Published in: Forest Biodiversity in North, Central and South America, and the Caribbean
F. Dallmeier and J.A. Comiskey, Editors
Man and the Biosphere Series Volume 21
The Parthenon Publishing Group, New York
1998
pages165-186

CHAPTER 9

RESPONSES OF PLANTS AND BIRDS TO HURRICANE DISTURBANCES IN A DRY TROPICAL FOREST OF QUINTANA ROO, MEXICO

Dennis F. Whigham and James F. Lynch

INTRODUCTION

Long-term studies of vegetation plots or permanently marked individual organisms can yield insights into the dynamics of communities and populations (e.g. Lack, 1966; Gill, 1985; Weatherhead, 1986; Foster, 1988; Streng *et al.*, 1989; Hubbell and Foster, 1990; Primack and Hall, 1992; Silvertown *et al.*, 1994). Repeated sampling over an extended period can help to illuminate the mechanisms of vegetational change and clarify the role of major disturbances in determining community patterns. A few examples illustrate the kinds of insights that are only possible through long-term monitoring of individuals or plots.

It has generally been thought that tree growth rates in the humid tropics show only minor annual variation and that differences in rainfall explain what little variation does exist (Swaine, 1989; Korning and Balslev, 1994). However, when Clark and Clark (1994) measured annual growth of marked saplings and adult trees over a 9-year period in a lowland neotropical rain forest, they found that growth rates actually varied significantly from year to year. These authors suggested that the observed pattern may be driven by annual variation in cloud cover, not variation in rainfall. This study provided the first field support for Raich *et al.*'s (1991) hypothesis that variation in the productivity of tropical forests is caused mainly by seasonal fluctuations in cloud cover, which in turn mediate the flux of photosynthetically active radiation.

In another example of the unique value of long-term plot studies, Silvertown *et al.* (1994) analyzed data from 90 years of sampling permanent grassland plots at the Rothamstead Experimental Station in the United Kingdom. These authors concluded that the grassland community has been remarkably stable for nearly a century. Seasonal differences in species abundance appeared to be a function of rainfall, which determines the biomass of grasses and hence the intensity of competition between grasses and forbs. This important insight could not have been gained without detailed, long-term monitoring of vegetation composition and local climatic conditions.

Permanent plots can also provide information on the responses of populations, communities, and ecosystems to natural and anthropogenic disturbances. The floristics, structure, and dynamics of forests in the Caribbean region appear to be significantly influenced by the frequent impact of hurricanes (Boose *et al.*, 1994), which may prevent pioneer tree species from living long enough to reach the forest canopy (Zimmerman *et al.*, 1994).

In most studies of major perturbations (e.g. wild fires, hurricanes, volcanic eruptions), permanent plots were established only after a disturbance occurred to assess the extent of damage (e.g. Smith *et al.*, 1994; Zimmerman *et al.*, 1994) and monitor ecosystem recovery. However in a few cases, long-term observations of a site prior to a natural disturbance have allowed direct before-and-after comparisons. As an example, Whigham *et al.* (1991) used four years of baseline data to assess hurricane damage to a dry tropical forest in Mexico's Yucatan Peninsula, finding that some effects of Hurricane Gilbert, which struck the area in September 1988, were immediate and severe (e.g. almost complete defoliation of the forest), but that few trees were killed directly by the hurricane and mortality returned to pre-hurricane levels within four to five years. Observations made during the first two years after the hurricane suggested that recovery would be rapid for plant (Whigham *et al.*, 1991) and avian (Lynch, 1991) components of the ecosystem.

We have continued our long-term observations at the Puerto Morelos study site, where we have compiled data for 12 years. In this paper, we re-evaluate our earlier predictions that plant and bird communities would rapidly recover from the immediate impact of Hurricane Gilbert (Lynch, 1991; Whigham *et al.*, 1991).

METHODS

Plant studies

In February and March of 1984, 12 permanent 40-m^2 plots were established in an area of semi-evergreen tropical forest at Rancho San Felipe, approximately 10 km south of the Caribbean coastal village of Puerto Morelos, Quintana Roo, Mexico (for location map see Lynch, 1991). Based on precipitation data, this vegetation would be classified as dry forest or very dry forest in the Holdridge *et al.* (1971) system. This medium-stature forest (canopy height varies from about 15 to 25 m) grows on very shallow soils that overlie limestone bedrock in a karstic landscape. In 1984, the 1.92 ha encompassed by the 12 plots contained more than 120 species of trees and shrubs (E. Cabrera and D. F. Whigham unpublished data). All trees >10 cm in diameter at breast height (dbh) were tagged and identified in 1984 and have been remeasured annually. Litter fall was studied from May 1984 through October 1992. Five 1-m^2 litter traps were placed at randomly determined locations within each plot. Fallen litter was collected regularly (usually 8 to 10 times each year) and separated into leaf material and reproductive materials. Dry weights of each component were obtained, and nutrient concentrations were determined from weight- and timecomposited yearly samples. Only phosphorus data for litter fall are discussed in this paper. Phosphorus concentrations were determined using plasma emission spectroscopy (Whigham and Richardson, 1988). In 1984, precipitation data obtained from the Cancun airport about 45 km north of the study site indicated 870 mm of rainfall occurred. Precipitation was measured at the study site from 1985 to 1992 and at Puerto Morelos (about 10 km north of the study site) from 1992 to 1995. Additional descriptive information on vegetation, soils, and woody debris can be found in Whigham *et al.* (1990, 1991) and Harmon *et al.* (1995).

Bird studies

The relative abundance of birds at the study site was assessed by two complementary sampling methods. Pairs of nylon mist nets (overall dimensions = 12 m × 12 m, mesh size = 32 to 38 mm) were operated in each of the 12 permanent plots for three successive mornings in late November 1984 and in February and March from 1985 to 1995 for a total of 72 net-mornings/year for 12 years. This plot-based information was supplemented by data from 15 to 24 nets placed in the same tract of forest immediately south of the permanent plots. Each captured bird was identified to species, weighed, sexed, and aged, where possible, and permanently identified with a unique combination of colored plastic leg bands.

To improve coverage for species that avoid the forest understory or are too large to be captured in fine-mesh nets, mist-netting data were supplemented by data from standardized point counts, which were conducted each year at 36 to 52 locations (Lynch, 1989, 1991). To obtain a sufficient number of point counts for statistical comparisons while still maintaining a sufficient distance (about 200 m) between points to assure the independence of each count, it was necessary to extend the area sampled by point counts well beyond the approximately 6 ha of forest occupied by the permanent plots and the adjacent supplemental netting site. Therefore, the point count results are not as directly comparable to the plant data from the permanent plots as are the mist-netting data. The discussion below is restricted to the mist-netting data.

RESULTS

Tree mortality

Between 1984 and 1988, annual tree mortality averaged 0.5%. Mortality increased five-fold to 2.6% immediately after Hurricane Gilbert (Whigham *et al.*, 1991) and reached 5.0% in 1989 (Figure 9.1). Most trees that died within the first 6 months after the hurricane suffered either a snapped bole or destruction of the canopy (Whigham *et al.*, 1991). Annual mortality of trees began to decline in 1990, and, by 1993, had reached pre-hurricane levels. One of the most interesting and unexpected findings to date was that the hurricane almost

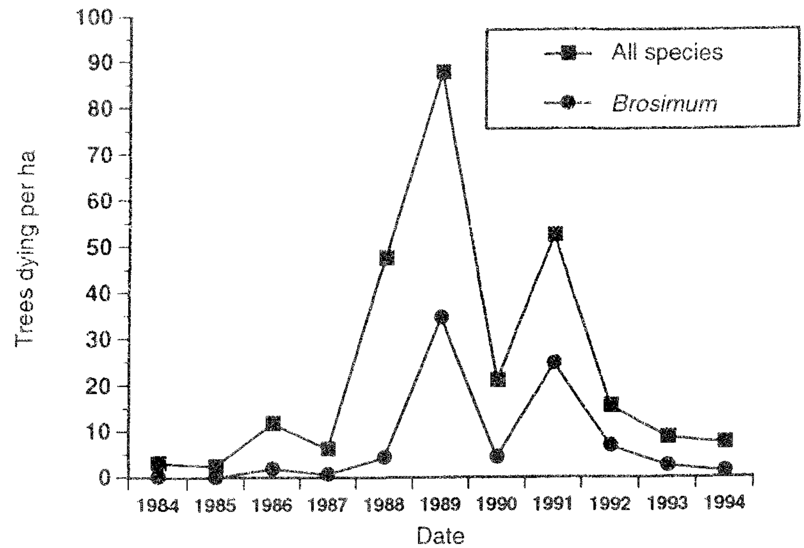


Figure 9.1 Annual mortality/ha for all tree species combined and for *Brosimum alicastrum* (Ramon) in 12 permanent plots at Rancho San Felipe. Hurricane Gilbert heavily damaged the study site in September 1988

completely eliminated one of the co-dominant species from the forest canopy (Figure 9.1). Ramon (*Brosimum alicastrum* Swartz.), a common tree in humid lowland forests of Mesoamerica, had been the second most abundant tree in the permanent plots in 1984 (143 individuals >10 cm dbh), and only 11 individuals died between 1984 and 1988. However, 56 *B. alicastrum* were killed outright by the hurricane or died within the following 3 months, and most remaining individuals sustained severe crown damage. Although surviving Ramon sprouted, the success of new sprouts was low compared with other local tree species. Ramon trees continued to die for several years after the hurricane, and, by 1995, only 4 barely surviving individuals remained of the original 143 on the permanent plots.

Tree growth

Average annual diameter growth and relative growth increased for all tree species after the hurricane (Figures 9.2A and 9.2B). Figure 9.3 shows annual growth rates of four abundant species in the plots: *Manilkara zapota* (L.) van Royer, *B. alicastrum*, *Bursera simaruba* (L.) Sarg, and *Drypetes lateriflora* (Swartz) Drug & Urban. The first three are canopy dominants, whereas *D. lateriflora* is an understory tree. *M. zapota* and *D. lateriflora* are relatively slow growing, but in four of five post-hurricane years, their annual growth rates exceeded the mean growth rate measured before the disturbance (Figures 9.3A and 9.3B). *B.*

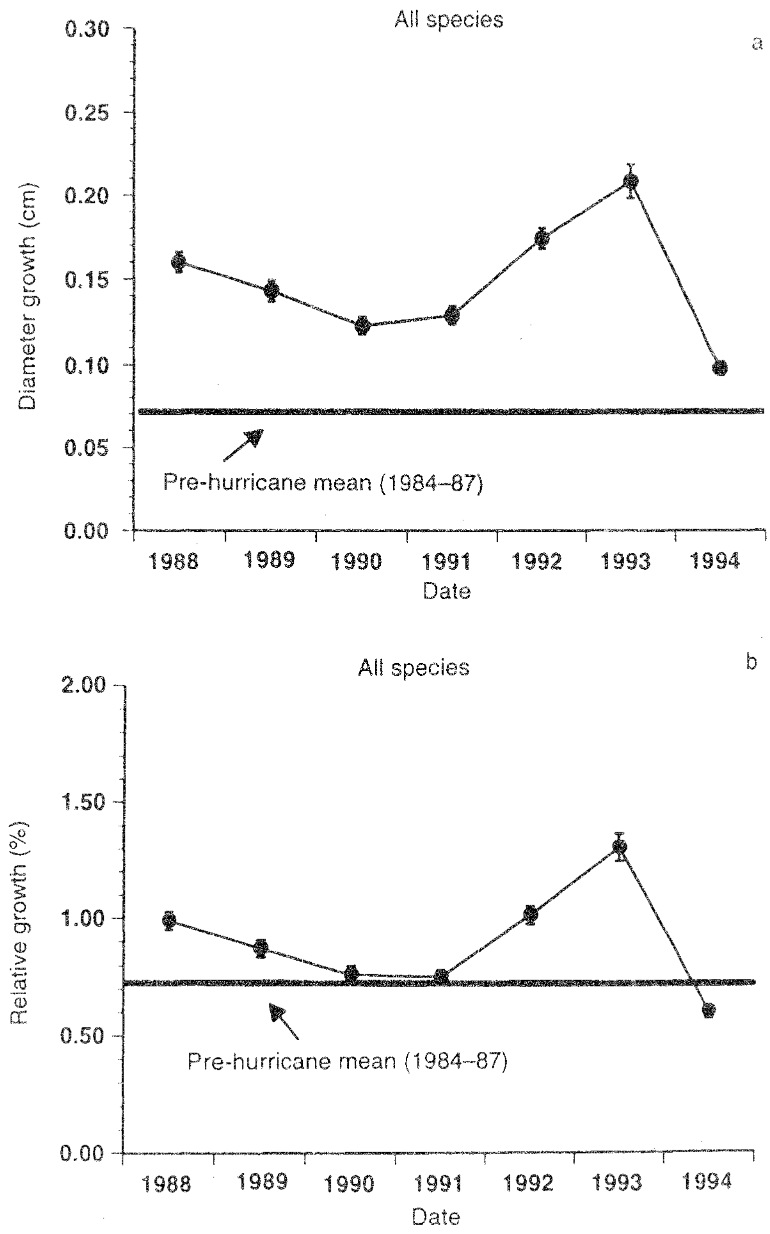


Figure 9.2 Average (± 1 standard error) annual diameter (A) and relative growth (B) rates of all species in 12 permanent plots at Rancho San Felipe. Annual diameter growth for each tree was calculated as: dbh increase = $dbh_{t+1} - dbh_t$ where dbh is tree diameter and t is year. Relative growth was calculated as: relative dbh increase = $(dbh_{t+1} - dbh_t)/dbh_t$

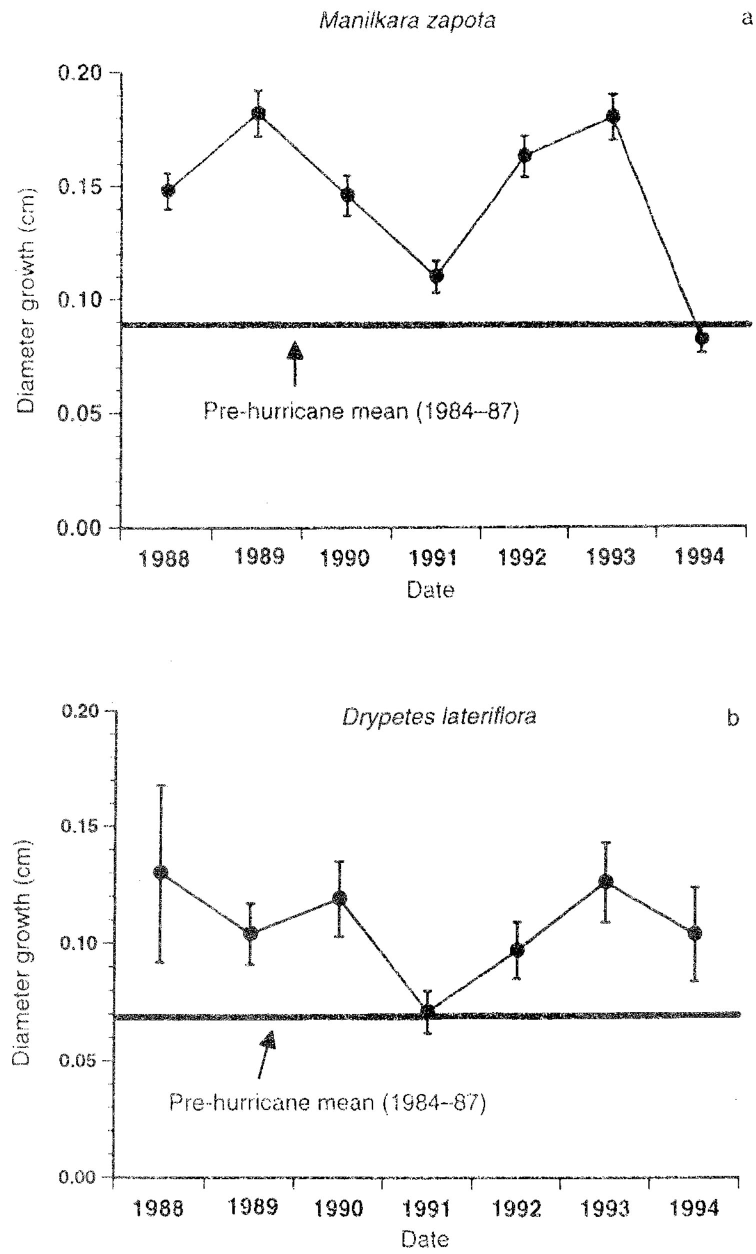
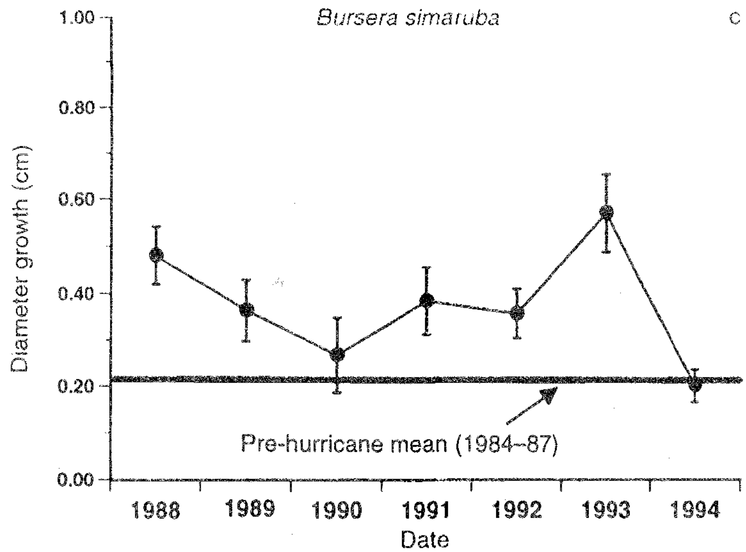
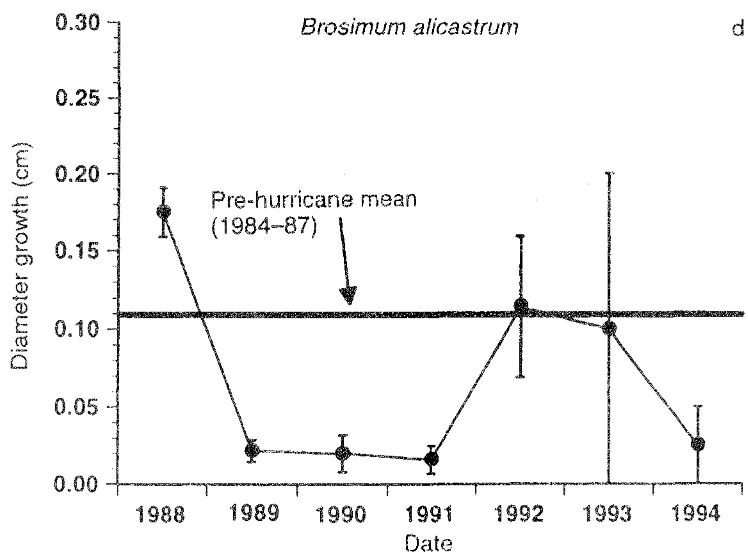


Figure 9.3 Annual growth (± 1 standard error) of *Manilkara zapota* (A), *Drypetes lateriflora* (B), *Bursera simaruba* (C), and *Brosimum alicastrum* (D) in 12 permanent plots at Rancho San Felipe. Growth was calculated as in legend for Figure 9.2


Bursera simaruba
c
Diameter growth (cm)
1.00
0.80
0.60
0.40
0.20
0.00
Pre-hurricane mean (1984–87)
1988
1989
1990
1991
1992
1993
1994
Date


Brosimum alicastrum
d
Diameter growth (cm)
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Pre-hurricane mean
(1984–87)
1988
1989
1990
1991
1992
1993
1994
Date

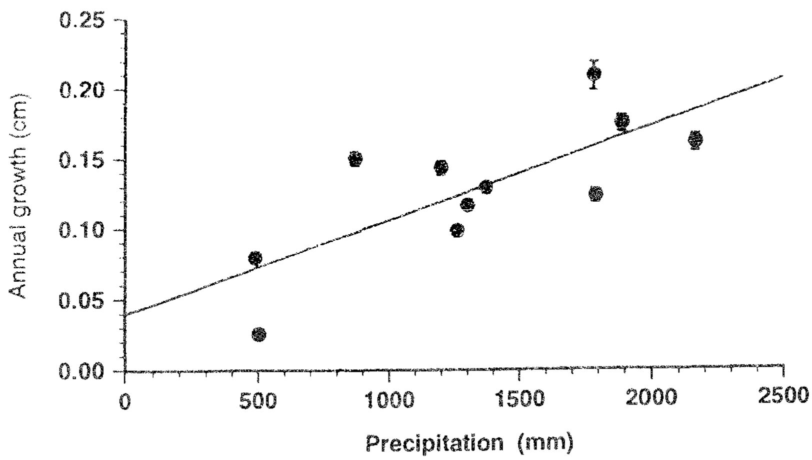


Figure 9.4 Regression relationship between annual precipitation (mm) and annual average growth (cm) from 1984 to 1994. Growth data are means ± 1 standard error for all species in 12 permanent plots at Rancho San Felipe. The linear regression equation is: growth = 0.000409 (precipitation) + 0.2257 ($r^2 = 0.56$)

simaruba was the fastest growing tree species in the plots before the hurricane, and its growth rate continued to exceed those of the other species in four of five post-hurricane years (Figure 9.3C). *B. alicastrum* was the only species that consistently showed lower growth rates after the hurricane (Figure 9.3D). As described above, *B. alicastrum* suffered almost complete mortality, and the few surviving adult individuals were obviously in poor health.

Annual tree growth was highly correlated with annual precipitation before the hurricane (Whigham *et al.*, 1990) and that relationship showed little change when pre- and post-hurricane data were combined (Figure 9.4). Thus, the annual variations in growth shown in Figure 9.3, including the higher average growth rates from 1989 to 1993, most likely reflect variation in annual rainfall.

Litter fall

More than 800 g/m^2 of leaf litter fell to the forest floor as a result of the hurricane (Whigham *et al.*, 1991), and the average phosphorus concentration in leaf litter generated by the hurricane was almost three times greater than the average concentration in the leaf litter collected during the four pre-hurricane years (Whigham *et al.*, 1991). Average annual litter fall of leaves and reproductive material (e.g. fruits, seeds, flower parts, etc.) in the four post-hurricane years were below the mean value for the four pre-hurricane years (Figures 9.5A and 9.6A). However, after the massive litter fall that was caused by the hurricane (Whigham *et al.*, 1991), subsequent annual differences in leaf litter fall seemed to reflect variation in rainfall more than response to the storm (Figure 9.7).

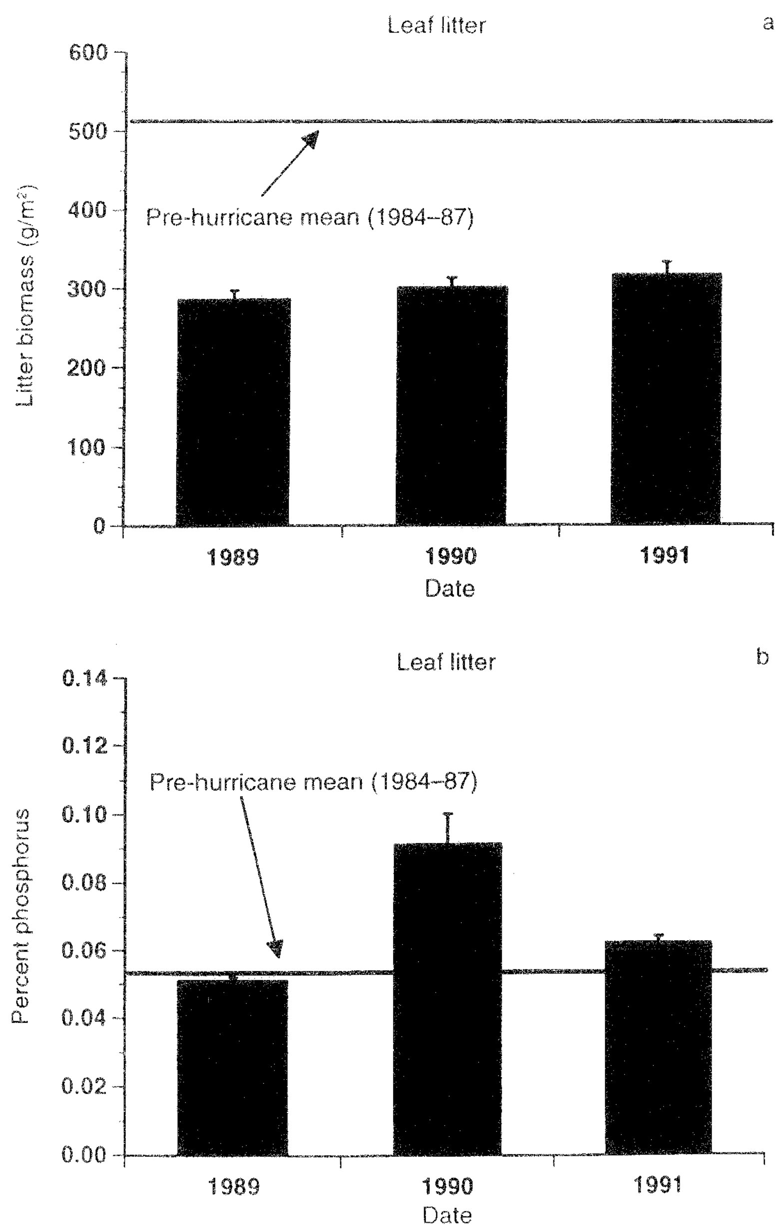
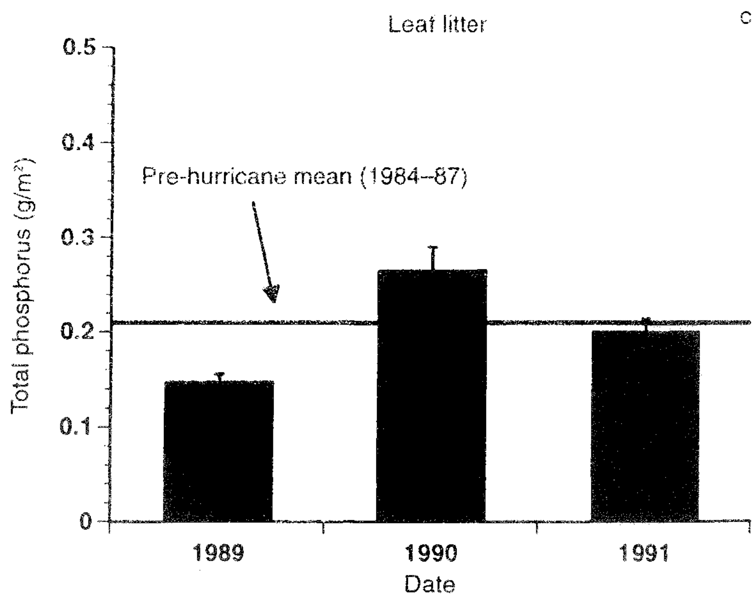


Figure 9.5 Comparison of annual leaf litter fall (A), litter phosphorus concentrations (B), and total phosphorus (C) in leaf litter during post-hurricane years compared to means for pre-hurricane years (1984 to 1987). All values are means ± 1 standard error



Excluding leaf litter fall associated with the hurricane event (see Whigham *et al.*, 1991 for data on hurricane effects), combining data for before and after Hurricane Gilbert resulted in a highly significant ($r^2 = 0.60$; $p < 0.001$) correlation between annual precipitation and annual leaf litter fall.

Higher phosphorus concentrations in post-hurricane leaf litter fall (Figure 9.5B) resulted in more total phosphorus in leaf litter fall by 1990, one year after the hurricane, even though total leaf fall was less in the post-hurricane years (Figure 9.5A). Phosphorus concentrations and total amounts of phosphorus in reproductive materials collected in the litter traps showed no clear response pattern by the end of the study (Figures 9.6B and 9.6C). Phosphorus concentrations in reproductive materials were lower than pre-hurricane levels for two of the three years.

Short-term responses of birds to the hurricane

Over extensive areas of northeastern Quintana Roo, Hurricane Gilbert opened up the forest by felling whole trees and major limbs (including associated lianas) and defoliating the canopy. Fallen trunks, branches, and lianas combined with rapidly growing seedlings, saplings, and shrubs to create a virtually impenetrable tangle of living and dead vegetation in the ground-shrub stratum. The post-hurricane forest combined the canopy height and tree distribution of intact forest with the high light intensity and dense understory of old fields and shrub communities (Lynch, 1991).

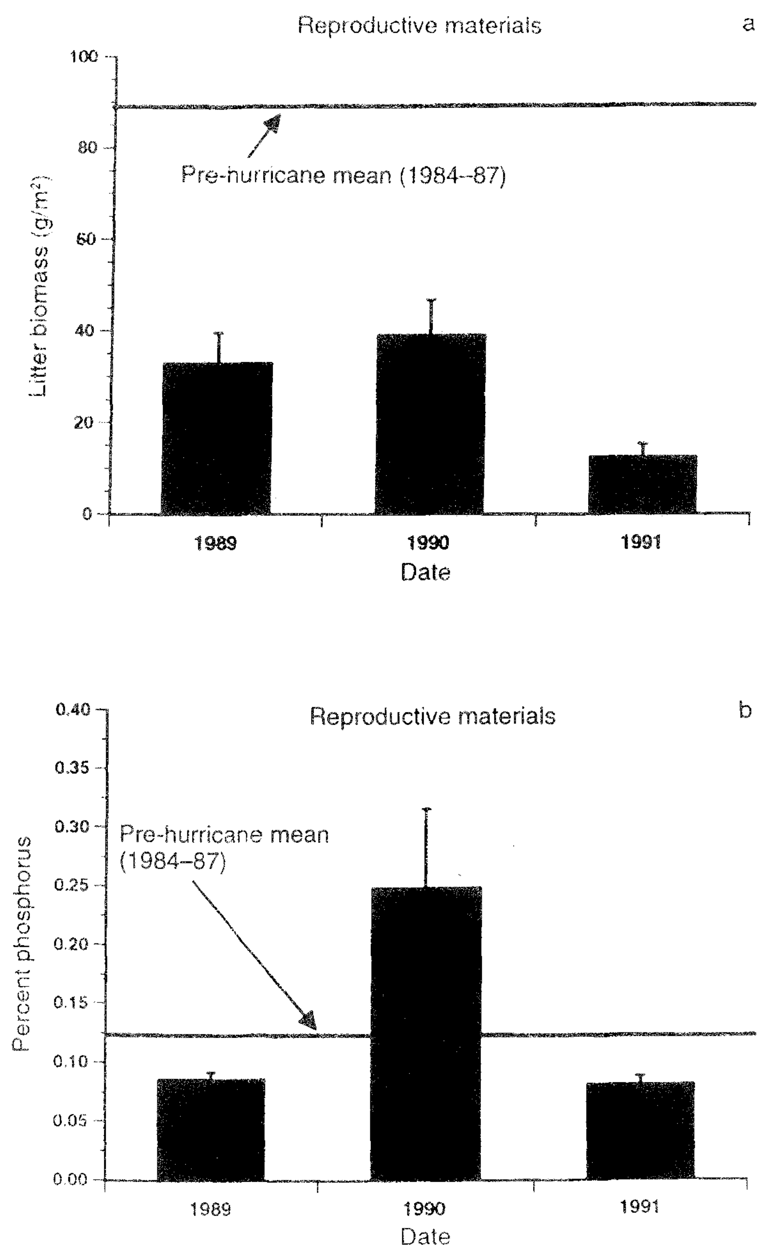
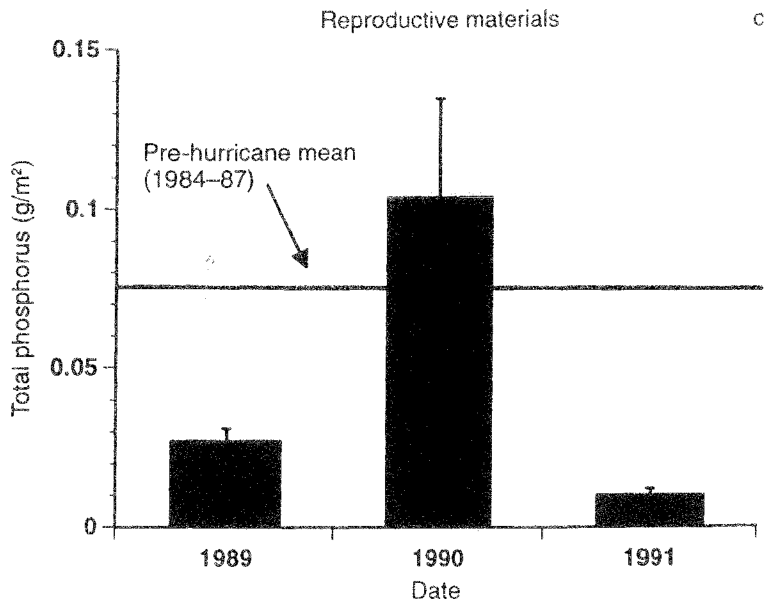


Figure 9.6 Comparison of annual reproductive litter fall (A), phosphorus concentrations (B), and total phosphorus (C) in reproductive litter during post-hurricane years compared to means for pre-hurricane years (1984 to 1987). All values are means ± 1



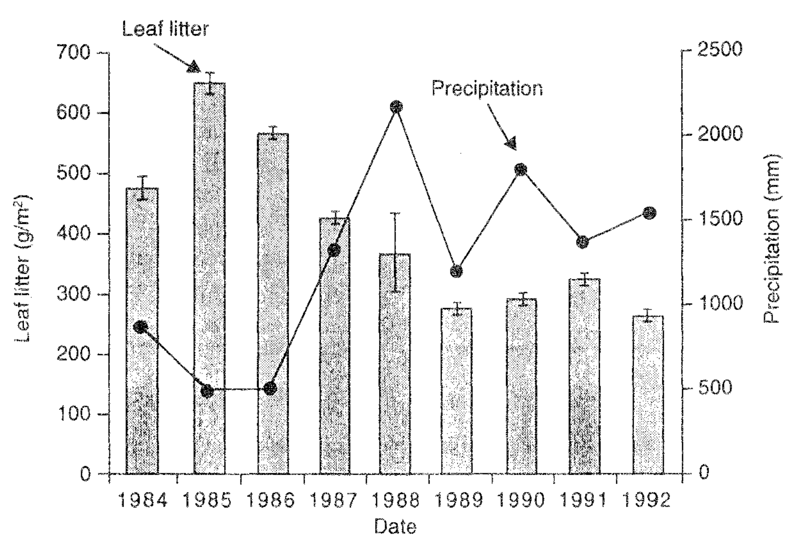


Figure 9.7 Comparison of annual leaf litter biomass and precipitation from 1984 to 1992. Data for litter biomass are means ± 1 standard error

Table 9.1 Species richness and capture rates (CR = 100 × individuals captured/net-hour) for mist-netted samples of migrant (Migr.) and resident (Res.) birds at Rancho San Felipe over 11 winters (Hurricane Gilbert struck the site in September 1988; the burned forest plot, just north of the unburned plot, was first sampled in February 1990, approximately six months after being swept by wild fire)

Year	*Net hours*	*Total Spp.*	*Migr. Spp.*	*Res. Spp.*	*Migr. CR*	*Res. CR*	*Total CR*
Unburned forest				Pre-hurricane			
1984–85	888	35	11	24	5.0	15.8	20.7
1985–86	918	21	7	14	3.3	3.5	6.8
1986–87	324	21	6	15	6.8	10.5	17.3
1987–88	331	22	8	14	7.2	10.0	17.2
Mean	615	25	8.0	16.8	5.6	10.0	15.5
				Post-hurricane			
1988–89	396	45	15	30	12.4	21.7	34.1
1989–90	662	42	14	29	8.8	15.7	24.5
1990–91	572	38	14	24	12.4	13.2	25.5
1991–92	612	39	15	24	12.4	11.6	24.0
1992–93	678	40	13	27	7.1	10.9	18.0
1993–94	618	32	8	24	3.1	8.7	11.8
1994–95	585	35	15	20	12.5	11.4	23.9
Burned forest				Post-hurricane			
1989–90	424	41	13	28	23.1	17.2	40.3
1990–91	360	47	16	31	45.8	27.8	73.6
1991–92	370	44	18	26	39.5	18.5	58.0
1992–93	386	47	16	31	23.6	18.6	42.2
1993–94	485	45	18	27	14.0	14.0	28.0
1994–95	469	61	20	41	23.2	27.7	51.0

Despite radical alteration of what had been a relatively open understory, most forest bird species showed only modest changes in abundance as measured by capture rates. At the community level, the most dramatic effect of the hurricane on understory birds was to double the overall capture rate (CR = 100 × individuals captured/net-hour) and increase the number of species captured/netting bout by about 70% (Table 9.1, Figures 9.8 and 9.9). Species diversity and density of individuals in the post-hurricane bird community closely resembled those that had been documented previously in a nearby old field that was five to seven years into secondary succession (Lynch, 1991). These patterns reflected three complementary trends: 1) most species present in the forest understory before the hurricane remained there afterward; 2) in response to the complete defoliation of the forest canopy, many birds that normally forage high in the forest moved lower into the densely vegetated understory; and 3) a number of bird species that are normally associated with early- to mid-successional habitats moved into the post-hurricane forest (Lynch, 1989, 1992). Forest-associated migratory

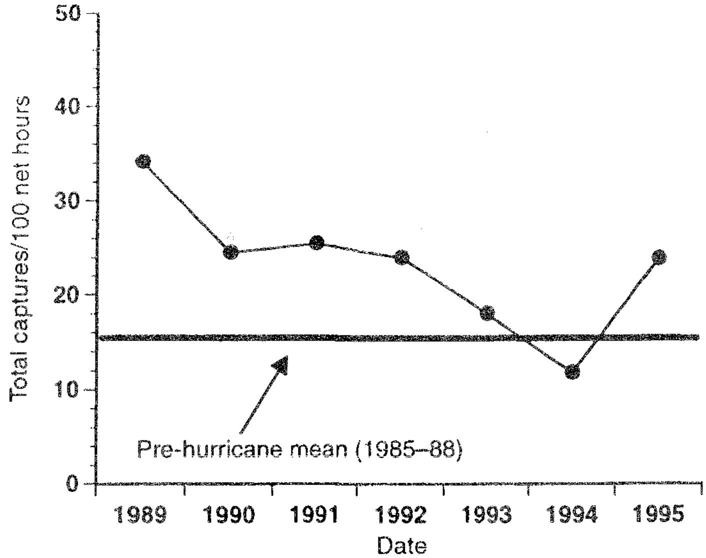


Figure 9.8 Capture rates (CR = 100 × individuals captured/net-hour) for birds at the Rancho San Felipe study site during post-hurricane years (1989 to 1995) compared with average value for four pre-hurricane years (1985 to 1988)

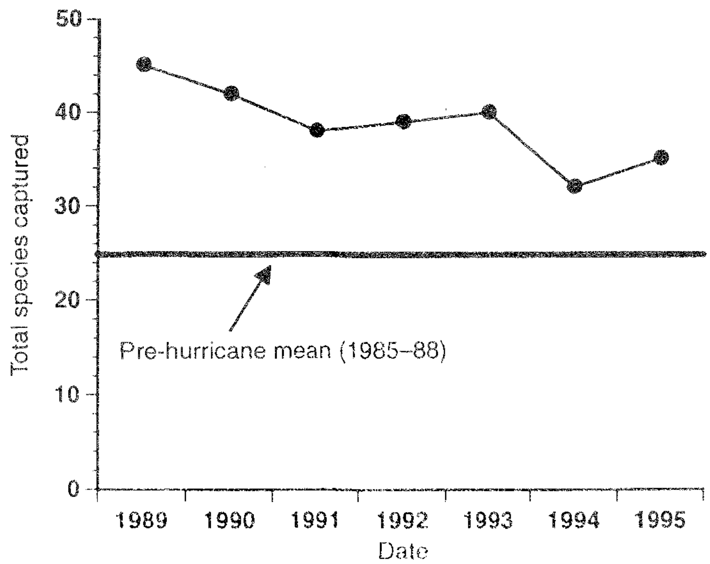


Figure 9.9 Number of bird species in mist-netted samples from Rancho San Felipe during post-hurricane years (1989 to 1995) compared with average value for four pre-hurricane years (1985 to 1988)

species seemed better buffered against hurricane effects than did residents, and shrub-associated migrants were more likely than shrub-associated residents to invade the understory of the post-hurricane forest (Table 9.1). As a result, the relative abundance of migrant individuals in our capture samples increased from 30% before the hurricane to 39% afterward (Lynch, 1989).

These community-level patterns are also evident at the individual species level (Table 9.2). Among the migrant species that were common in the forest understory prior to Hurricane Gilbert, only the wood thrush (*Hylocichla mustelina*) was completely absent six months after the storm (Table 9.2; Lynch, 1991). Capture rates for two of the most frequently netted species, the migratory hooded warbler (*Wilsonia citrina*) and the permanently resident red-throated ant-tanager (*Habia fuscicauda*), remained virtually unchanged after the hurricane (Figure 9.10, Table 9.2). The migratory magnolia warbler (*Dendroica magnolia*) exemplified a species that was common in the canopy of the pre-hurricane forest (as documented by point counts), but was only occasionally captured in mist nets (Lynch, 1989). After Hurricane Gilbert, the capture rate of this species increased seven-fold (Table 9.2). The indigo bunting (*Passerina cyanea*) and painted bunting (*Passerina ciris*), both migrants, exemplify old-field species that first appeared in the forest after the hurricane (Lynch, 1989; Table 9.2). The migratory white-eyed vireo (*Vireo griseus*) showed both horizontal and vertical migration into the forest understory after the hurricane. In northern Quintana Roo, this species is most abundant in brushy old fields, although it is also quite common in the canopy of mature forest. Before Hurricane Gilbert, white-eyed vireos were rarely captured in the forest, even though they were frequently detected in forest point counts and were abundant in nearby brushy old fields (Lynch, 1989). Capture rates increased more than 30-fold after the hurricane, at which time the white-eyed vireo became the most frequently netted species in the forest (Figure 9.11).

Longer-term responses of birds to the hurricane

Most community- and species-level responses of birds to Hurricane Gilbert proved to be ephemeral, and a return toward pre-hurricane conditions was already evident in the second year after the storm (Lynch, 1991; Lynch and Whigham, 1995; Tables 9.1 and 9.2). The elevated post-hurricane values for species richness and capture rate began to decline in the second winter and continued a negative trend in subsequent years (Figures 9.8 and 9.9). The post-hurricane invasion of the forest by birds found in early old fields was also transitory. Species such as the ruby-throated hummingbird (*Archilochus colubris*), bananaquit (*Coereba flaveola*), indigo bunting, and orchard oriole (*Icterus spurius*) were common in the forest a few months following Hurricane Gilbert (February to March 1989), but had disappeared or drastically declined by February to March 1991. On the other hand, the wood thrush, a previously common forest-associated species that was completely absent for two winters following the hurricane, exceeded

Table 9.2 Mist-net capture rates (CR = 100 × individuals captured/net-hour) for the most frequently netted migrant and resident bird species in unburned tropical semi-evergreen forest at Rancho San Felipe (Hurricane Gilbert struck the site in September 1988, 5 months before the 1989 sample; pre-hurricane (Pre-H) entries = means of four annual samples; * = species more abundant in old fields than in undisturbed forest)

	Pre-H	*1989*	*1990*	*1991*	*1992*	*1993*	*1994*	*1995*
Nearctic–neotropical migrants								
Ruby-throated hummingbird*	–	0.7	–	–	–	–	–	–
Least flycatcher*	–	0.5	0.2	0.2	–	0.5	–	0.2
Wood thrush	0.60	–	–	3.8	1.6	1.9	0.2	0.9
Gray catbird*	0.05	0.7	0.8	–	1.0	0.2	–	1.4
White-eyed vireo*	0.10	3.2	2.3	2.1	2.0	1.3	0.3	0.7
Hooded warbler	1.00	1.2	1.1	1.0	1.1	1.3	0.6	1.5
Kentucky warbler	0.50	0.5	0.8	1.2	1.5	0.4	0.3	2.0
Ovenbird	0.70	0.2	0.3	0.9	1.1	1.0	0.6	2.0
Yellow-breasted chat*	0.02	–	–	–	–	0.2	–	–
Common yellowthroat*	0.02	–	0.4	0.2	–	–	–	0.3
Worm-eating warbler	0.10	0.2	0.3	0.9	0.5	0.4	0.2	1.5
Swainson's warbler	0.02	–	–	0.2	0.3	0.2	–	0.5
Black-and-white warbler	0.20	0.3	0.9	1.1	0.3	0.6	0.6	0.7
Magnolia warbler	0.20	1.5	0.5	0.5	0.3	0.7	0.2	–
Blue-winged warbler*	–	0.2	0.2	0.2	0.3	0.2	0.2	–
American redstart	–	0.3	–	0.8	–	–	–	0.2
Summer tanager	–	–	–	–	0.2	–	–	0.2
Indigo bunting*	–	1.2	1.2	0.2	0.3	–	–	0.2
Painted bunting*	–	0.2	0.3	0.2	0.2	–	–	0.2
Orchard oriole*	–	1.2	–		–	–	–	–
Tropical residents								
Buff-bellied hummingbird*	0.2	–	0.2	0.2	–	–	0.2	0.5
Wedge-tailed sabrewing	0.4	–	1.1	–	0.8	0.4	0.5	0.2
White-bellied emerald	0.2	0.5	0.4	–	0.5	0.4	0.6	–
Ruddy woodcreeper	1.2	0.2	1.4	0.2	0.5	0.2	0.5	0.9
Ivory-billed woodcreeper	0.5	2.0	1.2	1.4	1.1	1.0	0.5	1.0
Olivaceous woodcreeper	0.2	1.8	0.6	0.5	–	0.1	0.3	0.3
Tawny-winged woodcreeper	0.3	0.2	0.4	0.2	0.3	0.9	0.5	0.7
Bright-rumped attila	0.3	0.5	0.6	0.5	0.8	0.7	0.5	0.5
Royal flycatcher	0.3	0.5	–	0.4	0.5	0.7	0.3	0.8
Stub-tailed spadebill	0.1	1.3	0.2	–	–	–	0.3	0.3
Northern bentbill	0.1	0.5	0.6	0.4	0.2	0.2	–	–
Spot-breasted wren*	–	1.0	0.4	0.9	0.2	0.6	–	0.5
Yucatan vireo*	0.1	0.2	0.6	0.5	0.3	0.3	0.3	–
Tawny-crowned greenlet	0.5	1.0	0.9	1.0	0.8	–	0.3	0.3
Red-throated ant-tanager	2.5	2.8	2.9	1.4	1.1	1.3	0.8	1.7
Rose-throated tanager	0.3	–	0.2	0.7	0.6	0.6	0.5	0.3
Bananaquit*	–	1.0	0.6	–	–	–	0.2	–
Blue bunting	0.3	0.8	1.4	0.4	1.5	0.6	0.3	0.5
Orange oriole*	–	–	1.0	–	–	–	–	–

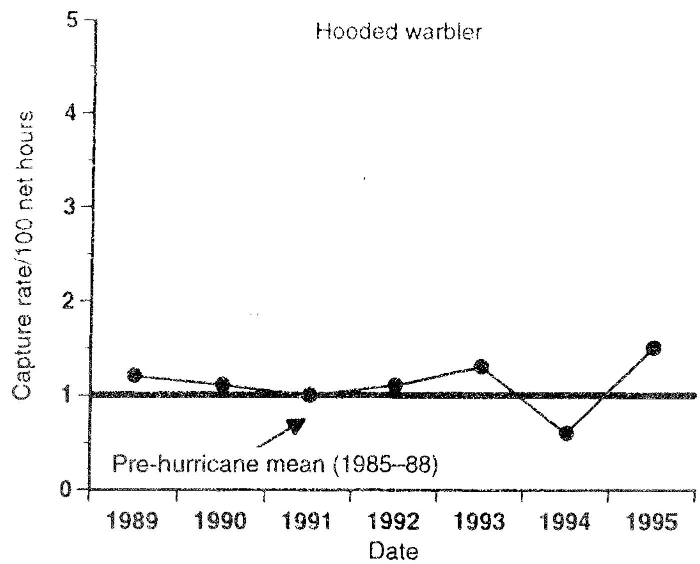


Figure 9.10 Capture rates for the hooded warbler (*Wilsonia citrina*) during post-hurricane years (1989 to 1995) compared with the average value for four pre-hurricane years (1985 to 1988). This common understory species showed little response to Hurricane Gilbert

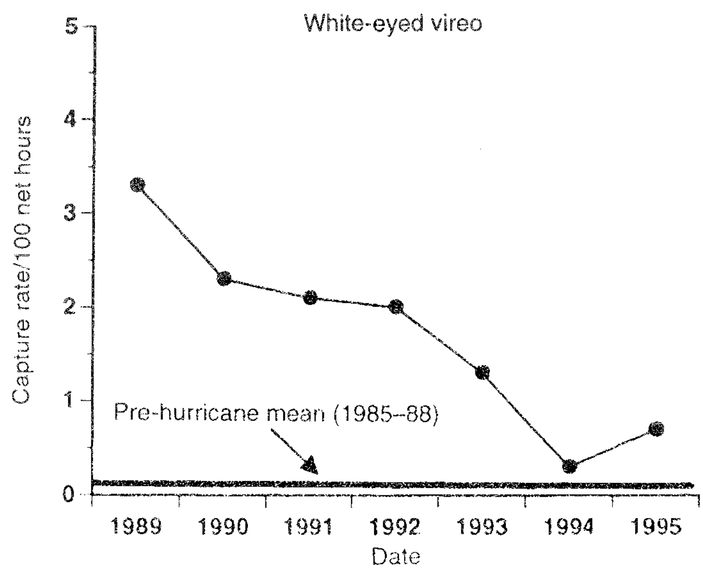


Figure 9.11 Capture rates for the white-eyed vireo (*Vireo griseus*) during post-hurricane years (1989 to 1995) compared with the average value for four pre-hurricane years (1985 to 1988). Large numbers of this shrub-forest species initially invaded the dense forest understory created by Hurricane Gilbert, but numbers subsequently declined

its pre-hurricane mean density in the fourth winter (Table 9.2). The descent into the understory of canopy-foraging species such as the magnolia warbler and American redstart (*Setophaga ruticilla*) also proved temporary, and capture rates for these species began to decline in the second winter after the storm (Table 9.2). Perhaps the longest lasting community effect the hurricane had on birds was to decrease the relative and absolute abundance of frugivorous and nectarivorous species. Because many frugivores species are too large and/or too low in density to be adequately sampled by standard mist nets, this trend was most evident in data from point counts (Lynch, 1991). Another fairly persistent effect of the hurricane was an increase in the prevalence of bird species that prefer dense leafy vegetation. Capture rates of species such as the spot-breasted wren (*Thryothorus maculipectis*), white-eyed vireo, and tawny-crowned greenlet (*Hylophilus ochraceiceps*) subsequently declined from their high post-hurricane values, but continued to exceed pre-hurricane levels for at least several years (Table 9.2).

DISCUSSION

Effects of the hurricane on the forest

Our long-term data on tree growth, litter fall, nutrients in litter fall, and bird occurrences have provided insights into how different components of a dry tropical forest respond to annual variations in precipitation and to catastrophic disturbances. Hurricane Gilbert altered the forest by completely defoliating the canopy and subcanopy and causing severe structural damage to most canopy trees (Whigham *et al.*, 1991). Within two to four years, most of the plant and bird variables that were measured before the hurricane had returned to pre-hurricane values. Canopy regeneration had already begun when we visited the site one month after the hurricane, and within two to three years, the leaf area index and phenological patterns (e.g. periodicity of leaf development and senescence, flowering and fruiting) had returned to their pre-hurricane configurations (I. Olmsted and D. F. Whigham unpublished data).

The rate at which phosphorus cycled through the leaf litter increased after the hurricane. We believe that this was because of two factors. First, higher-than-average rainfall in the post-hurricane years (Figure 9.7) was correlated with increased phosphorus concentrations of leaf litter fall (Figure 9.5B), especially in years when annual precipitation exceeded about 1500 mm (Whigham, 1994). Second, the hurricane deposited a large amount of phosphorus on the forest floor in the form of woody debris and leaf litter (Whigham *et al.*, 1991; Harmon *et al.*, 1995). The nearly three-fold increase in the total amount of phosphorus in the leaf litter should have resulted in higher release rates of phosphorus as the litter decomposed in the first few years after the hurricane. Lodge and McDowell (1991) found higher phosphorus concentrations in leaf litter in Puerto Rico following Hurricane Hugo, and Sanford *et al.* (1991), also working in Puerto Rico, predicted that a long-term increase in soil organic carbon associated with the hurricane would lead to a measurable and persistent increase in mineralized soil phosphorus.

Brokaw and Walker (1991) summarized a series of papers on hurricane damage and short-term recovery in the Caribbean region, and made several predictions. They suggested that hurricanes should not be viewed as catastrophic to tropical forests in the region because these storms kill only a small percentage of trees (i.e. where the storm impacts are most pronounced). This generalization is supported by our data, but may not apply to all Caribbean vegetation types, nor to other regions. For example, Ramon trees (this study) and mangrove forests (Smith *et al.*, 1994) appear to be highly susceptible to hurricane damage. Brokaw and Walker (1991) also predicted that hurricanes could be found to have longer-term impacts on forest structure and function, especially in areas where there would be changes in the abundance of pioneer species relative to species found in mature forests. Our data from Rancho San Felipe indicated that major structural attributes of the forest (e.g. tree density and basal area) were changed very little by the hurricane, even though the morphology of the forest canopy was considerably modified. Functional attributes (growth, litter production, nutrient cycling) were initially perturbed by the hurricane, but quickly returned to pre-disturbance levels.

Effects of the hurricane on birds

Recovery of the forest bird community was clearly underway by the second year after Hurricane Gilbert. Mist-net capture data alone do not allow one to fully separate the effects of localized movements (e.g. vertical migration from the canopy to the understory) from true changes in density for all bird species. However, capture data are reliable indicators of actual abundance for relatively small (< 75 g) species that are associated with the forest understory rather than the upper canopy. In this regard, it may be significant that most of the common forest understory specialists (e.g. tawny-crowned greenlet, hooded warbler, Kentucky warbler, ovenbird, red-throated ant-tanager) showed little or no response to the hurricane (Table 9.2). However, major changes in density did occur in some species. The spectacular post-hurricane increase in white-eyed vireo captures (Figure 9.11) and the complete disappearance of the wood thrush after the hurricane (Table 9.2) were confirmed by point count data, which took into account birds in the forest canopy as well as the understory (Lynch, 1991).

We have no way of knowing whether Hurricane Gilbert caused significant direct mortality on birds, as opposed to merely inducing emigration of certain species to less disturbed areas. Either or both mechanisms may have accounted for the post-hurricane density reductions we observed in some species. However, the high mobility and short generation time (typically one year) of most forest bird species would permit them to rapidly recolonize and repopulate suitable hurricane-impacted forest, given an adequate source of propagules. Such sources exist less than 20 km south of our study site, beyond the zone of intense storm damage.

In comparison to birds, larger and slower-growing organisms such as canopy trees may be more resistent to hurricanes and quicker to repair non-lethal hurricane damage. However, unlike birds, canopy trees require very long periods of time to recoup the effects of extensive hurricane-induced mortality. It will be many decades before the seedlings of *B. alicastrum* present at the time of the hurricane could possibly become dominants at the Rancho San Felipe site.

Compared with forest trees, birds showed more inter-specific variation in their short-term responses to Hurricane Gilbert. Many species (e.g. hooded warbler) were not measurably affected by the storm; others (e.g. wood thrush) completely disappeared from the storm-impacted area for one or more years; still other species (e.g. orchard oriole, indigo bunting) colonized the forest in the wake of the hurricane or showed dramatic changes in abundance (e.g. white-eyed vireo).

Because of their high mobility, even small species of birds may respond more to landscape-wide or (in migratory species) even trans-continental environmental factors than to conditions at the scale of our 0.16-ha permanent plots. Approximately 10 to 11 months after Hurricane Gilbert struck our study site, thousands of hectares in the surrounding region were swept by catastrophic wild fires that killed > 90% of all canopy trees and essentially obliterated the forest understory (Lynch, 1991). The pioneering bird community that initially occupied burned areas was dominated by field-shrub species. Most of the forest-associated species that persisted after the hurricane in unburned forest were absent from burned areas (Lynch, 1991, 1992). However, recapture data from permanently marked individuals showed that some individual birds routinely moved back and forth between burned and unburned vegetation and that directional movements (i.e. colonization events) into the burned area from the unburned forest also occurred over a period of several years (J. Lynch unpublished data). Burned sites underwent rapid secondary succession, and four to five years after the fire, shrubs and small trees covered the formerly barren landscape. Concurrently, the compositions of bird communities in burned and unburned habitats converged upon each other and upon the pre-hurricane bird community (Table 9.1; Lynch and Whigham, 1995). However, because the successional clock was set back to an earlier state in fire-impacted areas than in unburned forest, it may be decades before the former attain all of the floristic, physiognomic, and avifaunal characteristics of mature forest.

We conclude that the dry tropical forest we studied in the Yucatan is unusually resilient to disturbance, and that most functional elements of the community quickly recover from hurricane damage. The wild fires that typically follow hurricanes in the Yucatan region have greater and longer-lasting impact on local ecosystems than do hurricanes themselves, but even fire-damaged systems show a relatively rapid convergence toward pre-disturbance conditions.

ACKNOWLEDGMENTS

We thank Felipe Sanchez and Patricia Zugasty Towle for making their ranch available for our long-term research, and for helping us in many other ways. Connie Butcher provided rainfall data from Puerto Morelos. Assistance in the field was provided by Ed Balinsky, Toni Bava, Mauro Berlanga, Edgar Cabrera, Gilberto Chavez, Carin Chitterling (Bisland), Alan Curtis, Laurie Greenberg, Mark Harmon, Jamie Harms, Jim and Debbie Johnson, Arturo Lopez, Elizabeth Ley, Bill Mayher, Pat Mehlhop, Gene Morton, Ingrid Olmsted, Jay O'Neill, Jay Sexton, Martha Van der Voort, and several groups of volunteers from the Smithsonian Research Expeditions Program. Financial support was provided by the Smithsonian Institution (Environmental Sciences Program, International Environmental Sciences Program, Research Opportunities Fund) and the World Wildlife Fund (US).

REFERENCES

Boose, E.M., Foster, D.R. and Fluet, M. (1994). Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs*, **64**, 369–400

Brokaw, N.V.L. and Walker, L. R. (1991). Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica*, **23**, 442-7

Clark, D.C. and Clark, D.B. (1994). Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. *Journal of Ecology*, **82**, 865–72

Foster, D.R. (1988). Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, South-western New Hampshire, USA. *Journal of Ecology*, **76**, 105–34

Gill, D.E. (1985). Interpreting breeding patterns from census data: a solution to the Husting dilemma. *Ecology*, **66**, 344–54

Harmon, M.E., Whigham, D.F., Sexton, J. and Olmsted, I. (1995). Decomposition and mass of woody detritus in the dry tropical forests of the northeastern Yucatan Peninsula, Mexico. *Biotropica*, **27**, 305–16

Holdridge, L.R., Grenke, W.C., Hatheway, W.H.J., Liang, T. and Tosi, J.A. (1971). *Forest Environments in Tropical Life Zones. A Pilot Study*. Pergamon Press, New York

Hubbell, S.P. and Foster, R.B. (1990). Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. In Gentry, A.H. (ed.) *Four Neotropical Rainforests*. Yale University Press, New Haven, CT. pp.522–41

Korning, J. and Balslev, H. (1994). Growth rates and mortality patterns of tropical lowland tree species and the relation to forest structure in Amazonian Ecuador. *Journal of Tropical Ecology*, **10**, 151–66

Lack, D. (1966). *Population Studies of Birds*. Clarendon Press, Oxford

Lodge, D.J. and McDowell, W.H. (1991). Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica*, **23**, 373-8

Lynch, J.F. (1989). Distribution of overwintering Nearctic migrants in the Yucatan Peninsula, I: General patterns of occurrence. *Condor*, **91**, 515–44

Lynch, J.F. (1991). Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. *Biotropica*, **23**, 488–96

Lynch, J.F. (1992). Distribution of overwintering Nearctic migrants in the Yucatan Peninsula, II: Use of native and human-modified vegetation. In Hagan, J.M. and

Johnston, D.W. (eds) *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington, DC, pp.178–95

Lynch, J. F, and Whigham, D.F. (1995). The role of habitat disturbance in the ecology of overwintering migratory birds in the Yucatan Penisula. In Estrada, A.S., Sader, S. and Wilson, M. (eds.) *Conservation of Neotropical Migratory Birds in Mexico*. Miscellaneous Publication 727. Maine Agricultural Forest Experiment Station, Orono, MN, pp.199–214

Primack, R.B. and Hall, P. (1992). Biodiversity and forest change in Malaysian Borneo. *Bioscience*, **42**, 829–37

Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., Grace, A.L., Moore, B. and Vorosmarty, C.J. (1991). Potential net primary productivity in South America: application of a global model. *Ecological Applications*, **1**, 399–429

Sanford, R.L., Jr., Parton, W.J., Ojima, D.S. and Lodge, D.J. (1991). Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modeling. *Biotropica*, **23**, 364–72

Silvertown, J., Dodd, M.E., McConway, K., Potts, J. and Crawley, M. (1994). Rainfall, biomass variation, and community composition in the Park Grass Experiment. *Ecology*, **75**, 2430–37

Smith, T.J., III, Robblee, M.B., Wanless, H.R. and Doyle, T.W. (1994). Mangroves, hurricanes, and lightning strikes. *Bioscience*, **44**, 256–62

Streng, D.R., Glitzenstein, J.S. and Harcombe, P.A. (1989). Woody seedling dynamics in an east Texas floodplain forest. *Ecological Monographs*, **59**, 177–204

Swaine, M.D. (1989). Population dynamics of tree species in tropical forests. In Holm-Nielsen, L.B., Nielsen, L.B. and Balslev, H. (eds). *Tropical Forests: Botanical Dynamics, Speciation, and Diversity*. Academic Press, Inc., London, pp.101–10

Weatherhead, P.J. (1986). How unusual are unusual events? *American Naturalist*, **128**, 150–4

Whigham, D.F. (1994). Dry tropical forest responses to variations in precipitation, phosphorus addition and disturbance. In Tallis, J.J., Norman, H.J. and Benton, R.A. (eds) *Proceedings of the VI International Congress of Ecology*. Manchester, p.149

Whigham, D.F., and Richardson, C.J. (1988). Soil and plant chemistry of an Atlantic white cedar wetland on the Inner Coastal Plain of Maryland. *Canadian Journal of Botany*, **66**, 568–76

Whigham, D.F., Zugasty Towle, P., Cabrera Cano, E., O'Neill, J. and Ley, E. (1990). The effect of annual variation in precipitation on growth and litter production in a tropical dry forest in the Yucatan of Mexico. *Tropical Ecology*, **31**, 23–34

Whigham, D. F., Olmsted, I., Cabrera Cano, E. and Harmon, M.E. (1991). The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. *Biotropica*, **23**, 427–33

Zimmerman, J.K., Everham, III, E.M., Waide, R.B., Lodge, D.J., Taylor, C.M. and Brokaw, N.V. (1994). Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology*, **82**, 911–22