THE EFFECT OF ANNUAL VARIATION IN PRECIPITATION ON GROWTH AND LITTER PRODUCTION IN A TROPICAL DRY FOREST IN THE YUCATAN OF MEXICO

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Abstract: We describe the responses of a tropical dry forest to variations in rainfall over a four year period. Long-term study plots (1600 m^2) were established in 1984 and DBH measurements of trees were made annually. Leaf litter and litter of flowers, fruits, and other reproductive parts were measured regularly over the same time period. There were significant annual differences in tree growth and leaf litter production and the differences were correlated with differences in precipitation. Annual precipitation totals varied by almost 600 mm during the four years and the number of months with no precipitation during the dry season ranged from 5.5 to 0. Annual rates of tree growth were most closely related to the sum of precipitation in the current and previous year. Annual leaf litter production was correlated with the amount of precipitation in the current year. There were no annual differences in the biomass of reproductive materials collected in litter traps.

Résumé: Les auteurs ont dècrit les réponses d'une forét sèche tropicale aux variations des précipitations au cours de quatre ans. Les parcelles expérimentales (1600 m^2) pour une étude à long terme, ont été établies en 1984 et les mesures de DBH (DBH>10 cm) ont été effectuées chaque année. Les litiéres de feuilles, fleurs, fruits et autres organes de reproduction ont été mesurées réguliérement pendant la même période. On a observé des différences annuelles significatives en ce qui concerne la croissance des arbres et la production de la litiére de feuille; ces différences sont liées aux variations des précipitations. Les précipitations totales annuelles ont varié de presque 600 mm pendant les 4 ans et le nombre de mois sans précipitation pendant la saison sèche a varié de 0 a 5.5. Les taux annuels de la croissance des arbres montrent une relation étroite avec la somme des précipitations de l´année en cours et celles de l'année précédente tandis que la production annuelle de la litière de feuilles est liée à la précipitation de l'année en cours. On n'a pas relevé de différences annuelles dans la biomasse des organes reproducteurs récoltes dans les piāges ē litiére.

Resumo: Os autores descrevem as respostas de uma floresta tropical sêca as variaçaes da precipitação durante um período de quatro anos. Em 1984 foram establecidas parcelas premanentes de 1 600 m^2 tendo-se procedido à medida anual do DAP. A biomassa caída respeitante às folhas, flores, frutos e outros orgãos reprodutivos foi regularmente medida para os mesmos intervalos de tempo. Varificou-se existirem diferenças anuais significativas no crescimento arbóreo e na produção de folhada na dependência da precipitação. As precipitações anuais totais variaram quase 600 mm durante os quatro anos, e o número de meses sem precipitação durante a estação sêca variou entre os 5,5 e os 0. As taxas anuais de crescimento das árvores mostraram-se muito estreitamente relacionadas com com a soma da precipitação no ano corrente e no anterior. A produção anual da folhada esteve igualmente correlacionada com o quantitativo da precipitação do ano corrente. Não se verificaram diferenças anuais na biomassa do material reprodutivo colectado nos colectores de folhada.

Key Words: Yucatan, Mexico, tree growth, mortality, litter production, Neotropics, tropical dry forest, precipitation.

INTRODUCTION

Tropical dry forests cover more area than humid tropical forests yet there have been few studies of their structure and function even though they are heavily affected by man's activities (Murphy & Lugo 1986a). Although one of the most important features of tropical dry forests is the high seasonal and annual variation in precipitation (Murphy & Lugo 1986a, Kelly *et al.* 1988), there have been few multi-year studies of how tropical forests with a distinct dry season respond to variations in precipitation (Breitsprecher & Bethel 1990, Borchert 1980, Daubenmire 1972, Frankie *et al.* 1974, Lieberman 1982, Murphy & Lugo 1986b, Newton 1988, Reich & Borchert 1982, 1984). In this paper we report results from an ongoing long-term study in a tropical dry forest on the Yucatan Peninsula. Our objective is to characterize the effects of annual variation in precipitation on basal area growth, litter production, and mortality over a four year period when annual precipitation varied almost threefold.

LOCATION AND CHARACTERIZATION OF THE STUDY SITE

The study site is located south of Cancun near the village of Puerto Morelos (20°49´N, 87°7´W) in Quintana Roo (fig. 1). Longterm climatic data from weather stations across the Yucatan show that the entire peninsula is characterized by a distinct period of low precipitation (Walter & Lieth
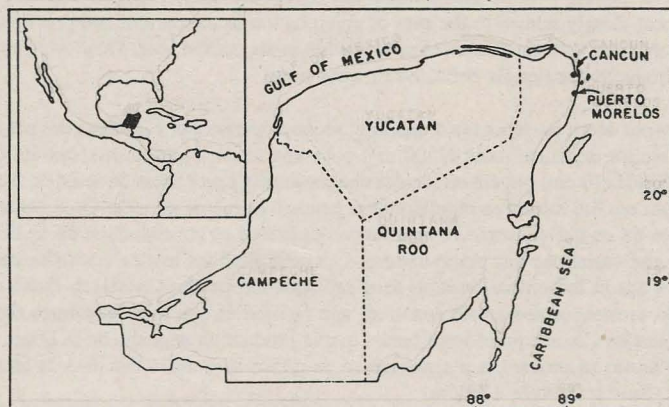

FIG. 1. Map of the Yucatan Peninsula showing the location of Puerto Morelos which is approximately 10 km North of the study site.

1967). Based on annual precipitation and temperature data at Valladolid (Fig. 2) the area would support either tropical dry or very dry forest in the Holdridge system (Holdridge *et al.* 1971). Miranda (1958) classified forests in the northeastern part of the Yucatan as Selva mediana subperennifolia because of the presence of both evergreen and deciduous species.

Prior to extensive damage caused by Hurricane Gilbert in September 1988 (Olmsted *et al.* 1989), there was no evidence of recent disturbance to the forest at the study site. Past human activities appear to have been limited to the extraction of sap used in chewing gum from *Manilkara zapota*
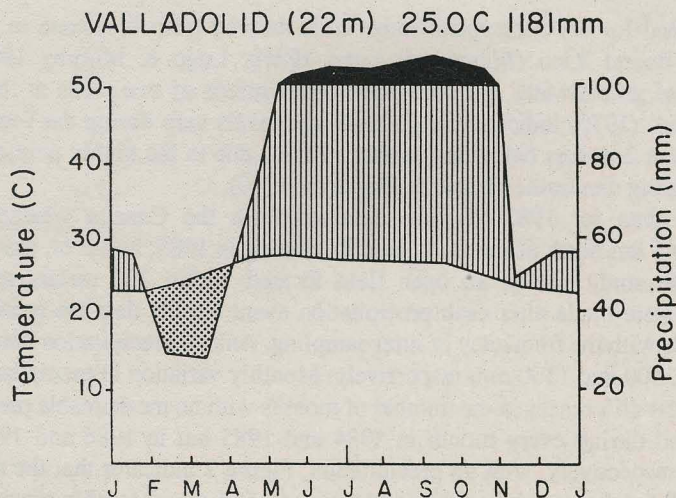
VALLADOLID (22m) 25.0 C 1181mm

FIG. 2. Climate diagram for Valladolid which is located approximately 135 km West of the study site. The long term mean for temperature and precipitation are given in the upper right corner. The relationship between temperature and precipitation suggest 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 temperture 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. Elevation of the station at Valladolid is 22 m.

(L.) van Royer and the removal of palms (*Thrinax radiata* Lodd. ex J.A. Schult, *Coccothrinax readii* Quero) and small understory trees (e.g., *Bursera simaruba* (L.) Sarg. and *Gymnanthes lucida* Swartz) for local construction materials. Historically, there has been minimal agricultural activity in this part of the Yucatan and the forests have been shown to provide important habitat for migratory birds (Lynch 1989, Lynch *et al.* 1985).

Canopy height is variable but is usually between 10 and 20 m. Fifty five species occurred in the three study plots and seven species (*Manilkara zapota, Talisia olivaeformis* (HBK.) Radlk., *Gymnanthes lucida* Swartz, *Brosimum alicastrum* Swartz, *Drypetes lateriflora* (Swartz) Drug & Urban, *Sapindus saponaria* L., and *Coccoloba diversifolia* Jacq. accounted for 64% of all individuals > than 10 cm in diameter. The mean basal area (24.7 ± 2.0 m²/ha and 343 ± 23 cm²/tree) and number of species in the three plots are at the low end of the ranges reported for dry tropical forests by Murphy & Lugo (1986a). We have recorded, however, more than 125 tree and shrub species in the vicinity of the plots which would place the forest in the range given for wet forests (Murphy & Lugo 1986a). Trees less than 30 cm DBH dominated the three plots as indicated by the following size-class distribution for the 346 individuals: 10-20 cm DBH = 236, 20-30 cm DBH = 75, 30-40 cm DBH = 19, 40-50 cm DBH = 10, > 50 cm DBH = 6).

Soil at the study site, called tzekel ekluum in the Mayan language, is classified as litosol-redzina (Escalante 1986) and is derived from weathered Miocene and Pliocene material (Back & Hanshaw 1970, West 1964). The soil is very shallow (Whigham & Cabrera. In press) and occurs in pockets between rocks exposed on the surface. The average (± 1 standard error) organic matter content (51.5 ± 5.1% ; N = 36) and pH (7.1 ± 0.1 ; N = 36) of soil samples collected at the site are similar

to those described for dry subtropical forest soils derived from limestone in Jamaica (Kelly *et al.* 1988) and Puerto Rico (Murphy & Lugo 1986b, Lugo & Murphy 1986). We have no measurements of groundwater but qualitative observations of two wells at the site and data in Back & Hanshaw (1970) indicate that groundwater levels vary during the year but that they ar usually more than 2 meters below the surface. This is due to the highly permeable nature of the soil and underlying limestone (Back & Hanshaw 1970).

Precipitation data for 1983-85 were obtained from the Cancun weather station, located approximately 45 km north of the study site. Beginning in 1985, however, precipitation was also measured at the study site in an open field located within 100 meters of the study plots. Measurements were made after each precipitation event but the data are reported on a monthly basis to coincide with the frequency of litter sampling. Annual precipitation between 1983-87 was 1331, 870, 485, 500 and 1100 mm respectively. Monthly variation in precipitation was large and there were annual differences in the number of months with no measureable precipitation (Fig. 3). Precipitation fell during every month in 1984 and 1985 but in 1986 and 1987 there were 5.5 and 2 months, respectively, with no precipitation. Figure 2 indicates that the minimal long-term monthly rainfall for the areas should be approximately 25 mm. Monthly precipitation at Cancun and/or the study site (Fig. 3) fell below that value on 14 occasions during the study period.

METHODS

We report data from three 40 x 40 m plots which were established in January-February, 1984. All trees > 10 cm DBH were tagged, identified and DBH was measured at a marked height. Nomenclature follows Chavelas (1982), Durán (1983), Olmstead *et al.* (1983), Sosa & Cabrera (1983), Sánchez (1987) and Tellez & Cabrera (1987). Plots were censused and trees measured during the same two week period each year. Annual growth was calculated on a basal area basis (cm^2/tree and m^2/ha) and for diameter increments (mm) of individual trees. When DBH decreased from one year to the next, a pattern that is not uncommon in dry tropical forests (Daubenmire 1972, Lieberman 1982, Murphy & Lugo 1986a), growth was assigned a value of zero. Trees which died during the study were not included in the data analysis.

Five litter collectors (each 1m × 1m) were randomly placed in each plot in Februrary 1984. The collectors, made of wood framed poultry wire lined with plastic window screen, were held above the soil with rocks. They were visited each month but litter samples were collected only if a measureable amount of material was present. In the field, litter samples were separated into leaves and reproductive parts (flowers, fruits, and floral parts) and weighed to the nearest 0.1gm. Subsamples were then dried to constant weight to determine the moisture content for conversion of wet weight data to dry weight equivalents.

Analysis to variance (ANOVA) was used to test for yearly differences in litter production and yearly differences in basal area growth on a plot basis. Repeated measures analysis of covariance (ANCOVA) was used to test for yearly differences in species basal area increments. Intial DBH was used as the covariate in the ANCOVA. Differences between means for litter production and basal area increments were compared with Tukey tests when the ANOVA and ANCOVA tests were significant at least at $P \leq 0.05$. Linear regression analyses were used to compare annual basal area increment and litter production with annual precipitation for the current and previous years. Leaf litter data for each sampling period were also compared with precipitation data for:1. the month that the litter was collected, 2. the month before the litter was collected, 3. the current month
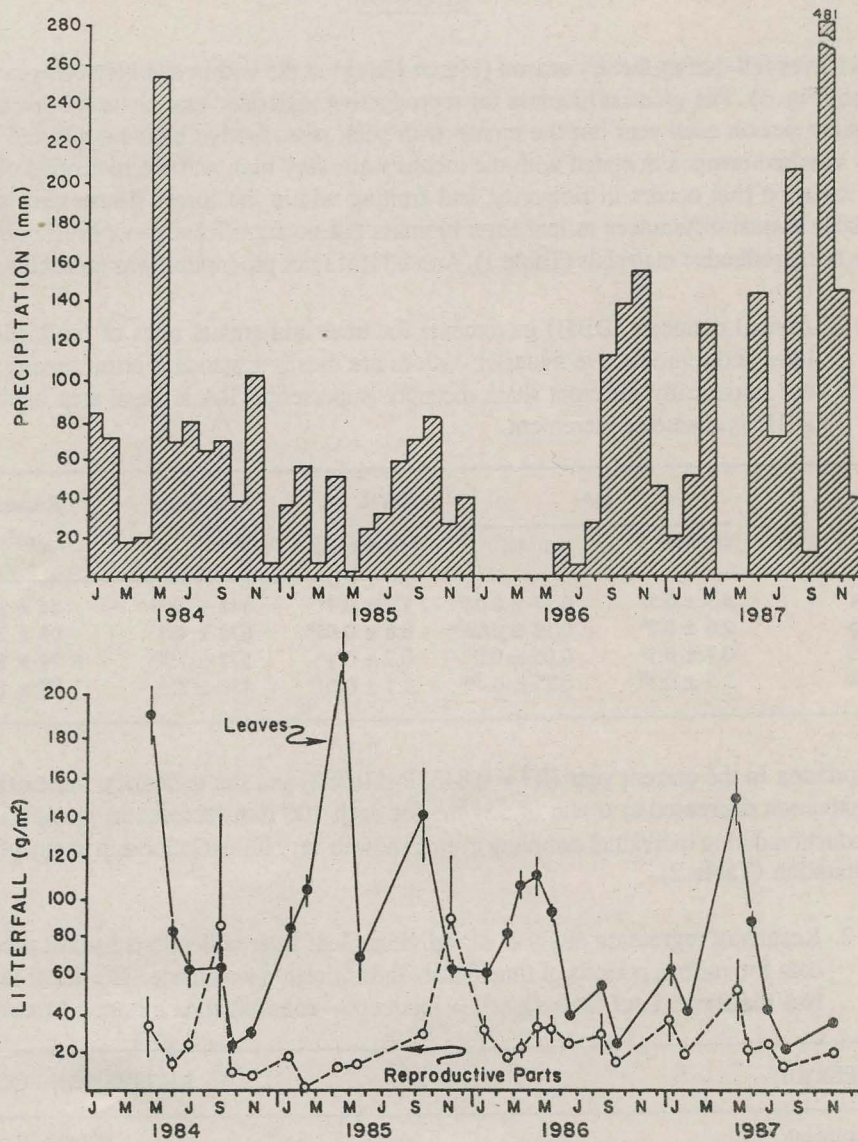
Fig. 3. Precipitation (mm) and litterfall production in g/m^2 (leaf and reproductive materials) between 1984 and 1987. Total yearly precipitation was 870 mm in 1984, 485 mm in 1985, 500 mm in 1986, and 1100 mm in 1987. Values for litter and reproductive material are means ± 1 standard error.

and month before the litter was collected, 4. two months before the litter was collected, 5. three months before the litter was collected, 6. four months before the litter was collected, and 7. the entire dry season. All statistical comparisons were made with PC-SAS (Joyner 1985).

RESULTS

Most leaves fell during the dry season (March-May) but the within and between year variation was high (Fig. 3). The greatest biomass for reproductive materials was measured toward the end of the rainy season each year but the month with peak reproductive biomass differed each year and the standard errors associated with the means were very high and are indicative of the large spatial variation that occurs in flowering and fruiting within the forest. There were singificant ($p \leq 0.001$) annual differences in leaf litter biomass but no significant annual differences in the biomass of reproductive materials (Table 1). Annual leaf litter production was most closely related

TABLE 1. Annual diameter (DBH) increments for trees and annual rates of production of leaf litter and reproductive material. Values are means ± standard error; means which are not statistically different share the same superscript. BA is basal area increment and DBH is diameter increment.

Year	BA		DBH	Leaf Litter	Reproductive
	cm^2/tree	m^2/ha	(mm/tree)	(g/m^2)	(g/m^2)
1984	5.5 ± 0.5^a	0.37 ± 0.04^a	1.7 ± 0.1^a	448 ± 38^{bc}	84 ± 28^a
1985	2.6 ± 0.2^b	0.18 ± 0.03^{bc}	0.8 ± 0.05^b	672 ± 45^a	95 ± 20^a
1986	0.7 ± 0.1^c	0.05 ± 0.1^c	0.2 ± 0.1^c	577 ± 15^{ab}	79 ± 11^a
1987	3.5 ± 0.3^b	0.25 ± 0.4^{ab}	1.1 ± 0.01^b	430 ± 25^c	72 ± 10^a

to precipitation in the current year ($R^2 = 0.843$, $P \leq 0.082$) and the regression indicates that leaf litter production decreased at a rate of $35g/m^2$ for each 100 mm increase in precipitation. Leaf litter production during individual sampling events showed very little relationship to any prior period of precipitation (Table 2).

TABLE 2. Results of regression analysis of individual leaf litter collections against precipitation data for various periods of time before the collection was made. The linear regressions had the form: Leaf litter (g/m^2) = intercept - constant (precipitation in mm).

TIME PERIOD	R^2	REGRESSION EQUATION
Current month	0.004	78.981 - 0.044 (ppt)
Current and previous month	0.075	89.299 - 0.099 (ppt)
Previous month	0.112	86.900 - 0.167 (ppt)
Two previous months	0.078	90.267 - 0.118 (ppt)
Three previous months	0.066	91.524 - 0.089 (ppt)
Four previous months	0.068	93.201 - 0.076 (ppt)
Dry season	0.230	343.134 - 0.198 (ppt)

There were significant ($p \leq 0.001$) between-year differences in annual rates of basal area increase and on an individual tree basis, only 1985 and 1987 were not significantly different from each

other (Table 1). On a plot basis (m^2/ha) the annual pattern was similar but the yearly differences were not as distinct due to the larger variation (Table 1). The relationship between basal area increase and the sum of precipitation in the current and previous year was highly significant (Fig. 5; R^2= 0.986; $p \leq 0.007$). The slope of the regression equation indicates that a 100 mm increase in precipitation for the two years combined resulted in a 0.4 cm^2/tree increase in basal area.
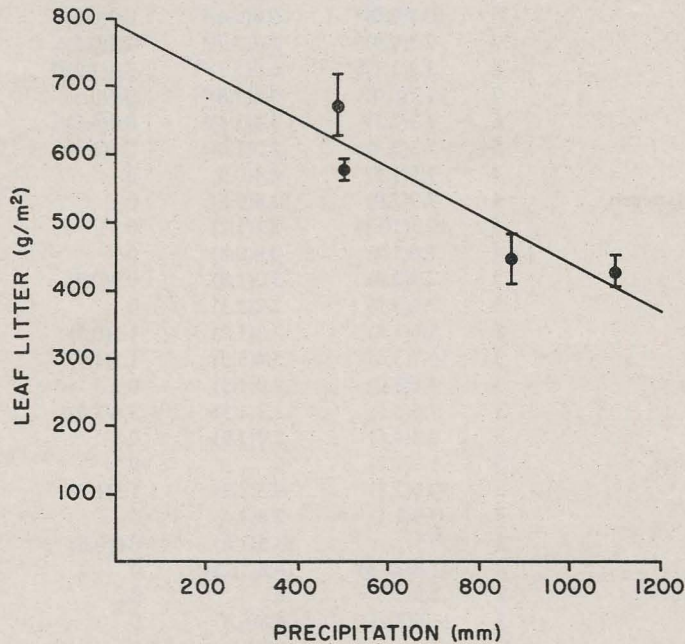

FIG. 4. Comparison of leaf litter production (g/m^2) and precipitation (mm) in the current year. The equation for the linear regression line is: Leaf litter production = 790.17 - 0.35 (precipitation) [$R^2 = 0.843$, P \< .082]. Values are means ± 1 standard error.

Annual patterns of basal area increase were similar for almost all tree species, although between-year differences were statistically significant only for the most abundant species (ie., > 6 individuals in the three plots; Table 3). When data for species with five or fewer individuals were combined, annual basal area increase was significantly different for all years (Table 3). Many species showed no measurable growth in 1986, but growth was positive in the other three years (Table 3). Tree mortality totals were: 1984 = 0, 1985 = 2, 1986 = 6, 1987= 1.

TABLE 3. Basal area increase of species in the study plots. Growth is given as basal area increment per year (cm^2/tree). N is the number of individuals in the three plots. Values are means ± 1 standard error in parenthesis. For species with N ≥ 6, years that did not differ significantly (P ≤ 0.05) share the same superscript. The last entry in the table represents mean values for all species with 5 or fewer individuals. Authorities for the species are given at the end of the table.

SPECIES	N	1984	1985	1986	1987
Manilkara zapota	74	6.2(0.9)[a]	3.1(0.4)[b]	0.2(0.1)[c]	4.8(0.5)[ab]
Talisia olivaeformis	40	2.3(0.7)[a]	1.3(0.3)[ab]	0.4(0.2)[b]	0.9(0.3)[b]
Gymnanthes lucida	41	1.9(0.3)[a]	1.3(.03)[ab]	0.7(0.2)[b]	1.2(0.3)[ab]
Brosimum alicastrum	30	9.1(1.7)[a]	2.1(0.4)[bc]	0.3(0.3)[c]	4.2(1.3)[b]
Drypetes lateriflora	29	3.0(1.0)[a]	1.6(0.4)[ab]	0.5(0.2)[b]	3.3(0.7)[a]
Sapindus saponaria	13	10.2(3.0)[a]	0.8(0.6)[b]	0.9(0.6)[b]	3.8(1.5)[b]
Coccoloba diversifolia	12	2.3(0.9)[a]	2.7(0.7)[a]	1.3(0.5)[a]	1.4(0.8)[a]
Beaucarnea pliabilis	8	3.2(1.1)[a]	6.0(1.3)[ab]	2.3(1.2)[ab]	0.7(0.4)[b]
Bursera simaruba	7	11.7(6.0)[a]	5.6(1.8)[b]	0.9(0.5)[c]	12.3(3.8)[a]
Myrcianthes fragrans	6	2.3(2.3)[a]	3.4(3.4)[a]	6.6(4.6)[a]	15.8(6.1)[a]
Neea psychotrioides	5	7.3(3.4)	2.0(1.0)	0.4(0.4)	2.3(0.8)
Tabebuia chrysantha	4	1.5(1.5)	4.4(0.9)	0	6.7(2.7)
Mastichodendron foetidissimum	4	7.9(7.9)	12.8(9.6)	0	8.8(3.3)
Ceiba aeseulifolia	4	17.3(10.3)	2.1(1.2)	0	4.5(3.7)
Antirhea lucida	4	1.6(1.2)	0.8(0.8)	0	1.7(1.0)
Calyptranthes pallens	3	2.9(2.9)	5.0(1.9)	0.9(0.9)	0
Nectandra coriacea	3	7.8(3.5)	2.2(2.1)	0	0.7(0.7)
Exothea diphylla	3	1.8(1.8)	2.3(1.2)	1.3(0.5)	1.6(1.6)
Acacia dolichostachya	3	16.7(3.4)	5.4(3.5)	1.1(1.1)	7.4(3.8)
Maytenus guatemalensis	3	4.8(3.0)	2.9(1.5)	0	1.2(1.2)
Thouinia paucidentata	3	7.6(5.5)	1.3(1.3)	3.8(3.8)	5.5(0.6)
Guettarda combsii	3	9.4(4.6)	2.7(1.9)	0	5.5(0.6)
Gymnopodium floribundum	3	1.9(1.1)	0	0	0.6(0.6)
Gliricidia sepium	3	12.6(2.3)	5.5(2.8)	1.5(1.5)	5.6(3.8)
Krugiodendron ferreum	3	3.9(2.1)	2.4(1.4)	0	3.2(2.1)
Wimmeria sp.	3	0	3.5(1.8)	0.6(0.6)	1.9(1.1)
Vitex gaumeri	2	41.8(24.8)[a]	16.8(16.8)[a]	0	0
Coccoloba spicata	2	2.9	0	0	8.2
Cordia gerascanthus	2	11.8(8.2)	6.8(6.8)	0	10.7(3.8)
Coccoloba acapulcensis	2	0	2.0	0	0.9
Enriquebeltrania sp.	2	4.5	1.8	0	2.6
Lonchocarpus rugosus	2	5.8(5.8)	0	0	5.9(1.2)
Malmea depressa	2	4.4(0.9)	1.8(0.0)	0	3.5(0.1)
Bumelia laetevirens	2	0	3.5(1.8)	0	0.9(0.9)
Guaripa linearibracteata	1	11.1	7.4	0	3.7
Astronium graveolens	1	0	12.3	0	0
Casearia nitida	1	7.7	0	0	3.9
Lonchocarpus yucatanensis	1	0	1.7	0	0
Acacia gaumeri	1	0	0	0	7.1
Spondias sp.	1	0	0	3.8	0
Schoepfia schreberi	1	10.5	2.7	2.7	2.7
Jacquinia schippii	1	0	0	2.0	0
Pouteria unilocularis	1	0	2.2	2.2	0
Swartzia cubensis	1	0	9.4	0	3.3
Caesalpinia yucatanensis	1	1.1	0	1.9	3.9
Eugenia sp.	1	1.6	2.7	0	3.2
Metopium brownei	1	0	0	0	0
Lysiloma latisiliquum	1	3.1	3.1	0	6.3
Coccoloba swartzii	1	0.	0	0	7.6
Adelia barbinervis	1	3.5	1.8	0	1.8
Unknown species	1	0	0.7	0	6.6
Species with ⩽ 5 individuals	69	5.8(1.0)[a]	2.6(0.4)[b]	0.6(0.2)[c]	3.1(0.5)[b]

Authorities for species given in the table: *Manilkara zapota* (L.) van Royer, *Talisia olivaeformis* (HBK.) Radlk., *Gymnanthes lucida* Swartz, *Brosimum alicastrum* Swartz, *Drypetes lateriflora* (Swartz) Drug & Urben, *Sapindus saponaria* L., Coccoloba diversifolia Jacq., *Beaucarnea pliabilis* (Baker) Rose, *Bursera simaruba* (L.) Sarg., *Myrcianthes fragrans* (Swartz) McVaugh, *Neea psychotrioides* Donn. Smith, *Tabebuia chrysantha* (Jacq.) Nicholson, *Mastichodendron foetidissimum* subsp. *gaumeri* (Pittier) Cronq., *Ceiba asculifolia* (HBK.) Britton & Baker, *Antirhea lucida* Swartz., *Calyptranthes pallens* Griseb., *Nectandra coriacea* (Swartz) Griseb., *Exothea diphylla* (Standl.) Lundell, *Acacia dolichostachya* Blake, *Maytenus guatemalensis* Lundell, *Thouinia paucidentata* Radlk., *Guettarda combsii* Urban, *Gymnopodium floribundum* var *antigonoides* (Robin) Standl. & Steyerm, *Gliricidia sepium* (Jacq.) Steud., *Krugiodendron ferreum* (Vahl) Urban, *Vitex gaumeri* Greenm, *Coccoloba spicata* Lundell, *Cordia gerascanthus* L., *Coccoloba acapulcensis* Standl., *Lonchocarpus rugosus* Benth., *Malmea depressa* (Baillon) E.E. Fries, *Bumelia laetevirens* Hemsl., *Guaripa linearibracteata* (heimerl) Lundell, *Astronium graveolens* Jacq., *Casearia nitida* Jacq., *Lonchocarpus yucatanensis* Pittier, *Acacia gaumeri* Blake, *Schoepfia schreberi* Gmel., *Jacquinia schippii* Standl., *Pouteria unilocularis* (Donn. Smith) Baehni, *Swartzia cubensis* (Britt & Wils.) Standl., *Caesalpinia yucatanensis* Greenm., *Metopium brownei* (Jacq.) Urban, *Lysiloma latisiliquum* (L.) Benth., *Coccoloba swartzii* Meisner, *Adelia barbinervis* Cham. & Schlecht.

DISCUSSION

Murphy & Lugo (1986a) reviewed the literature on dry tropical forests and emphasized the overriding importance of the relationship between precipitation and soil water availability. They concluded that leaf turnover is sensitive to water availability, that leaf fall occurs earlier during dry years, and that extremely dry years play a key role in molding structural characteristics of dry forests. Borchert (1980), Daubenmire (1972), and Reich & Borchert (1984) found that seasonal patterns of tree development were highly variable among species and that growth and development were influenced by variations in tree water stress more than by differences in the availability of soil water. Most generalizations about ecological processes in dry tropical forests have, however, been based on short-term studies and Murphy & Lugo (1986a) suggested that long-term studies will be required to test the generality of their findings. The first four years of this ongoing study encompassed almost a three-fold difference in annual precipitation and the results to date can be used to evaluate some of the generalizations summarized above.

As predicted (Leigh & Smythe 1978; Proctor 1984; Lugo *et al.* 1978), litter fall was greatest during the dry season and annual leaf litter production was negatively related to annual precipitation (Fig. 4). As predicted by Murphy & Lugo (1986a), leaf fall also began earlier during the years with the least total precipitation (Fig. 3). Annual leaf litter production was not, however, influenced by the distribution of precipitation within the dry season as we found no significant relationship when litter production during individual sampling events was compared to recent amounts of precipitation or precipitation during the dry season (Table 2). Extended periods with little or no precipitation also appeared to have little influence on litter production. Both leaf litter production and total precipitation were quite similar in 1985 and 1986, even though there were 5.5 months without measurable precipitation in 1986 compared with 0 months in 1985. Similarly, leaf litter production in 1984 and 1987 were not statistically different even though there were two months without any measurable precipitation in 1987. These findings support the suggestion that precipitation may only have a very general control on leaf fall. This conclusion is also supported by Wright & Cornejo (1990) who have been working in Panama in a wet tropical forest but with a distinct dry season. They hypothesized that vapor pressure dificits cue leaf fall because leaf loss was related to water stress in very few species.

Variation in either the total amount or the temporal pattern of precipitation seems to have little
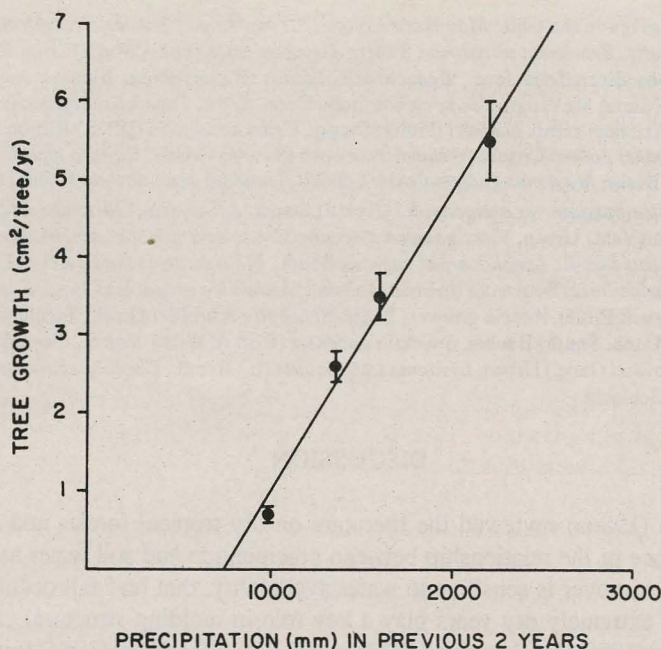
effect on the annual production of reproductive materials, but this conclusion must be tentative as much of the fruit and seed production may have been consumed by animals before being sampled. The large standard errors that characterized the data for reproductive parts (Fig. 3) also reflects the spatial and temporal variability of reproductive output within the forest.

Annual rates of basal area increment were much more sensitive to variations in precipitation than were annual rates of leaf litter production. Annual basal area increase varied nearly eightfold (0.7-5.5 cm²/tree) during the four years, whereas variation in leaf litter production was much less (430-672 g/m²). Although the data only cover four years, we found a highly significant relationship between annual rates of basal area increment and total annual precipitation in the current and previous years. Reich & Borchert (1984) also found evidence for moisture stress control on tree growth in dry tropical forests in Costa Rica. Breitsprecher & Bethel (1990), however, found litttle relationship between tree growth and precipitation and proposed that variations in daily solar radiation were the most important environmental triggers of growth. Their findings from the wetter forests at La Selva, however, might not be as applicable to dry tropical forests. Comparison of annual rates of basal area increase for individual species lends further support for the importance of precipitation in dry tropical forests. In three out of four years, annual rates of basal area increase varied dramatically among the twelve most abundant tree species (Table 3), but interspecific differences were virtually nonexistent in 1986 when the increment rates for all species except *Sapindus saponaria, Coccoloba diversifolia, Beaucarnea pliabilis* (Baker) Lundell, and *Myrcianthes fragrans* (SW.) McVaugh were less than 1.0 cm²/tree. *Beaucarnea* is the only one of the latter

species that is typically associated with dried habitats (1.Olmsted, personal communication), but low rates of basal area increment in 1987 indicate that this species also was severely stressed during the two driest years. The other three species may have roots that penetrate the limestone substrate and utilize groundwater.

The low amounts of precipitation in 1985 and 1986 and the lack of any precipitation for 5.5 months in 1986 may have represented one of the unusual stress periods that Murphy & Lugo (1986a) suggested are so importnat to thê dynamics of dry tropical forests. For species with at least two individuals, fifteen had no measurable increase in diameter in 1986 and six trees died. The number of species with two or more individuals and no measurable basal area increase ranged from 0-3 in the other three years and the maximum number of trees which died was 2. Most species, however, resumed positive growth during 1987, suggesting that they are quite resilient to drought conditions.

Although data from the first four years of this study have provided additional support for the suggestions of Murphy & Lugo (1986a), they have also extended beyond earlier findings to demonstrate the existence of quantitative relationships between annual precipitation and the dynamics of basal area increment and leaf litter production. In future years, this study should continue to provide useful information about the relationship between ecosystem dynamics and key driving variables (e.g., precipitation). The importance of other variables (availability of nutrients and response to hurricane disturbance) are also being examined at the site.

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