soil seed banks in forests on the peninsula clearly needs further study as the forests studied by Rico-Gray and Garcia-Franco (1992) in Yucatán state, which mostly had seeds of early successional species, were different from the forest that occur in much of Quintana Roo.

Rancho San Felipe, as well as other nearby sites not impacted by fire, shared a common type of structural change with all other hurricane-damaged forests in the region. The basal area of live trees decreased from approximately 26 to 21 m^2 $ha.^{-1}$ at Rancho San Felipe; similar values (27.3 and 24.8 m^2 $ha.^{-1}$) were measured at the two other sites that were impacted by Hurricane Gilbert, but had not burned. Unlike most other forests that have been examined, however, the increase in basal area at our site has been minimal. Based on the annual census data and inclusion of in-growth measurements (see Figure 10.2), we have found almost no increase in basal area, and we anticipate that it will take several decades for the forest to return to pre-hurricane levels. The rate of recovery of forest basal area appears to be much lower than the recovery rate that has been reported for other forests where tree growth rates are higher (Dallmeier, Comiskey, and Scatena 1998; Weaver 1998b).

Hurricane Gilbert had no detectable short-term or long-term influence on tree growth. Relative growth rates were higher in the first few post-hurricane years for all trees combined and for some species. Increased growth, however, was a reflection of higher amounts of rainfall during the same period, rather than a hurricane response (Whigham and Lynch 1998). In contrast, changes in growth rates—either positive or negative—have been found in other hurricane-impacted forests in the region. Reilly (1998) found lower post-hurricane growth rates in St. John Island forests following Hurricane Hugo. Vandermeer, Granzow, and Boucher (1997), as well as Vandermeer, Brenner, and Granzow (1998), found higher growth rates following Hurricane Joan in Nicaragua, especially in forests that had been heavily damaged. Scatena, Moya, Estrada, and Chinea (1996) also found evidence for high growth rates of trees and understory plants following Hurricane Hugo in Puerto Rico.

The lack of a clear growth response at the Rancho San Felipe is due to two related factors. First, a positive relationship between precipitation and growth (Whigham et al. 1990). We believe that this pattern is characteristic of dry tropical forests that occur in areas with an extensive and variable dry season. Second, the soils at Rancho San Felipe are very shallow, typically less than 20 cm (Whigham and Cabrera 1991). The combination of shallow soils, which dry very quickly after rain events, and a distinct dry season result in a strong climatic control of tree growth.

Higher annual precipitation in the first few post-hurricane years also resulted in less annual leaf litterfall compared to prehurricane years (Whigham and Lynch 1998). The close relationship between annual leaf litterfall and precipitation in pre-hurricane and post-hurricane years suggests, however, that hurricanes had little impact on annual litter production in post-hurricane years. There was an increase, however, in the concentration of phosphorus in leaf litter after a hurricane (Whigham and Lynch 1998). This result can be interpreted as an increase in rates of nutrient cycling, most likely due to the release of phosphorus from decomposing organic debris generated by hurricanes (Scatena et al. 1996). Scatena, Moya, Estrada, and Chinea (1996) found that leaf litterfall was lower in the first post-hurricane year and returned to pre-hurricane levels by the third year.

The results described to this point are appropriate for forests that do not burn following a hurricane. In general, fire has not been reported to be an important post-hurricane factor in wetter forests (e.g., Vandermeer, Brenner, and Granzow de la Cerda 1998; Weaver 1998b; Foster, Fluet, and Bosse 1999) or drier forests on Caribbean islands (Weaver 1998a). Fire is, however, clearly an important factor in Quintana Roo. Snook (1993, 1998) reviewed the literature on fires and found that fires are caused by natural and anthropogenic activities. The largest recorded fires in the region followed hurricanes in 1942, 1974, and 1988 (Snook 1993). When burned and unburned forest areas in the northern part of the peninsula are compared, data clearly shows that fires have a much greater influence on forest structure and species composition. Fire-damaged areas that were sampled and fire-damaged forests in the southern portion of the peninsula (Snook 1993) had lower basal area of live trees. It also appears that few species are able to survive intense fires, especially in areas where the soils also burn because they are very shallow and have a high content of organic matter.

Postfire vegetation proceeds through successional pathways that differ from those associated with hurricane damage, especially in areas that have been severely burned. Many more trees survive hurricanes than fires; as was found at Rancho San Felipe, there are few changes in species composition in hurricane-damaged forests. The models developed by Vandermeer et el. (1996) appear to apply to hurricane-damaged forests in the Maya zone that do not burn. Successional pathways following fire depend on the intensity of the fire. In areas that are severely burned, shade-intolerant species (e.g., *Bursera simaruba*, *Vitex gaumeri*, *Metopium brownei*) are common (Snook 1993; Olmsted et al. 1991); they are also abundant in areas that were cleared for agriculture, and then abandoned. In areas where fires were less intense, succession is dominated by tree species that can sprout following nonlethal fires (e.g., *Dendropanax arboreus*, *Guettarda combsii*) and understory species that generate better under "light shade." Olmsted et al. (1991) found *B. simaruba*, *D. arboreus*, *G. combsii*, *Gymnanthes lucida*, *V. gaumeri*, and *M. brownei* sprouting from burned saplings in intensely burnt forest in northern Quintana Roo, some of them sprouting roots.

Modern-day forest vegetation in the Yucatán Peninsula appears to be influenced primarily by historic patterns of land clearing (Gómez-Pompa, Flores, and Sosa 1987; White and Darwin 1995; Mizrahi, Ramos-Prado, and Jiménez-Osornio 1997) and by the combined impacts of hurricanes and fire (Snook 1998; Olmsted and Loope 1983). Studies in the northern part of the peninsula demonstrate that there are few long-term direct impacts of hurricanes, except for a decrease in basal area of the forest that will persist for decades. Forests in the northern portion of the peninsula are clearly adapted to a climatic regime that includes frequent disturbance. The forests are quite resistant to hurricane damage, but are also quite resilient when disturbances (e.g., fire) result in major changes in structure. Furthermore, medium-scale to large-scale disturbances caused by hurricanes and fires may play an important role determining the abundance of important species such as Mahogany (*Swietenia macrophylla*) in southern Quintana Roo (Snook 1993; Dickinson and Whigham 1999) and *Manilkara zapota* throughout the peninsula (Olmsted et al. 1991).

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