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THE PRODUCTIVITY AND COMPOSITION OF MANGROVE FORESTS, LAGUNA DE TÉRMINOS, MEXICO

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ABSTRACT

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The composition and productivity of two mangrove sites surrounding the Laguna de Términos, Mexico, were studied from March 1979 to January 1984. Measurements were made of the tree composition, above-ground woody biomass changes, and litterfall production at a high-salinity fringing site and a low-salinity riverine site. *Rhizophora mangle* L. was the dominant tree at the fringing site, but occurred only at the water's edge at the riverine site. *Avicennia germinans* L. dominated the inland area of the riverine site. *Laguncularia racemosa* Gaertn. f. had a more even distribution from shore to inland and from site to site. Average diameter at breast height (DBH) was greater at the riverine site for each of the three species; however, tree density (trees > 2.5 cm DBH) was more than twice as high at the fringing site (7510 ha^{-1}) than at the riverine site (3360 ha^{-1}). Wood production (1206 g m^{-2} $year^{-1}$ vs. 772 g m^{-2} $year^{-1}$) and litterfall (1252 g m^{-2} $year^{-1}$ vs. 835 g m^{-2} $year^{-1}$) were higher at the riverine site than at the fringing site. Total estimated above-ground net production was 2458 g m^{-2} $year^{-1}$ at the riverine site and 1607 g m^{-2} $year^{-1}$ at the fringing site.

INTRODUCTION

Mangroves dominate approximately 75% of the world's coastline between latitudes 25°N and 25°S (McGill, 1959). Mangrove species are adapted to areas characterized by high temperatures, fluctuating salinities and shifting, anaerobic substrates (Odum et al., 1982). Many studies have been conducted on mangroves — over 7000 titles (Snedaker, 1982). Species zonation has been

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a dominant theme in the literature while the productivity and functioning of the mangrove forests have been neglected. In the Gulf of Mexico area, Florida, mangroves have received the most intensive study (Heald, 1969; Odum, 1970; Miller, 1972; Carter et al., 1973; Lugo et al., 1975; Teas, 1979; Twilley, 1982). Others have studied mangrove forests in Puerto Rico (Golley et al., 1962; Pool et al., 1975, 1977; Cintrón et al., 1978) and the West Indies (Woodroffe, 1982). However, very few studies have been done of mangrove forests in Mexico (Thom, 1967; Pool et al., 1977; Rico-Gray and Lot, 1983).

Mangrove forests play an important role in the functioning of tropical coastal systems. Data from Florida (Heald, 1969; Odum, 1970; Lugo and Snedaker, 1975; Lugo et al., 1975, 1980; Twilley, 1982), Puerto Rico (Golley et al., 1962) and Australia (Boto and Bunt, 1981) indicate that mangrove forests tend to be net exporters of organic matter. Heald (1969) and Odum (1970) documented the dependence of south Florida's sport and commercial fisheries on the net production of red mangroves via the detritial energy pathway. Carter et al. (1973) suggested that 57–80% of the total organic budget of Fahkahatchee and Fahka Union Bays, Florida, was provided by export from the mangrove forests surrounding the bays.

The Laguna de Términos is the largest coastal lagoon as well as the port for the largest fishing fleet in Mexico. The economic importance of the lagoon has meant that there have been a series of studies carried out to understand the basic processes and history of the lagoon and the structure and function of fish communities within it (see Phleger and Ayala-Castañares, 1971; Yáñez-Arancibia et al., 1980; Yáñez-Arancibia and Day, 1982, and references contained therein). Day et al. (1982) briefly addressed mangrove productivity in a discussion of the overall productivity of the lagoon, but there have been no detailed ecological studies of mangroves bordering the lagoon.

The lagoon is almost completely surrounded by mangrove forests, covering an area nearly as large as the open-water area of the lagoon itself (Fig. 1). Therefore, the mangroves are a significant part of the lagoon ecosystem. We began this study with two general objectives. The first was to study the mangroves as part of the larger program of study of the Laguna de Términos being carried out by the Universidad Nacional Autónoma de México. The second, and equally important, objective was to conduct the research within the context of current thinking about the ecology of mangroves. In designing the study, we relied on the classification of mangrove structure and productivity which has evolved over the past decade from the original description of Lugo and Snedaker (1974), who identified several major mangrove-community types based on differences in soil type, nutrient input, and hydrology. At present, there are considered to be three main forest types: basin, fringe, and riverine (R. Twilley, personal communication, 1986; see also Cintrón et al., 1980; Brown and Lugo, 1982; Odum et al., 1982). Each community type has a characteristic structure and range of productivity, litter decomposition, and detritus export.

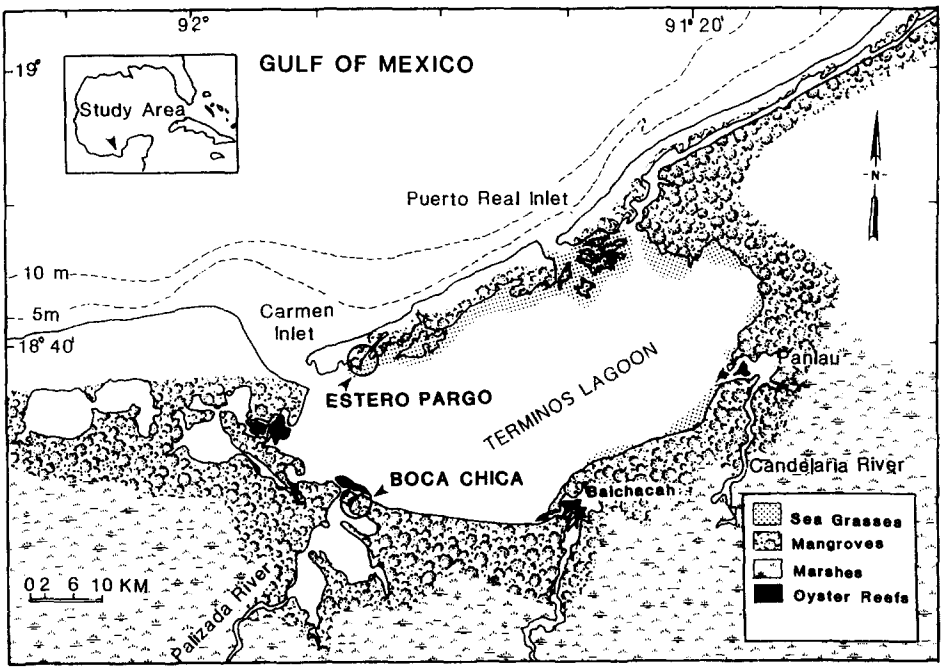

Fig. 1. Map of the Laguna de Términos showing the distribution of major habitats and the locations of the two mangrove study areas.

Generally, total biomass, tree height, litterfall and decomposition, and freshwater turnover increase from basin to riverine forests (Pool et al., 1975, 1977; Brown and Lugo, 1982). The two dominant forest types surrounding Laguna de Términos appear to be fringing and riverine and we chose study sites in each area. These two sites are different in terms of species composition and tree height, with the riverine site being visibly more robust. We wanted to see how the structural and productivity characteristics of the site fit the classification mentioned above.

AREA DESCRIPTION

Laguna de Términos is a large (approximantely 2500 km^2), shallow (mean depth 3.5 m) coastal lagoon located at the base of the Yucatan peninsula in the state of Campeche, Mexico (Fig. 1). It is connected to the Gulf of Mexico through two passes, one at each end of Isla del Carmen which is a barrier island that separates the lagoon from the open gulf. The lagoon has a net inflow through the eastern inlet at Puerto Real and a net outflow through the western inlet at Carmen (Mancilla and Vargas, 1980; Graham et al., 1981) as evidenced by the formation of a floodtide delta on the lagoon side of Puerto Real inlet. This net westerly flow is mainly the result of the trade winds that blow from

the east most of the year. Maximum wind speeds (50—60 km h^{-1}) occur during the season of winter storms, or "Nortes".

Average annual precipitation (1680 mm $year^{-1}$) is seasonal, with a dry season from February to May and a wet season from June to January. The same pattern exists over the entire drainage basin of the lagoon, producing a similar pattern of flow in the three main rivers entering the lagoon. Peak river discharge occurs in the months of September, October and November.

The lagoon is bordered almost completely by extensive mangrove swamps. Three tree species dominate: *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* L. (black mangrove), and *Laguncularia racemosa* Gaertn. f. (white mangrove). A fourth species, *Conocarpus erecta* L. (buttonwood), grows only along the landward fringes of the swamp. Beds of seagrasses, *Thalassia testudinum* Banks ex König, *Halodule* sp. and *Syringodium filiforme* Kütz. occur along the lagoon side of Carmen Island, on the delta of Puerto Real inlet and along the eastern and southeastern shores of the lagoon.

METHODS

Study sites

After a visual survey of the mangrove forests, two areas were selected for studies of mangrove productivity: a forest at Boca Chica, bordering the mouth of the Palizada River, and a forest along Estero Pargo, a 5.3-km-long tidal channel on the lagoon side of Isla del Carmen (Fig. 1). The width of the mangrove zone at Estero Pargo, between the tidal stream and the upland, varies between 50 and 150 m. The mangroves at Boca Chica are part of a band of mangroves that grow around the entire periphery of the lagoon and extend several kilometers inland. In the rainy season, during the period of high river flow, the forest at Boca Chica is continuously flooded with freshwater, while in the dry season the forest floor is almost always free of standing water. At Estero Pargo there is regular tidal inundation and exposure throughout the year. Water salinities in Estero Pargo and Boca Chica range from 20 to 40 ppt and from 0 to 5 ppt, respectively. Both areas are extremely flat. Depressions of several centimetres occur throughout both areas, but there is no consistent elevation change in either. Mangroves are harvested for charcoal or timber and it was evident that harvesting had occurred in both study areas in the past.

Forest composition

Trees with diameter at breast height (DBH) (or diameter above the highest prop root in the case of *R. mangle*) greater than 2.5 cm were sampled using the point-centered quarter method (Cottam and Curtis, 1956; Cintrón et al., 1978) with points 10 m apart. At Estero Pargo, two 130-m transects approximately

50 m apart were run from the channel's edge to a point near the upland boundary. At Boca Chica, three 90-m transects were run from the stream's edge inland. Frequency, density, basal area, average diameter and importance values were calculated for each mangrove species (Curtis and McIntosh, 1951; Mueller-Dombois and Ellenberg, 1974), and the complexity index was calculated for each site (Holdridge et al., 1971).

Above-ground woody biomass production

In March 1982 the DBH of 100 trees within each study area was measured and the trees tagged for future measurements. Approximately 30 trees of each of the three main tree species representing all diameter sizes were selected for diameter measurements. The trees were remeasured in February 1983 and their initial and final biomass estimated using procedures described below. Unfortunately, nearly 50% of the *Avicennia germinans* and *Laguncularia racemosa* at Boca Chica were harvested by local woodcutters just before the second measurement, so that calculations of biomass increase at that site were based on fewer trees (about 15 for each species).

In order to estimate biomass of mangrove trees, 10 trees of each of the three species were harvested at Estero Pargo and Boca Chica (total of 20·per species). The trees varied in size from 1 to 10 cm DBH. After the trees were felled, total height was measured and the leaves were stripped from the branches. Fresh weights of all branches, trunks and prop roots (for *Rhizophora mangle*) were determined in the field. Subsamples of all components were taken to the laboratory, dried at 70°C to a constant weight and then weighed. The dry weights of all components were calculated using the dry—wet ratios of the subsamples for each species. Regression equations of tree diameter as the independent variable and the weights of specific components as the dependent variable were developed. A t-test of the slope values (B) showed that there was no significant difference between the regressions from each site ($P<0.05$). Therefore, one set of regression equations was formulated for each species using the trees harvested from both sites (Table I).

Total annual net woody growth was estimated as described below. Woody biomass was calculated for each tree using DBH from the two measurement periods and the regression equations formulated from the harvest data (Table I). The increase in woody biomass was calculated by subtracting the initial biomass from the final biomass. Initial diameter was then plotted against the increase in biomass (Fig. 2) and regression equations formulated so that for any diameter we could predict the biomass increase. The transect data were arranged according to species and by 2-cm-diameter classes. The number of trees per hectare in a given diameter class was then multiplied by the predicted biomass increase for that diameter class. The sum of the biomass increases for

TABLE I

Regression coefficients used to estimate above-ground standing biomass. The equations are of the form $\log_e Y = A + B \log_e X$, with Y = dry weight (kg), X = DBH (cm), and r^2 = percent variance accounted for by the regression

Species	Plant component	A	B	r^2
Avicennia germinans	Trunk	−2.0199	2.4399	97
	Branches	−2.5845	1.8200	84
	Total	−1.5852	2.3023	97
Laguncularia racemosa	Trunk	−2.0794	2.3861	99
	Branches	−2.9622	1.7299	68
	Total	−1.5919	2.1924	97
Rhizophora mangle	Trunk	−1.9122	2.4120	93
	Branches	−2.8633	2.3286	90
	Prop roots	−4.4565	3.1828	83
	Total	−1.5605	2.5072	94

all diameter classes of each species resulted in the total net woody growth of the mangroves at each study site.

Litterfall

From March 1979 until April 1980, litter was collected every 2–4 weeks from 10 1-m^2 traps at Estero Pargo and 11 traps at Boca Chica. The traps with screen bottoms were randomly placed from the streamside to 50 m inland. Litter from each trap was dried to constant weight at 70 °C, sorted into leaves, woody material, flowers and fruits, and weighed. In addition, the fruits were divided by species and counted.

Soil salinity

Soil salinity in each mangrove site at Estero Pargo and Boca Chica was measured monthly from a series of ground-water wells from January 1983 to January 1984. Soil salinity was measured again in April 1985 at Estero Pargo. The wells were spaced at 20-m intervals on a transect from the water's edge to the inland extent of mangroves at Estero Pargo and for 100 m at Boca Chica. The wells were constructed of 3-cm-diameter plastic pipes placed in the soil to a depth of 0.5 m. The wells extended above the soil surface to a level higher than the highest tides. A refractometer was used to measure salinity on a water sample taken from each well which had refilled after being pumped out.

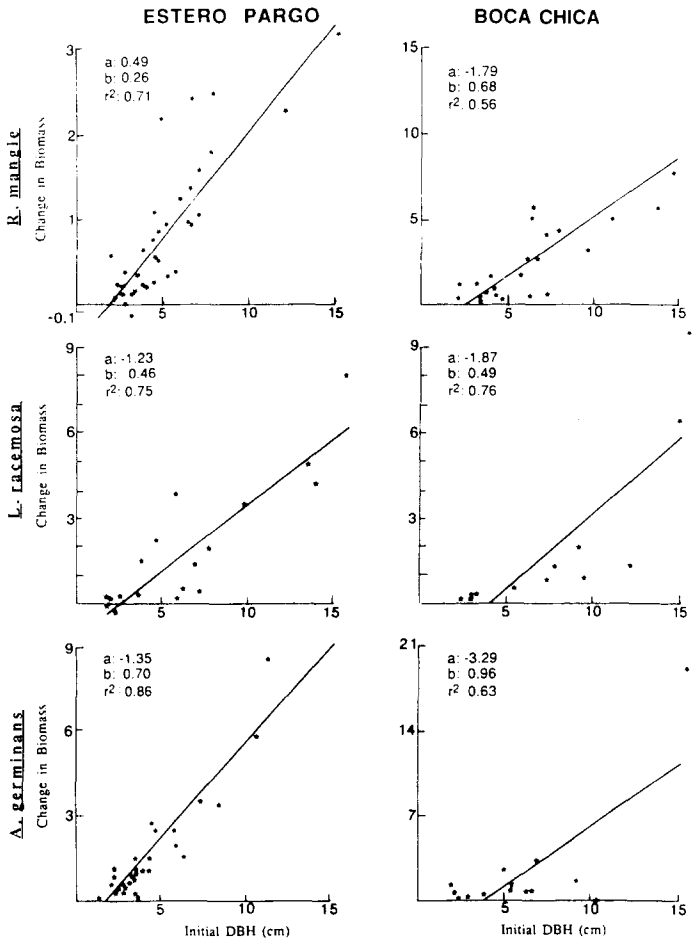

Fig. 2. Plots of initial DBH measurements and change in biomass for *Rhizophora mangle* L., *Laguncularia racemosa* Gaertn. f. and *Avicennia germinans* L. at Estero Pargo and Boca Chica.

RESULTS

Forest composition

The same three species of mangrove were encountered on the transects at both study sites: *Rhizophora mangle, Avicennia germinans* and *Laguncularia racemosa.* A fourth species, *Conocarpus erecta,* was present in the vicinity of both areas but was not encountered on transects at either study site.

At Boca Chica, *A. germinans* had the highest importance value and *R. mangle* the least (Table II). The reverse was true at Estero Pargo. *L. racemosa* had about the same importance value at both sites. At Boca Chica there were fewer trees, but they were larger and their basal area was greater.

TABLE II

Tree composition of Boca Chica and Estero Pargo mangrove forests (trees > 2.5 cm DBH)

	Mean canopy height (m)	Frequency[1]	Density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Average diameter (cm)	Complexity index[2]	Importance value[3]
Boca Chica	20					68.9	
Avicennia germinans		56.2	1890	21.0	8.6		54.8
Laguncularia racemosa		28.6	960	11.5	10.5		32.6
Rhizophora mangle		15.2	510	1.7	5.3		12.6
Total			3360	34.2			100.0
Estero Pargo	6					31.5	
Rhizophora mangle		61.1	4591	12.9	5.1		57.0
Laguncularia racemosa		34.3	2574	9.5	6.5		38.0
Avicennia germinans		4.6	345	0.9	5.3		5.0
Total			7510	23.3			100.0

[1]Percent of total number of trees.
[2]Complexity index = canopy height × basal area × stem density × No. species × 10^{-5} (adapted from Holdridge et al., 1971, by Brown and Lugo, 1982).
[3]Importance value is the sum of the relative frequency, relative density and relative dominance divided by 3.

Annual above-ground woody biomass production

The average rate of basal area increase and net woody above-ground production per tree for all three mangrove species was greater at Boca Chica than at Estero Pargo (Table III). *R. mangle* had the smallest basal area increase of the three species at both sites (0.89 and 2.74 cm^2 at Estero Pargo and Boca Chica, respectively). However, the amount of prop roots associated with red mangrove is not apparent from the basal area figures. Even though *R. mangle* had a fairly high rate of woody growth at Boca Chica as compared to Estero Pargo, this species contributed only 99.5 g m^{-2} (8%) to the total above-ground wood production of the area (Table III) because of the fewer number of trees present at the site. This situation was reversed at Estero Pargo. *R. mangle* had the smallest basal area increase and wood production per tree, but because of the number of trees (Table II), the total above-ground wood production of this species was large (46% of the total productivity). Average woody biomass at

TABLE III

Average basal area (BA) change, average woody growth per tree and total annual woody growth of mangrove trees measured at Boca Chica and Estero Pargo, Laguna de Términos, Mexico, March 1982 — February 1983

	Average BA change (cm^2)		Average woody growth (kg tree $year^{-1}$)		Total woody growth (g m^{-2} $year^{-1}$)	
	Boca Chica	Estero Pargo	Boca Chica	Estero Pargo	Boca Chica	Estero Pargo
Avicennia germinans	3.81	2.70	2.21	1.56	802.3	73.1
Laguncularia racemosa	3.69	3.33	1.72	1.53	304.0	345.5
Rhizophora mangle	2.74	0.89	2.69	0.74	99.5	353.3

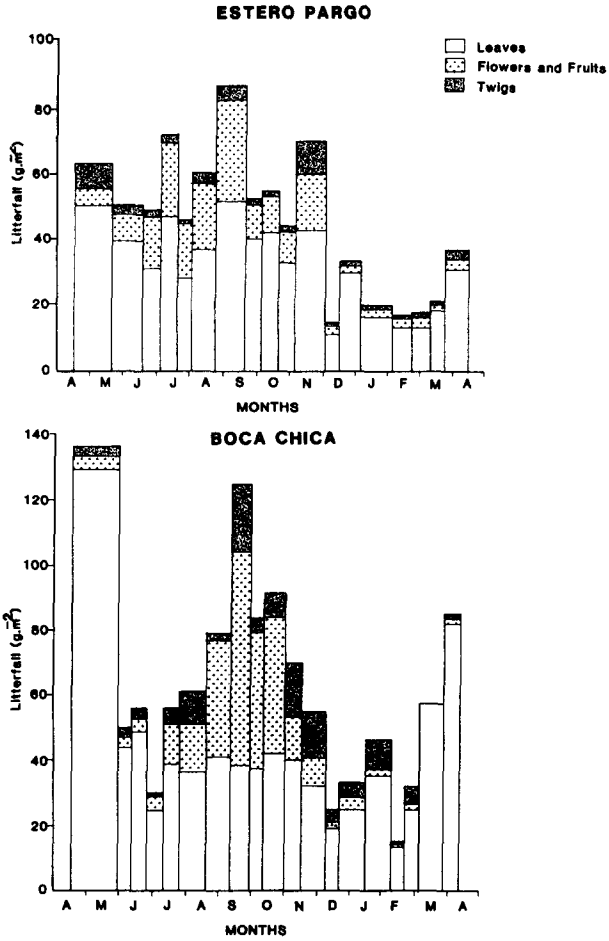

Fig. 3. Seasonal patterns of litterfall at the two study sites. The width of the bars indicates sampling interval.

Estero Pargo and Boca Chica was calculated to be 12.0 and 13.5 kg m^{-2}, respectively.

Litterfall

Leaf-fall was the dominant component of litterfall throughout the year at both sites, with the exception of one period in September, when fruit-fall was greater at Boca Chica (Fig. 3). There were definite peaks in litterfall: leaf-fall was highest during the dry season (February to May) at Boca Chica and lowest at Estero Pargo. The rates at the two sites were very similar during the rest of the year. The fall of flowers, fruits and wood showed strong peaks during the rainy season at Boca Chica. In Estero Pargo, the fall of flowers and fruits was

TABLE IV

Estimated above-ground net primary production of mangrove species at Boca Chica and Estero Pargo (g m^{-2} $year^{-1}$). The litterfall values are revised from those reported by Day et al. (1982)

Component	Location	
	Boca Chica	Estero Pargo
Woody growth		
Avicennia germinans	802.3	73.1
Laguncularia racemosa	304.0	345.5
Rhizophora mangle	99.5	353.3
Total	1205.8	771.9
Litterfall		
Leaves	880.8	594.2
Flowers and fruits	252.7	191.9
Wood	118.4	48.0
Total	1251.9	834.1
Annual above-ground net primary production	2457.7	1606.0

generally higher in the rainy season, while wood-fall was uniform throughout the year. The fruits of *R. mangle* dominated by weight because of their much larger individual size. However, the smaller fruits and flowers of *A. germinans* and *L. racemosa* were more numerous, even in Estero Pargo where *R. mangle* trees were more abundant. The total fruit-fall was higher at Boca Chica. Total litterfall for the entire year, as well as the component totals in each category, were highest at Boca Chica (Table IV).

Total above-ground net primary production

Even though the litterfall data were collected prior to the stem-growth study, we have combined the two sets of data (litterfall and woody biomass) to obtain estimates of net primary productivity of 2458 g m^{-2} $year^{-1}$ at Boca Chica and 1607 g m^{-2} $year^{-1}$ at Estero Pargo (Table IV). We realize that litterfall values can vary from year to year because of variations in fruit production and because of storm activity (Woodroffe, 1982). Our values for litterfall are similar to the average values for fringe (906 ± 89 g m^{-2} $year^{-1}$) and riverine (1187 ± 76 g m^{-2} $year^{-1}$) forests in Florida (Twilley, 1982). In addition, we monitored the growth of 15 trees at each site during 1980, 1981 and 1982 and found no significant differences in growth rates during those years. Thus, we are fairly confident that our values give a reliable estimate of total average annual production for these two sites.

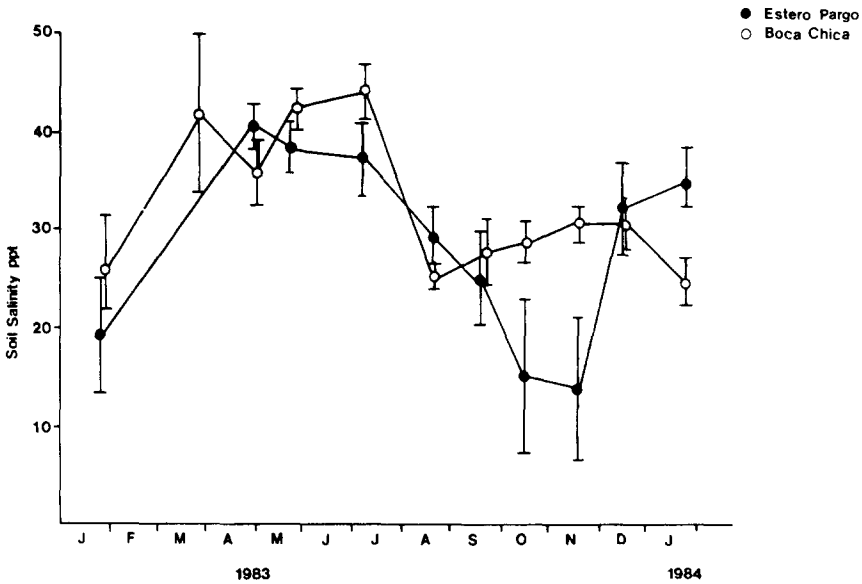

Fig. 4.Seasonal soil salinity variations at the two study sites. Vertical bars are ± 1 standard error.

Soil salinity

Contrary to our expectations, there was no consistent difference in soil salinity between the two sites in 1983–84 (Fig. 4). Both sites showed a seasonal trend with a generally lower salinity in the wet season. The salinity in Estero Pargo was significantly lower than in Boca Chica in October and November and significantly higher in January 1984 ($P < 0.05$). Mean salinity in 1983–84 was never higher than 45‰ and only one measurement was higher than 50‰ (Boca Chica, March, 56‰). In April 1985, soil salinity at Estero Pargo was between 65 and 72‰, with the exception of the well nearest the upland which was 28‰. These measurements were taken the day after a heavy rain, indicating that precipitation passed through the sandy soil and lowered the salinity at the station nearest the upland.

DISCUSSION

Composition

The structural characteristics of the vegetation at Boca Chica (Table II) are very similar to the mean values calculated for canopy height, basal area and number of species for riverine forests in the literature (Brown and Lugo, 1982). Brown and Lugo (1982) also described riverine forests as forests with *Rhizophora* dominating the periphery and *Avicennia* and *Laguncularia* dominating the inner forest, just as we observed at Boca Chica.

The mangrove forest at Estero Pargo is frequently flooded by tide waters and is composed predominantly of *R. mangle*. *L. racemosa* occurs from the shore inland, whereas *A. germinans* is found mainly in shallow depressions throughout the forest. Thom (1967) and Rabinowitz (1975) reported that *Laguncularia* has less stringent habitat requirements than either *Avicennia* or *Rhizophora* and is capable of growing in any of the mangrove zones.

Above-ground production

Wood production

There have been very few studies in which the wood production of mangroves has been measured and nearly all of the available estimates are for *Rhizophora* (Brown and Lugo, 1982). To our knowledge, this is the first report of wood production by *L. racemosa*. Golley et al. (1962) estimated production in a *Rhizophora* forest in Puerto Rico to be 307 g m^{-2} $year^{-1}$, while Clough and Attiwill (1982) estimated that in an *Avicennia* forest in Australia to be 356 g m^{-2} $year^{-1}$. Other estimates of *Rhizophora* production include 2000 g m^{-2} $year^{-1}$ in Thailand (Christensen, 1978) and 2100 g m^{-2} $year^{-1}$ in Florida (Teas, 1979). Values for wood production at Boca Chica and Estero Pargo (1206 and 772 g m^{-2} $year^{-1}$, respectively) fall within the range of reported values.

The regression equations calculated in this study were compared with regression equations for *Rhizophora* formulated by G. Cintrón (personal communication, 1980) using data from Golley et al. (1962). Cintrón's equations for biomass were: (1) $\log_e$ (stem biomass) $= \log_e 201.76 + 2.136 \log_e$ (DBH); (2) $\log_e$ (branch biomass) $= \log_e 69.82 + 2.324 \log_e$ (DBH), (3) $\log_e$ (prop root biomass) $= \log_e 72.63 + 2.481 \log_e$ (DBH). The DBH data of *Rhizophora* from Golley et al. (1962) were used in our equations and those of Cintrón to estimate biomass. The branch-biomass equations gave the most comparable results with our equations, underestimating Cintrón's by 18%. The largest discrepancy occurred in the prop root estimations, where our equations underestimated Cintrón's by 70%. Our stem biomass estimates were 17% less than Cintrón's for stem diameters <2 cm, 5% over for 2–3 cm, and 10% less for 3–5-cm diameters. These results indicate the error level which can be introduced by applying regression equations from one area to other areas.

Litter production

Mangroves are thought to be significant contributors to estuarine and inshore productivity via litterfall. Litterfall is the most common productivity value in the mangrove literature because it is the most easily measured component of total net primary productivity. Mangrove leaves are shed continuously throughout the year, with rates varying from habitat to habitat. Scrub or stunted forests are the least productive (122 ± 36 g m^{-2} $year^{-1}$) of the mangrove for-

ests (Pool et al., 1975; Snedaker and Brown, 1981; Teas, 1979). Fringe forests average 906 ± 89 g m^{-2} $year^{-1}$ (Twilley, 1982). The highest values for litterfall are from riverine forests where litterfall values average 1100–1200 g m^{-2} $year^{-1}$ (Twilley, 1982; Brown and Lugo, 1982). Litter production at Estero Pargo (835 g m^{-2} $year^{-1}$) and Boca Chica (1252 g m^{-2} $year^{-1}$) agree with reported values for fringing and riverine forests.

Throughout the range of mangroves there seems to be a general trend for peak litterfall to occur during the rainy season (Heald, 1969; Pool et al., 1975; Williams et al., 1981; Bunt, 1982; Twilley, 1982). This peak litterfall, at a time when there is abundant water flowing through the area, may help to account for the high export of material from the forests. In our study, the highest litterfall at Boca Chica occurred just before the rainy season began, while most of the litter at Estero Pargo fell during the rainy season.

Total above-ground net primary production (NPP)

Reported values of total above-ground NPP in mangrove forests range from a low of 380 g m^{-2} $year^{-1}$ for a scrub forest in Florida (Teas, 1979) to 5475 g m^{-2} $year^{-1}$ for a mixed forest in Florida (Carter et al., 1973). The values generally fall within the range that might be expected for woody plants. The different methods used may account for some of this variability. The assumption that total above-ground NPP for mangroves is three times total litterfall (Teas, 1979) is not supported by our results, in which NPP was approximately twice the amount of litterfall. Teas (1979) based the 3:1 ratio on Bray and Gorham (1964), who derived the ratio from terrestrial forests. Bray and Gorham (1964) recommended that further productivity research be conducted to refine the NPP/litterfall ratio. In freshwater forested wetlands of southeastern U.S.A., the NPP/litterfall ratio is 2.3 ± 0.1 (Carter et al., 1973; Conner and Day, 1976; Schlesinger, 1978; Mitsch and Ewel, 1979; Mulholland, 1979; Brown, 1981; Conner et al., 1981). These results suggest that the NPP/litterfall ratio for both freshwater and saltwater is about 2:1. This shows that such ratios for one forest type (e.g. terrestrial) should not be applied to other forest types (such as mangroves). Our values for Estero Pargo (1607 g m^{-2} $year^{-1}$) and Boca Chica (2458 g m^{-2} $year^{-1}$) are comparable with many of the published production values.

Until recently, researchers have tended to think that community structure in mangrove systems is related to soil-salinity gradients (see Lugo and Snedaker, 1974). However, salinity does not seem to be an important factor in affecting community structure or productivity in this study. The data for 1983 indicate that, in general, there does not seem to be a consistent difference between the two sites. The one set of measurements in April 1985 indicates that occasionally soil salinities may reach 70‰. In general, however, the results suggest that salinity is below 50‰ in both areas. Information summarized by

TABLE V

Mean nutrient concentrations in waters of Estero Pargo, Laguna de Términos and Boca Chica. Concentrations are in μM

Nutrient	Estero Pargo[1]	Laguna de Términos[2]	Boca Chica[2]
NH_4^+	14.6	4.0	2.0
NO_3^-	3.9	0.5	2.5
Total inorganic N	18.5	4.5	4.5
PO_4^{3-}	0.6	0.15	0.5
N:P	30.0	30.0	9.0

[1]Ley-Lou, 1985.
[2]Yañez-Arancibia and Day, 1982.

Brown and Lugo (1982) indicates that salinities below this do not significantly affect structure or productivity. Nickerson and Thibodeau (1985) reported that the distributions of *Avicennia* and *Rhizophora* were closely correlated with the amount of hydrogen sulfide in the soil. They found that when compared with vegetation distant from the streamside, vegetation fringing streams was taller, more robust and grew in soils with lower hydrogen sulfide levels. This suggests that the concentration of hydrogen sulfide is an important factor regulating both primary production and forest structure at the two Laguna de Términos sites. We hypothesize that the hydrogen sulfide content is lower in the soils at Boca Chica because of low sulfate concentrations in river water, especially in comparison with sea water.

The data suggest that the differences in primary production at our study sites are influenced mainly by nutrient loading and freshwater turnover. Pool et al. (1975) suggested a direct relationship between productivity and freshwater turnover for mangrove forests. Clearly, Boca Chica has the highest freshwater input, at least in surface water. It is interesting to note that water concentrtions of inorganic nitrogen (N) and phosphorus (P) are highest in Estero Pargo (Table V). However, the loading of N and (especially) P must be higher at Boca Chica due to riverine input. In nutrient analyses of decomposing litter in litter bags placed on the forest floor, Day et al. (1982) measured higher concentrations of N and P at Boca Chica than at Estero Pargo. Decomposition rates were also higher at Boca Chica. Since the N:P ratio in the water is low at Boca Chica, this suggests that N-fixation may be important in supplying nitrogen and that the river is important in supplying P. A number of workers have shown that increased nutrient availability, especially P, is related to higher productivity in mangroves (Onuf et al., 1977; Snedaker and Brown, 1981; Brown and Lugo, 1982; Boto et al., 1984).

Mangroves are generally productive due to a number of factors including high solar radiation and temperatures, a year-long growing season and generally abundant nutrients in the soil. Our calculations indicate that the ratios of

net above-ground productivity (kg m^{-2} $year^{-1}$) to biomass (kg m^{-2}) for the two sites (Estero Pargo = 0.13, Boca Chica = 0.18) are significantly higher than the average of 0.042 for upland hardwoods and conifers (Whittaker, 1966; Whittaker and Woodwell, 1968; Whittaker et al., 1974). This difference in productivity/biomass ratios is due to both higher productivity and lower biomass at the two Laguna de Términos sites as compared to upland forests. Higher productivity is related to the factors listed above. The lower biomass of the mangrove sites may be due to stresses such as salinity, anaerobic conditions and high hydrogen sulfide concentrations in the soil. Thus more of the available energy from primary production must be used to deal with stress and less is available to build structure.

The differences between Estero Pargo and Boca Chica illustrate this balance between production and biomass. Productivity and biomass as well as the productivity/biomass ratio were higher at Boca Chica which has a high freshwater input. It has been demonstrated that high freshwater input leads to higher productivity and higher biomass in mangroves. This is probably caused by a number of factors which include lower salinity, higher nutrient inputs (especially P) and a lower hydrogen sulfide level due to lower sulfate concentrations in freshwater. Since stresses are lower, productivity is higher and more energy can be used for building biomass, resulting in a higher productivity/biomass ratio at Boca Chica.

The information developed in this study, in combination with other research in the area, is useful in developing plans for management and conservation of the natural resources of the Laguna de Términos region. We have demonstrated that the mangrove forests are very productive. Other studies have shown that mangrove litter decomposes rapidly and is flushed to the lagoon (Day et al., 1982). The Laguna de Términos region is the most important commercial fishery area in Mexico. Organic detritus from the mangroves is an important dietary item for many fish species and the mangrove area is an important fish habitat (Yáñez-Arancibia et al., 1980; Yáñez-Arancibia and Day, 1982). Dissolved organic substances from decaying mangrove leaves have been shown to stimulate aquatic primary productivity in the lagoon (C. Madden, personal communication, 1986). Thus, the productivity and extent of mangrove forests in the area are directly related to high fisheries productivity.

Our results also suggest how the forests can be managed to maintain high productivity. Riverine input is important as a source of nutrients and freshwater, and therefore upstream activities such as dams and diversions would lead to lower productivity. Local management practices should avoid activities which lead to increased stress on mangroves. Changes, such as impoundment or channelization, which cause increased anaerobiosis and hydrogen sulfide concentrations or lead to hypersalinity should be avoided. In general, a high degree of flushing by both tide and river should be maintained.

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