

Ecophysiology of a Mangrove Forest in Jobos Bay, Puerto Rico

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ABSTRACT.—We studied gas exchange, leaf dimensions, litter production, leaf and litterfall chemistry, nutrient flux to the forest floor, retranslocation rates, and nutrient use efficiency of mangroves in Jobos Bay, Puerto Rico. The fringe forest had a salinity gradient from the ocean (35‰) to a salt flat (100‰) and a basin (about 80‰). Red (*Rhizophora mangle*), white (*Laguncularia racemosa*), and black (*Avicennia germinans*) mangroves were zoned along this gradient. Photosynthetic rates, stomatal conductance, leaf area and weight, leaf specific area, and nutrient use efficiency decreased with increasing salinity, while xylem tension, nutrient retranslocation, and leaf respiration increased with increasing salinity. The concentration of some leaf elements increased with salinity (N, P, Mg, Na) while others decreased (Ca). Leaf specific area was less variable than leaf area or weight. Maximum photosynthesis ($12.7 \mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), leaf conductance ($283 \text{ mmol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), and litterfall ($16.9 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) in the fringe were high in comparison with those of other world mangroves. Nutrient flux to the forest floor was also high and nutrient use efficiency was low in this forest. Part of the reason for these high values and low use-efficiencies was the high proportion of nutrient-rich flowers and propagules in litterfall. Nevertheless, access to freshwater in the form of groundwater discharge and about 1 m of annual rainfall play a role in the high productivity of the Jobos mangroves.

INTRODUCTION

The literature on mangrove forests is abundant (Rollet 1981) and only recently have there been quantitative studies on the ecophysiological responses of trees to environmental gradients. For example, Feller et al. (2002) studied phosphorus limitation across an ecotonal gradient that included several edaphic variables, Lovelock and Feller (2003) focused on a salinity gradient, and McKee et al. (2002) studied a nutrient gradient in Belize, Florida, and Panamá, respectively. A review of fringe mangrove forest's literature (Lugo 1990) uncovered a wide gap between the description of vegetation zonation in fringe forests domi-

nated by *Rhizophora mangle* (there are many) and studies of environmental gradients and vegetation response (very few). Yet, progress in understanding the responses of mangrove species to variable conditions requires precise paired measurements of biotic responses and gradients of abiotic conditions. Without such paired measurements, very little generalization will be possible because short distances in a fringe mangrove may involve a large range of environmental conditions (Cintrón et al. 1978, Feller et al. 2002). These broad ranges are not usually included in experiments on the ecophysiology of mangroves. For example, Björkman et al. (1988) and Ball and Pidsley (1995) studied gas exchange and tree growth (respectively) in mangrove trees and seedlings but restricted their salinity experiment to values between seawater strength (35‰) and 90% dilution

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(or less than 5‰). However, salinity ranges of 0 to 100‰ are common in mangroves, particularly in arid coastlines or on steep topographic gradients (Cintrón et al. 1978). Lovelock and Feller (2003) studied photosynthetic performance of Florida mangroves at salinities as high as 55‰ as did Feller et al. (2003), but most other ecophysiological research is at lower salinities (Feller et al. 1999, Cheeseman and Lovelock 2004, Lovelock et al. 2004).

We expand previous analyses of mangrove vegetation response to pore salinity (Cintrón et al. 1978) to studies of ecophysiological responses to salinity gradients. By relating structural and ecophysiological responses of mangrove species to specific environmental conditions, we contribute to the understanding of robust relationships between mangroves and their environment.

METHODS

We conducted measurements in two adjacent fringe forests. One was an inland fringe forest lining a dead-end canal that connects the forest to the Mar Negro in Jobos Bay National Estuarine Research Reserve in Puerto Rico. We will refer to this site as the inland fringe forest (IFF). Lugo (1987), Montero and Soler (1987), Dávila (1987) and Ruiz Bernard and Lugo (1999) have described the site. Between October 11, 1985 and January 11, 1987, we collected litterfall monthly in this forest. A second mangrove stand fringed the ocean and was located just southwest of the IFF, across a dirt road. We will refer to this site as the ocean fringe forest (OFF). On December 6, 1986 we established a 100 m × 2 m transect in the OFF and conducted the following measurements: vegetation profiles, topographic relief, environmental conditions, leaf photosynthesis, stomatal conductance, water potential, leaf specific area, and nutritional status of leaves of various sizes and appearance. These measurements occurred at the end of the rainy season.

All the work in the OFF was along the 100-m transect that originated at the ocean edge and ended inland in a basin after crossing a salt flat (salina). We identified

trees to species, mapped their location, and measured tree height. Land elevation relative to sea level was measured along the transect using a level and readings to a precision of 1 cm. We used a refractometer calibrated for seawater to measure pore and surface water salinity.

We measured photosynthetically active radiation (PAR) with a light integrator (Li190 quantum sensor, Li-Cor, Lincoln, NE) and air temperature and humidity with an aspirated psychrometer. Xylem tension was measured with a Scholander pressure chamber (Scholander et al. 1965). Leaf samples used for measurement of leaf sap osmotic pressure were cleaned in the field by washing the leaf surface with distilled water (to eliminate external sea salt deposition), dried with paper towels, and enclosed inside tight glass vials. The vials were frozen in dry ice, transported to the laboratory, and boiled for 2 h. We extracted leaf sap from the samples with a hand press providing a pressure of about 100 psi, and measured the osmolality of cell sap with a water vapor osmometer (Wescor, Logan UT) calibrated against NaCl solutions of known concentration. We transported subsamples of pore water taken at 30 cm depth to the laboratory for the measurement of osmolality with a water vapor osmometer. Salinity (‰) measured with a hand refractometer and osmolality (mol kg⁻¹) measurements of soil water samples were highly correlated as expected:

$$\text{Osmolality (mmol kg}^{-1}\text{)} = 33.9098 \times \text{salinity (‰)} - 231.8243, r^2 = 0.99$$

For natural waters, this equation has a negative independent term due to the presence of organic compounds that influence the refraction index without affecting salinity.

Photosynthetic rate, stomatal conductance, leaf temperature, and incident photon flux density on leaves were measured along the transect every 3 h from dawn to dusk using a portable gas exchange system (ADC-LCA-2, Analytical Development Corp., Hoddesdon, UK), operating in the open mode (Long and Hålgren 1985). Every

3 h we conducted triplicate measurements on mature leaves of red mangroves (*Rhizophora mangle*) on the water's edge, white mangroves (*Laguncularia racemosa*) on the water's edge, and those two species plus black mangroves (*Avicennia germinans*) in the basin behind the salina (basin).

Leaf Characteristics, Litterfall, and Nutrient Cycling

We collected leaves still attached to the trees to study their area/weight characteristics and nutritional status by species and location along the OFF transect. We classified leaves by their appearance and location on the branch. The leaf categories were mature (fully expanded), old mature, yellow, and senescent. Senescent leaves were still attached to the stem but were already brown in color. We ignored young leaves that had yet to expand to full size. Leaf collections included 10 leaves each of mature, old mature, yellow, and senescent leaves. We measured leaf area in the laboratory with a leaf area meter (Li-cor model 3100, Lincoln NE). Leaves were dried to constant weight at 70°C, ground, ashed, and analyzed for N, P, K, Ca, Mg, and Na. Thirty-two samples were chemically analyzed (two replicates for each combination of leaf type, species, and location in the transect). We compared these results with similar determinations on mature red mangrove leaves (Serrano and Monefeldt 1987), ground litter (Varela and Berrios 1987), and fresh leaf litter collected over a period of 16 mo at the IFF. The comparison was limited to red and white mangroves because black mangroves did not grow in the IFF. Serrano and Monefeldt measured 1500 red mangrove leaves at the IFF while Varela and Berrios harvested thirty three-0.25 m² plots of litter.

Comparisons of dimensions and nutrient concentrations between leaf types and species were made on the basis of 95% confidence intervals of the sample means. In this analysis, means without overlapping confidence intervals are statistically different. This was considered more appropriate than a standard analysis of variance because leaf types represented a developmental age gradient, being produced sequentially on each

branch sampled. Nutrient concentrations were expressed on an area basis using specific leaf areas, to avoid errors estimating absolute amounts of a given nutrient in the leaf tissue derived from increasing accumulation of minerals in older leaves.

Litterfall was collected in the IFF using two 0.5 m × 4.0 m baskets constructed of plastic screen mesh located in the field on September 11, 1985. Collections from these baskets were monthly. Litterfall was initially separated into leaves, and miscellaneous between October 11, 1985 and January 11, 1986. After February 11, 1986 we separated leaves by species and between May 11, 1986 and January 11, 1987, we separated flowers and propagules by species. Samples were oven dried to constant weight at 70°C. We used these samples for chemical analyses (N, P, K, Ca, Mg, and Na). Litterfall material from each basket was analyzed separately for each date of collection and after sorting into leaves, flowers, and propagules by species plus fine wood and miscellaneous. In total, we analyzed 95 samples for the six elements as follows: 36 leaf samples (18 white and 18 red mangrove), 27 flower and propagule samples (11 white and 16 red mangrove), 18 fine wood samples, and 14 miscellaneous samples.

We estimated the nutrient flux in litterfall by multiplying the concentration of an element in a litterfall component by the mass of that component. We integrated monthly measurements of litterfall to obtain an annual litterfall rate by component. From monthly data of nutrient flux, we calculated the ratio of nutrient to mass and multiplied this ratio by the annual litterfall mass by component. This gave us an estimate of annual nutrient flux by litterfall compartment. We calculated the mass concentration of nutrients in litterfall by dividing the annual nutrient flux by the annual mass fall of litterfall by compartment and species. The inverse of this concentration, expressed in the same units (g g⁻¹), is the nutrient use efficiency *sensu* Vitousek (1984).

We used individual leaf data to calculate leaf specific area (leaf area in cm²/dry weight in g). We also used leaf chemical

data to estimate retranslocation rate and instantaneous nutrient use efficiency of P and N. Absolute retranslocation was the difference in nutrient content between senescent and mature leaves, expressed in mmol m^{-2} . We also expressed this value as a % of mature leaf nutrient concentration. The inverse of the nutrient concentration in senescent leaves, expressed in g g^{-1} , was an instantaneous measure of the Vitousek's nutrient use efficiency.

Laboratory Analyses

Oven dried vegetation samples were ground through a Wiley mill with a mesh size of 0.85 mm (20 mesh) stainless steel mesh, ashed in a muffle furnace at 450°C for four hs, to determine ash content, and dissolved in HCL. We used a Beckman Spectra Span V Plasma Spectrophotometer using the digestion method recommended

by Luh Huang and Schulte (1985) for determination of P, K, Ca, Mg, and Na. We analyzed for nitrogen in samples digested with concentrated H_2SO_4 and a catalytic mixture of CuSO_4 and K_2SO_4 using a semi-micro Kjeldahl procedure (Chapman and Pratt 1979). We also ran a standard citrus leaf sample from the National Bureau of Standards after every 24 determination, to assure the precision of the analysis.

RESULTS

Vegetation and Environment

The 100-m transect through the OFF had strong gradients of salinity and structural characteristics of vegetation (Fig. 1). There was a berm at 20 m from the ocean edge, another berm behind the salina, a lagoon adjacent to the road, and another lagoon behind the road. In fact, road construction

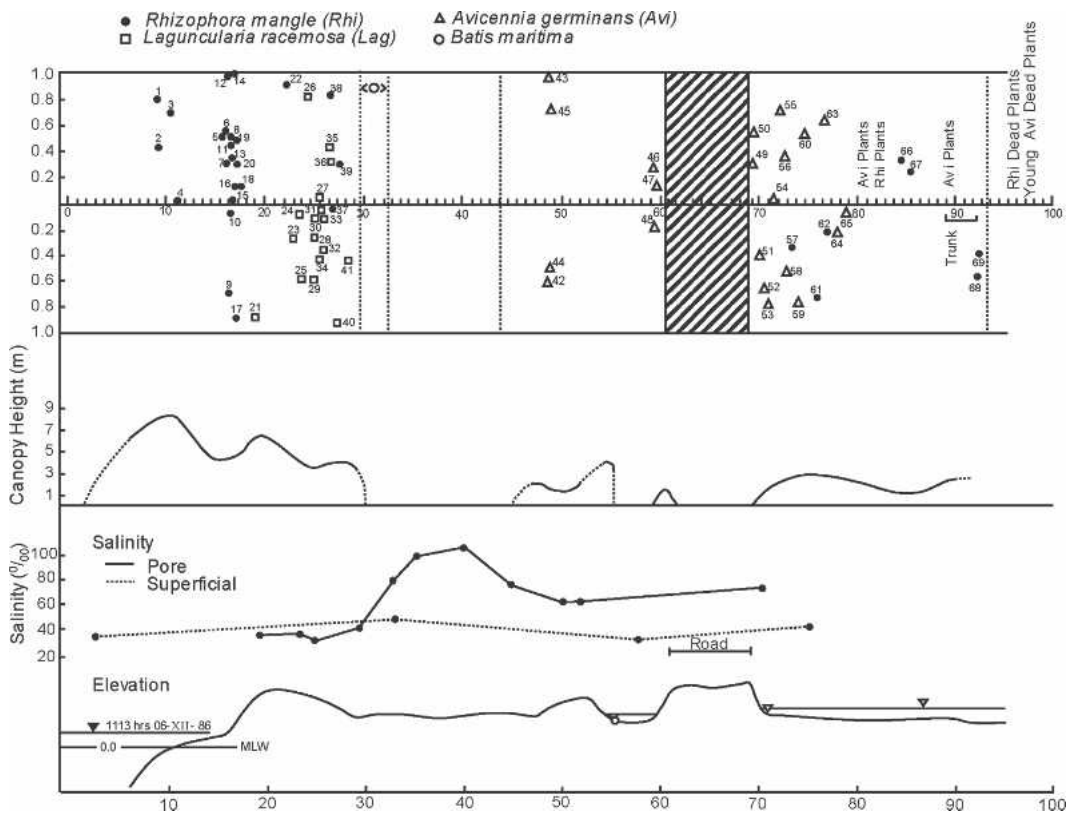


FIG. 1. Vegetation profile, topography, and pore salinity in an ocean fringe forest in Jobos, Puerto Rico. The upper panel shows the location of the 100 m x 2 m transect from the ocean (left) towards inland (right). The road is shown in the upper panel with dashed oblique lines.

filled a portion of the lagoon behind the salina, thus creating the impression that there are two lagoons. The water level at the lagoon was above mean low water and above the level of the ocean at the time of the survey. This reflects recent rainfall and explains the surface water salinity at 40‰ or below. The lagoon floor was at sea level. Pore salinity in the ocean fringe was the same as seawater and it increased rapidly behind the fringe from about 38‰ to about 100‰ in the salina. Pore salinity decreased behind the salina to about 60‰ and increased again slightly behind the road. The basin is the area behind and immediately before the road (Fig. 1).

Tree height was inversely proportional to pore salinity. The tallest trees grew just in front of the oceanic berm (Fig. 1) and decreased in height both towards the salina on the ocean side and away from the salina on the roadside. Mangrove species exhibited zonation and the distribution of trees was associated with the berm. Red mangroves grew mostly on the ocean side of the fringe with few scattered individuals fringing the inland lagoon. White mangroves predominated behind the oceanic fringe while black mangroves grew most densely on the fringes of the salina. Wherever there was a berm, trees clustered along its long axis. This suggests regeneration by floating propagules stranded along a topographically high point in the swamp.

Leaf Ecophysiology

Leaf environment.—Input of PAR to the forest on December 6, 1986 was 36.5 mol m^{-2} and the day was sunny throughout with high air temperature, low relative humidity (about 60% between 10:00 and 15:00 h), and high air saturation deficits (averaging 12 g m^{-3} between 10:00 and 16:00 h, Fig. 2). Air temperature increased from 24°C in the early morning to a maximum of 32.1°C at 13:30 h. The relative humidity decreased from about 84% early in the day to about 60% through mid-day. The air saturation deficit, increased until approximately 14:00 h when it began to decrease sharply as moist offshore winds increased the water

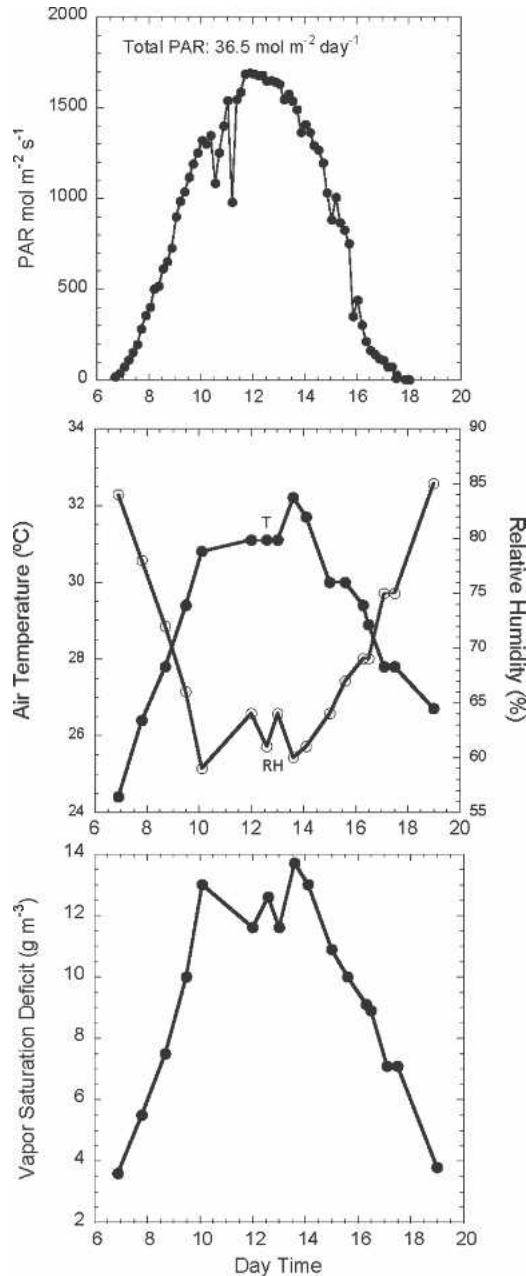


FIG. 2. Environmental conditions on December 6, 1986 in an ocean fringe forest at Jobos, Puerto Rico.

content of the air and air temperature decreased.

Osmotic pressure of leaf cell sap and pore salinity.—The salinity of pore water ranged from 36‰ at the water's edge (Fig. 1), equivalent to 989 mmol kg^{-1} , to 100‰ or

about 3160 mmol kg⁻¹ at the salina. These concentrations correspond to osmotic pressures, at 25°C, of 2.1 to 2.5 MPa at the water's edge and more than 7.0 MPa in the salina. Osmolality of leaf sap changed according to pore salinity (Table 1). Osmotic pressure of leaf cell sap was always higher than that of soil water. White mangroves, regardless of where they grew, had the lowest osmotic concentrations (Table 1). Black mangroves growing around the salina had the highest cell sap concentration. Black mangroves grew in the highest pore salinity conditions. Red and white mangroves, even those growing away from the water's edge, grew under lower pore salinity conditions.

Daily course of xylem tension.—Leaf xylem tension changed little during the day (9:00 to 15:00 h; Fig. 3); it averaged 3.6 MPa in red mangrove and 3.2 MPa in white mangroves (Table 1). Xylem tension in black mangroves was considerably higher and remained around 5.0 MPa during the same period. Measured xylem tensions at noon were larger than the osmotic pressure of pore water and of the leaf cell sap, except in red mangroves.

Gas exchange.—Photosynthetic rates were higher in trees by the water's edge than in trees in the basin (Figs. 4 to 6, Table 2). Red and white mangroves had higher photosynthetic rates and leaf conductance during the morning hours than in the afternoon (Figs. 4 and 5). Trees growing at the water's edge showed a reduction in photosynthetic rates after 14:00 hr, when due to solar

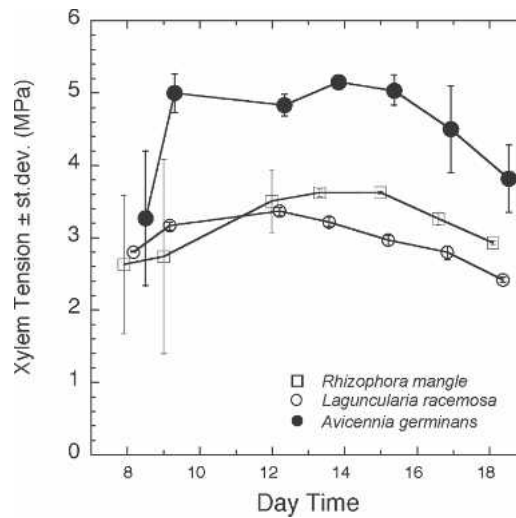


FIG. 3. Diurnal course of xylem tension of three mangrove species in an ocean fringe forest in Jobos, Puerto Rico. Standard deviation of the mean are shown.

angle, leaves were shaded from direct sunlight and photon flux density decreased markedly. Black mangroves in the basin maintained low but steady photosynthetic rates until about 16:00 h, probably because photon flux density remained around 1,000 mmol m⁻²s⁻¹ (Fig. 6). In this species a sharp decrease in leaf conductance was observed between 12 and 15 hours, but we did not consider it a midday depression because it was not accompanied by a parallel decrease in photosynthesis. In all species, the rather large leaf conductance allowed leaf temperatures to remain about 2 to 3°C below

TABLE 1. Paired osmolality values of soil water and leaf sap, and mid-day xylem tension of mangrove species. Cell sap osmolalities are the average of three replicates sampled in the morning. Standard deviation was less than 3%. Xylem tension is the average of 12 measurements per species taken between 0900 and 1500 h at Jobos Bay, Puerto Rico, December 1986. Standard deviation is in parenthesis.

Species	Pore water		Cell sap		Xylem tension (MPa)
	(mmol kg ⁻¹)	π MPa @ 25C	(mmol kg ⁻¹)	π MPa @ 25C	
<i>Rhizophora mangle</i>					
Fringe	860	2.1	1305	3.2	
Basin	1025	2.5	1489	3.7	3.6 (0.6)
<i>Laguncularia racemosa</i>					
Fringe	860	2.1	988	2.4	3.4 (0.6)
Basin	1025	2.5	1178	2.9	
<i>Avicennia germinans</i>					
Basin	1633	4.0	1799	4.4	5.1 (1.0)

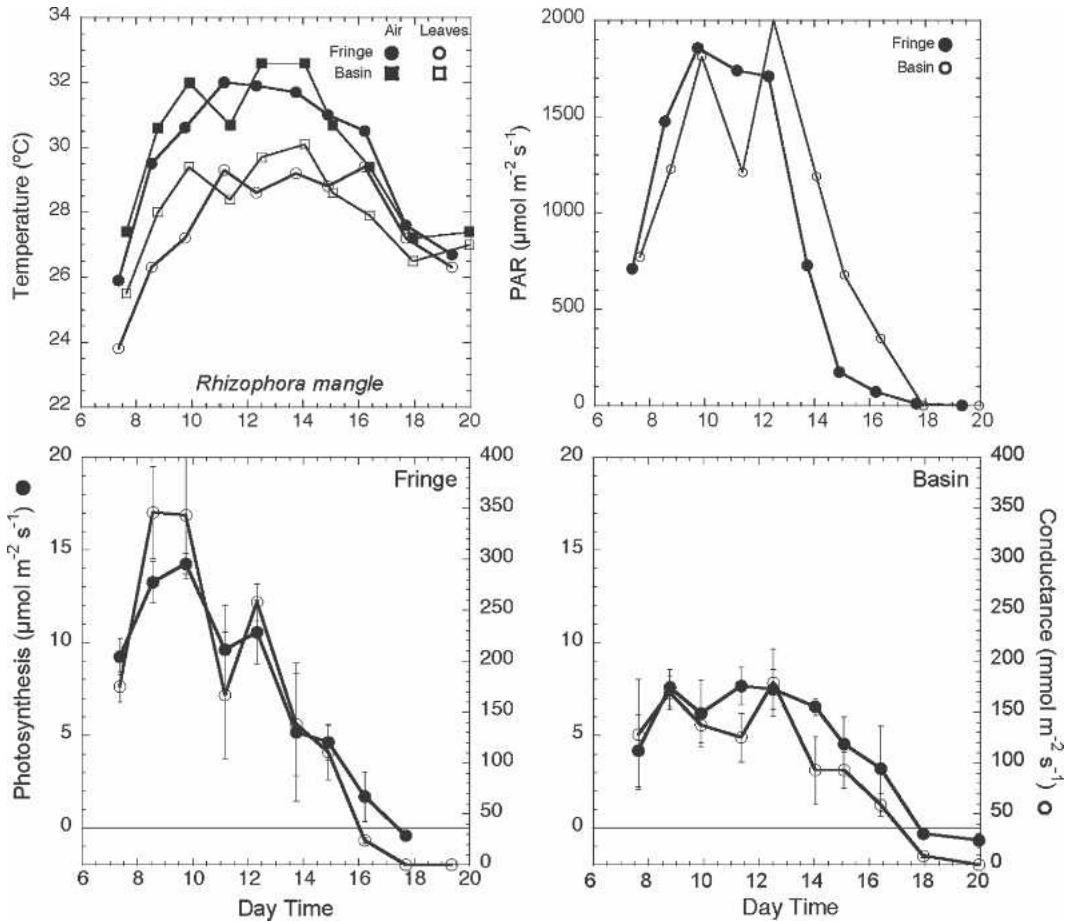


FIG. 4. Diurnal course of net photosynthesis and stomatal conductance in mature sun leaves of *Rhizophora mangle* in two contrasting locations (fringe and basin) in an ocean fringe forest in Jobos, Puerto Rico. Leaf and air temperature and photon flux density during the measurement period are also shown.

air temperature (Figs. 4 to 6). Leaf temperature was below 30°C most of the time. The light saturation of the photosynthetic rate of all three species appeared to be approximately at 1,000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Fig. 7). Red and white mangrove trees from the water's edge had consistently higher photosynthetic rates than those from the basin site (Table 2). Leaf respiration increased with salinity and with increasing salinity within species. Red mangroves had the lowest leaf respiration rates while black mangroves had the highest ones.

The relation between leaf conductance and photosynthetic rate is nearly linear and similar for red and white mangroves from fringe and basin sites (Fig. 8). This was not

the case for black mangroves because stomatal conductance was abnormally high in the early morning and late afternoon (Fig. 6).

Leaf Characteristics and Chemistry

Leaf characteristics changed with appearance, species, and location of the tree, i.e., fringe, or basin (Table 3). Leaf expansion reached a peak in mature stages except in black and red mangrove in the basin. In those stands, old mature leaves had higher leaf area than mature leaves and in all cases old mature leaves had the highest weight. Leaf weight was lower in yellow and senescent stages except for red mangroves in

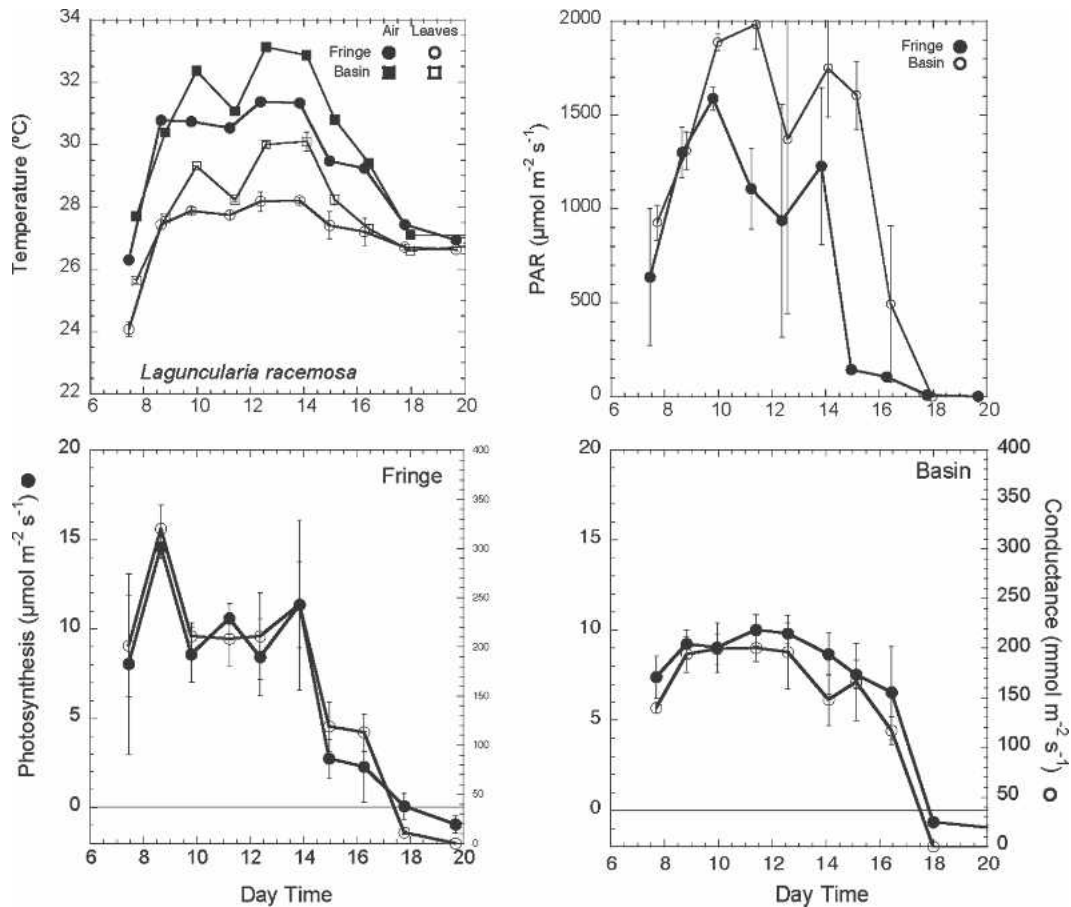


FIG. 5. Diurnal course of net photosynthesis and stomata conductance in mature sun leaves of *Laguncularia racemosa* in two contrasting locations (fringe and basin) in an ocean fringe forest in Jobos, Puerto Rico. Leaf and air temperature and photon flux density during the measurement period are also shown.

the fringe. However, leaf area was much smaller in senescent leaves of all species compared to their respective old mature leaves. As a result, the specific leaf area did not change as much as was expected from changes in leaf weight.

Red mangroves had the largest and heaviest leaves among species studied while black mangroves had the smallest and lightest (Table 3). Red mangrove leaves appeared to be larger and heavier when growing at the fringe compared to those growing in the basin near the salina. The specific leaf area was highest for mature leaves and decreased in the other leaf types. Mature leaves of red mangroves in the fringe had similar specific leaf area as white mangroves in the basin. However,

mature leaves of red mangroves in the basin had similar specific leaf area as black mangroves in the basin. As leaves changed in appearance, the difference in specific leaf area between species decreased although red mangroves in the basin had the lowest values at senescence.

Leaf nutrient concentrations based on leaf area varied according to species, appearance, and location of the tree (Fig. 9a-f). With the exception of P in senescent leaves, red mangrove leaves from trees in the fringe had lower N, P, and Na (Fig. 9a-c) concentrations than those of the same species growing in the basin. With two exceptions, of the mangrove species growing in the basin, leaves of black mangroves had the highest N, P, and Mg concentrations

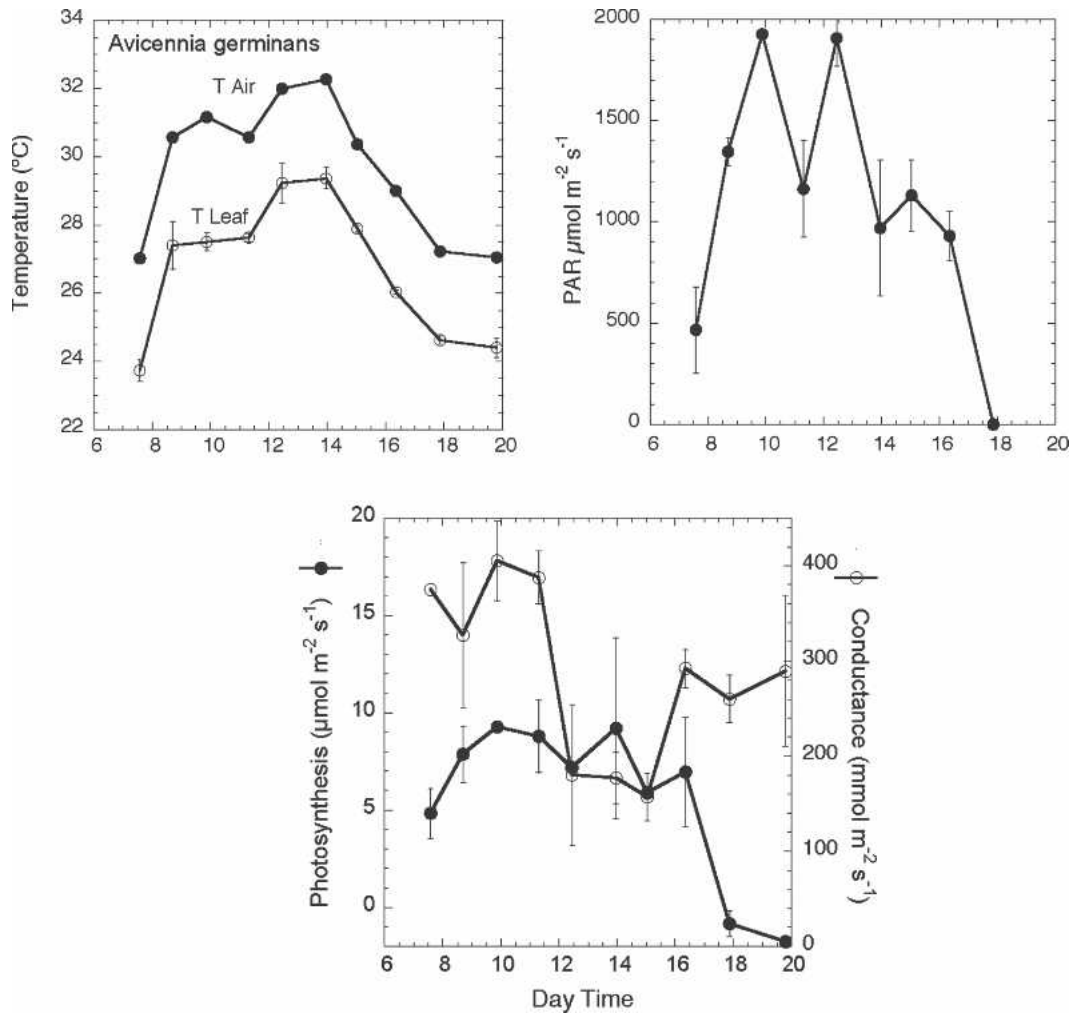


FIG. 6. Diurnal course of net photosynthesis and stomatal conductance in mature sun leaves of *Avicennia germinans* in two contrasting locations (fringe and basin) in an ocean fringe forest in Jobos, Puerto Rico. Leaf and air temperature and photon flux density during the measurement period are also shown.

TABLE 2. Average maximal rates of photosynthesis, respiration, and leaf conductance of mangrove species measured along a salinity gradient in Jobos Bay, Puerto Rico. Values are average of 4 to 6 measurements with three replicates each. Standard deviation is in parenthesis.

Process	<i>Rhizophora mangle</i>		<i>Laguncularia racemosa</i>		<i>Avicennia germinans</i>
	Fringe	Basin	Fringe	Basin	Basin
Average Maximum Photosynthesis ($\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$)	12.7 (1.4)	7.1 (0.7)	10.7 (2.5)	9.0 (0.9)	7.9 (1.4)
Respiration ($\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$)	0.4	0.7 (0.4)	0.9 (0.5)	1.0 (0.2)	1.8 (0.2)
Average maximum conductance ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)	283 (94)	141 (32)	241 (54)	184 (21)	185 (29)

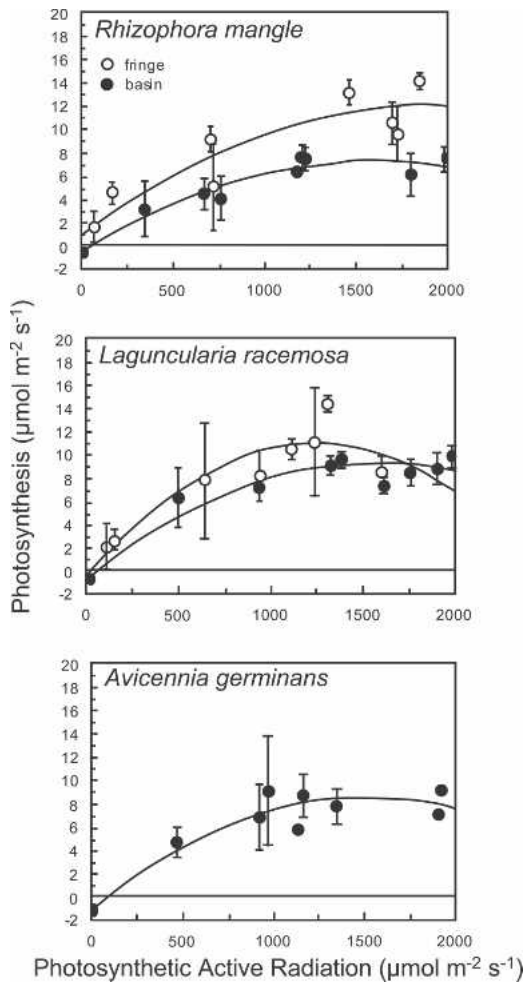


FIG. 7. Light-photosynthesis curves for three mangrove species in Jobos, Puerto Rico.

and the lowest Ca concentration (Fig. 9 a, b, e, and f). The exceptions were the P concentration of senescent leaves and the Mg concentration of mature leaves. Except for N and Mg, mature leaves of white mangroves always had higher nutrient concentrations than those of nearby red mangroves. Nutrient concentrations changed substantially as leaves senesced. Concentrations of N and P decreased from mature to senescent leaves (Fig. 9 a-b). Those of Ca increased with the exception of white mangroves Fig. 9f), whereas Mg increased with age in red mangrove, but concentrations in mature and older leaves did not differ significantly in black and white mangroves

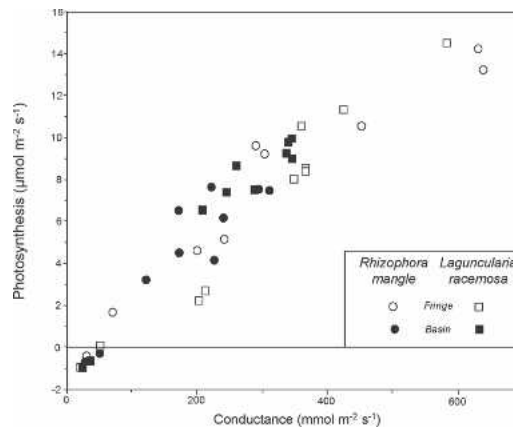


FIG. 8. Relationship between photosynthetic rate and stomatal conductance in two mangrove species in Jobos, Puerto Rico.

(Fig. 9e). Concentrations of Na and K increased from mature to senescent leaves in some species but decreased in others (Fig. 9c-d).

Retranslocation accounted for about 54 to 69% of the N and 43 to 83% of the P in mature leaves (Table 4). Retranslocation was higher in the basin compared to the fringe. Black mangroves had the highest P retranslocation of all species. Irrespective of location in Jobos, instantaneous P use efficiency was high while N use efficiency was low compared to values in Vitousek (1984). Black and red mangroves in the basin had the highest N and K use efficiency.

Litterfall and Nutrient Flux

We measured a large pulse of litterfall in October 1985 and afterwards the rate decreased to about $1.5 \text{ g m}^{-2} \text{ day}^{-1}$ in February and increased slowly to about $5 \text{ g m}^{-2} \text{ day}^{-1}$ (Fig. 10). The October pulse was associated with an October 7, 1985 rainfall event of 312 mm. Leaves comprised 60% of litterfall and red mangrove leaf fall was higher than white mangrove leaf fall (Table 5). Flowers and propagules exceeded fine wood fall and had a large pulse in October 1985. The contribution of flowers and propagules to total litterfall was 31%, slightly below the 40% contributed by red mangrove leaves.

TABLE 3. Dimensions of leaf types sampled for nutrient analyses. Values are averages of 10 leaves per type with 95% confidence intervals in parenthesis.

Location/Species	Area (cm ²)	Weight (g)	Specific area (cm ² /g)
Basin			
<i>Laguncularia racemosa</i>			
Mature	20.2 (2.7)	0.33 (0.05)	62 (2)
Old mature	22.4 (3.1)	0.57 (0.09)	40 (2)
Yellow	10.3 (1.8)	0.23 (0.05)	48 (4)
Senescent	9.1 (2.7)	0.19 (0.05)	47 (6)
<i>Avicennia germinans</i>			
Mature	11.2 (1.4)	0.21 (0.03)	55 (6)
Old mature	15.6 (1.8)	0.37 (0.04)	42 (2)
Yellow	11.1 (2.4)	0.25 (0.06)	45 (4)
Senescent	11.0 (2.5)	0.23 (0.05)	49 (2)
<i>Rhizophora mangle</i>			
Mature	18.8 (1.4)	0.36 (0.04)	54 (2)
Old mature	45.0 (8.2)	0.95 (0.17)	47 (4)
Yellow	24.0 (6.7)	0.52 (0.15)	47 (2)
Senescent	18.1 (3.7)	0.44 (0.10)	41 (2)
Fringe			
<i>Rhizophora mangle</i>			
Mature	51.1 (6.1)	0.88 (0.14)	60 (2)
Old mature	52.2 (6.3)	1.07 (0.13)	49 (1)
Yellow	49.1 (5.3)	0.99 (0.11)	50 (2)
Senescent	29.6 (7.1)	0.62 (0.15)	48 (4)

The concentration of nutrients in litterfall varied with species, litter component, and time as illustrated by the temporal variation for leaf fall (Fig. 11a to c). Concentrations changed with abrupt changes in the rate of leaf fall. In some cases nutrients increased in concentration when leaf fall decreased (December data for N and P) and in others, nutrient concentrations followed the pattern of leaf fall (K in red mangrove). The concentration of P and N in leaves was remarkably constant, except for the pulses in December and January. The mass-weighted element concentration data for litterfall components (Table 6) show small differences in N, high Ca and Na in white mangrove leaves, high P in white mangrove flowers and propagules, and low Mg in flowers in general. The inverse of the concentrations in Table 5 is the nutrient use efficiency of litterfall components. It shows white mangrove leaves with the highest P use efficiency, followed by red mangrove leaves. Conversely, white mangrove flowers and propagules had the lowest P use efficiency. The use efficiency values for N are all similar.

The flux of nutrients to the forest floor varied with species and litterfall component (Table 5). Leaves contributed N and K in proportion to their mass and their Ca, Mg, and Na fluxes were of a higher proportion to the total flux than their mass was to total litterfall. The P flux in flowers and propagules was 88% of the total P flux in litterfall. The absolute amounts of K and Mg, and those of Na and Ca in litterfall were similar. Except Na, all element fluxes were higher in red mangrove leaves than in white mangrove leaves.

DISCUSSION

Physiognomy and Ecophysiology

The physiognomy of the OFF mangroves involves small trees and an abundance of stunted trees growing around hypersaline lagoons. Tree height, density, and species zonation of the mangrove stands in this study (Fig. 1) correspond to those reported by Cintrón et al. (1978) for this region of Puerto Rico. The tallest trees grow near the

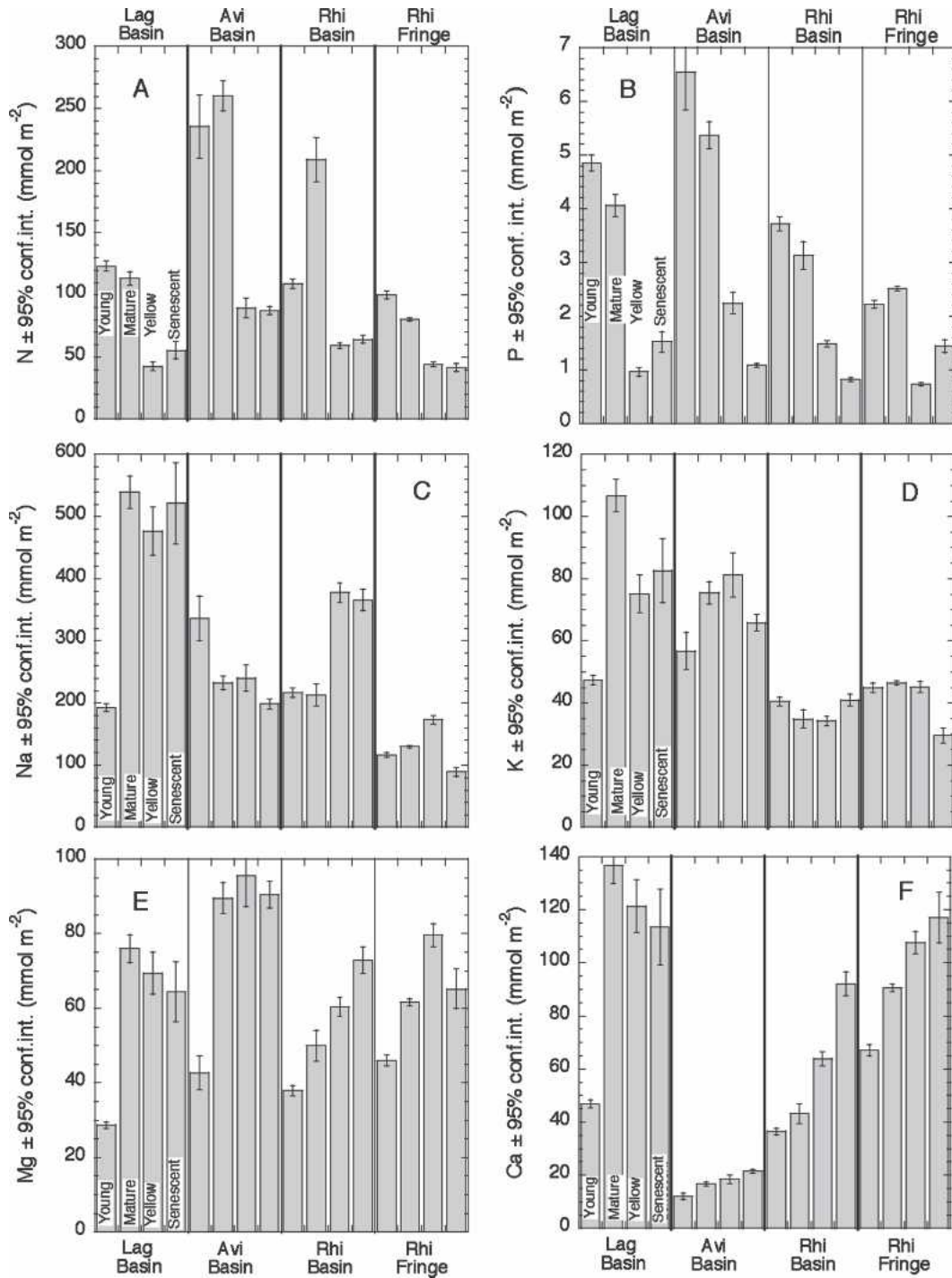


FIG. 9. Leaf nutrient concentrations expressed on a unit area basis (a to f) in different types of leaves and for different mangrove species in fringe and basin conditions in Jobs Bay, Puerto Rico. Vertical lines represent 95% confidence intervals.

TABLE 4. Retranslocation and instantaneous nutrient use efficiency (*sensu* Vitousek 1984) in senescent mangrove leaves in Jobos Bay. Retranslocation as % of the nutrient concentration at leaf maturity is in parenthesis.

Species and location	Retranslocation (mmol cm ⁻²)		Nutrient use efficiency (kg mass/kg nutrient)		
	N	P	N	P	K
Fringe					
<i>Rhizophora mangle</i>	58 (58)	1.1 (43)	357	4,684	180
Basin					
<i>Rhizophora mangle</i>	144 (69)	2.9 (78)	270	9,615	152
<i>Avicennia germinans</i>	173 (66)	5.5 (83)	167	6,098	79
<i>Laguncularia racemosa</i>	68 (54)	3.3 (69)	274	4,525	66

*Based on senescent leaves and the maximum concentration of mature leaves.

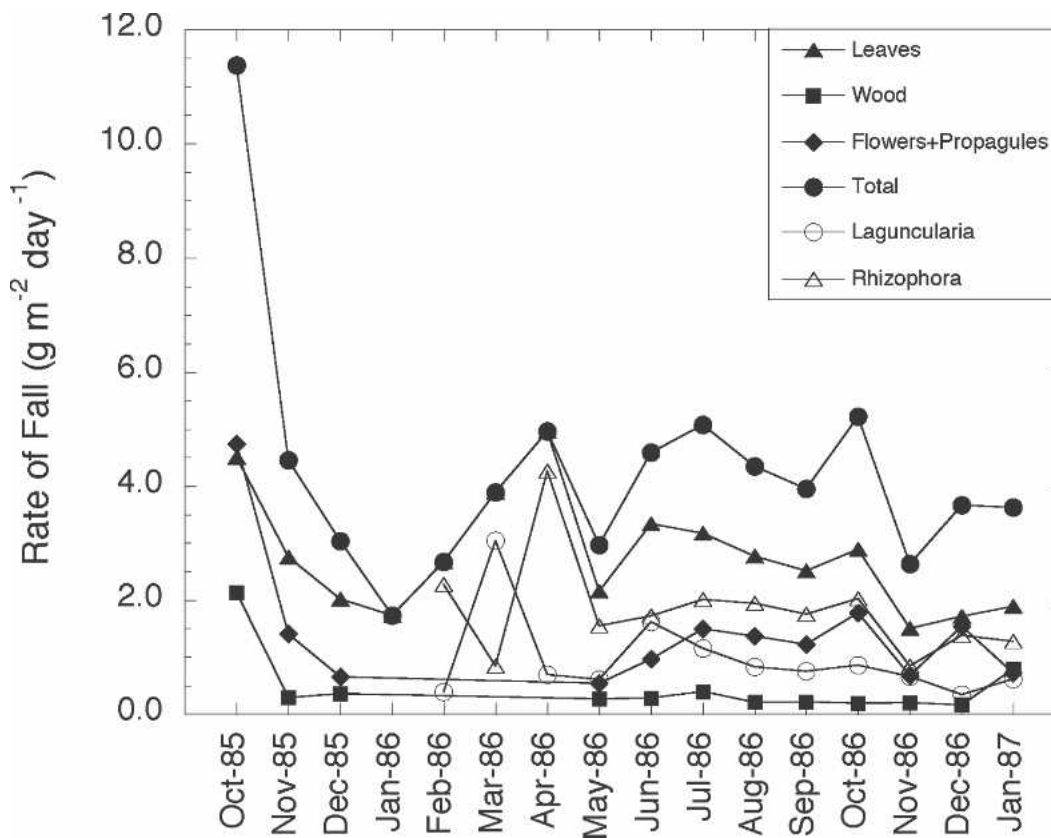


FIG. 10. Monthly litterfall rate in a fringe mangrove forest in Jobos Bay, Puerto Rico.

ocean fringe where pore salinity is lower. No mangrove trees occurred in the salina with pore salinities near 100‰. Red and white mangroves clustered along the ocean fringe with pore salinities below 40‰. Black mangroves predominated far from ocean water at pore salinity near 80‰. Scattered individuals of red and white

mangroves grew in the basin. In contrast to the OFF, white and red mangrove trees in the IFF reached 10 m in height at salinities that are normally similar to those at the OFF (Dávila 1987). However, because of their connection with Mar Negro, and ground water discharge (Quiñones Aponte et al. 1996), the IFF experiences more fre-

TABLE 5. Annual mass, nutrient, and Na flux (kg ha^{-1}) by litterfall of a fringe mangrove forest at Jobos Bay, Puerto Rico. We rounded litterfall data to the nearest kg, and integrated over different intervals, therefore, columns do not add to the total.

Compartment	Mass	N	P	K	Ca	Mg	Na
<i>Rhizophora</i> leaves ^a	6698	44	2	41	120	46	44
<i>Laguncularia</i> leaves ^a	3553	20	1	17	85	18	88
All leaves ^b	10160	63	2	57	204	63	200
Flowers and propagules ^c	5265	35	7	32	20	9	46
Fine wood ^c	1694	13	1	6	49	63	13
Total litterfall ^c	16872	108	8	91	274	80	262

^aIntegration of data from February 11, 1986 to January 11, 1987.

^bIntegration of data from September 11, 1985 to January 11, 1987.

^cIntegration of data from October 11, 1985 to December 11, 1985; and May 11, 1986 to January 11, 1987.

quent events of salinity reduction than the fringe at OFF and this might explain the larger trees. In the OFF, the continuous contact with the ocean maintains stable year-round salinity.

The zonation of mangrove species coincides with their xylem tension (Table 1, Fig. 3). Black mangroves, growing at the highest pore salinities maintained higher xylem tensions than red and white mangroves. If xylem tension in these mangrove species is a good measure of leaf water potentials (Miller et al. 1975), then it appears that the extraction of leaf sap underestimates the true value of the osmotic pressure. If cell sap π gets near the leaf water potential, turgor pressure should approach zero, causing a reduction in stomatal opening, but we observed stomata open all day long (Figs. 4 to 6). Differences between π measured in extracted cell sap and that determined by pressure/volume curves have been estimated to be 0.2 MPa or more (Tyree and Jarvis 1982).

The results of gas exchange measurements conform to observations in other mangrove forests (Medina 1999). For example, net photosynthesis was higher in the fringe at lower salinities than in the basin at higher pore salinities (Figs. 4 to 6). Red and white mangroves exhibited higher photosynthetic rates in the fringe than in the basin (Table 2). However, red mangroves had peak photosynthetic rates early in the day and decreased the rate in the afternoon, regardless of location. The white and black mangroves sustained their photosynthetic rates during the daytime. The

photosynthetic rate of black mangroves in the basin was similar or lower than the rates of white and red mangroves in the basin, but their respiration was the highest among all species. In general, the peak rates of photosynthesis of red mangroves were high compared to literature reports elsewhere, while the rates in white and black mangroves were in the same order as reported for mangroves elsewhere (Table 7). The leaves that we measured had lower temperatures than the air, in some cases by several degrees (Figs. 4 to 6), so it is possible that high temperature was not limiting to the rate of carbon assimilation. Ball et al. (1988) found optimal photosynthetic rates when leaf temperature in six mangrove species was 30°C. In addition, the light curves (Fig. 7) show that the three species had high photosynthetic rates at the light levels measured during the study (Figs. 2 and 4 to 6). Moreover, the time of our study at the end of the rainy season also help explain the high photosynthetic values that we measured. Sobrado (1999b) found that mangroves in Venezuela had peak rates of photosynthesis during the rainy season and rates fell to lower values as the dry season progressed.

Smith et al. (1989) measured the effect of salinity and drought on photosynthesis of black mangroves growing in coastal salt flats in northern Venezuela. Maximum photosynthetic rate during the rainy season was lower than rates measured in this paper ($<6 \mu\text{mol m}^{-2}\text{s}^{-1}$), and it was reduced by 30% during the peak of the dry season. Cheeseman and Lovelock (2004) measured

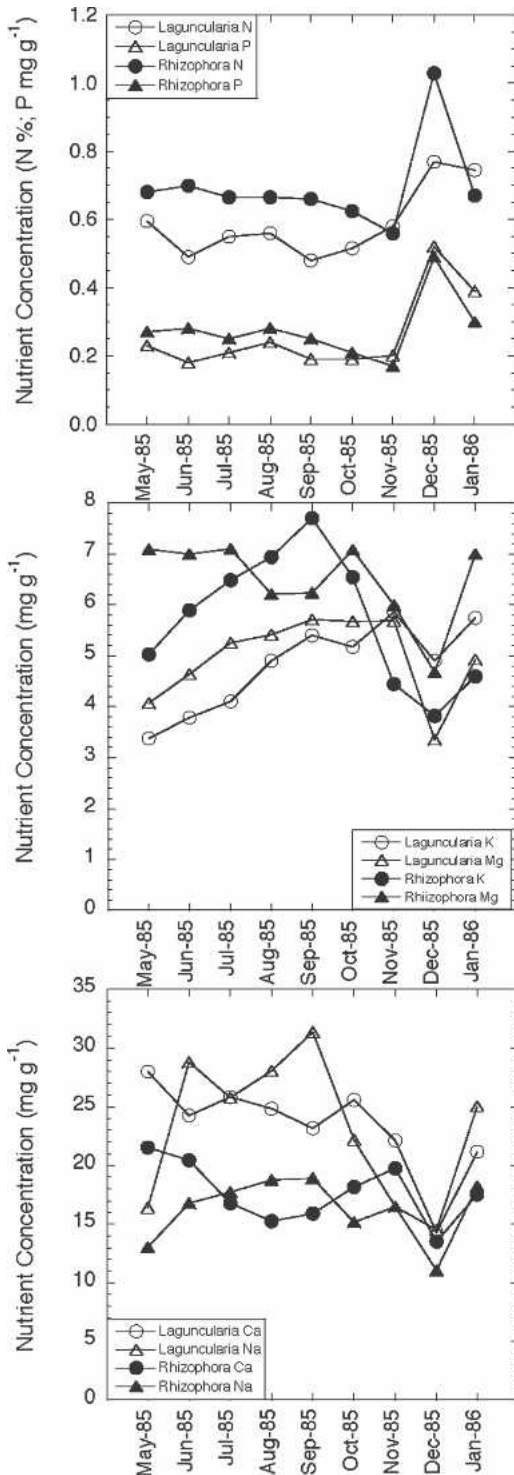


FIG. 11. Nutrient (a, b) and element (c) concentration of falling leaves for two mangrove species in a fringe forest in Jobos Bay, Puerto Rico.

photosynthesis in red mangroves along a nutrient gradient in Belize and found that maximum photosynthesis rate was higher in fringe mangrove (LAI = 2.3) than in dwarf, P-limited mangroves (LAI = 0.7) (9.9 vs. $5.3 \mu\text{mol m}^{-2}\text{s}^{-1}$). Photosynthetic rates were even lower in June and September, and differences between sites were smaller, and showed an inverse relationship. Leaf conductance followed the same pattern, maximal conductance being around $100 \text{ mmol m}^{-2}\text{s}^{-1}$, being reduced to ≈ 70 in fringe and ≈ 60 in dwarf mangroves during the less favorable months. These authors showed remarkably low light saturation intensities ($\approx 500 \mu\text{mol m}^{-2}\text{s}^{-1}$) that were not confirmed in our field study. Lovelock et al. (2004) measured photosynthesis in mangrove communities along a soil nutrient gradient in Panama, and found that photosynthesis per unit leaf area was conservative. The main effect of nutrient deficiency was to change the biomass allocation patterns. This conclusion was supported by fertilization experiments that showed similar results to those reported by Feller (1995) in Belize. It may be concluded that photosynthesis and conductance are significantly affected by salinity, whereas leaf gas exchange behaves more conservatively along gradients of P availability.

Specific leaf area values of leaves past the old mature stage (Table 3) were similar to those of sclerophyll plants (Medina et al. 1989). The size of red mangrove leaves in the fringe forest is large, reflecting lower salinity stress because red mangrove leaves become smaller and thicker at higher salinities (Lugo et al. 1981, Camilleri and Ribi 1983). Senescent leaves are much smaller than the old mature ones (Table 3). This suggests that production of leaves of different sizes occur at various time intervals, or alternatively, that differential mortality is occurring as leaves develop. The fall of large leaves with low specific area could act as a mechanism for reducing the salt content within the tree. However, in the IFF stand that we studied, white mangrove leaf fall had the largest quantity of sodium and higher Na concentration than those of red mangroves (Table 5, Fig. 11). White mangroves have a tendency to develop leaf suc-

TABLE 6. Mass-weighted (mg g^{-1}) and nutrient molar ratios of litterfall and its components in a fringe mangrove forest at Jobos Bay, Puerto Rico. Data for mature leaves are included for comparison.

Compartment	N	P	K	Ca	Mg	Na	N/P	K/Na	Ca/Mg
	Litterfall								
<i>Rhizophora</i> leaves	6.5	0.3	6.1	17.9	6.8	16.7	11.3	0.6	4.3
<i>Laguncularia</i> leaves	5.5	0.2	4.7	23.8	5.2	24.9	11.8	0.3	7.5
All leaves	6.2	0.3	5.6	20.0	6.2	19.6	11.2	0.5	5.3
<i>Rhizophora</i> flowers and propagules	6.6	0.7	5.5	3.4	1.7	9.4	4.5	1.0	3.3
<i>Laguncularia</i> flowers and propagules	7.4	5.2	8.9	6.0	1.5	4.9	0.6	3.1	6.6
All flowers and propagules	6.7	1.3	6.0	3.8	1.6	8.8	2.4	1.2	3.9
Fine wood	7.4	0.4	3.5	28.6	2.9	7.3	8.2	0.8	16.3
Miscellaneous	6.3	0.5	4.5	7.9	2.6	9.0	5.8	0.9	5.0
All litterfall	6.4	0.5	5.4	16.3	4.7	15.5	6.2	0.6	5.7
	Mature leaves								
<i>Laguncularia racemosa</i> -Basin	10.7	0.9	11.5	11.7	4.3	27.5	5.2	0.7	4.5
<i>Avicennia germinans</i> -Basin	18.2	0.1	12.2	2.7	5.7	42.5	7.4	0.5	0.8
<i>Rhizophora mangle</i> -Basin	8.3	0.6	8.6	7.9	5.1	26.9	6.1	0.5	2.6
<i>Rhizophora mangle</i> -Fringe	8.4	0.4	10.5	16.1	6.7	16.1	9.3	1.1	4.0

culence with age, a process that dilutes the osmotic concentration of leaf sap (Biebl and Kinzel 1965). Red mangrove leaves in the fringe were larger and heavier than red mangrove leaves in the basin (Table 3).

Red mangrove leaves in the fringe had low concentration of N, P, and Na relative to the other species (Fig. 9), low rates of retranslocation, and high nutrient use efficiency (Table 4). These results suggest a response to the effects of tidal action which removes nutrients from the site, but also ventilates roots and maintains constancy in the nutrient and salinity level of water. The concentrations of other elements varied with the species as expected from other studies. For example, Lugo (1998) reported that, worldwide, *Avicennia* spp has low concentration of Ca. This pattern is related to oxalate accumulation characteristic of this genus (Popp 1984). Red mangrove had low concentration of K.

Using N and P concentration data in Serrano and Monfeldt (1987) we estimates a similar percentage retranslocation value for the IFF forest as those in Table 4 for the OFF and basin. Our retranslocation results are similar to those reported by Lovelock et al. (2004) for P-fertilized Panamanian mangroves and Feller et al. (2002) for Belizean mangroves, suggesting a P-rich environment for our IFF. The control sites studied by Lovelock et al. (2004) and Feller et al. (2002) had a higher P retranslocation rate

and lower N retranslocation rate (the dwarf mangroves in Belize only) than our IFF site. Although there is a clear tendency to transport a larger percentage of P than N from the amounts accumulated in mature leaves, the absolute molar N/P retranslocation ratios decrease from 50 in *Rhizophora*, to 30 in *Avicennia*, and 20 in *Laguncularia*. The physiological significance of these ratios in mangroves remains to be established.

Productivity and Nutrient Use Efficiency

Heavy rains induced the initial peak in flower, propagule, and litterfall (Table 5, Fig. 10). Litterfall increases in mangroves during heavy rains (Twilley 1982). However, even if we subtract the unusual event in 1985, the leaf and total litter production by the IFF was still high. For example, between February 11, 1986 and January 11, 1987, leaf fall was 10.3 Mg ha^{-1} , a high value when compared to other mangroves (Table 7). A significant portion of litterfall was mangrove flowers and propagules, so that leaf fall was only 60 % of the total fall. This is a low contribution by leaves because in many mangroves leaf fall exceeds 70% of litterfall (Twilley et al. 1986). However, this difference is due to the inclusion of heavy propagules in our data.

Because of the high rate of flower and propagule fall and the high nutrient concentration of these materials, the nutrient

TABLE 7. Comparison of ecophysiological parameters measured in the Jobos Bay mangrove forest with those of other mangroves around the world. Results for red and black mangroves, respectively, represent fringe and basin conditions in Jobos. The other mangroves include many species, including species in the genera *Rhizophora*, *Avicennia*, and *Laguncularia*. Locations involve mostly Venezuela, Australia, Florida, and Puerto Rico.

Parameter	Jobos Bay		Other Mangroves		
	Fringe	Basin	Range	Condition	Reference
Maximum photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)	12.7	7.9	3.9-14.6	Fringe to hypersaline	Attiwill and Clough 1980; Björkman et al. 1988; Ball et al. 1988; Sobrado 1999a and b, 2000; Sobrado and Ball 1999; Lovelock and Feller 2003; Lovelock et al. 2004; Cheeseman and Lovelock 2004
Maximum conductance ($\text{mmol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)	283	185	125-210	Fringe to hypersaline	Björkman et al. 1988; Ball et al. 1988; Sobrado 2000
Leaf area (cm^2)	31-52*	15.6			
Leaf weight (g)	0.6-1.1*	0.37			
Specific leaf area ($\text{cm}^2 \text{ g}^{-1}$)	53-60*	55	45-123	Fringe to hypersaline and riverine	Medina and Francisco 1997; Sobrado 1999b, 2000; Sobrado and Ball 1999; Lovelock and Feller 2003; Lovelock et al. 2004
Litterfall ($\text{Mg ha}^{-1} \text{ yr}^{-1}$)	16.9	—	6.0 9.0 13.0	Basin Fringe Riverine	Twilley et al. 1986, 1997
Leaf fall ($\text{Mg ha}^{-1} \text{ yr}^{-1}$)	10.2	—	2.0-9.4	Basin	Twilley et al. 1986
N flux ($\text{kg ha}^{-1} \text{ yr}^{-1}$)		—	15-67	Basin	
P flux ($\text{kg ha}^{-1} \text{ yr}^{-1}$)	8	—	4.8	Inland fringe	Lugo and Musa 1993
K flux ($\text{kg ha}^{-1} \text{ yr}^{-1}$)	108	—	48	Inland fringe	Lugo and Musa 1993
Mass/N	154-357†	167	100-300	Basin	Twilley et al. 1986
Mass/P	3846-9091†	6250	1519	Inland fringe	Lugo and Musa 1993
Mass/K	164-179†	72	151	Inland fringe	Lugo and Musa 1993
N retranslocation (%)	52-60†	63	44-54		Lovelock et al. 2004
P retranslocation (%)	69	84	65-82		Lovelock et al. 2004

*The first value is for the Inland Fringe Forest (Serrano and Monefeldt 1987) and the second for the Ocean Fringe Forest.

†The first value is from annual litterfall and the second is from individual leaves.

flux to the forest floor was high in spite of the retranslocation by leaves (Table 5). The variation in nutrient concentration of mangrove parts (Table 6) reflects the variation in nutrient use efficiency in this forest. White mangrove leaves had a higher N and P nutrient use efficiency than red mangrove leaves. However, the flowers and propagules of white mangroves had a higher N and P nutrient use efficiency than flowers and propagules of red mangroves. In general, the N use efficiency in these

mangroves was low, while that for P averaged low for all litter, and was within the higher values measured for leaves in other mangrove forests (Table 7).

We found higher instantaneous nutrient use efficiency (Table 4), than estimates based on annual leaf fall. The difference is due to two factors. First, nutrient concentration of leaf fall is not constant but changes over time (Fig. 11). This variation reduces the estimate of efficiency because falling green leaves, for example, contrib-

ute to a reduction in the efficiency ratio. Second, the fall of large mature and old mature leaves with higher nutrient concentrations than yellow or senescent leaves (Fig. 9) also reduced the efficiency ratio. The instantaneous use efficiency ratio was high because the senescent leaves used for the calculation had the lowest nutrient concentrations of all leaves on the tree.

The ratios of N to P and Ca to Mg were higher in leaf litter than in mature leaves (Table 6). However, the K to Na ratio was similar in mature leaves and leaf litter. The largest difference was in the N/P, which suggests that litter is enriched in N after falling on the forest floor as observed frequently during the process of litter decomposition (Twilley et al. 1986) or that P is released faster than organic matter (Table 6). This was particularly true in white mangrove leaves, which exhibited the largest change in N/P between mature leaves and leaf litter. Red mangrove leaves had a higher N/P and K/Na than other mangrove species and white mangroves had the lowest N/P. As expected, wood litter had a high Ca/Mg while flowers had very low N/P, particularly those of white mangrove.

From the work of Varela and Berrios (1987) and our leaf fall data (Table 5), we estimated the ratio of leaf fall to leaf litter mass in the IFF. The concentration of N, P, and K in leaf litter was 1.17, 0.04, and 0.29 mg g⁻¹, respectively. Leaf litter standing stock was 0.53 Mg ha⁻¹ and the standing stock of N, P, and K was 6.2, 0.21, and 1.6 kg ha⁻¹, respectively. The ratios of fall to stock were 19.2, 10.2, 9.5, and 35.6 for mass, N, P, and K, respectively. These ratios are similar to those reported for Joyuda Lagoon, an inland fringe forest on the west coast of Puerto Rico (Lugo and Musa 1993), and they are high in comparison to mangroves elsewhere (Twilley et al. 1986, 1997). In fact, the Jobos Bay mangroves have litter turnover ratios similar to those of riverine forests. The reason for these high ratios is the high rate of litter fall and the removal of litter at the fringe by tidal action.

CONCLUSION

The measurements of litterfall, net daytime photosynthesis, and nutrient use effi-

ciency showed that under favorable conditions the mangroves in Jobos are capable of high rates of production and fast circulation of nutrients (Table 7). Although we found differences between red mangroves in the OFF and IFF, they were small. The IFF had larger trees, higher N and P concentration, and smaller leaves, but similar retranslocation rates. Both fringe forests evidenced capacity for high productivity and high turnover of nutrients and mass. The flushing of forest floor litter maintains a low litter stock, which coupled to the high rate of litterfall results in high litter turnover. Waters in the canal at the IFF are black waters rich in particulate and dissolved organic materials. The black waters indicate a slower water turnover than at the OFF, where tides and waves flush the system daily. We believe that this difference in hydrology is critical for the functioning of mangroves because they cause changes in the salinity and root environment of the respective forests. At the OFF, salinity levels are more constant at about seawater strength and roots are ventilated more often than at the IFF. The IFF is subject to salinity change, dilution during rainfall events, and concentration during drought. The annual rainfall at Jobos is about 1 m, at the transition between moist and dry forest conditions. Given the annual variability in rainfall and freshwater discharge from the regional aquifer in this region (Quiñones Aponte et al. 1996), the IFF experiences more environmental change over the long-term than does the OFF. The salinity of the OFF is buffered by the ocean, and is thus less likely to experience frequent reductions in salinity. We believe the long-term accumulation of low salinity events favor the greater structural development in the IFF relative to the OFF. Because we conducted our litterfall measurements during a period of high rainfall and our gas exchange measurements during clear conditions after the rainy season, our results document the optimal productivity of this mangrove forest. It is possible that the influence of tidal motion along with rainfall act as the primary factors regulating ecosystem function in these fringe forests. The picture that emerges from our measure-

ments and observations is a forest of low biomass storage and high turnover in a variable environment. Measurements of these parameters during the drought cycle will certainly yield a different level of productivity and turnover. This underscores the need for long-term research in mangrove forests.

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Errata

The values for table 6 published in the article below are incorrect. Please use the values in the table below, these are the correct ones.

Lugo, A.E.; Medina, E.; Cuevas, E.; Cintron, G.; Laboy Nieves, E.N.; Schaeffer Novelli, Y. 2007. Ecophysiology of a mangrove forest in Jobos Bay, Puerto Rico. *Caribbean Journal of Science*. 43(2): 200-219.

Table 6 . Mass-weighted concentration (mg g⁻¹) and nutrient ratios of litterfall and its components in a fringe mangrove forest at Jobos Bay, Puerto Rico. Data for mature leaves are included for comparison.

Compartment	----- mg/g -----						--- molar ratio ----		
	N	P	K	Ca	Mg	Na	N/P	K/Na	Ca/Mg
Litterfall									
Rhizophora Leaves	6.5	0.26	6.1	17.9	6.8	16.7	55	0.21	1.6
Laguncularia Leaves	5.5	0.21	4.7	23.8	5.2	24.9	58	0.11	2.8
All Leaves	6.2	0.25	5.6	20	6.2	19.6	55	0.17	2.0
Rhizophora Flowers and Propagules	6.6	0.67	5.5	3.4	1.7	9.4	22	0.34	1.2
Laguncularia Flowers and Propagules	7.4	5.19	8.9	6	1.5	4.9	3	1.07	2.4
All Flowers and Propagules	6.7	1.27	6	3.8	1.6	8.8	12	0.40	1.4
Fine Wood	7.4	0.41	3.5	28.6	2.9	7.3	40	0.28	6.0
Miscellaneous	6.3	0.49	4.5	7.9	2.6	9	28	0.29	1.9
All Litterfall	6.4	0.47	5.4	16.3	4.7	15.5	30	0.20	2.1
Mature Leaves									
Laguncularia racemosa-Basin	10.7	0.9	11.5	11.7	4.3	27.5	26	0.25	1.7
Avicennia germinans-Basin	18.2	1.0	12.2	2.7	5.7	42.5	40	0.17	0.3
Rhizophora mangle-Basin	8.3	0.6	8.6	7.9	5.1	26.9	31	0.19	0.9
Rhizophora mangle-Fringe	8.4	0.4	10.5	16.1	6.7	16.1	46	0.38	1.5