

# MODERN ECOLOGY

## Basic and Applied Aspects

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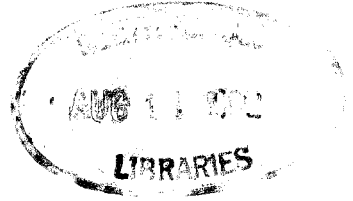
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## Chapter 4

# Survival and growth beneath and near parents: The case of *Myrcianthes* *fragrans* (Myrtaceae)

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### 4.1 Introduction

Discussions of the fate of seedlings in tropical forests have mostly focussed on whether or not they become established beneath the canopy of their parents and the importance of gap versus non-gap environments to their growth and survival (CLARK and CLARK 1984). In the early 1970's, CONNELL (1971) and JANZEN (1971) independently proposed that seedling establishment would be lower near parents because of disproportionately high mortality associated with seed predation, herbivory, and pathogens. CLARK and CLARK (1984) reviewed 24 studies on this topic published between 1970 and 1984 and found general support for either density-dependence or distance-dependence in progeny mortality. Additional support for the CONNELL-JANZEN hypothesis was provided by AUGSPURGER (1984a) who found that seedlings of eight out of nine wind-dispersed species in Panama

had higher survival rates away from parents. Others have found different results. KITAJIMA and AUGSPURGER (1989) found that, seedlings of *Tachigalia versicolor* had a higher survival rate with increasing distance from the parent, but that few seedlings persisted beyond 40 m from parents. SCHUPP (1988) found that seed survival of *Faramaea occidentalis* was greatest beyond the canopy of the parent but that mortality of established seedlings was similar beneath and away from parents. HUBBELL (1980) also noted that juveniles can reach maturity immediately adjacent to an adult of the same species.

A number of investigators have examined the role of tree gaps as sites for successful establishment and growth of seedlings (SCHUPP 1988, AUGSPURGER 1983, AUGSPURGER 1984b, AUGSPURGER and KELLY 1984, BROKAW 1985, BROKAW 1987, DENDLOW et al. 1990, DE STEVEN and PUTZ 1984, UHL et al. 1988). In most of these studies, seedling survival and growth rates were greater in tree gaps. SCHUPP (1988), however, found that predation was higher in gaps and concluded that long-term seedling survival might be best in the forest understory.

Given the high diversity of trees in most tropical forests compared to the few species that have been studied, it is not surprising that a variety of relationships between adults and their offspring have been described. More studies are needed before generalizations can be made either about the JANZEN-CONNELL hypothesis or about the importance of tree gaps to the dynamics of humid and dry tropical forests.

In this paper we address the issues of parent-offspring growth and survival by using results of a six year study of *Myrcianthes fragrans* (Sw.) McVAUGH (Myrtaceae) in a dry tropical forest in the Yucatan Peninsula of Mexico. *Myrcianthes fragrans* occurs from northern South America through the West Indies and into southern Florida (McVAUGH 1963). We have three objectives: 1) to evaluate factors affecting seedling survival by: a. characterizing distance relationships between adults and between adults and smaller individuals, and by b. evaluating the growth and mortality of seedlings in long-term plots located at three distances from parent trees, 2) to determine the relationship between seedling growth and soil depth. Soils at our study site are shallow, usually less than 20 cm, and we hypothesized that seedling growth would be negatively related to soil depth, and 3) we address the hypothesis that seedlings respond positively to canopy opening using measurements of seedling growth and mortality prior to and following complete canopy defoliation caused by Hurricane Gilbert in September, 1988.

## 4.2 Study site

The studies were conducted in a dry tropical forest ("selva mediana subperennifolia" (MIRANDA 1958) on the Yucatan Peninsula. The site, hereafter called Rancho San Felipe, is located approximately 10 km south of the village of Puerto Morelos (20° 49' N, 87° 7' W) in the Mexican state of Quintana Roo. Canopy height at the site varies between 15 and 25 meters. Twelve long-term study plots (40 × 40 m)

were established in February 1984. All trees with a diameter (DBH) greater than 10 cm were tagged and identified in each plot. The twelve plots contained 1508 individual trees that belonged to 79 species. Nine species (*Manilkara zapota* (L.) VAN ROYER, *Talisia olivaeformia* (HBK.) RADLK., *Gymnanthes lucida* (SWARTZ), *Brosimum alicastrum* SWARTZ, *Drypetes lateriflora* (SWARTZ) DRUG and URBAN, *Sapindus saponaria* L., *Coccoloba diversifolia* JACQ, *Beaucarnea pliabilis* (BAKER) LUNDELL), and *Myrcianthes fragrans* accounted for approximately 60% of all individuals. Thirty-eight *Myrcianthes* trees occurred in eleven of the plots and its density ranged from 1 to 6 per 1600 m<sup>2</sup>. DBH of *Myrcianthes* ranged from 14.7 to 69.2 cm (mean 36.4 cm; SD±14.0).

There are no long-term climatic data from Rancho San Felipe but relevant data are available from the Cancun airport (25 km), Felipe Carillo Puerto (185 km) (LOPEZ ORNAT 1983), and Valladolid (135 km) (WALTER and LIETH 1967). The climate is strongly seasonal with a distinct period of low precipitation that usually lasts from November through May (Fig. 4.1). Annual precipitation is approximately 1100 mm, but the amount and seasonal distribution are highly variable (WHIGHAM et al. (in press)). The average annual temperature at Valladolid and Felipe Carillo Puerto is 25°C and the monthly mean varies from approximately 26 to 22°C. Maximum temperatures occur between May and August (ca. 40–33°C) and minimum temperatures between January and March (ca. 18–8°C).

The shallow azonal soil, classified as a litosol-rendzina and derived from weathered Miocene and Pliocene parent material (WEST 1964, BACK and HANSHAW 1970), occurs in pockets between exposed limestone rocks. The soil has an almost neutral pH ( $7.1 \pm 0.1$ ) and the organic matter content is high ( $51.5 \pm 5.1\%$ ).

Average light conditions in the forest understory were determined prior to Hurricane Gilbert. Shaded areas in long-term seedling plots (see page 65) received an average of  $1.0 \pm .5\%$  (1 standard error) of full sunlight (N= 34; PAR measurements made in a nearby field and at the soil surface in seedling plots during cloudless conditions on 16 February, 1985 between 11AM and 12PM using a LI-COR Model 185B light meter). During the same sampling period, sunflecks (N= 14) in the seedling plots received an average of  $12.3 \pm 11.4\%$  (Range: 40.0–1.7%) of full sunlight. No light measurements were made immediately after Hurricane Gilbert but the canopy was completely defoliated and light intensities were accordingly quite high (Ingrid Olmsted, personal communication).

### 4.3 Methods

**Distances between juveniles, saplings, and trees.** We measured interplant distances between all *Myrcianthes* individuals > 10 cm DBH in the 1600 m<sup>2</sup> plots. We also measured the distances between each individual tree and all juveniles (plants less than 1 m in height), saplings (plants greater than 1 m in height and less than 10 cm DBH), and trees within a ten meter radius. A ten meter sampling radius was chosen to represent areas beneath (0–5 m) and beyond (5–10 m) the

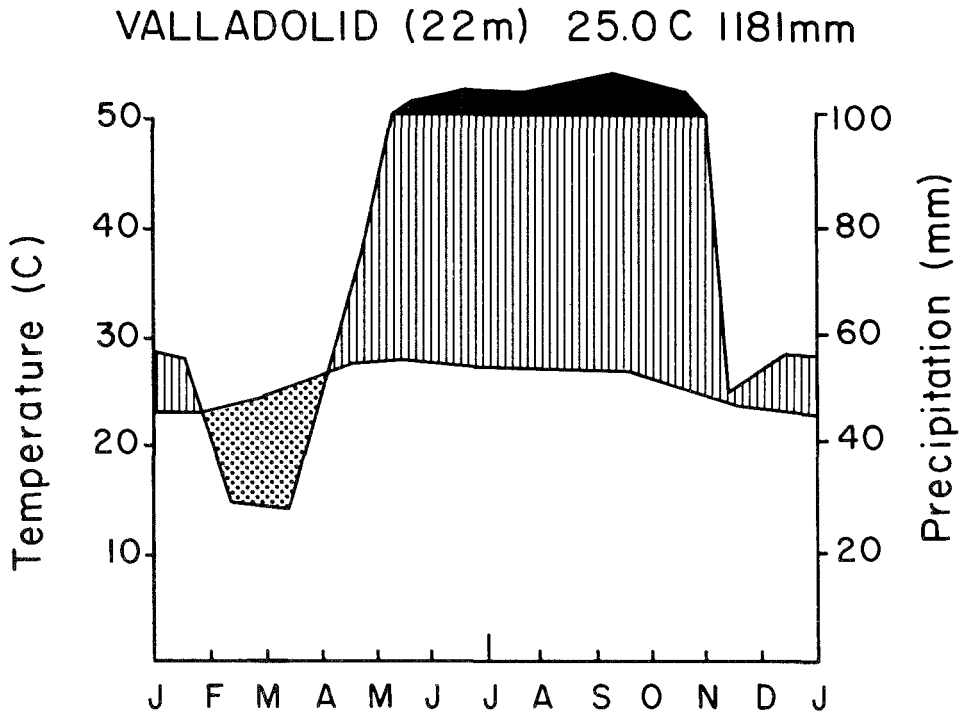


Figure 4.1: Climate diagram (WALTER and LIETH 1967) for Valladolid (elevation 22 meters). The long-term mean for temperature and precipitation are given in the upper right corner of the diagram. The relationship between temperature and precipitation suggests periods of excess or deficit water conditions. The dotted area is a period of relative drought when the precipitation curve falls below the temperature curve. The vertically shaded area is the humid season when the precipitation curve is above the temperature curve. The black area represents the part of the year when precipitation exceeds 100 mm per month and the scale is reduced to 1/10.

canopy of each tree, and to include the distribution of virtually all seedlings. Differences between the density of *Myrcianthes* juveniles, shrubs, and trees within the 10 m sampling radius were compared with ANOVA and the Tukey-Kramer test (WILKINSON 1989).

**Seedlings in long-term plots.** In February 1984, we established nine plots (1 × 1 m) around each of five trees. Plots, three per transect, were positioned between 1–2, 5–6, and 10–11 meters from the boles of the putative source trees. These plots will hereafter be referred to as 1, 5, and 10 meter distances. A cohort of *Myrcianthes* seedlings had germinated during the previous 2–3 months. Cotyledons were still attached and most seedlings had produced the first true leaves. We counted the number of seedlings in each plot and fitted their stems with small numbered aluminum tags. In most plots we tagged all seedlings but in plots with more than 100 individuals, only a subset (approximately 50%) of the seedlings were tagged. Since 1984, the plots have been censused yearly at approximately the same time to determine the number and height of live seedlings. Height and density data were analyzed with a nested ANOVA model (quadrat nested within tree and distance) and means compared with the Tukey test (JOYNER (ed.) 1985). Seedling survival at 1, 5, and 10 meters was compared with the Peto and Peto's Logrank Test (PYKE and THOMPSON 1986).

**Depth of the soil-litter layer.** The potential rooting depth available to seedlings was evaluated by measuring the depth (cm) of the litter-soil layer at 10 cm from the trees and then at 50 cm intervals along three randomly located 10 m transects per tree (Total = 15 transects). The litter-soil layer was defined as the distance between the top of the litter layer and solid rock. Depth was measured by inserting a wooden stick into the soil and marking it at the top of the soil-litter layer after the stick had reached solid rock. The distance from the bottom of the stick to the mark was then measured. Statistical comparisons of the depth of the litter-soil layer at different distances from parent trees were made using ANOVA (quadrats nested within trees) and means were compared with the Tukey-Kramer test (WILKINSON 1989).

**Seedling growth and microhabitat characteristics.** In February 1990, we harvested 300 seedlings from the 1984 cohort. Twenty seedlings were collected along each of three randomly located 10 m transects at each of the five trees described on page 65. The following data were collected in the field: 1. distance (m) between parent and seedling, 2. qualitative assessments of light conditions were made by evaluating the percent canopy above each seedling. Three categories were used: A. shade – seedling judged to be completely shaded by leaves of overhead vegetation, B. partial shade – seedlings mostly shaded by overhead vegetation but judged to receive some direct light during the day, C. sun – seedlings covered by little overhead vegetation and judged to receive large amounts of direct light during the day, 3. depth of soil (cm) immediately beneath the seedling, 4. number of leaves and branches, 5. shoot height (cm), 6. length (cm) of the root divided into vertical and/or horizontal components. The latter division was necessary because *Myrcianthes* roots begin to grow horizontally after they have reached the bottom of the soil profile. Plants were dried to constant weight in the sun, and biomass (g)

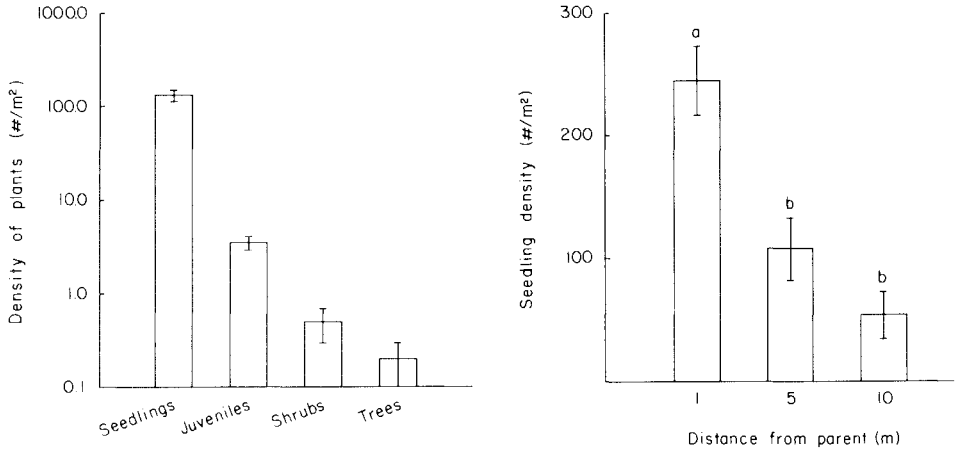


Figure 4.2: Density (log scale) of *Myrcianthes fragrans* seedlings, juveniles, saplings, and trees. Values are means  $\pm$  1 standard error.

(a) Seedling data are from the long-term plots (see page 65). Juvenile, sapling, and tree data represent densities within 10 meters of individual trees (see page 63).

(b) Mean density ( $\pm$  1 standard error) of seedlings in long-term study plots. Means that are not different at  $P < .05$  share the same letter.

determined for leaves, shoots, branches, vertical roots, and horizontal roots. Using a nested (transect nested within tree) ANOVA model, the data were analyzed using the GLM procedure in SAS (JOYNER (ed.) 1985).

## 4.4 Results

**Density and distance relationships** The mean and standard deviation of the distance between trees in the 11 plots was  $22.8 \pm 11.2$  meters ( $N = 62$ ; max = 51.3 m, min = 1.9 m). Within 10 m of each tree, the average distances to juveniles ( $7.0 \pm 1.9$ ), shrub-sized individuals ( $6.4 \pm 2.0$ ), and tree-sized individuals ( $6.2 \pm 1.5$ ) were not statistically different. Densities were, however, significantly different ( $P < .0001$ ) with juveniles  $>$  shrubs = trees (Fig. 4.2a). Within the long-term plots, seedling densities in 1984 differed significantly ( $P < 0.01$ ) as a function of distance to the source tree, with  $1 > 5 = 10$  m (Fig. 4.2b).

**Growth and mortality in long-term plots.** The shape of the mortality curves were similar for all three distances but the slopes were significantly different ( $P < .001$ ) and survivorship was greater at 5 and 10 m (Fig. 4.3). After almost 60

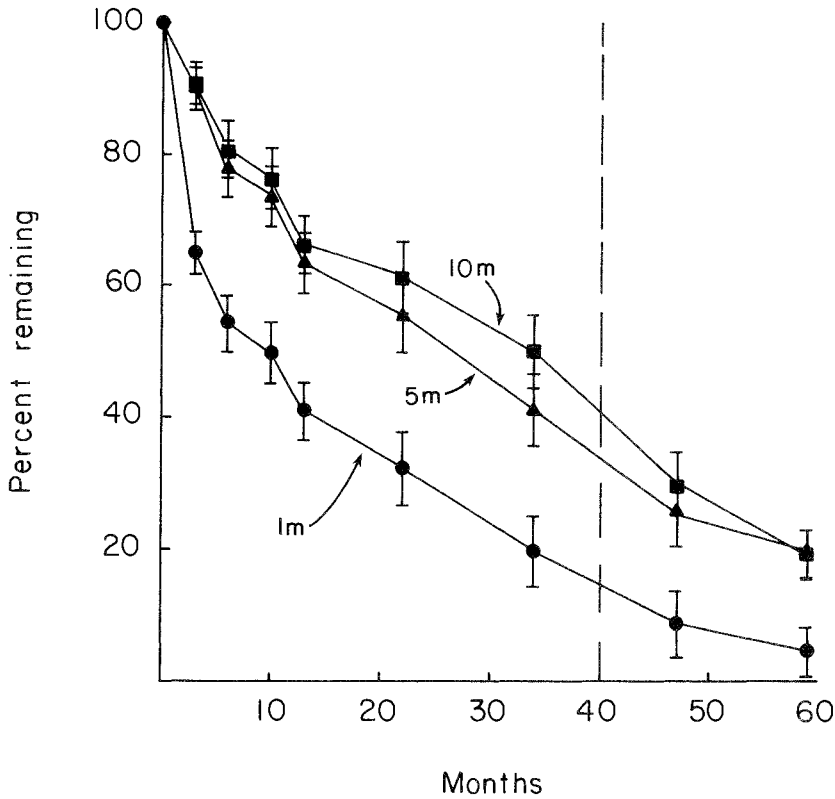


Figure 4.3: Survivorship curves for seedlings in long-term study plots at 1, 5, and 10 meters from parent trees. The vertical dashed line indicates when Hurricane Gilbert struck the study area in September, 1988.

months, only  $4.5 \pm 1.2\%$  of the original cohort of seedlings were alive at 1 m, compared with  $19.5 \pm 3.8$  and  $19.2 \pm 3.8\%$  at 5 and 10 m respectively. At each census, we were able to locate almost all seedlings and it was apparent that few had suffered from herbivore damage. Most dead seedlings were upright and had dried intact leaves attached. Most seedlings appeared to have died from drought stress although a few had been physically damaged from falling debris and a few others appeared to have died from shading as a result of being covered by fallen bark.

From April, 1985 to February, 1988, mean seedling height increased less than 1 cm at 1 and 5 m and only about 1.5 cm at 10 m (Fig. 4.4). Average annual height growth prior to the hurricane did not differ significantly between the three distances (Fig. 4.5). Annual growth rates increased significantly following the hurricane but



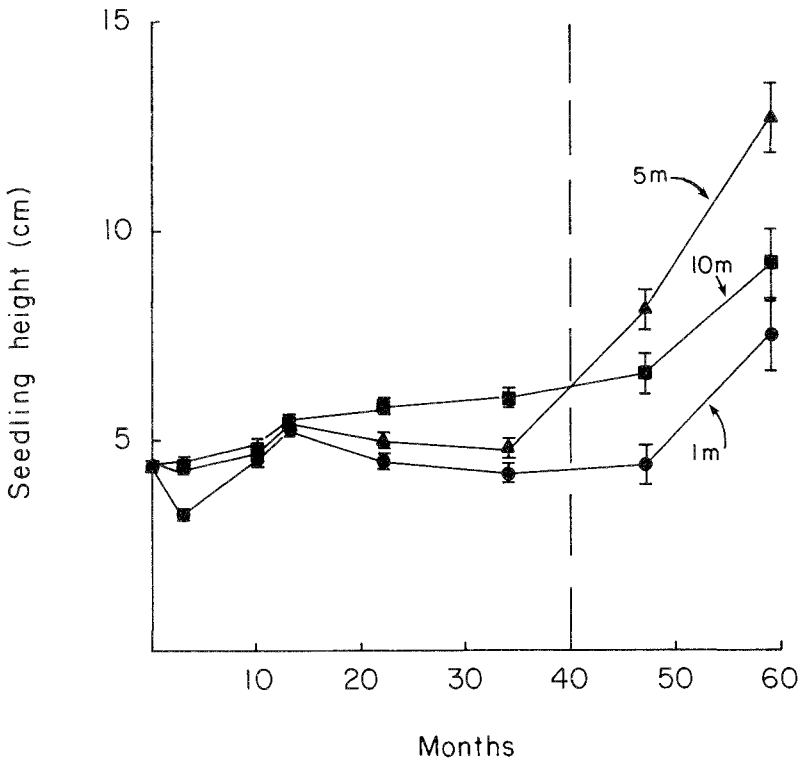


Figure 4.4: Height (cm  $\pm$  1 standard error) of seedlings at 1, 5 and 10 meters from parent plots. The vertical dashed line indicates when Hurricane Gilbert struck the study area in September, 1988.

the three distances were not significantly different even though the growth rate was less at 1 m (Fig. 4.5).

**Soil depth and distance from parent trees.** Large amounts of bark exfoliates from the trunk and large branches of *Myrcianthes* and a mound of litter develops that extends outward from the base of the tree to about 2.5 m (Fig. 4.6). Depth of the litter-soil layer at 0.1 m was significantly more ( $P < 0.01$ ) than greater distances. Depth of the litter-soil layer was also significantly greater at 0.5, and 1 m but there were no significant differences beyond 1.5 m where the soil depth was approximately 10 cm.

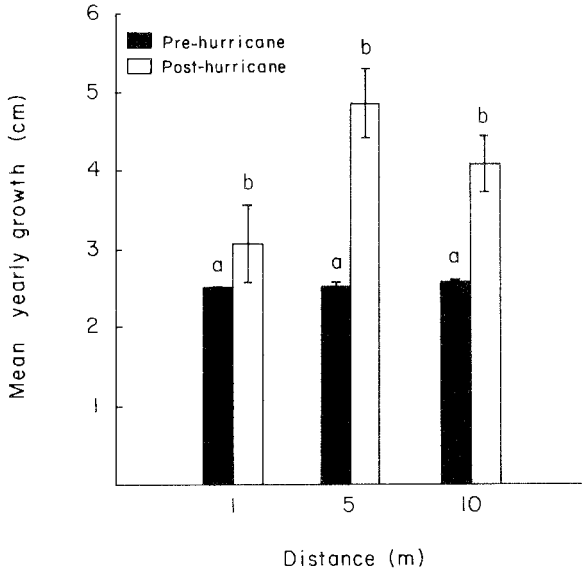


Figure 4.5: Average annual growth in height of *Myrcianthes* seedlings before (black bars: March 1984–March 1987) and after (Open bars: September 1988–March 1990) Hurricane Gilbert. Values are means  $\pm$  1 standard error.

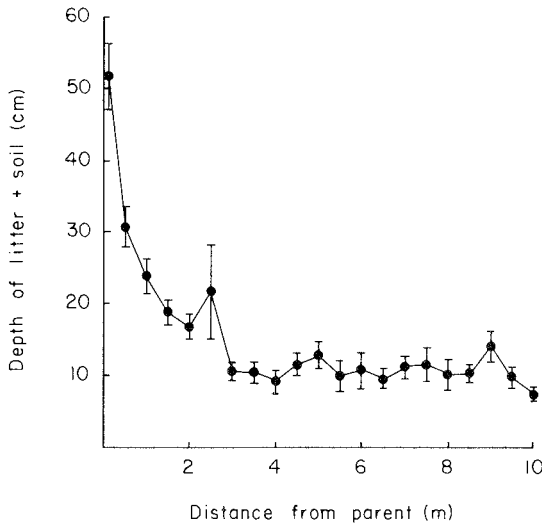


Figure 4.6: Depth of the litter-soil layer as a function of distance from trees. Values are means  $\pm$  1 standard error. Methods for sampling see page 65.

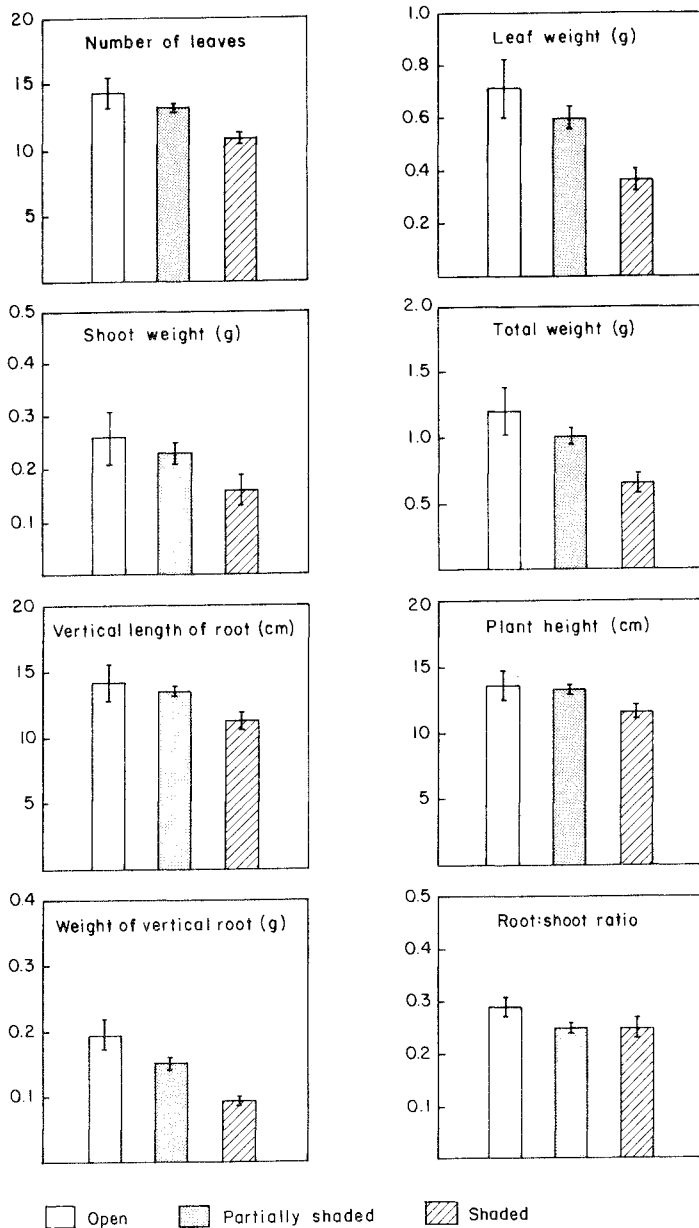


Figure 4.7: Growth parameters for *Myrcianthes* seedlings in shaded, partially shaded, and open microhabitats. Values are means  $\pm$  1 standard error. Microhabitat designations are as shown at the bottom of the figure.

Table 4.1: Results of linear regression analysis of growth variables against soil depth. N= 300.

VARIABLE	R <sup>2</sup>	INTERCEPT	SLOPE
Length of vertical root (cm)	.358	5.678	.560
Weight of vertical root (g)	.090	0.074	.005
Number of leaves	.058	10.475	.188
Length of horizontal root (cm)	.053	4.381	-.162
Plant height (cm)	.036	10.990	.158
Number of branches	.035	.144	.024
Weight of horizontal root (cm)	.035	.050	-.002
Weight of leaves (g)	.030	.395	.013
Weight of branches (g)	.023	.157	.005
Root:shoot ratio	.004	.266	-.001

**Seedling growth and microhabitat characteristics.** After 6 years of growth, soil depth showed almost no statistically significant relationship to any of the variables measured on harvested seedlings (Table 4.1). Length of the vertical root was the only variable for which soil depth accounted for more than 10 percent of the variance.

Although there were no significant differences in seedling growth rates with distance, there were significant microhabitat effects on growth following Hurricane Gilbert. In comparison with seedlings in open and partially shaded microhabitats, seedlings in shaded microhabitats were significantly shorter ( $P < .001$ ), had fewer leaves ( $P < .008$ ), less leaf biomass ( $P < .009$ ), shorter and smaller vertical roots ( $P < .046$ ), and less shoot and total biomass ( $P < .009$ ) (Fig. 4.7).

## 4.5 Discussion

Initially, seedling densities were highest beneath parent trees. Seedling mortality was greatest near the parent tree as predicted by the JANZEN-CONNELL hypothesis. However, herbivory or pathogens probably were not responsible for the higher levels of mortality observed near parent trees. As indicated, almost all marked seedlings appeared to have died from physical damage (crushing or breaking of the stems), shading, drought stress or some combination of those factors.

AIDE (1987) and CLARK and CLARK (1989) found that seedling mortality due to physical damage was common in moist tropical forests. Mortality due to direct physical damage was of minimal importance in this study, even during the most intense hurricane ever measured in the Western Hemisphere. We found very few

seedlings that had died as a result of direct impact (i. e., broken stems) from fallen branches. A few seedlings were killed by direct impact from fallen objects before and after the hurricane but most appeared to die from shading that resulted from being covered by exfoliated bark (before the hurricane) or by woody debris (after the hurricane).

Although we have no direct measurements of seasonal variation in available soil water, we believe that drought was the primary cause of mortality. The soils are very shallow (Fig. 4.6) and contain very little water, especially during the dry season when many plants appear to be water stressed. These results contrast with AIDE and ZIMMERMAN (1990) who suggested that seedling growth in the forest understory may be enhanced during dry periods because of increased light and soil moisture due to less evapotranspiration from leafless canopy trees. Other factors such as nutrient availability may also be important but soil depth is not as it was related to only one seedling growth parameter, length of the vertical root.

Light also appeared to be an important factor that limited seedling growth and perhaps survivorship (AUGSPURGER 1984a, AUGSPURGER 1984b, BROKAW 1985, DENSLOW et al. 1990, UHL et al. 1988, CLARK and CLARK 1989, DENSLOW 1987). Prior to the hurricane, light levels were very low (mostly < 1%) in the forest understory and the average seedling height increased very little during the 40 months before the hurricane. Seedling growth measured after the hurricane indicated that seedling in shaded microhabitats grew significantly less than seedlings growing in open and partially shaded areas. These findings agree with those of others (e. g., UHL et al. 1988, AIDE and ZIMMERMAN 1990) who have found that variations in light conditions played an important role in controlling the growth of woody seedlings in moist tropical forests.

Following the seedlings stage, patterns of mortality must remain spatially constant for many years. We found surprisingly constant mean distances (ca. 7 m) from parent trees to juveniles and saplings. Survival to tree size near parent trees can occur (HUBBELL 1980) in tropical forests but is probably uncommon. The average distance between adults exceeded 20 meters and, within the 1600 m<sup>2</sup> plots, only three of the sixty-two nearest neighbor interplant distances were less than 5 meters.

We do not know the causes of mortality for individuals larger than seedlings but hurricanes may be more important than all other factors combined. Of 38 *Myrcianthes* trees in the eleven 1600 m<sup>2</sup> plots, one (2.6%) died (cause of mortality unknown) between 1984–1988, compared with 12 (31.6%) as a result of Hurricane Gilbert. Trees of all species in the forest were defoliated and suffered varying degrees of canopy damage during the hurricane. For *Myrcianthes*, two large (DBH > 50 cm) individuals were uprooted during the hurricane, two completely defoliated trees never sprouted, and the other eight individuals died even though they had initially sprouted.

Perhaps more damaging to trees, however, were widespread fires which occurred during the dry season after the hurricane. Although Rancho San Felipe itself was

mostly protected, two small areas burned when fire jumped the fire lane that had been cut around the ranch. In one of these areas, we established four 1600 m<sup>2</sup> plots and sampled all trees greater than 10 cm DBH. The number of trees in the four plots averaged  $93 \pm 15$  (1 standard error) and mortality averaged  $89.3 \pm 3.9\%$ , a mortality level typical of other areas in northern Yucatan that burned during the same period (Ingrid Olmsted, personal communication). All 18 *Myrcianthes* trees in the plots were killed and we found only two surviving saplings in one of seventy-two plots (each plot was 4 × 4 m) sampled within the four larger plots. Clearly, the distribution and abundance of *Myrcianthes* can be influenced by both hurricanes and subsequent fires.

In summary, we found evidence to support almost every hypothesis about the distribution, abundance, and growth of seedlings and trees. Data from long-term plots support the hypothesis that mortality is greatest near parents. Mortality of *Myrcianthes* seedlings was greatest within one meter of parent trees but the primary cause did not appear to be herbivory and disease but physical damage and shading caused by exfoliated bark. These findings support the hypothesis that direct and indirect damage caused by fallen objects may be one of the most important causes of seedling mortality (AIDE 1987, CLARK and CLARK 1989). Between-tree distance data support the hypothesis that few plants survive beneath their parent but, like HUBBELL (1980), we found a few individuals growing close to each other.

Our data suggest that *Myrcianthes* has adopted a "sit-and-wait" approach to reproduction and growth. Individuals do not produce seeds regularly (ca. only once in the six years of this study) and seedlings growth in the understory is very slow and appears to be primarily light limited. If seedlings can survive long enough, however, a canopy disturbance (i. e., single-tree death or large disturbances such as those caused by the hurricane) may occur and subsequent growth may no longer be as strongly light-limited. In the case of single-tree disturbances, we agree with UHL et al. (1988) who suggested that individuals that are recruited into gaps or are present as seedlings would only reach the canopy after multiple disturbances. Seedlings, juveniles, and saplings would have a greater probability of reaching the sub-canopy or canopy following a single large-scale disturbance that defoliates and causes extensive damage to trees. Even in this instance, however, it seems likely that only larger (i. e. small tree-sized individuals) would reach the canopy after a single disturbance event because the canopy reforms rather quickly (unpublished data). Perhaps most important, this study demonstrates that endogenous (e. g., seed dispersal, seedling predation and herbivory etc.), factors that control the distribution patterns of trees in dry tropical forests may be less important than exogenous factors (e. g., hurricanes, fires). Because most seedling studies have been conducted in moist tropical forests, many more species-specific comparisons of this sort are needed before we can begin to understand the dynamics of tree populations in dry tropical forests.

## Acknowledgments

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