BIOTROPICA 23(4a): 434–441 1991

The Impact of Hurricane Gilbert on Trees, Litterfall, and Woody Debris in a Dry Tropical Forest in the Northeastern Yucatan Peninsula[1]

Dennis F. Whigham

Smithsonian Environmental Research Center, Box 28, Edgewater, Maryland 21037, U.S.A.

Ingrid Olmsted

A. P. 1209, Cancún, Quintana Roo, México 77500

Edgar Cabrera Cano

Centro de Investigaciones de Quintana Roo, Box 424, Chetumal, Quintana Roo, México 77100

and

Mark E. Harmon

Department of Forest Science, Oregon State University, Peavy Hall 154, Corvallis, Oregon 97331-5705, U.S.A.

ABSTRACT

Hurricane Gilbert struck the northeastern portion of the Yucatan Peninsula in an area where we have been conducting studies of the vegetation and avifauna in a dry tropical forest since 1984. All trees in our study area were completely defoliated and most suffered heavy structural damage. Although few trees were killed outright, many died over the next 17 months, especially those that had been heavily damaged. Tree recovery was rapid as relative diameter growth for most species for the first year after the hurricane were greater than average diameter growth rates for three of the five prehurricane years. Biomass of litterfall (leaves and wood less than 10 cm in diameter) and nutrients generated by the hurricane exceeded the totals produced during any of the five previous years. The hurricane increased the mass and nutrients in coarse woody debris (wood greater than 10 cm in diameter) by approximately 50 percent. Mortality caused by fire was much greater than mortality caused by the hurricane.

RESUMEN

El Huracán Gilberto azotó la parte noreste de la Península de Yucatán en un área donde hemos estudiado la vegetación y avifauna en un bosque seco tropical desde 1984. Todos los árboles en nuestra área de estudio fueron defoliados totalmente y la mayoría sufrió daños estructurales muy severos. Aunque pocos árboles fueron destruídos por el huracán, muchos murieron durante los 17 meses después, especialmente aquellos que sufrieron mayor daño. La recuperación de los árboles fue rápida para la mayoría de las especies, según lo indica el crecimiento relativo del diámetro de la mayoría de las especies durante el primer año después del huracán, que fue mayor que el crecimiento promedio del diámetro para tres de los cinco años antes del huracán. La biomasa de hojarasca (hojas y madera de diámetro menor de 10 cm) y nutrimentos generados por el huracán excedieron los totales producidos durante cualquiera de los cinco años anteriores. El huracán incrementó en aproximadamente 50 por ciento la masa y nutrimentos de residuos grandes de madera (madera mayor de 10 cm de diámetro). La mortalidad causada por incendios fue mayor que la mortalidad causada por el huracán.

HURRICANES CAN HAVE DRAMATIC EFFECTS on the structure of tropical forest (*e.g.*, Crow 1980, Lugo *et al.* 1983, Thompson 1983, Weaver 1986, Boucher 1990, Brokaw & Walker, 1991) and it is important to know not only how different types of forests are affected by hurricanes but how they subsequently recover. Hurricanes are common in the Caribbean and Gulf of Mexico (Gleason 1984, Conner *et al.* 1989). The northeastern Yucatan Peninsula has been hit by 31 tropical depressions between 1871 and 1975 (Jáuregui *et al.* 1980). Hurricane Gilbert, the strongest tropical depression (885 mb) ever measured in the Western Hemisphere, struck our research site in northeastern Quintana Roo, Mexico on 14 September 1988, with winds of approximately 300 km/hr.

The availability of predisturbance information on the vegetation (Whigham *et al.* 1990, Whigham

---

[1] Received 9 January 1991, revision accepted 17 May 1991.

& Cabrera 1991) and avifauna (Lynch 1989, Lynch, in press; Lynch 1991) of this region provides us with an opportunity to characterize hurricane impacts at the level of individual tree and bird species as well as at the community and ecosystem levels. We have four objectives in this paper: to document the impacts of the hurricane on trees; to characterize its impacts on the production of leaf litter and coarse woody debris; to describe initial recovery of the forest; and to describe the additional effects of fires on the hurricane-damaged forest that occurred in the study area during the dry season following the hurricane. Information on the responses of birds to Hurricane Gilbert can be found in Lynch (1991).

Although Lundell (1934) provides useful qualitative descriptions, there have been few quantitative studies of Yucatan Peninsula forests (Olmsted & Durán, in press), that today represent one of the most extensive remaining forested areas in Mexico. The dominant vegetation types are low, medium, and tall forms of semievergreen (selva subperennifolia) and semideciduous (selva subcaducifolia) forests (Miranda 1958, Miranda & Xolocotzli 1963). Forests in most of the peninsula would be classified as tropical dry or very dry in the Holdridge system (Whigham *et al.* 1990).

In 1984 we began work at Rancho San Felipe, approximately 10 km south of the village of Puerto Morelos in the northeastern portion of Quintana Roo, Mexico (for a map showing the study site location see Lynch 1991). Precipitation averages approximately 1100 mm per year, but is annually and seasonally quite variable (Whigham *et al.* 1990). Canopy height is between 15 and 25 m and the ten leading dominant species are *Manilkara zapota* (L.) van Royer, *Talisia olivaeformis* (HBK.) Radlk, *Gymnanthes lucida* Swartz, *Brosimum alicastrum* Swartz, *Drypetes lateriflora* (Swartz) Drug & Urban, *Sapindus saponaria* L., *Coccoloba diversifolia* Jacq., *Beaucarnea pliabilis* (Baker) Rose, *Bursera simaruba* (L.) Sarg., and *Myrcianthes fragrans* (Sw.) McVaugh, but more than 125 tree and shrub species have been identified in the plots that are described in the next section. The shallow and highly organic soils (Whigham *et al.* 1990) are classified as litosol–redzina and they are derived from Miocene and Pliocene materials (Back & Hanshaw 1970, Escalante 1986).

METHODS

Twelve plots (40 × 40 m) were established in February–March 1984, and all trees greater than 10 cm dbh were tagged and identified. Tree diameters have been measured yearly between mid-February and early March. Relative diameter growth rates for each tree were calculated for each year (t) as follows: Relative diameter growth = $((\mathrm{dbh}_{t+1} - \mathrm{dbh}_t)/\mathrm{dbh}_t) \times 100$. Litterfall has been measured at approximately monthly intervals since March 1984 using 60 litter traps (5 randomly positioned 1 × 1 m traps per plot). Samples were divided into leaf and reproductive parts (fruits, seeds, floral parts, etc.) and wet weights were determined in the field. Dry weights were determined on subsamples which were then ground in a meat grinder and stored dry. Litter samples were then returned to the Smithsonian, dried a second time, and ground in a Wiley Mill. Yearly composite samples of the leaf and reproductive categories were made by combining the monthly samples based on weight. Composited samples were analyzed for P, Ca, K, Mg, and Mn using plasma emission spectroscopy (see Whigham & Richardson 1988 for details of analytical procedures). Nutrient concentration and biomass data were combined to estimate annual rates of nutrient deposition for each litter box. Woody material less than 10 cm in diameter were collected in the litter boxes only in 1984.

Posthurricane damage was assessed within one month after Hurricane Gilbert by evaluating the conditions of trees in the 12 plots. All but 29 of the 1486 trees were located at that time. The following damage categories were used: 1 = crown completely removed but the trunk not snapped; 2 = only largest branches remaining; 3 = most large branches remaining; 4 = only twigs and small branches removed; 5 = trunk snapped; 6 = tree uprooted.

Litterfall samples were collected from the 60 litter traps within three months of Gilbert. The samples were divided into leaves, twigs, and 4 classes of wood (<2.5 cm, 2.5–5 cm, 5–10 cm, >10 cm). Processing of materials from the litter boxes was as described above. There was no material in the reproductive category. The amount of coarse woody debris (>10 cm in diameter) on the forest floor in the 12 plots before and after the hurricane was estimated using procedures described by Harmon *et al.* (1986). Subsamples of coarse woody debris (N = 51) were also collected, dried, ground, and analyzed for P, Ca, Mg, Mn, and K. In addition, nitrogen in the posthurricane litterfall and in the coarse woody debris was determined using standard Kjeldahl procedures.

Extensive fires swept through the northeastern Yucatan during the summer dry season (June–Au-

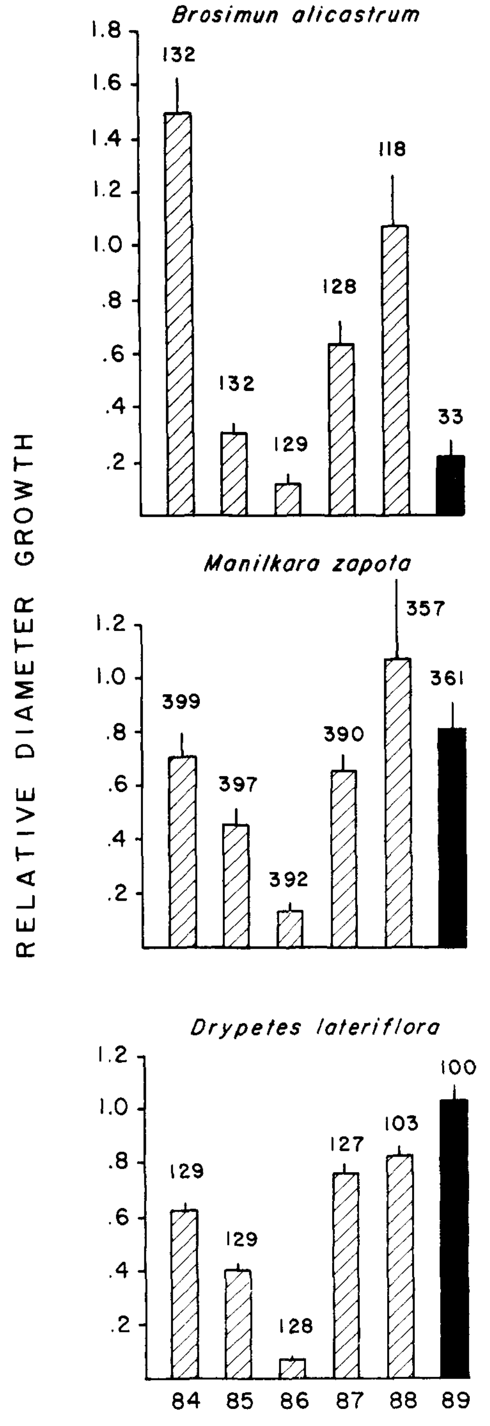

FIGURE 1. Relative annual growth rates for three dominant tree species at Rancho San Felipe. Relative diameter growth for each tree was calculated for each year (t) as follows: Relative diameter growth = $((dbh_{t+1} - dbh_t)/dbh_t) \times 100$. Values for each year are means ± 1 standard error. Sample sizes are shown above each bar.

←
Hatched bars are prehurricane years and the solid bar is the first posthurricane year. Seven months of 1988 were prehurricane and five were posthurricane. We believe that most of the 1988 growth had occurred during the prehurricane months as all trees were defoliated by the hurricane and tree canopies had only started to develop during the five posthurricane months. Years are indicated on the X axis as 1984 = 84, 1985 = 85, etc.

gust 1989) following Hurricane Gilbert. Although Rancho San Felipe was protected by fire lanes and active fire suppression by the owners, fires burned a few small areas, including less than 5 percent of 2 of our 12 long-term study plots, before they could be extinguished. In February 1990 we established four plots (each 40 × 40 m) in one hurricane-damaged area on the ranch that had also burned. All trees greater than 10 cm dbh were identified and measured.

RESULTS

TREE DAMAGE, MORTALITY, RECOVERY, AND RESPONSE TO FIRE.—During the 5 years prior to the hurricane, 39 (2.6%) of the trees originally tagged had died. Of the 39 trees, most (80.8%) died in 1986 and 1987, which were years with low total annual precipitation (450–500 mm), having from 2–5 months without any measurable precipitation (Whigham *et al.* 1990). The prehurricane annual mortality rate (average of 0.5% per year) was low compared to moist tropical forests where 1.0–2.2 percent per year has been reported (Lieberman *et al.* 1985).

All trees were damaged and defoliated by Hurricane Gilbert and most had only their largest branches remaining (Table 1). Smaller numbers and percentages of trees had their trunks snapped, crowns completely removed, minor crown damage, or were uprooted. By January 1989, 4 months after the hurricane, 38 (2.6%) trees were dead, out of the 1447 that were alive when Hurricane Gilbert struck. The number of dead trees had increased to 72 (5.0%) by March 1989, 162 (11.2%) by February 1990, and 182 (12.6%) by September 1990. Fifteen (9.2%) of the trees that were dead by February 1990 were killed by ground fire that burned small portions of plots 1 (N = 5) and 2 (N = 10). Mortality was not evenly distributed among the damage classes ($X^2(180.49) > X^2_{.001(5)}(20.515)$) and appeared to be related to the degree of damage (Table 1). Trees that had snapped suffered the highest mortality followed, in order, by trees with only the largest branches remaining > trees that had

TABLE 1. *Damage to trees following Hurricane Gilbert and mortality of trees in each of the damage classes. The total number of trees at the time of the hurricane was 1447. Percent mortality (mort.) was calculated as the number of individuals dying divided by the number of trees. All trees in the plots were damaged.*

Damage type	Hurricane damage *N*	Hurricane damage %	Mort. (17 months) *N*	Mort. (17 months) %
Crown removed, trunk not snapped	143	10.7	14	8.6
Only largest branches remaining	554	41.3	32	19.8
Most large branches remaining	420	31.3	20	12.3
Only twigs and small branches removed	98	7.3	1	0.6
Trunks snapped	167	12.4	47	29.0
Tree uprooted	60	4.5	26	16.0
Fire killed			15	9.3

been uprooted > trees with most large branches remaining > trees with the crowns removed but trunks not snapped > trees with minor crown damage. Percent mortality was highest in *Brosimum* (*N* = 46; 31.3% of all trees that died) and 15 percent or less for the other 9 dominant species: *Drypetes* (*N* = 22; 15.0%), *Manilkara* (*N* = 15; 10.2%), *Talisia* (*N* = 6; 4.1%), *Myrcianthes* and *Gymnanthes* (*N* = 10; 6.8%), *Beaucarnea* (*N* = 4; 2.7%), *Sapindus, Coccoloba,* and *Bursera* (*N* = 2; 1.4%). Mortality based on dbh size classes was: 10–20 cm = 51.2%, 20–30 cm = 23.5%, 30–40 cm = 10.5%, +40 cm = 5.6%.

Substantial canopy development had occurred during the first 17 posthurricane months (I. Olmsted & D. Whigham, pers. obs.) and, for most species, relative diameter growth during the first year following the hurricane was higher than it had been in three of the five previous years (*e.g., Drypetes lateriflora* and *Manilkara zapota* in Fig. 1). *Brosimum alicastrum* was the only species that had a very low average relative growth rate following the hurricane (Fig. 1).

Fires had an even greater impact on tree mortality than the hurricane. Fire damage was widespread throughout the northeastern portion of the Yucatan Peninsula and many areas suffered extensive tree mortality (I. Olmsted, pers. obs.). In the 4 plots in the burned area at Rancho San Felipe, 85.4 ± 4.1 percent of the 401 trees were killed.

LEAF LITTERFALL AND COARSE WOODY DEBRIS.—Hurricanes can potentially influence patterns of nutrient cycling by quickly transferring large amounts of nutrients from storage in living biomass to storage in the litter pool. Average leaf litterfall biomass and total amounts of P, K, Ca, Mg, and Mn after the hurricane were greater than the totals for any of the previous five years (Table 2). Concentrations of Ca and Mg in the leaf litterfall produced by the hurricane were similar to values measured in annually composited leaf litterfall samples from the five previous years. In contrast, concentrations of P and K in leaf litterfall produced by the hurricane were higher than values measured in previous years (Table 2).

Biomass of twigs and other woody materials generated by the hurricane and collected in the litterfall traps during the first month after the hurricane were higher than the amounts collected for all of 1984 (Fig. 2). The hurricane increased the amount of coarse woody debris biomass in the plots from an average of 31 Mg/ha prior to the storm to 47 Mg/ha after (Fig. 3). The standing stocks of Ca, K, Mg, N in the coarse woody debris increased between 22–36 percent as a result of the hurricane. In contrast, P and Mn increased 57 percent. Although we made no quantitative measurements, it was obvious that posthurricane fires consumed almost all surface leaf litter, coarse woody debris and much of the organic matter in the soil.

DISCUSSION

Physical damage of forests associated with hurricanes has been documented (*e.g.,* Lugo *et al.* 1983, Thompson 1983, Weaver 1986), but there have been few instances where pre- and posthurricane data could be compared. The forest canopy at Rancho San Felipe was completely defoliated and most trees were heavily damaged. The amount of damage, however, does not appear to be unusual (Brokaw & Walker 1991) and was very similar to that described for forests struck by hurricanes in Belize (Johnson & Chaffey 1973) and Dominica (Lugo *et al.* 1983). Wadsworth and Englerth (1959) sampled hurricane damaged forests on limestone soils in Puerto Rico and found that stem breakage was

TABLE 2. *Biomass, nutrient concentrations, and amounts of nutrients in leaf litterfall (fine litter) measured 3 months after Hurricane Gilbert compared to the range of values measured for leaf litterfall during the previous four years. All values are means ±1 standard error* (N = 60).

	After hurricane	Previous 4 years
Biomass (g/m^2)	836 ± 65	422 ± 12–647 ± 18
Total P (g/m^2)	0.7 ± 0.1	0.2 ± 0.01–0.3 ± 0.01
Total K (g/m^2)	17.9 ± 1.4	6.2 ± 0.2–9.3 ± 0.3
Total Ca (g/m^2)	28.0 ± 2.3	12.0 ± 0.4–19.6 ± 0.6
Total Mg (g/m^2)	2.4 ± 0.2	1.2 ± 0.03–1.8 ± 0.1
Total Mn (mg/m^2)	0.3 ± 0.02	0.1 ± 0.003–0.2 ± 0.01
% P	0.08 ± 0.002	0.03 ± 0.001–0.05 ± 0.001
% K	2.17 ± 0.03	0.45 ± 0.02–1.52 ± 0.01
% Ca	3.31 ± 0.03	2.84 ± 0.02–3.04 ± 0.05
% Mg	0.29 ± 0.004	0.29 ± 0.003–0.31 ± 0.004
Mn (microgram/gm)	31.1 ± 0.9	28.1 ± 0.07–30.6 ± 0.6

more common than windthrow. Trees that were uprooted, had their trunks snapped, or had heavy crown damage suffered the highest amounts of post-hurricane mortality (Table 1). This indicates that the severity of damage will play a key role in determining overall rates of mortality in hurricane damaged forests.

Data from the few long-term studies of recovering forests in the region (Crow 1980, Weaver 1986) support the statements of Lugo *et al.* (1983) and Boucher (1990), who suggested that steady state forests probably do not develop in hurricane-prone regions. It is still too early to determine how much change in forest composition or structure will occur at our site or how long such changes will persist, but the low rates of tree mortality suggest that forest composition will change relatively little. Few tree species have invaded the forest and most have been scattered individuals of *Cecropia peltata* L. (now considered by some taxonomists to be *Cecropia schreberiana*) and *Carica papaya* L., both short-lived successional species.

The only unexpected response to the hurricane has been the high mortality and slow recovery of *Brosimum alicastrum*. Most individuals sprouted af-

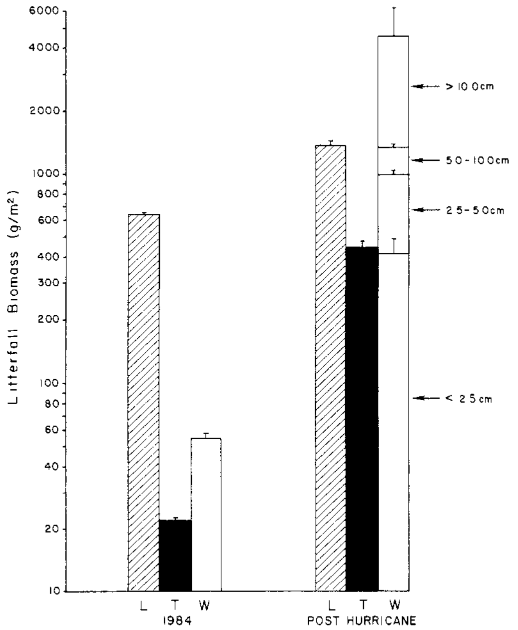

FIGURE 2. Comparison of litterfall collected in litter traps for all of 1984 with litterfall in litter traps 3 months after Hurricane Gilbert. Values are means ± 1 standard error. L = leaves, T = twigs, W = wood. In 1984 the wood category was not subdivided into the size classes shown for the posthurricane data. *N* = 60.

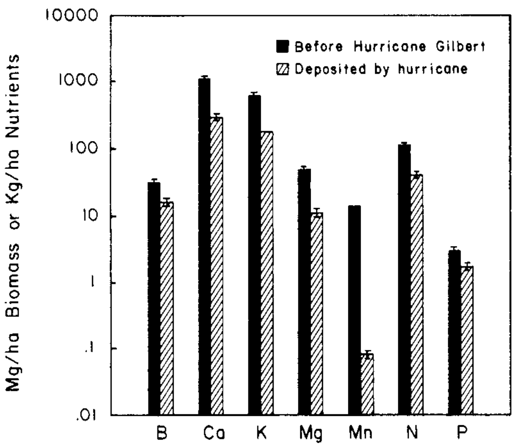

FIGURE 3. Biomass (B) and nutrients (Ca, K, Mg, Mn, N, and P) in coarse woody debris before and after Hurricane Gilbert in the study plots at Rancho San Felipe. Values are means ± 1 standard error. *N* = 12.

ter the hurricane but they only produced a few branches that were short-lived. By February 1990 it appeared that *Brosimum* had accounted for approximately 45 percent of all trees that had died. Some individuals that appeared to be dead in February 1990, however, produced a few new shoots in 1990, and by February 1991 the number of dead *Brosimum* had dropped from about 45 to 30 percent of all dead trees. The individuals that were alive in February 1991, however, did not appear to be very healthy and survival is by no means assured. In contrast, individuals of all other species have recovered dramatically. The response of *Brosimum* was not expected, as it is very widespread throughout the region and is known to respond well to pruning (Parado-Tejeda & Muñoz 1981; P. Zugasty Towle, pers. comm.).

Recovery of the forest has been rapid. During the 17 months after Hurricane Gilbert relative growth rates of most tree species were higher than in most previous years and the leaf area index of the forest almost doubled from February 1989 to February 1990 (data not shown). Similar posthurricane recovery of trees has been noted in Mississippi (Van Hooser & Hedlund 1969), Dominica (Lugo *et al.* 1983), and Australia (Webb 1958). Our leaf litterfall data suggest that the recovery of canopy productivity was also rapid. After one year, annual leaf litter production was only about 15 percent less than the lowest amount measured in the preceding 5 yr.

We believe that several factors may explain the rapid recovery of the forest. As in Dominica (Lugo *et al.* 1983), most tree species at our study site resprouted within one month, and the canopies of most trees had recovered dramatically within one year. Rapid canopy development was most likely supported by resources stored in woody tissues, but once new leaves and shoots were produced, photosynthetic products must have been responsible for growth.

High relative growth rates also may have reflected 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 availability of additional phosphorus may have been particularly important (*e.g.,* Vitousek 1984, Jordan 1985). If phosphorus limitation is a factor controlling productivity in tropical forests, one might predict that trees should remove P from leaves prior to senescence (Jordan 1985), and concentrations of P in leaves deposited before a hurricane would be expected to be lower than in leaves removed by the storm. Our data show that phosphorus concentrations in leaves collected after Hurricane Gilbert were almost twice as high as they were in naturally senesced leaves during any of the 5 previous years, and that the total P in leaf biomass deposited by the hurricane was approximately 15 times greater than the total for any previous year (Table 2). As most leaves completely decompose within six months (D. Whigham, pers. obs.), large amounts of P would potentially be available to support growth immediately after a major hurricane such as Gilbert.

The biomass and nutrient content of woody debris present in the forest before the hurricane were large, and were almost doubled by the storm. Leaching and decomposition of this woody material represent another potential source of nutrients to support short and long-term growth of the forest. In the future, information on the role of woody debris as sources or sinks for nutrients will be provided by decomposition experiments we are conducting at the site.

Finally, Furley and Newey (1979) found that hurricane-damaged forests in Belize suffered additional damage as a result of fire. Our results were similar and suggest that the fires which frequently follow in the wake of hurricanes can have a very important influence on forest structure and may be more important than direct hurricane damage. Fire may be especially important in areas where shallow and highly organic soils, such as at our site (Whigham *et al.* 1990, Whigham & Cabrera Cano 1991), may be highly combustible.

ACKNOWLEDGMENTS

This work has been supported by the World Wildlife Fund, Smithsonian Environmental Sciences Program, Smithsonian International Environmental Sciences Program, and the Smithsonian Research Expedition Program. National Science Foundation Grants BSR-8514325 and BSR-8918643, in part, supported MEH. We would like to thank Patricia Zugasty Towle and Felipe Sánchez Román for the use of Rancho San Felipe, for their help in data collection, and for their continuing support of our work. Jim Lynch, Jay O'Neill, Zhigang Wang, and Jess Zimmerman reviewed the manuscript. The manuscript was also improved by comments from Julie Denslow, Nicholas Brokaw, Jack Putz, and two anonymous reviewers. Liz Ley, Ed Balinsky, Jim Johnson, Catin Chitterling, and members of the 1990 Smithsonian Research Expedition team (Owen Lavin, Sol Courtman, Sherley Higuera, Margery Plymire, Shirley and James Virosco, and William McNiven) helped collect data.

LITERATURE CITED

Back, W., and B. B. Hanshaw. 1970. Comparison of chemical hydrogeology of the carbonate peninsulas of Florida and Yucatan. J. Hydrol. 10: 330–368.

Boucher, D. H. 1990. Growing back after hurricanes. BioScience 40: 163–166.

Brokaw, N. V. L., and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23: 442–447

Conner, W. H., J. W. Day, Jr., R. H. Baumann, and J. M. Randall. 1989. Influence of hurricanes on coastal ecosystems along the northern Gulf of Mexico. Wetland Ecol. Manag. 1: 45–56.

Crow, T. R. 1980. A rain forest chronicle: a 30-year record of change in structure and composition at El Verde, Puerto Rico. Biotropica 12: 42–55.

Escalante Rebolledos, S. E. 1986. La flora del Jardin Botánico del Centro de Investigaciones de Quintana Roo. A.C. Tesis. Universidad Veracruzana, Xalapa, Veracruz, México.

Furley, P. A., and W. W. Newey. 1979. Variations in plant communities with topography over tropical limestone soils. J. Biogeogr. 6: 1–15.

Gleason, P. J. Editor. 1984. Environments of South Florida: present and past II. Miami Geological Society, Coral Gables, Florida.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, J. D. Lattin, N. H. Anderson, S. V. Gregory, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. The ecology of coarse woody debris in temperate ecosystems. Recent Adv. Ecol. Res. 15: 133–302.

Jáuregui, E., J. Vidal, and F. Cruz. 1980. Los Ciclones y tormentas tropicales en Quintana Roo durante el período 1871–1975. *In* Memorias de Problemática y Perspectiva de Quintana Roo, pp. 47–63. Instituto de Geografía, UNAM, y CIQRO, Cancún, México.

Johnson, M. F., and D. F. Chaffey. 1973. An inventory of the Chiquibul Forest Reserve, Belize. Land Resource Study No. 14. Foreign and Commonwealth Office, Overseas Development Administration, Land Resources Division, Surrey, England.

Jordan, C. F. 1985. Nutrient cycling in tropical forest ecosystems. John Wiley & Sons, New York, New York.

Lieberman, D., M. Lieberman, R. Peralta, and G. S. Hartshorn. 1985. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. J. Ecol. 73: 915–924.

Lugo, A. E., M. Applefield, D. J. Pool, and R. B. McDonald. 1983. The impact of Hurricane David on the forests of Dominica. Can. J. For. Res. 13: 201–211.

Lundell, C. L. 1934. Preliminary sketch of the phytogeography of the Yucatan Peninsula. Carnegie Inst. Contr. Amer. Archaeol. 12: 257–321.

Lynch, J. F. 1989. Distribution of overwintering nearctic migrants in the Yucatan Peninsula, I: general patterns of occurrence. Condor 91: 515–544.

———. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. Biotropica 23: 488–496.

———. In press. Distribution of overwintering nearctic migrants in the Yucatan Peninsula, II: use of native and human-modified vegetation. *In* J. Hagen and D. Johnston (Eds.). Distribution, Ecology, and Conservation of Nearctic Migratory Landbirds. Smithsonian Institution Press, Washington, D.C.

Miranda, F. 1958. Estudios acerca de la vegetación. *In* E. Beltrán (Ed.). Los recursos naturales del sureste y su aprovechamiento. Tomo II, pp. 215–271. IMRNR, México, D.F.

———, and E. H. Xolocotzli. 1963. Los tipos de vegetación de México. Bot. Soc. Bot. Mex. 28: 29–179.

Olmsted, I. C., and R. Durán García. In press. Los tipos de Vegetación. *In* D. Navarro and J. Robinson (Eds.). Diversidad Biológica en Sian Ka'an, Quintana Roo, México, CIQRO and University of Florida Press, Gainesville, Florida.

Parado-Tejeda, E., and C. Sánchez Muñoz. 1981. *Brosimum alicastrum.* A potentially valuable tropical forest resource. Instituto Nacional de Investigaciones sobre Recursos Bióticos. Xalapa, Veracruz, México.

Thompson, D. A. 1983. Effects of Hurricane Allen on some Jamaican forests. Commonw. For. Rev. 62: 107–115.

Van Hooser, D. D., and A. Hedlund. 1969. Timber damaged by hurricane Camille in Mississippi. U. S. Dep. Agric. For. Serv. Research Note SE-96. Southern Forest Experiment Station, New Orleans, Louisiana.

Vitousek, P. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285–298.

Wadsworth, F. H., and G. H. Englerth. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. Caribb. For. 20: 38–51.

Weaver, P. L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. Caribb. J. Sci. 22: 53–70.

Webb, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, North Queensland. Aust. J. Bot. 6: 220–228.

Whigham, D. F., and C. J. Richardson. 1988. Soil and plant chemistry of an Atlantic white cedar wetland on the Inner Coastal Plain of Maryland. Can. J. Bot. 66: 568–576.

———, P. Zugasty Towle, E. Cabrera Cano, J. O'Neill, and E. Ley. 1990. The effect of annual variation in precipitation on growth and litter production in a tropical dry forest in the Yucatan of Mexico. Trop. Ecol. 31: 23–34.

———, AND E. CABRERA CANO. 1991. Survival and growth beneath and near parents: the case of *Myrcianthes fragrans* (Myrtaceae). *In* G. Esser and D. Overdieck (Eds.), Facets of modern ecology, pp. 61–76. Elsevier, Amsterdam, The Netherlands.