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NUTRIENT CYCLING BY THE RED MANGROVE, *RHIZOPHORA MANGLE L.*, IN JOYUDA LAGOON ON THE WEST COAST OF PUERTO RICO.

BY

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ABSTRACTO

La Laguna Joyuda representa un ecosistema casi cerrado, excelente para propósitos de estudio. El presente estudio examina las tasas de flujo de nutrientes entre la comunidad de mangles de borde y la laguna. Por medio de muestreos, experimentos, transectos, análisis químicos, y la comparación de fotografías aéreas, se documenta el ciclo de nitrógeno en este sistema.

Se encontró que el tiempo de residencia del nitrógeno en el agua de la laguna es corto; la biomasa de mangles es de aproximadamente 720 toneladas; la tasa de remoción de nitrógeno es de 15.9 toneladas por año; la tasa de retorno de nitrógeno a la laguna es de 1.92 toneladas por año; y la tasa de crecimiento de los mangles es de aproximadamente 1,960 metros cuadrados por año o 2.97 toneladas nitrógeno por año.

Se presentan recomendaciones para estudio subsiguientes.

WE ARE THE MANGROVES

Our lives

intertwined

hopeful, helpless

we are the mangroves,

graciously

hooking a tapestry

of roots

on the coast

of a tropical

island.

We know with our hearts

that only our love

will nourish

this cyclic growth

of healthy

knotted roots.

Come grow strong with me.

Judy Berk-Levine

ACKNOWLEDGEMENTS

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INTRODUCTION

Joyuda Lagoon represents a fairly closed system, which is excellent for study purposes. Previously, the levels of nutrients and their seasonal variations within the lagoon were unknown. The food webs occurring here also remained unstudied. Being almost entirely fringed by red mangroves (*Rhizophora mangle* L.), it is believed that the organic detritus from these trees constitutes a major fraction of the base of this food web. Investigations for a predictive model are needed to help evaluate the potential impact of development and future recommendations for management of the lagoon.

This study is concerned with the nutrient turnover rates between the mangroves and the lagoon. Through sampling, experiments, transects, chemical analyses, and the comparison of aerial photographs it is the aim of this work to document the nutrient cycling between the fringing mangrove community and the lagoon.

The main concerns of this project were to quantify the rates of removal of nitrogen (in the form of ammonium) from water by the mangrove, and conversely, the amount of nitrogen returned to the lagoon by the mangroves and its seasonal variations. Nitrogen and phosphorus have been chosen, in particular, because they are traditionally identified as limiting nutrients to primary production in marine environments and are of extreme biological importance.

Towards these aims this study has provided quantitation of the

amount of litter-fall from the mangroves and its inherent nutritional value; monitored the level of nutrients in the lagoonal water and different compartments of the mangroves (leaves, propagules, roots, flowers, and wood); determined the rate of uptake of ammonium by mangrove roots; and documented the rate of mangrove leaf decay. The standing crop (biomass), species composition, and growth of the fringing mangroves have also been calculated.

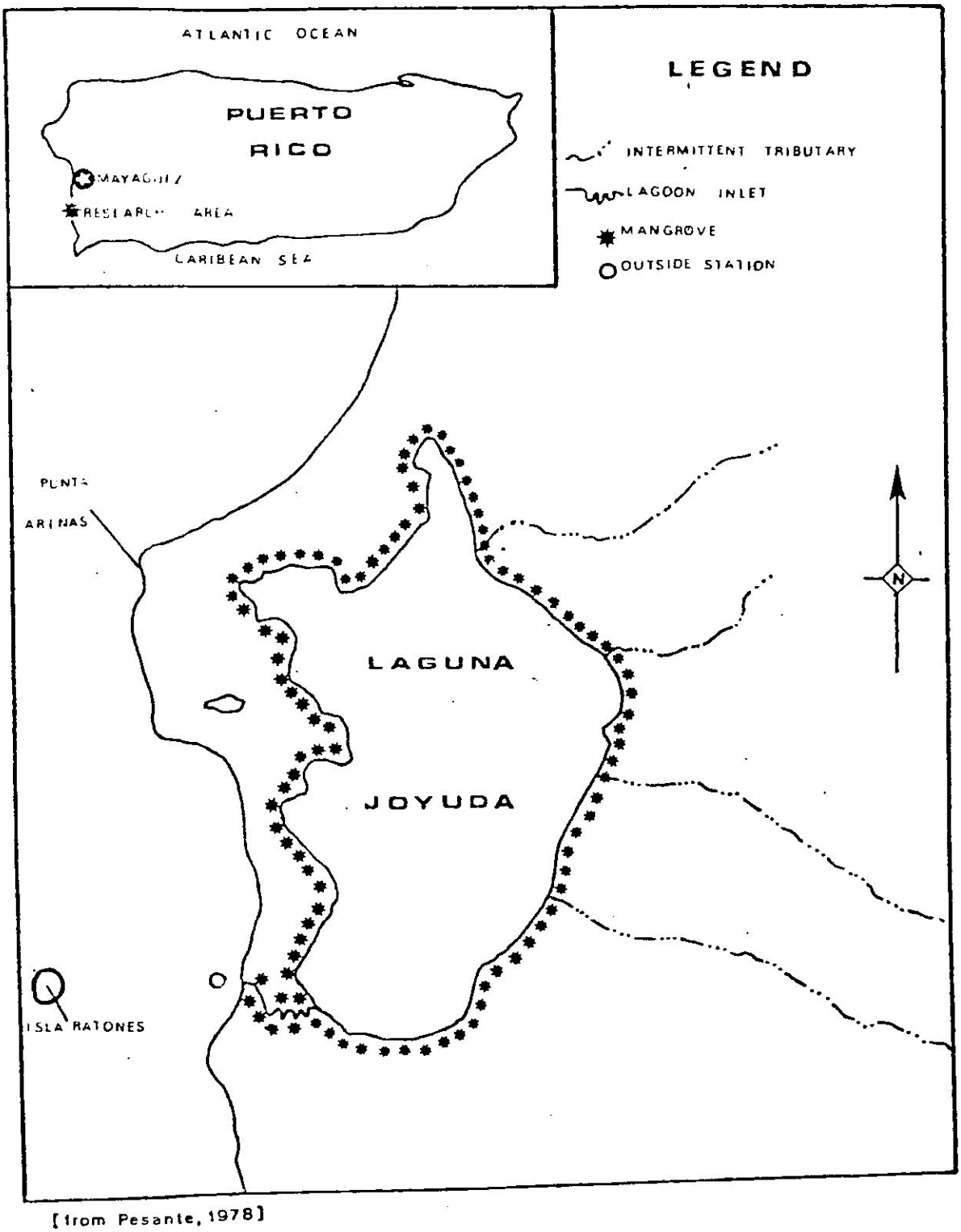
DESCRIPTION OF STUDY AREA

Joyuda Lagoon is located on the west coast of Puerto Rico, at approximately 67° 10' 45" W longitude and 18° 07' 30" N latitude. This is about 5 miles (8 km) south of Mayagüez (Fig. 1, from Pesante, 1978). The climatic classification of the area is a Subtropical Moist Forest (Ewel and Whitmore, 1973). The average yearly rainfall for the study period was 1730 mm (68.21 inches). According to Carvajal, et al. (1980) the minimum and maximum annual precipitation varies between 1,000 and 2,000 mm, respectively.

This lagoon, which is considered brackish, has a surface area of 121.4 hectares (about 300 surface acres)(Pagán and Austin, 1967). The lagoonal basin area is 1.37 km^2 and the drainage area surrounding the lagoon is 5.95 km^2 (Carvajal, et al., 1980). Highway number 102 runs along the sand bar separating Joyuda Lagoon from the Mona Passage. There is a canal of approximately 0.5 km length, which connects the lagoon to the ocean. The average depth of the water in the lagoon is 1.5 m with two deeper areas of 2 and 2.5 m (Pesante, 1978).

Historic data on Joyuda Lagoon salinity shows great variations with time. Carvajal, et al. (1980) report recorded salinities from 8°/$_{oo}$ to 44°/$_{oo}$. According to Pesante (1978), salinity measurements taken in the lagoon during his study indicated that the lagoon is homogeneous on a vertical and longitudinal plane. He further suggests that this is so because of the shallowness of the system (1.5 m) coupled with

Figure 1. Location of Joyuda Lagoon in Puerto Rico (from Pesante, 1978).



[from Pesante, 1978]

continuous winds which effectively mis the water. Carvajal, et al. (1980) agree with this statement and add that this system is also homogeneous with regard to temperature and dissolved oxygen.

The sediments, studied by Comer (1969) are described as a grayish-black mud with varying amounts of shell material. Comer (1969) also states that due to the activity of burrowing organisms there is no perceptible stratification of bottom sediments, and that mangrove swamp material is the major source of fine sediments. *Ruppia maritima*, a seagrass, grows profusely along the west and south coast shores of the lagoon (Pesante, 1978).

A fringe of mangrove, predominantly *Rhizophora mangle*, the red mangrove, grows around the lagoon, covering over 75% of the shoreline. This fringe varies in width from 5 to over 40 meters. Also found growing along the shore and further inland are *Avicennia germinans*, the black mangrove; *Laguncularia racemosa*, the white mangrove; and *Conocarpus erectus*, the buttonwood. The mangroves in Joyuda Lagoon are among the tallest in Puerto Rico, having been measured to over 22 meters (Carvajal, et al., 1980).

At the south end of the lagoon, a bird rookery has been established in a stand of red mangroves. Birds frequently observed at the lagoon include both terrestrial and aquatic species. Some of these include: The cattle egret (*Bubulcus ibis*), Leashes' petrel (*Oceanodroma leucorhoa*), the Purple Martin (*Megaceryle alcyon*), the Cave Swallow (*Detrochelidon fluva fluva*), and the Brown Pelican (*Pelecanus occidentalis*) (Carvajal, et al., 1980).

A species list of fish and invertebrates inhabiting the lagoon was compiled by Pagán and Austin (1967) while investigating a fishkill in the lagoon during that year. The Department of Natural Resources has compiled another list of phytoplankton, zooplankton, as well as fish of Joyuda Lagoon (Carvajal, et al., 1980). Pesante (1978) was the first to describe the zooplankton populations in this lagoon.

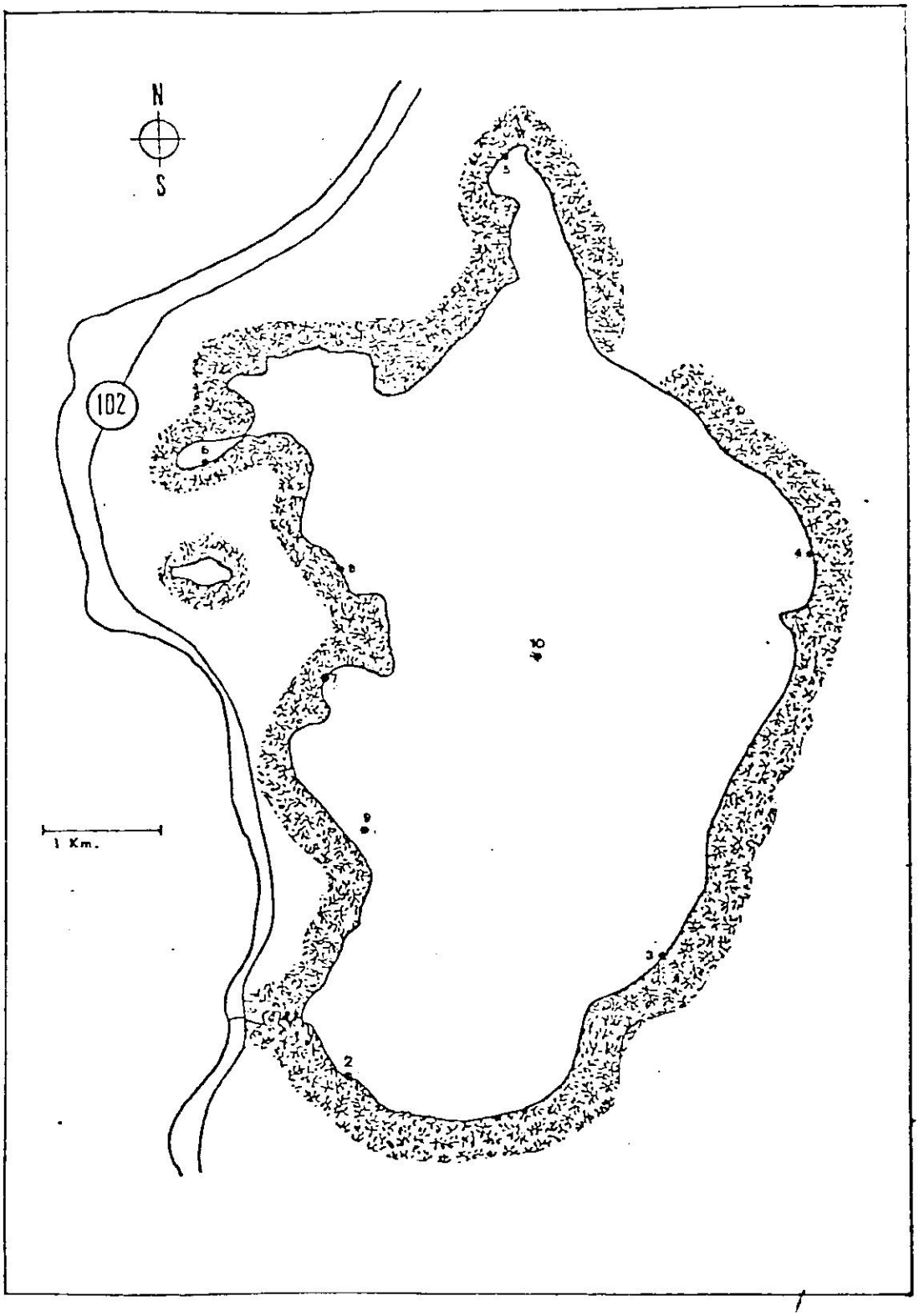
At present, two students in the Department of Marine Sciences, University of Puerto Rico, are completing their work in Joyuda Lagoon. García (1981) is describing the fish population with regard to their parasites, and Castro (1981) is doing work on the bottom communities of the lagoon. Carvajal has done work involving bioluminescense by the dinoflagellate *Pyrodinium bahamense* and the ctenophore *Mnemiopsis* spp. in Joyuda Lagoon.

The land surrounding the lagoon contains high quantities of Nickel (Ni) and Iron (Fe), which are believed to be in concentrations of possible commercial importance (Carvajal, et al., 1980).

There are many families residing in the area surrounding Joyuda Lagoon who, directly or indirectly, sustain themselves by fishing in the lagoon. At present, legislation is pending in the House of Representatives to make Joyuda Lagoon a nature preserve as recommended by the Department of Natural Resources and the Puerto Rico Coastal Management Program and Final Environmental Impact Statement written by the U.S. Department of Commerce (1978).

Sampling sites 1 through 8 (Fig. 2) were used to collect data on litter-fall, mangrove species composition, water nutrient concentrations, interstitial water, and mangrove leaf decay rates. Stations 9 and 10

Figure 2. Location of sampling stations in Joyuda Lagoon marked with a star (*).


N
S
102
1 Km.
1
2
3
4
5
6
7
8
9
10

were used solely for water samples to determine nutrient concentration. Station 9 was located at the tide gauge and station 10 in the middle of the lagoon.

METHODS

López and Teas (1978) have developed a model for determining cycling of trace metals in mangroves. With proper modification, the model has been applied to this study of nutrient cycling in the mangrove-lagoon ecosystem. The model consists of a sequence of discreet compartments. Each compartment is described in terms of the product of its biomass and nutrient content. The rate of exchange between these compartments represents turnover rates of biomass or rates of cycling.

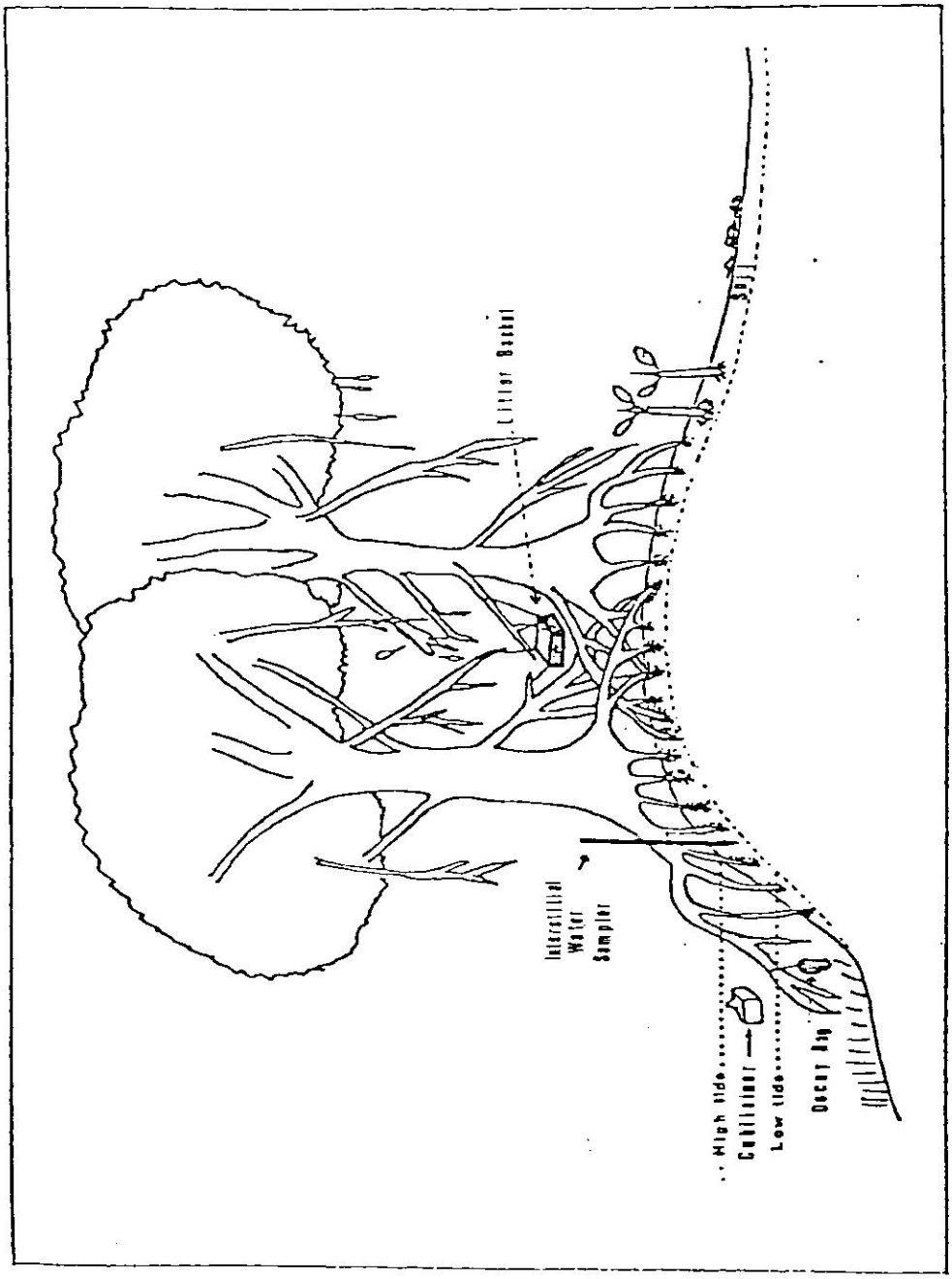
For Joyuda Lagoon, biomass (standing crop) and average concentration of nutrients in various compartments (leaves, seedlings, feeding roots, aerial roots, flowers, and wood) of the red mangrove (*Rhizophora mangle*) have been measured. With estimates of rates of fall of red mangrove biomass and nutrient content per unit biomass, the turnover rate of nutrients through mangroves is assessed. Nutrient content in the water and sediment compartments have also been assessed.

Leaves, propagules, flowers, feeding roots, and wood were collected at selected sites around the lagoon. Each sampling station consisted of approximately a 25 m stretch of fringing red mangrove. About 200 full size leaves that looked green and healthy were picked, one by one, randomly from the lower, middle, and upper parts of the trees. Also, about 100 yellow, dying leaves were picked in the same manner as healthy leaves. About 25 propagules and 50 flowers were picked in the same manner. Aerial roots are those projecting from the tree into the

air or water but not buried in the bottom mud. Sections of these were cut from various trees throughout each sampling area. Feeding roots include rhizomes and were dug out of the mud, again from various trees throughout the section of the forest sampled. Analogously, sections of hardwood were cut from growing limbs ranging from 3 to 5 cm in diameter. Each type of tree compartment (leaves, etc.) was stored in separate plastic bags as to make up samples that were composites over the forest. All samples were oven-dried at 70°C after chopping the larger pieces into smaller ones. A subsample from each mixed, dried sample was ground into a powder in an Osterizer and with a mortar and pestle, then tested for total nitrogen content according to the method for total Kjeldahl nitrogen in the U.S.E.P.A. Manual of Methods for Chemical Analysis of Water and Wastes (1974), in duplicate.

Water samples throughout the lagoon were obtained at approximately monthly intervals using plastic "Cubitainers." Figure 3 shows a schematic illustration of sampling techniques employed. Ten sampling stations were established. Caution was exercised to avoid contamination from the boat. Samples were filtered through Millepore (0.45 μ pore size) filters and frozen prior to analysis. Nutrient content determinations were then made in duplicate. Autoanalysis methods as per Gilbert and Loder.(1977) and Zimmermann, et al. (1977) were used for nitrate and nitrate determinations in a Technicon Autoanalyzer II at the Center for Energy and Environment Research laboratory. Strickland and Parsons (1972) methods were followed for ammonium and reactive phosphate determinations.

Figure 3. Representation of sampling techniques employed in this study.


Litter Basket
Interstitial Water Sampler
High tide
Low tide
Ocean Bay

For estimates of litter production the model of Pool, et al. (1975) was followed. Eight baskets of known area (0.108 m^2) were placed at intervals among the fringe mangroves. The baskets, with small holes in the bottom to allow rain water to drain out yet retain the litter, were elevated to avoid waterlogging at high tide (Fig. 3). Litterfall is considered to include leaves, seedlings, wood, and miscellaneous items (unidentifiable and extraneous objects). Leaves, branches, or seedlings partially in the basket were cut, and only that part inside the basket was included in the sample. Litter from the baskets was collected every 28 to 35 days in order to minimize weight loss to decay. Samples were dried to a constant weight and separated into compartments. From this, litter production per unit time has been calculated.

Transects were made through the surrounding mangrove forest at each of the 7 fringing stations which remained at that time, to determine species composition and zonation. Transects consisted of walking a measured line through the forest and noting the species encountered. Total biomass was calculated by multiplying total area covered by mangroves times the biomass per unit area (Golley, et al., 1962). Aerial photographs from 1936, 1951, and 1976 were compared to estimate mangrove growth through those time periods and to estimate the area presently covered by mangroves.

Interstitial water from the mangrove peat was sampled once during the year, by means of a sampling device designed and constructed by this investigator (Fig. 3). Levels of nitrate, nitrite, ammonium, and reactive phosphate were monitored. Again, samples were filtered through

Millipore (0.45 μ) filters and frozen until analyzed. With this data together with the constant computed from the uptake experiments, it was possible to formulate a model for nutrient uptake.

To determine the rate of ammonium uptake by the mangroves, isolated seedlings were placed in a plastic tank with seawater of known ammonium concentration. The change in concentration over time was measured for a 24 hour period. This was accomplished by direct wet chemical analysis for ammonium, the predominant nutrient found in the interstitial water. For 12 hours prior to the beginning of these experiments, the seedlings were allowed to stabilize in a solution of the same concentration and recover from any shock involved in transplanting.

It has been demonstrated that uptake of nutrients by algal cells and higher plants obey saturation kinetics (Dugdale, 1976). The rate of uptake may be fitted into a mathematical expression, known as the Michaelis-Menten equation of saturation kinetics. This mathematical model has been applied here to the saturation kinetics in the uptake of ammonium displayed by the mangrove seedlings.

The decay rate of *Rhizophora mangle* leaves was determined according to the methods of Heald (1971). Collection of dead, yellowed leaves in which the abscission process was virtually complete was made. If a leaf detached easily when touched it was judged ready to fall and included in the sample. Samples of 100 grams fresh weight were weighed and placed in nylon mesh bags (mesh size 1/8 inch square). Each bag was weighed and placed in the study area so that their contents were subject to the brackish water environment (Fig. 3).

Additional replicate samples were oven-dried until a constant weight was obtained. The relationship between fresh weight and dry weight was thus obtained and provided a conversion factor applied to the fresh weights of leaves used in this field experiment.

One bag was retrieved from the lagoon at approximately monthly intervals. A count was kept of the number of crabs and worms found within the decay bags. The samples were weighed, dried, then reweighed. The recorded weight of each sample was then compared to its calculated dry weight at the start of the experiment. This produced a measure of loss per unit time.

Climatological data was monitored at the Center for Energy and Environment Research, which is located 2 miles north of the lagoon. A tide gauge was installed in the lagoon by the Department of Natural Resources for continuous sensing of tidal variations. Both sets of data are available from the respective institutions.

Open ocean water samples were collected near the mouth of the canal. These were taken seasonally. The samples were filtered through Millipore (0.45μ) filters and frozen, then analyzed for the same nutrients as within the lagoon. Data were then compared to that obtained within the lagoon.

TRANSECTS

The purpose of these transects is to give a visual picture of the sites of litter basket placement. The vegetation, as marked on the transect lines in Figure 4, are the dominant mangrove species encountered. All transects were run in an approximately east-west orientation through the litter basket collection sites.

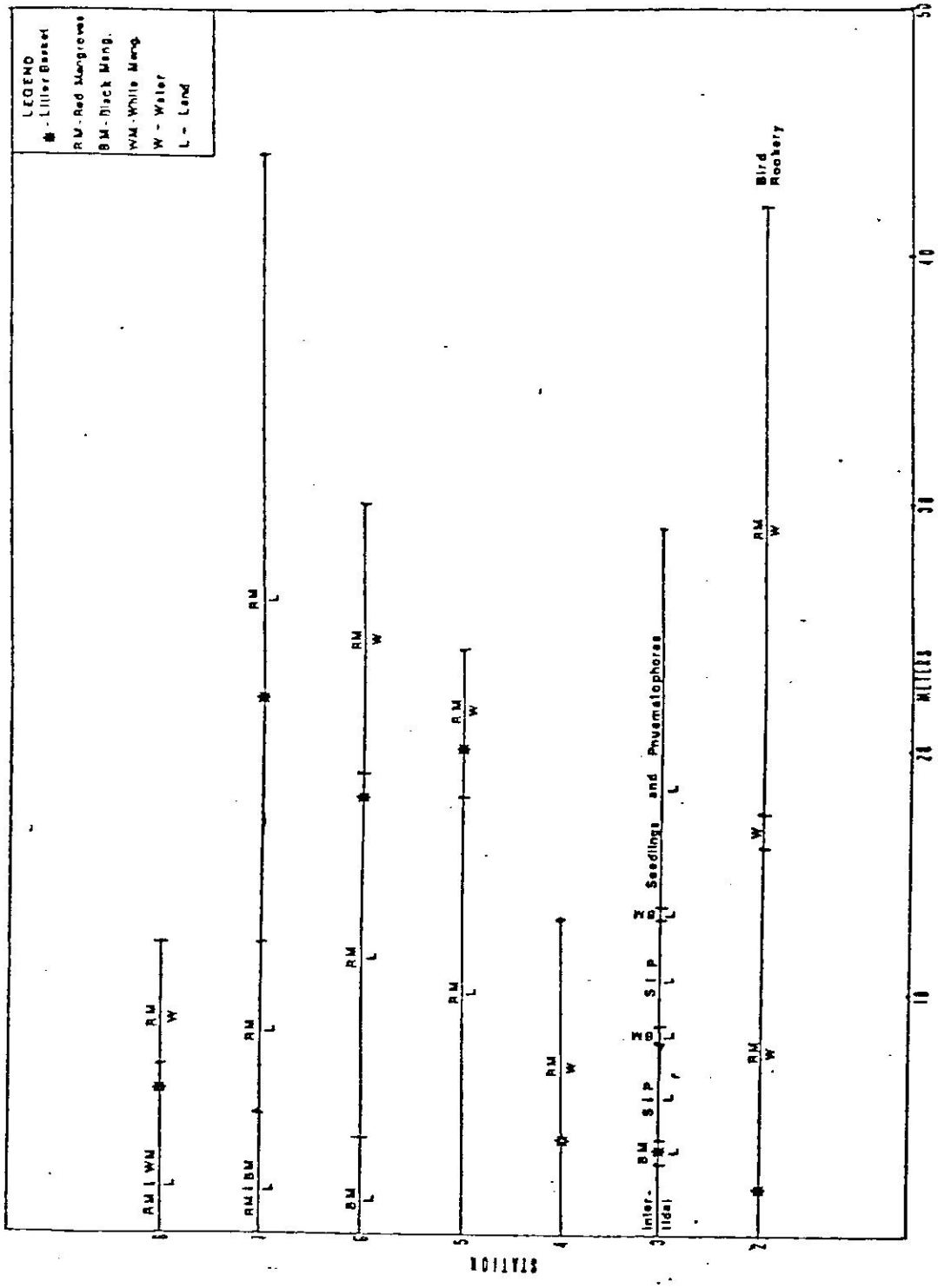
Station 1 was located in the canal connecting Joyuda Lagoon with the Mona Channel. However, due to unnatural interference, this station had to be abandoned.

The southern tip of the lagoon where station 2 was located is the site of a bird rookery. These mangroves are among the tallest in the lagoon. Here the litter basket was suspended over water, beneath a canopy of red mangroves. This area is a convolution of mangroves indenting into the lagoon. An area of water crosses the stand of mangroves.

Transect 3 began in an intertidal region of red mangrove seedlings on the east shore of the lagoon. The basket was located beneath a black mangrove. This was the only basket located in an area other than red mangrove. Many black mangrove pnuematophores and red mangrove seedlings cover the ground. It appears as though this area is in the process of being colonized by red mangroves since the red greatly outnumber the black mangrove seedlings.

The area of stations 4 and 5 is entirely red mangrove. Here

Figure 4. Transects through mangroves at litter stations in Joyuda Lagoon.


LEGEND
- Litter Basket
RM - Red Mangroves
BM - Black Mang.
WM - White Mang.
W - Water
L - Land
Bird Rookery
Seedlings and Physmatophores
Inter-tidal
STATION
METERS

again the baskets were elevated over water. Station 4 was located on the east shore and station 5 at the northern tip of the lagoon.

Station 6 was located in an area called La Lagunita. This is an area of Joyuda Lagoon which through time and growth of the surrounding mangroves has had its access gradually narrowed. At present, the opening is just wide enough to allow a small boat through. The water in this area is anoxic. During the course of this investigation two large red mangrove trees have died here. Proceeding from the water inland, the dominant red mangroves give way to a black mangrove zone.

At station 7 the basket was located in another red mangrove peninsular convolution of the shoreline. Proceeding west from the water the red mangrove zone becomes mixed with white mangroves.

The basket at station 8 was located in a mixed red and white mangrove stand. However, this is predominantly red mangrove. Proceeding towards the water (easterly) the area becomes totally red mangrove.

LITTER PRODUCTION

Litter was collected in 0.108 m^2 plastic containers for 17 months. From the actual amount of litter collected results were extrapolated to grams of litter per meter square per year ($g/m^2/yr$) for both fresh weight and dry weight. The total amount of litter collected in the 17 months, from 23 March, 1979 to 16 July, 1980, was 3881 grams wet weight (gww), 1812 grams dry weight (gdw), and total leaf-fall was 2023 gww and 1005 gdw (Tables 1 and 2).

From these figures it was possible to calculate the annual litter-fall budget of Joyuda Lagoon. Annually, 1919 gdw/m^2 and 945 gdw/m^2 of total litter and leaf litter, respectively, can be expected to fall in this environment. These figures were further broken down to 5.25 $gdw/m^2/day$ total litter and 2.56 $gdw/m^2/day$ for leaves.

In comparison with data in Table 3 it can be seen that Joyuda Lagoon produces more litter (both total and leaf) than the mean values computed for various other mangrove ecosystems. The greater rate of leaf litter production reported by Carvajal, et al. (1980) for Joyuda Lagoon (approximately 200 $g/m^2/yr$ greater) was not an actually measured rate, but a mathematical estimation based on tree density and basal area.

Separating the litter collections into compartments (Table 4 and Figures 5-7) the highest percentage of total collected litter was leaves, ranging from 28 to 72% in sampling periods, and 49% of the total litter produced in the 17 months; seedlings ranged from 2 to 46%, and were 26%

Table 1. Actual weight, in grams, of total litter and leaves collected, given in both wet and dry weights.

TABLE 1

Date	TOTAL Wet	TOTAL Dry	LEAF Wet	LEAF Dry
4/27	332	205	131	88
5/11	125	51	84	31
6/08	274	122	176	69
7/13	624	210	247	83
8/13	399	90	173	63
9/10	560	192	263	73
10/11	246	133	124	70
11/15	183	86	118	63
12/10	175	91	91	51
1/16	146	84	93	62
2/17	114	71	92	56
3/18	136	93	92	64
5/08	214	123	135	85
7/16	353	261	204	147
TOTAL	3881	1812	2023	1005
MEAN	277	129	146	72
STANDARD DEVIATION	161	63	60	26

Table 2. Grams dry weight of litter per meter square at each sampling data, presented by compartment.

TABLE 2

Date	Leaves	Seedlings	Twigs	Miscellaneous	Total
4/27	102	104	24	7	237
5/11	36	19	0	4	59
6/08	91	70	34	25	219
7/13	110	133	30	53	326
8/13	83	54	57	37	230
9/10	96	160	71	21	348
10/11	92	37	0	34	164
11/15	83	38	4	30	156
12/10	67	36	0	17	120
1/16	82	5	8	28	123
2/17	74	3	13	30	120
3/18	84	5	11	22	121
5/08	112	17	3	48	180
7/16	226	23	60	5	314
TOTAL	1339	704	315	361	2718

$g/m^2/yr$ = 1919 (total litter) and 945 (leaf litter)

$g/m^2/day$ = 5.25 (total litter) and 2.59 (leaf litter)

Table 3. Comparison of litter production from different ecosystems, in grams dry weight per meter square per year.

TABLE 3

Site	Forest Type	Litter Production leaf/total (% leaf)	Reference and Comments
Australia	*Avicennia marina*	1330	Briggs, 1977 (total litter)
Australia	*A. marina*	460/580 (79%)	Goulter and Allaway, 1975
Thailand	*Rhizophora apiculata*	670	Cromack and Monk, 1975 (leaf litter)
North Carolina (U.S.A.)	Hardwood Forest	270/437 (64%)	
	Pine Forest	319/325 (98%)	
Britain	Oak Forest	386	(leaf litter)
Britain	River Thames	23.2	Mathews and Kowalczewski, 1969 (total litter)
Florida	*R. mangle*	880	Odum and Heald, 1975 (total litter)
Florida	Mangrove Forest	485/650 (75%)	Lugo and Snedaker, 1975
Florida	Mangrove Forest	850	Pool, et al., 1975 (mean total litter)
Puerto Rico	Mangrove Forest	975	
Puerto Rico (Guayanilla Bay)	*R. mangle*	660/870 (76%)	López and Teas, 1978
Puerto Rico	Mangrove Forest S.	507-624 (81%)	Lugo and Cintrón, 1975 (southern type and northern)
	N.	931/1325 (70%)	
Puerto Rico	*R. mangle*	580	Golley, et al., 1962 (leaf litter)
Puerto Rico (Joyuda Lagoon)	Fringing Mangrove	1164	Carvajal, et al., 1980 (leaf litter est.)
Puerto Rico (Joyuda Lagoon)	Fringing Mangrove	945/1919 (49%)	This study

Table 4. Percent dry weight of total sample by compartment.

TABLE 4

Date	Leaves	Seedlings	Twigs	Miscellaneous
4/27	43	44	10	3
5/11	61	33	0	6
6/08	42	32	16	10
7/13	34	41	9	16
8/13	36	24	25	15
9/10	28	46	20	6
10/11	56	23	0	21
11/15	53	25	3	19
12/10	56	30	0	14
1/16	67	4	6	23
2/17	62	2	11	25
3/18	70	3	9	18
5/08	63	10	1	26
7/16	72	7	19	2
% of total collection	49	26	12	13
Mean	53	23	9	15
Standard deviation	14	16	8	8

Figure 5. Percentage of monthly litter collections by compartment, by dry weight. Arrow indicates change from 1979 to 1980.

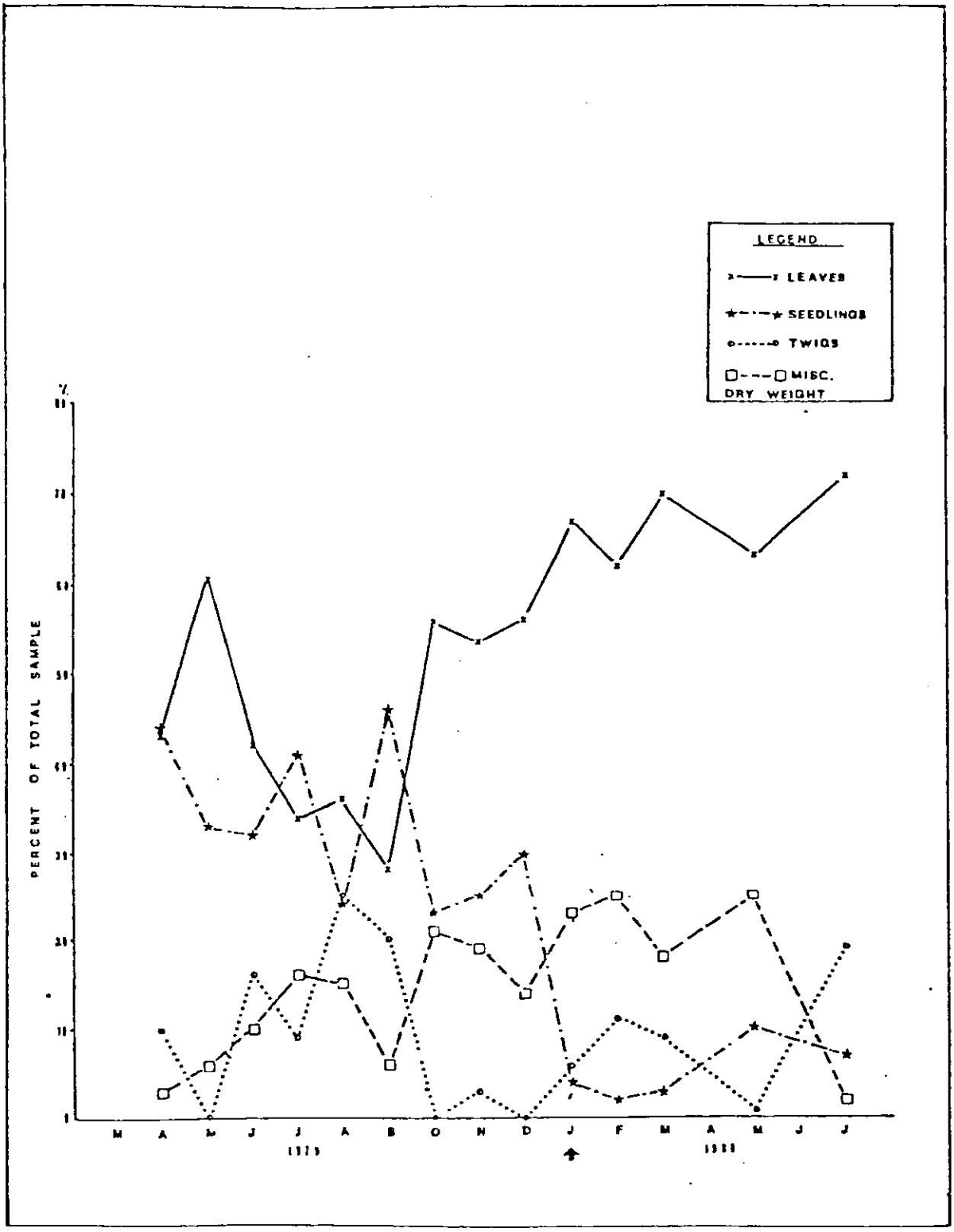

LEGEND
LEAVES
SEEDLINGS
TWIGS
MISC.
DRY WEIGHT
%
PERCENT OF TOTAL SAMPLE
M A M J J A S O N D J F M A M J J
1979
1980

Figure 6. Breakdown of monthly litter collections by compartment, in grams dry weight. No collection in April or June 1980. Arrow indicates change from 1979 to 1980.

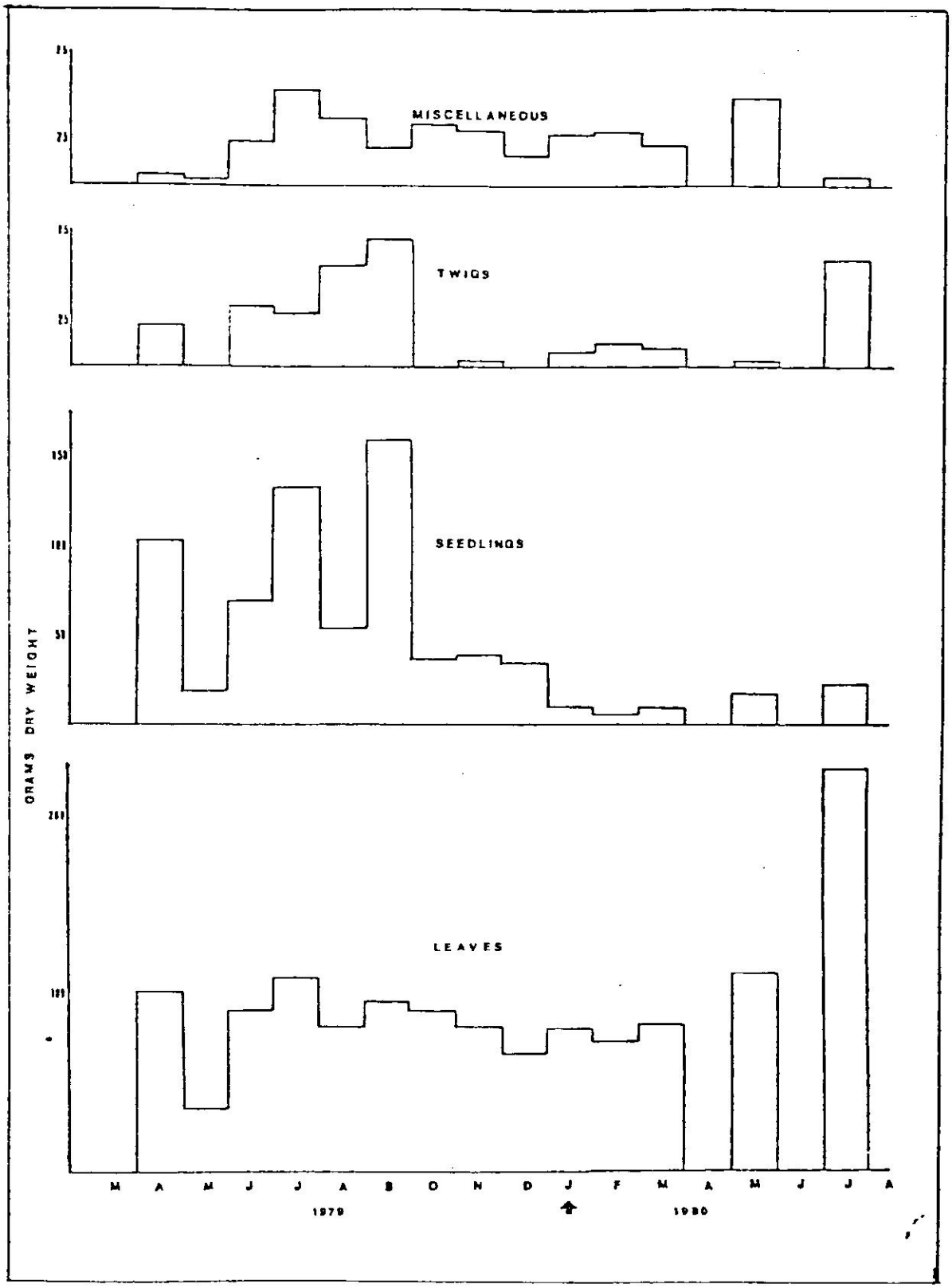
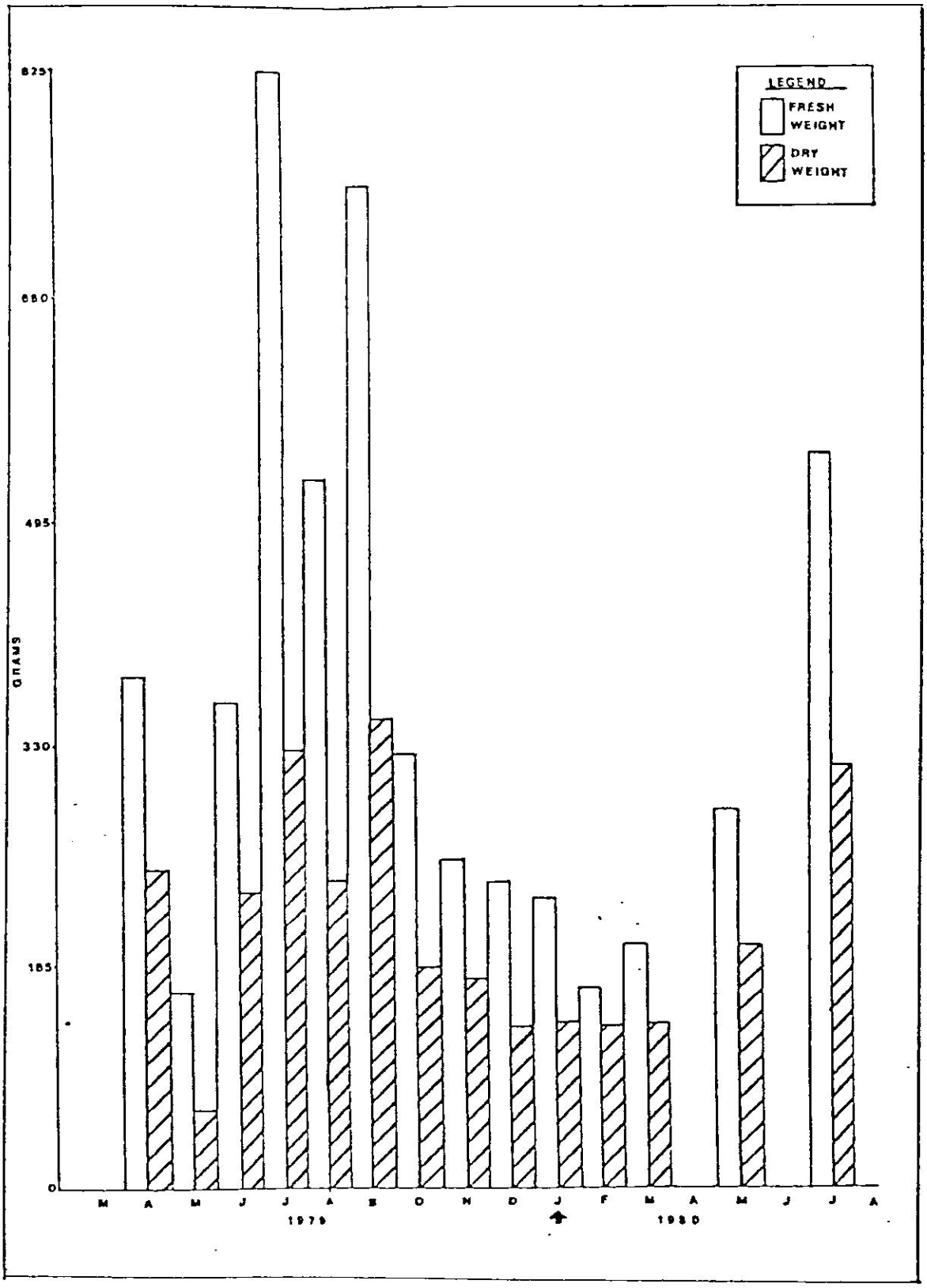

MISCELLANEOUS
TWIGS
SEEDLINGS
LEAVES
GRAMS DRY WEIGHT
M A M J J A S O N D J F M A M J J A
1979
1980

Figure 7. Monthly comparison of fresh and dry weight of litter collected, in grams. No collection in April or June 1980. Arrow indicates change from 1979 to 1980.


LEGEND
FRESH WEIGHT
DRY WEIGHT
825
660
495
330
165
0
GRAMS
M A M J J A S O N D J F M A M J J A
1979
1980

of the total; miscellaneous items ranged from 2 to 25%, and were 13% of the total; and twigs ranged from 0 to 25%, and were 12% of the total.

Pool, et al. (1975), in Florida, found mangrove leaf-fall to be the most important compartment in total litter-fall (from 68 to 86% of of total litter produced), wood-fall ranged from 3 to 15%, and miscellaneous items from 8 to 21%. Goulter and Allaway (1979), working in Australia with *Avicennia marina*, found leaf-fall to be 75% of the total.

Miscellaneous material was considered mangrove material unclassifiable into one of the three other categories or extraneous material not of mangrove origin (i.e. cane ash, insects, feathers, bird droppings, etc.). The greatest amount of miscellaneous matter was collected at station 2 (Table 5), in the bird rookery. Due to the presence of bird guano in the collection basket, large numbers of insects and crabs were contained in these samples. The guano was also found covering many of the leaves which had fallen into the basket.

As can be seen in Table 5, station 2 consistently contained the highest amounts of miscellaneous material, except after the passing of two hurricanes in early September. At this time station 3 contained the same amount of miscellaneous material as station 2, and station 7 contained about three times as much. This was probably due to the absence of birds in the rookery at this time. The miscellaneous matter in station 7 consisted mostly of dead crabs.

From this data it can be seen that the bird rookery area represents a large potential nutrient source for this lagoon.

Seedling production was high in April, July, and September when

Table 5. Comparison of miscellaneous items collected at each station, in grams dry weight.

TABLE 5

Date	STATION 2	3	4	5	6	7	8
4/27	2	2	0	0	0	1	1
5/11	2	1	0	0	0	0	0
6/08	14	1	1	1	0	1	1
7/13	32	3	1	0	1	1	3
8/13	23	1	1	1	0	0	1
9/10	3	3	1	0	0	10	0
10/11	25	0	1	0	0	0	0
11/15	21	1	1	0	0	0	0
12/10	13	0	0	0	0	0	0
1/16	19	1	0	1	0	0	0
2/17	21	1	0	1	0	0	0
3/18	15	1	0	0	0	0	0
5/08	30	2	1	1	0	2	0
7/16	missing	0	2	1	0	0	0
TOTAL	220	17	9	6	1	15	6
Mean	17	1.2	0.6	0.4	0.1	1.1	0.4
Standard deviation	10	1	2.4	1.6	0.5	4	1.6

it peaked (Table 6). During these three periods seedlings accounted for over 40% of the total collections. After September, seedling production was reduced and in December there was a sharp decline (Figs. 5 and 6). Mosura and Estevez (1977) also found greatest rates of seedling-fall in Florida occurred in August and declined by November, and virtually no seedlings were dropped from November to April.

Leaf litter throughout the year was fairly constant (Table 7 and Fig. 8), the mean being 2.8 gdw/m^2/day. Heald (1971) found leaf-fall to average about 1.3 g/m^2/day in May, and Pool, et al. (1975) found mean rates of leaf-fall are fairly constant for all mangrove forest studied (overall mean = 2.2 g/m^2/day, SD = 1.06).

Only during the three seedling peaks previously mentioned were leaves not the major contributor to total litter-fall. The peak leaf-fall periods were the summer of 1979 and again in the summer of 1980.

In comparing mean daily leaf litter-fall (Fig. 8) with mean monthly precipitation (Fig. 9) there is no significant correlation between amount of rain and leaf-fall at the 0.01 significance level, r = 0.07 (Schefler, 1979). As can be seen in Figure 9 precipitation peaked both in August and May, while leaf-fall was fairly evenly distributed throughout the study period.

When comparing daily total litter-fall to precipitation there is a positive correlation at the 0.01 significance level, r = 2.609 (Schefler, 1979). As rainfall increased so did total litter-fall.

In Florida, Pool, et al. (1975) also found peak litter-fall rates occurred between the months of August to October, which also corresponded with the highest intensity of rain and wind storm frequency.

Table 6. Comparison of seedling weights collected at each station, in grams dry weight.

TABLE 6

Date	STATION						
	2	3	4	5	6	7	8
4/27	0	0	9	62	0	9	8
5/11	0	1	6	0	1	0	0
6/08	20	3	0	24	0	6	0
7/13	0	12	3	47	7	6	26
8/13	3	9	0	24	2	1	1
9/10	14	0	12	12	1	81	0
10/11	13	3	1	0	3	4	3
11/15	15	0	2	0	9	2	1
12/10	21	0	1	0	0	4	0
1/16	1	0	1	0	0	1	0
2/17	0	0	0	1	0	1	0
3/18	0	0	1	1	0	1	0
5/08	0	0	1	1	0	11	0
7/16	missing	3	1	5	0	5	1
TOTAL	87	31	38	177	22	132	40
Mean	6.7	2.2	2.7	12.6	1.6	9.4	2.0
Standard deviation	24.1	8.3	10.2	47.3	5.9	35.3	10.7

Table 7. Mean daily rate of litter-fall (total and leaf) per day per sampling period, in grams dry weight per meter square per day (g.d.w./m^2/day).

TABLE 7

Sampling Period	Days	Litter Collected (Total/Leaves)	Total/Leaves g.d.w./m^2/day
3/23 - 4/27	35	237 / 102	6.8 / 2.9
4/28 - 5/11	14	59 / 36	4.2 / 2.6
5/12 - 6/08	28	219 / 91	7.8 / 3.3
6/09 - 7/13	35	326 / 110	9.3 / 3.1
7/14 - 8/13	31	230 / 83	7.4 / 2.7
8/14 - 9/10	28	348 / 96	12.4 / 3.4
9/11-10/11	31	164 / 92	5.3 / 3.0
10/12-11/15	35	156 / 83	4.5 / 2.4
11/16-12/10	25	120 / 67	4.8 / 2.7
12/11 - 1/16	37	123 / 82	3.3 / 2.2
1/17 - 2/17	30	120 / 74	4.0 / 2.5
2/18 - 3/18	30	121 / 84	4.1 / 2.8
3/19 - 5/08	51	180 / 112	3.5 / 2.2
5/09 - 7/16	69	314 / 226	4.6 / 3.3
TOTAL	479	2718 /1339	82.0 /39.1
Mean	34.2	194 / 96	5.9 / 2.8
Standard deviation	128.0	726.4/357.9	21.9 /10.5

Figure 8. Graphic representation of total litter-fall and leaf litter-fall per meter square per collection period. All values in grams dry weight.

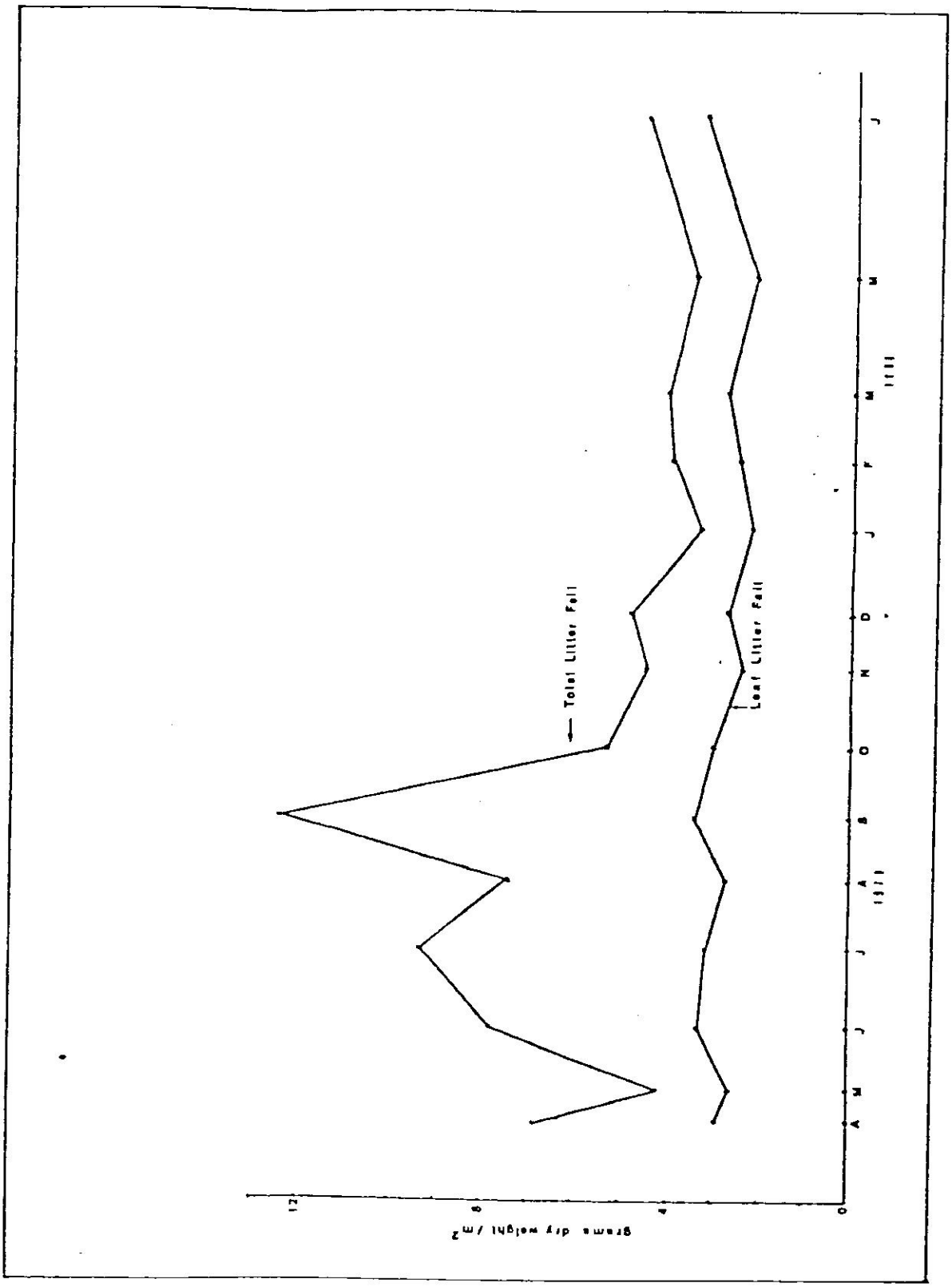
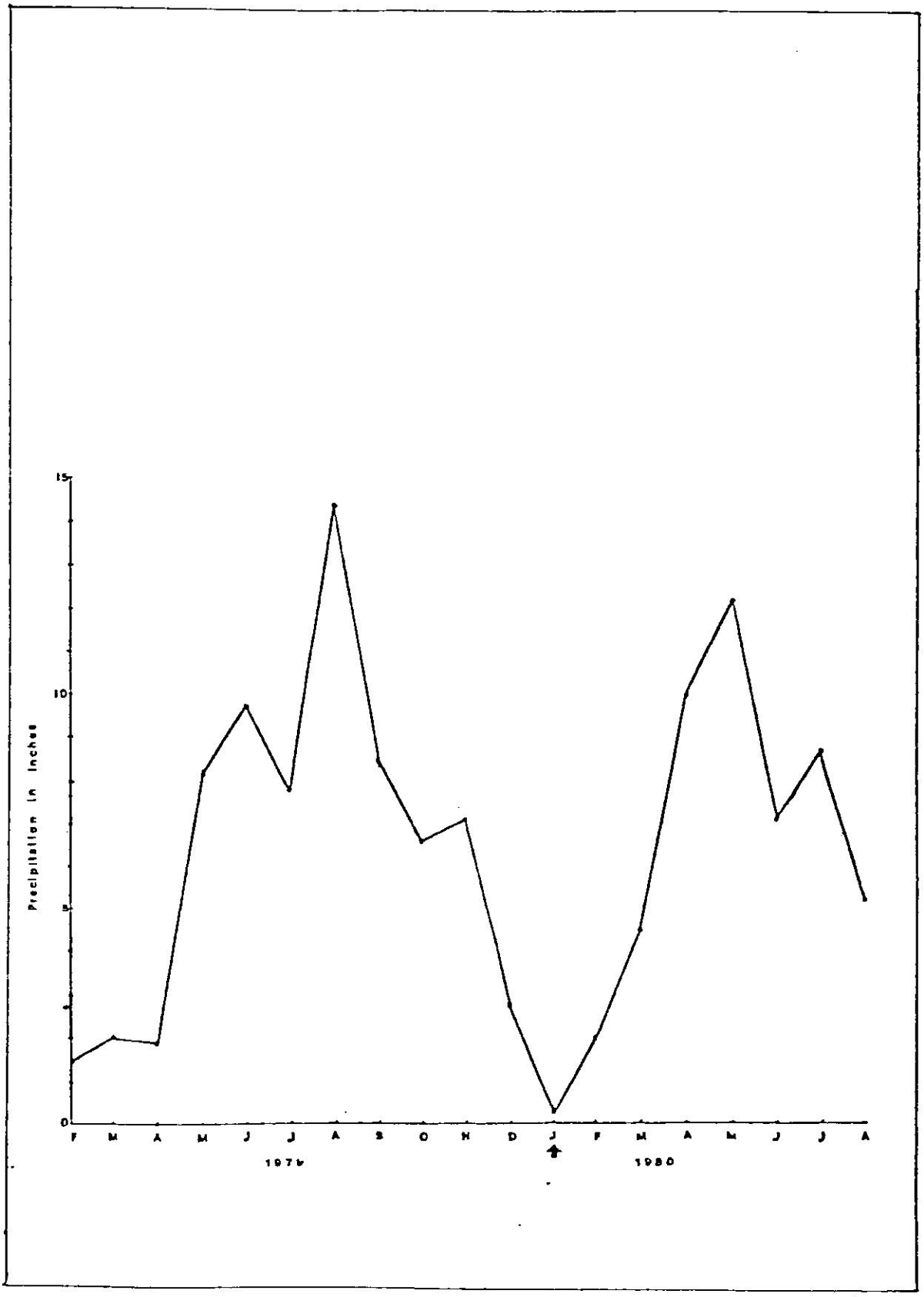

Grams dry weight / m²
0
4
8
12
A M J J A S O N D J F M A M J J
1977
1978
Total Litter Fall
Leaf Litter Fall

Figure 9. Graphic representation of mean monthly precipitation, in inches, during the study period.


Precipitation in Inches
15
10
5
0
F M A M J J A S O N D J F M A M J J A
1979
1980

As moisture became available, new leaves were produced and old ones dropped. During short dry periods, litter-fall decreased but seemed to increase during long droughts.

This is in agreement with Heald (1971) and Goulter and Allaway (1979) whose data showed monthly leaf-fall was greatest in the summer months. Heald (1971) believed that the operating mechanism is simply replacement of old leaves by new ones. Thus, annual leaf-fall is approximately equal to standing crop and there is a complete turnover of leaf material each year.

Pool, et al. (1975) found that mangroves in Florida and Puerto Rico had developed a leaf-fall strategy whereby leaves are dropped throughout the year, with higher rates during the wet season and lower rates during the dry season which coincides with lower temperatures. These findings are in agreement with this study.

It is hypothesized (Lugo and Snedaker, 1975) that leaf-fall patterns are sensitive to stresses such as salinity (fluctuating with precipitation) which increases the energetic cost of maintaining photosynthetic tissue. There must be an environmental threshold when it is metabolically less costly to drop leaves than to overcome the stress. At this point, leaf-fall rates increase above normal. Under normal conditions, leaf-fall occurs in phase with the production of new leaves in such a manner that the photosynthesis rate remains constant.

The highest precipitation and the highest litter-fall coincide with the passing of hurricanes David and Frederick from 30 August to 5 September, 1979. Several other investigators have dealt with the effects of hurricanes on mangroves.

Goulter and Allaway (1979) also found that occasional storms coincided with increased litter-fall. They state that the large quantity of material collected on these occasions might represent material that ordinarily would not have fallen during the whole experiment, but was broken from the trees by rough weather. If so, this single very high value introduces error into the total for the whole year, if this is to be regarded as an index to productivity. Alternatively, the high wind and rain might have caused abscission of material that was due to fall in the later sampling periods during the experiment; in this case error is not introduced into the annual total. Of these two possibilities they favor the latter due to the low litter-fall in collections immediately following. The same is the case here at Joyuda Lagoon.

The effects of hurricanes controlling the amount of wood-fall is mentioned by Pool, et.al. (1975). In their study wood-fall, including twigs, branches, and stems, was low in all sites except for periods of high winds and storms. This suggests that hurricanes are significant factors controlling this pathway.

Here in Puerto Rico, Lugo and Cintrón (1975) note the effects of hurricanes in controlling the size of mangrove trees. They found larger trees located in more protected areas, such as basin mangroves, that have escaped hurricane damage. This, in turn, affects a given area's productivity in that very large mangrove trees shed proportionally more leaves than do small and medium trees (Heald, 1971).

Comparisons of studies of the mangroves of Florida and Puerto Rico have been noted throughout this work. According to López and Teas

(1978) the pathways of energy flow in Puerto Rico mangroves should be essentially similar to that established by Odum and Heald (1975) in their trophic analysis of an estuarine mangrove community in Florida. Also, Pool, et al. (1975) found no statistical differences in the rate of litter-fall between Florida and Puerto Rico.

Pool, et al. (1975) found mangrove leaf-fall rates to be among the highest reported for any forest ecosystem (Table 3). Although mangrove productivity is high, its higher litter-fall rates do not necessarily imply higher productivity than surrounding forests.

Since the rate of litter production provides an indirect estimate of primary productivity, total litter-fall may reflect the nutrient status of the mangrove forest and surrounding water sheds (Pool, et al., 1975).

Water content of litter as a percentage of weight is shown in Tables 8 and 9. These percentages were calculated as the ratio of material dried at 70°C to constant weight divided by the weight of freshly collected litter. In all cases the mean percentage for the wet season was greater than those for the dry season. On the average leaves contained 31 percent more water during the wet season than during the dry season; seedlings 22 percent; wood 36 percent; and total litter contained 27 percent more water.

These findings differ from those found by Golley, et al. (1975) for tropical moist forest vegetation in Panama. In their study the average percentage of water in the biomass was 65.7 percent in the wet season and 51.8 percent in the dry season. Their litter compartment

Table 8. Percentage water content of leaves and total litter. Comparison between wet (more than 6 inches precipitation per month) and dry (less than 6 inches precipitation per month) seasons. All weights in grams.

TABLE 8

Date	Leaves Dry/Wet	% Water	Total Dry/Wet	% Water	Dry Months	Wet Months
4/27	88/131	33	205/332	38	X	
5/11	31/ 84	63	51/125	59		X
6/08	69/122	43	176/274	36		X
7/13	83/211	61	247/624	60		X
7/13	63/ 90	30	173/399	57		X
9/10	73/192	62	263/560	53		X
10/11	70/133	47	124/246	50		X
11/15	63/ 86	27	118/183	35		X
12/10	51/ 91	44	91/175	48	X	
1/16	62/ 84	26	93/146	36	X	
2/17	56/ 71	21	92/114	20	X	
3/18	64/ 93	31	92/136	33	X	
5/08	85/123	31	135/214	37		X
7/16	147/261	44	204/353	42		X
Mean	72/127	40	147/277	43		
Standard deviation	26/ 57	14	65/161	12		

Table 9. Percentage water content of seedlings and wood. Comparison between wet (more than 6 inches precipitation per month) and dry (less than 6 inches precipitation per month) seasons. All weights in grams.

TABLE 9

Date	Wood Dry/Wet	% Water	Seedlings Dry/Wet	% Water	Dry Months	Wet Months
4/27	22/27	22	90/161	44	X	
5/11	0	0	17/ 34	50		X
6/08	26/30	13	53/ 97	45		X
7/13	5/34	88	26/200	87		X
8/13	43/55	22	41/127	68		X
9/10	54/69	22	121/267	55		X
10/11	0.3/1	66	28/ 57	49		X
11/15	3/ 4	25	29/ 45	46		X
12/10	0	0	27/ 49	45	X	
1/16	6/10	40	4/ 7	43	X	
2/17	10/12	16	2/ 3	33	X	
3/18	8/10	20	3/ 6	50	X	
5/08	2/ 4	50	13/ 20	45		X
7/16	39/54	28	15/ 31	52		X
Mean	18/27	34	34/ 79	51		
Standard deviation	18/24	23	34/ 81	13		

reflected the greatest difference in water content (20.9 percent for the dry season and 72.4 percent for the wet season). Fruits and leaves contained the greatest quantities of water for any compartment in both seasons.

These differences are probably due to the greater amount of precipitation in Panama and also the vegetation types studied.

DECAY RATES

Plant debris has been recognized as a major nutritional source in the detrital food web of many varied ecosystems. Cammen (1975), Odum and de la Cruz (1967), Burkholder and Bornside (1957), and Gallagher, et al. (1976) have discussed the role of plant detritus in the salt marsh ecosystem; Darnell (1967 a and b) and Stephens (1967) in estuaries; Ovington (1965), Cromack and Monk (1975), Triska and Sedell (1976), and Cummins, et al. (1980) in woodlands; Gasith and Hassler (1976) and Rau (1978) in lakes; Mathews and Kowalczewski (1969) in the River Thames; and Hesse (1961), Heald (1971), Odum (1971), Pool, et al. (1975), Clough and Attiwill (1975), Fell, et al. (1975), Onuf, et al. (1977), Walsh (1967), Mosura and Estevez (1977), and Goulter and Allaway (1979) in mangrove forests.

In addition to works in specific areas, Darnell (1967b), in his general review, states that through its contribution to turbidity, sedimentation, and chemical alteration of the environment, organic detritus must influence every major process active in aquatic communities. For this reason emphasis in this study has been placed on the amount of mangrove litter produced around the lagoon and its rate of decay.

For the purpose of clarification of terms used in this work, the following definitions, taken from Heald (1971) are presented here:

The term debris is used to designate dead plant material such as mangrove leaves and twigs in various stages of decomposition. Thus,

debris is roughly equivalent to the term "litter" commonly used to describe decaying plant material in more fully terrestrial communities.

Detritus is debris fragmented to the point where individual particle size does not exceed 2 or 3 mm in smallest dimension. The important mechanisms of degradation include chemical dissolution, autolysis, hydrolysis, oxidation, mechanical attrition and fragmentation, enzymatic lysis by bacteria and fungi, and the activities of scavenging organisms.

A detrital particle is the product of these continuous degradation processes which cause a reduction in the size of a fragment of debris until its component parts can no longer be considered particulate. At this point it enters the ill-defined realm of "colloidal" or "dissolved organic" material so important in detrital food chains. Dimunition in size does not necessarily result in a decline in energy content; as Odum and de la Cruz (1967) demonstrated, reduction in particle size is accompanied by enrichment and increased metabolic activity as a result of adsorbed microbiota.

The capacity to retain and hold nitrogen by decomposing litter may be based on four possible processes: nitrogen immobilization by incorporation into fungal and microbial protein as carbon is mineralized; uptake of nitrate from water; nitrogen fixation; and exchange of ammonia on organic substrates (Triska and Sedell, 1976).

The work of Burkholder and Bornside (1957) demonstrated the relationship between seawater enriched by marsh grass decomposition and the appreciable number of bacteria that were found growing well in the medium; indicating the great potential value of this primary source of organic matter for supporting the complex flora and fauna of coastal waters.

As Darnell (1967b) points out, it would be a remarkable feat of selection for most estuarine species to avoid ingesting this material in quantity. While they derive little caloric value from the small amounts consumed, the significance of this material as a source of vitamins and

other micronutrients remains a distinct possibility. From the nutritional standpoint it makes little difference whether the consumer ingests such material through choice or not.

To determine the rate of decay of red mangrove leaves a year long litter bag study was undertaken. In this experiment a known weight of *R. mangle* leaves was placed in mesh bags and submerged in the lagoon water. The bags were retrieved periodically throughout the year and weight disappearance was measured.

The fate of a falling leaf is variable. It may fall onto dry ground or into water. Newly shed leaves may float for a maximum of six days (Heald, 1971), during which time they may travel out of the lagoonal system. The decay of leaves on land is a slower process than in water (Heald, 1971). Rates of decomposition in water are temperature and salinity dependent. Higher rates of decay have been recorded at increased temperature and increased salinity (Heald, 1971).

At Joyuda Lagoon weight loss in the first months was quite rapid (Table 10, Fig. 10). In the first 40 days 66 percent of the dry weight was lost. For the next 130 days weight loss was slower, yet perceptible, with an average monthly loss of about 4 percent. In mid-February there was a 12 percent drop in dry weight remaining. However, this increased weight loss was followed by no weight loss the following month. After approximately 280 days only two percent of the original dry weight remained in the mesh bag. By day 355 of the experiment no red mangrove leaves were present in the bag.

In comparing the decay rate found in this experiment with that

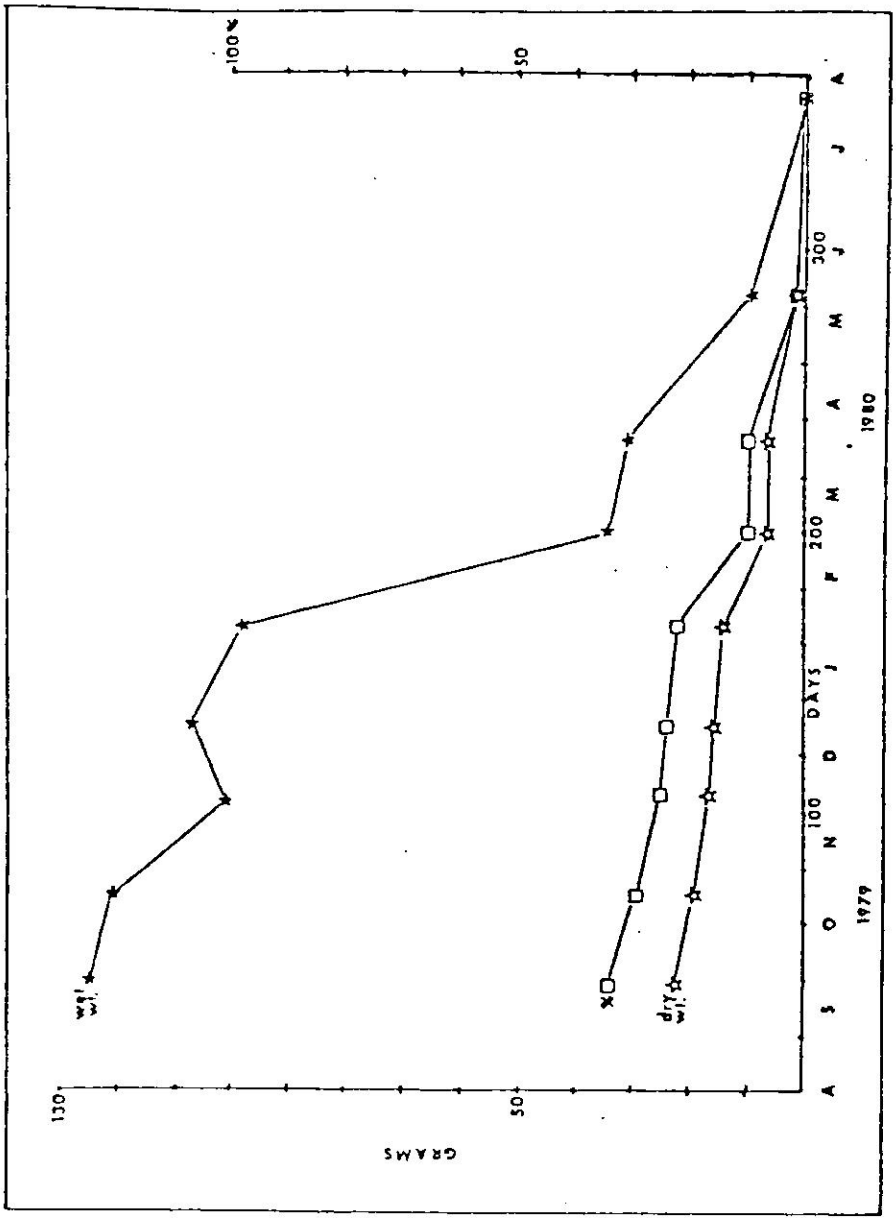
Table 10. Decay of red mangrove leaves submerged in Joyuda Lagoon water.

TABLE 10

Date	Grams Dry Weight	% Remaining
8/01	66	100
9/10	23	34
10/11	19	29
11/15	17	25
12/10	16	24
1/16	15	22
2/17	7	10
3/18	7	10
5/08	1	2
7/16	0	0

Figure 10. Decay rate of *Rhizophora mangle* leaves in Joyuda Lagoon water. Percent scale represents amount of litter remaining compared to starting dry weight.

Figure 11. Nitrogen and protein content of mangrove compartments, in percent dry weight.


GRAMS
130
50
100
50
DAYS
100
200
300
A S O N D J F M A M J J A
1979
1980
wet wt.
dry wt.

of Heald (1971) for red mangrove leaves, in brackish water in Florida, the two slopes of the regression lines proved not to be significantly different at the 99% confidence level ($p < 0.01$, $t=0.11$) using the Student t test (Zar, 1974).

It is evident from the graph of decay rate (Fig. 10) during the "winter" months (October-February) the slowest decay rates were observed. The temperature of the environment might be expected to affect degradation rates through its influence on the rates of chemical reactions, the activity of enzymes, and the metabolism of organisms (Heald, 1971).

Many crabs, amphipods, and worms were observed inside the mesh bags. An increase in the number of these aquatic organisms grazing on the organic matter was noted during the course of this experiment.

Red mangrove leaves are not heavily grazed while alive. Heald (1971) found an average of 5.1 percent of the leaf consumed by terrestrial organisms. However, once the leaf was submerged the amount of grazing increased steadily.

Another environmental factor affecting decay rates is the presence or absence of oxygen. Litter processing is fastest in primarily aerobic accumulations largely by biological actions rather than by physical abrasion (Cummins, et al., 1980). Processing in habitats that are primarily anaerobic involves little or no utilization by aquatic fungi or shredders and occurs at a much slower rate (Cummins, et al., 1980).

Conditions within the mesh litter bags could be observed to be anaerobic in the clumped mass of leaves, as evidenced by its black color

indicating reducing conditions. Leaves exposed at the mesh surface were in contact with the aerobic lagoon environment. For this reason it is possible that the degradation rate demonstrated in this experiment might be slightly slower than occurring naturally in the lagoon.

The daily decay rate calculated for this experiment was 0.27 percent. Lugo and Snedaker (1975) calculated a mean rate of decay of 0.233 percent per day.

NITROGEN CONTENT OF MANGROVES

After digestion of 1.0 gram of dried, ground sample from each of the mangrove compartments (leaves, branches, feeding roots, aerial roots, seedlings, flowers, and dead leaves) the percentage of total Kjeldahl nitrogen was determined. Subsequent multiplication of percent nitrogen by 6.25, the general conversion factor (Patrick and Delaune, 1976), yielded percentage protein.

Figure 11 illustrates the percent nitrogen measured and percent protein calculated. The difference between growing leaves and yellow dying leaves of the mangroves shows a removal of 33 percent nitrogen and protein before leaf fall. Clough and Attiwill (1975) after analysis of *Avicennia marina* found slightly higher values (Table 11), but percent withdrawal prior to abscission was also one third for nitrogen and phosphorous from leaves. Heald (1971) found an actively photosynthesizing *Rhizophora mangle* leaf contained 6.1 percent protein (0.98% N). Mobilization and withdrawal of proteins and some soluble carbohydrates during the process leading to abscission resulted in a decrease in protein content to 3.1 percent (49% removal) immediately before leaf fall.

The values reported by Clough and Attiwill (1975)(Table 11) were generally about 58 percent greater than those found in this study for nitrogen content. It is assumed that this difference is due to the different species of mangroves being analyzed. Heald's (1971) values for the same species as this study were very close.

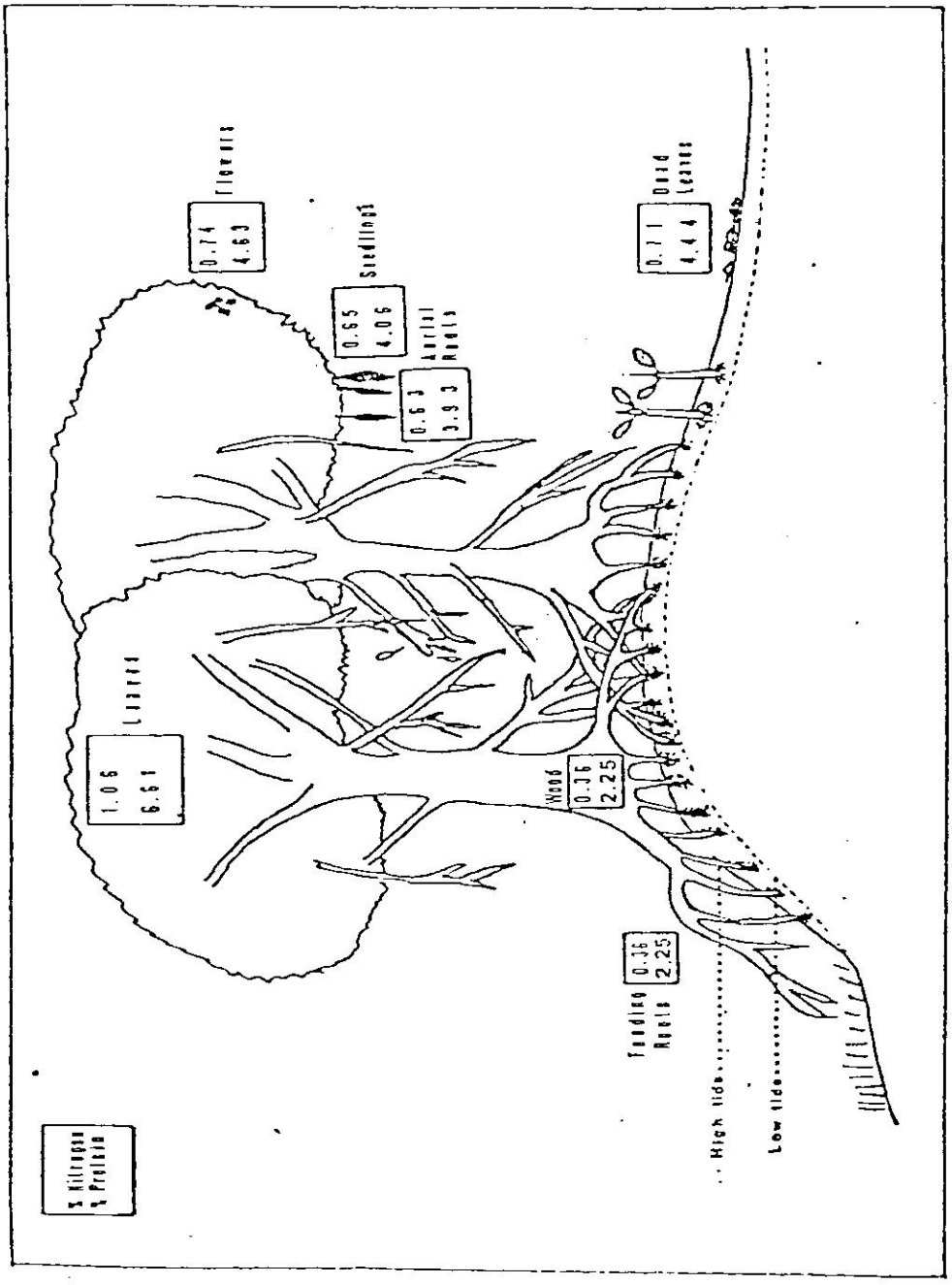

% Nitrogen
% Protein
1.06
6.61
Leaves
0.74
4.63
Flowers
0.65
4.06
Seedlings
0.63
3.93
Aerial Roots
Wood
0.36
2.25
0.11
4.44
Dead Leaves
Feeding Roots
0.36
2.25
High tide
Low tide

Table 11. Comparison of nitrogen concentrations (percent dry weight), by compartment, between *Rhizophora mangle* in Joyuda Lagoon (this study), and *Avicennia marina* in Westernport Bay, Australia (Clough and Attiwill, 1975).

TABLE 11

A. marina	% N	% N	*R. mangle*
Leaves	2.11	1.06	Leaves
Branches	0.61	0.36	Branches
Trunk	0.49	----	----
Main Root	0.68	0.36	Feeding Root
Fibrous Root	1.20	----	----
Pneumatophores	0.74	0.62	Aerial Root
Dead Leaves	1.23	0.71	Dead Leaves
Fruit	1.60	0.65	Seedlings
----	----	0.74	Flowers

Table 12. Nitrogen production by litter in Joyuda Lagoon. The TOTAL column is the sum of the three compartments listed, not including roots and flowers. Therefore, these values are lower than actual.

In comparison to other ecosystems, the red mangroves of Joyuda Lagoon had a greater nitrogen content than hardwood and pine forests in the United States (Cromack and Monk, 1975). Patrick and Delaune (1976) report higher values for protein content of *Spartina alterniflora*. Golley, et al. (1975) found an average of 1.2 percent nitrogen (by dry weight) for tropical forests, which is about twice the mean found in this study.

Clough and Attiwill (1975) found the percentage concentration of nitrogen in all mangrove compartments was within the range found in most plants (*Salicornis* sp.--1.57, *Eucalyptus* sp.--1.82, *Acacia* sp.--2.59, *Phragmites* sp.--3.10, and Seagrass spp.--1.3 to 2.0). Phosphorous content was found to be much higher than normally found in species from other natural ecosystems. However, they found the aerial parts of mangroves have higher concentrations per unit dry weight of both nitrogen and phosphorous than all but one of the forest species presented in their work.

Roots have almost twice as much biomass as tops in mangroves. The size of the energy and carbon pools is directly proportional to biomass, hence the large pool of energy and carbon held in mangrove roots (Clough and Attiwill, 1975). This compartment, however, was not measured quantitatively in this study.

It can thus be seen that the major pathway for nutrient cycling must be through turnover of leaves and roots.

The leaf litter cycle for the whole lagoon would contain approximately 67.1 kg nitrogen per hectare per year (Table 12). There

TABLE 12

	Annual Leaf-Fall	Annual Seedlings	Annual Wood-Fall	TOTAL
g/m^2	945	497	222.4	1664
% N	0.71	0.65	0.36	
g N/m^2	6.71	3.23	8.01	17.95
Kg N/ha	67.1	32.3	80.1	179.5

being 47.61 hectares of mangrove surrounding Joyuda Lagoon (Carvajal, et al., 1980), this yields approximately 3,195 kg nitrogen annually in leaf litter alone.

NUTRIENT CONCENTRATIONS IN THE WATER

The nutrient concentrations of Joyuda Lagoon water varied throughout the study period, as can be seen in Figure 12. In October, the results for ammonium have a point represented by a dot (•); this indicates an unusually high reading due to a number of dead fish left by fishermen at sampling site 8. This data point has not been included in calculations.

No data is available for March, June, and July for ammonium due to problems with reagents, hence the samples were unfortunately lost in analysis.

Tables 13 through 16 present all the nutrient data collected from each of ten stations in Joyuda Lagoon, and the mean nutrient concentration for the sampling period.

As is evident from Figure 12 there were two nutrient peaks, the first in September 1979 and the second in May 1980. The ammonium concentration also shows slightly higher readings for October and November. The nutrient peaks are at the end of summer and the end of winter. These peaks coincide with the two peaks in monthly precipitation (Fig. 9). It can also be seen that ammonium showed the greatest seasonal fluctuations, followed by nitrate. Nitrite was found at low, but fairly constant levels. Phosphate had a tendency to disappear below the limit of detection during the winter months.

Similar observations were made by Valiela, et al. (1978) and

Figure 12. Nutrient content of Joyuda Lagoon water, in ug·at/liter, during each sampling period. Circles, o, represent mean value for sampling period. Bars represent the range of concentrations found in each sampling period. Non-detectable nutrient levels are represented by n-d. Points plotted with an x represent unusually high readings thought to be due to experimental error, and thus disregarded from all calculations. Limit of detection: PO_4^{-3} = 0.03 ug·at/liter; NO_2^- =0.01; NO_3^- = 0.05 ug·at/l liter; NH_4^+ = 0.1 ug·at/l liter.

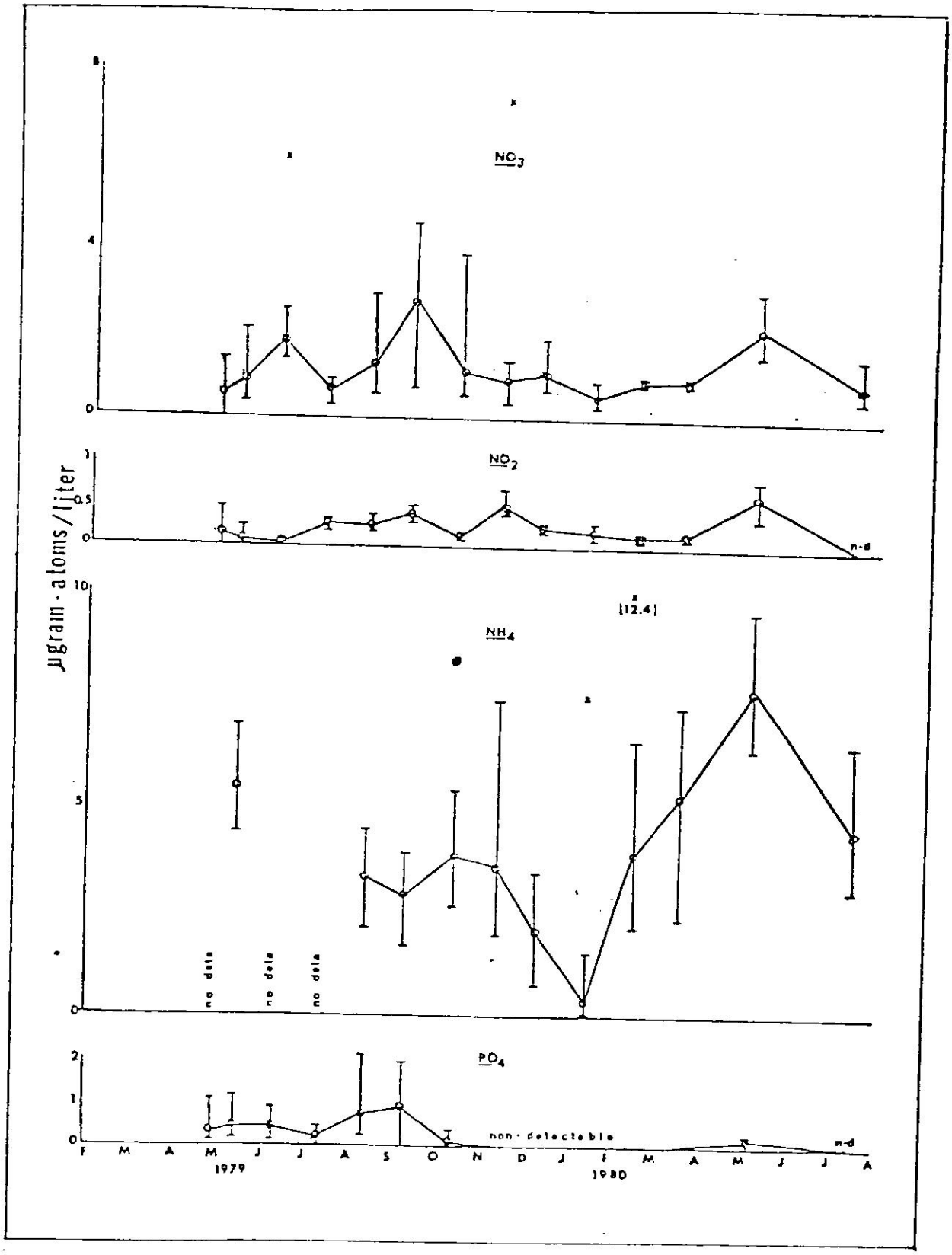

NO3
NO2
NH4
PO4
μgram - atoms / liter
[12.4]
no data
no data
no data
non - detectable
n-d
n-d
F M A M J J A S O N D J F M A M J J A
1979
1980

Table 13. Ammonium concentrations (ug·at NH_4^+-N/liter) in Joyuda Lagoon water, on each collection date, at each station. Concentrations marked with an (*) were questionable results, and therefore not included in the calculation of mean values.

TABLE 13

Station	DATE												
	4/27	5/11	6/08	7/13	8/13	9/10	10/11	11/15	12/10	1/16	2/17	3/18	5/08	7/16
1		4.33			2.84	2.91	3.85	4.41	3.34	7.47*	2.43	3.68	7.67	3.20
2		5.01			3.27	2.46	3.47	3.41	2.35	1.14	3.56	2.50	6.34	4.30
3		5.29			3.80	2.36	5.33	3.19	2.54	0	3.92	5.40	7.48	5.50
4		4.43			3.33	2.69	4.51	1.76	0.81	0.25	2.89	7.11	8.17	3.70
5		4.64			4.47	3.23	4.75	2.69	2.49	1.15	12.42*	7.32	8.50	3.90
6		5.58			3.04	3.89	3.30	7.44	1.60	1.10	6.31	2.30	6.45	6.40
7		6.86			4.22	1.66	2.57	2.77	1.60	0	2.12	5.90	7.34	2.90
8		6.86			2.09	2.95	8.35*	1.92	2.28	0	3.51	6.28	9.55	3.90
9		4.53			2.61	2.02	3.21	4.25	0.74	0.27	6.50	4.90	7.33	4.50
10		6.45			2.69	3.84	3.48	3.14	2.16	0	4.12	5.57	7.89	5.00
Mean		5.40			3.24	2.80	3.83	3.50	1.99	0.43	3.93	5.20	7.67	4.33
Standard deviation		1.00			0.75	0.72	0.87	1.63	0.81	0.53	1.55	1.70	0.95	1.07

Table 14. Nitrate concentrations (ug·at NO_3^--N/liter) in Joyuda Lagoon water, on each collection date, at each station. Concentrations marked with an (*) were questionable results, and therefore not included in the calculation of mean values.

TABLE 14

Station	DATE													
	4/27	5/11	6/08	7/13	8/13	9/10	10/11	11/15	12/10	1/16	2/17	3/18	5/08	7/16
1	1.37	2.07	1.58	0.77	1.37	4.55	0.63	7.35*	1.20	0.6	0.8	0.4	1.81	1.45
2	0.64	0.90	2.55	0.35	1.17	4.46	0.90	1.25	1.90	0.4	0.8	0.9	1.5	0.45
3	0	1.07	1.60	0.98	1.10	3.23	0.58	0.70	0.70	0.3	0.8	0.8	2.0	0.85
4	0.67	0.46	1.50	0.65	1.60	2.17	0.98	0.40	0.70	0.4	0.9	1.0	1.75	0.70
5	0.40	1.41	6.03*	0.87	0.75	1.63	1.13	0.65	0.80	0.9	1.0	1.0	3.0	0.78
6	0.38	0.67	1.43	0.48	2.90	0.75	3.85	0.60	1.10	0.7	0.8	0.8	1.81	0.43
7	0.44	1.15	2.54	0.48	0.95	3.60	0.70	0.95	0.90	0.5	0.8	1.0	2.75	0.65
8	0.40	0.55	1.63	0.57	0.62	2.55	0.87	1.40	0.90	0.3	1.0	1.0	2.25	0.75
9	----	0.61	1.43	0.63	1.80	2.35	0.70	1.00	0.90	0.4	0.9	0.9	2.06	0.80
10	----	0.49	1.80	0.72	0.75	2.55	0.80	0.50	0.90	0.9	0.9	0.9	1.88	1.26
Mean	0.54	0.94	1.78	0.65	1.30	2.75	1.11	0.83	1.01	0.53	0.9	0.9	2.08	0.81
Standard deviation	0.39	0.51	0.45	0.19	0.68	1.20	0.98	0.34	0.35	0.23	0.08	0.08	0.47	0.32

Table 15. Nitrite concentrations (ug·at $NO_2^=$-N/liter) in Joyuda Lagoon water, on each collection date, at each station. Samples on 7/16 were all below the limit of detection.

TABLE 15

Station	DATE													
	4/27	5/11	6/08	7/13	8/13	9/10	10/11	11/15	12/10	1/16	2/17	3/18	5/08	7/16
1	0.48	0	0.05	0.35	0.27	0.30	0.13	0.40	0.30	0.30	0.15	0.15	0.35	n
2	0.29	0	0.05	0.28	0.25	0.38	0.10	0.40	0.20	0.10	0.15	0.15	0.40	o
3	0.13	0.05	0.05	0.23	0.40	0.35	0.13	0.68	0.20	0.10	0.15	0.15	0.50	n
4	0.01	0.24	0.04	0.28	0.32	0.41	0.15	0.40	0.20	0.10	0.20	0.15	0.50	-
5	0.50	0.21	0.05	0.30	0.25	0.50	0.13	0.65	0.30	0.30	0.15	0.20	0.70	d
6	0.15	0	0.04	0.30	0.30	0.30	0.10	0.45	0.20	0.20	0.15	0.15	0.65	e
7	0.19	0.05	0.02	0.03	0.02	0.43	0.13	0.50	0.20	0.20	0.15	0.20	0.70	t
8	0.05	0.16	0.04	0.38	0.30	0.50	0.15	0.60	0.30	0.20	0.15	0.20	0.80	e
9	----	0.12	0.01	0.37	0.20	0.40	0.15	0.45	0.20	0.20	0.15	0.20	0.80	c
10	----	0.11	0.02	0.33	0.20	0.45	0.17	0.50	0.30	0.20	0.10	0.15	0.80	t
Mean	0.17	0.09	0.04	0.29	0.25	0.40	0.13	0.50	0.24	0.20	0.15	0.17	0.62	a
Standard deviation	0.15	0.09	0.15	0.10	0.10	0.07	0.02	0.11	0.05	0.07	0.02	0.03	0.17	b
														l
														e

Table 16. Phosphate concentrations (ug·at PO_4^{-3}-P/liter) in Joyuda Lagoon water, on each collection date, at each station. Concentration marked with an (*) was questionable, and therefore not included in the calculation of the mean. On dates marked non-detectable, all samples were below the limit of detection.

approximately constant proportion of 15:1 (N:P, by atoms) by phytoplankton as they grow, and that ocean waters at all depths usually contain these elements in a similar ratio (Riley and Chester, 1971). However, there are a number of exceptions. The ratio is often low in coastal waters and may show a seasonal effect (Riley and Chester, 1971).

In analyzing the nutrient data for Joyuda Lagoon water, assuming the Redfield ratio holds for mangroves, it appears that phosphorous is the limiting nutrient for most of the year (October-July) with ratios over 100:1. For June through September the ratio of N:P varied from 16:1 to 6:1. Here nitrogen could have been the limiting nutrient. Seasonally, nitrogen seems to be limiting during the summer months (of high litter productivity) and phosphorous limiting during the winter months (with lower litter productivity).

In most marine ecosystem studies nitrogen has been identified as the limiting nutrient (Valiela, et al., 1978; Patrick and Delaune, 1976; and Pomeroy, 1975). Kuenzler, et al. (1979) found in the Pamlico River estuary, that inorganic nitrogen was the most limiting nutrient during the summer months and its appearance in the winter seemed to trigger the dinoflagellate bloom. Phosphate was usually abundant and exhibited a summer maximum. Barnes (1957) states that as a result of the length of its cycle, nitrate is more likely to be a limiting factor in growth than phosphate.

From Table 17 it can be seen that Joyuda Lagoon nutrient concentrations are within values reported for other coastal areas.

Analysis of water samples from mid-lagoon, the canal connecting

Table 17. Comparison of nutrient concentrations in water. All values in ug-at/liter.

Table 17

NO_2^-	NO_3^-	NH_3^+	PO_4^{-3}	Reference and Area
----	0.4-1.5	----	0.6-1.7	Walsh, 1967. Hawaiian mangrove swamp.
----	30-100	----	1.0-1.5	Carpenter, et al., 1969. Chesapeake Bay, Maryland.
0-0.5	0-2.5	0-11	0-4	Valiela, et al., 1978. Great Sippewissett Marsh, Massachusetts.
----	0.1-4.5	1	0.3-0.8	Jackson, 1977. California.
----	----	----	1.3-10.1	Nicholas, 1967. Mexico.
0.1-0.6	1-25	1-15	2-12	Kuenzler, et al., 1979. Pamlico River, N. C.
----	0.8-3.5	0.6-2.3	----	Naiman and Sibert, 1978. British Columbia.
0-0.8	0.1-4.6	0-9.6	0-2.2	This study. Joyuda Lagoon, Puerto Rico.

the lagoon and the ocean, and the ocean revealed higher nutrient concentrations in the lagoon.

	(ug·at/l)			
	NH_3^-	NO_3^-	NO_2^+	PO_4^{-3}
Ocean	1.3	3.9	1.8	0.3
Canal	2.9	7.4	2.6	0.5
Mid	8.2	6.0	2.2	0.4

In October 1979, when the samples were taken in the canal, the tide was ebbing from the lagoon. This probably accounts for the higher nitrate, nitrite and phosphate levels in the canal. This result is not surprising.

Valiela, et al. (1978) found nutrient concentrations in offshore bay water to be two or three orders of magnitude lower than those in the marsh. Similar findings are reported by Nicholas (1967). It is generally accepted that there are significant differences between the coastal waters and open ocean in regard to the general nutrient deficiencies and relative scarcities of organisms and particles in surface layers of the latter (Goldberg, et al., 1973).

This is evidence of export of nutrients from the lagoon to the surrounding ocean area. The belief that mangroves are exporters of organic matter has been central to the description of these ecosystems as well as a prime argument for their conservation.

In studying different types of marine ecosystems Pomeroy (1975) concluded that, where essential elements are present in excess of needs, populations of high stability develop. Where nutrients are available, though not in great excess, communities of intermediate

stability develop. Where nutrients are in short supply and where specific limiting elements may change with time and space, communities are unstable. The relationship between species diversity and stability seems less clear-cut than the relationship between stability and availability of essential elements.

Due to the high nutrient concentrations in Joyuda Lagoon available to the mangroves and the demonstrated export of nutrients from the ecosystem, it appears from the previous discussion that the mangrove community fringing Joyuda Lagoon should be very stable.

The calculated mean nutrient concentrations for the entire study period are: 3.85 ug·at NH_4^+-N/l; 1.15 ug·at NO_3^--N/l; 0.23 ug·at $NO_2^=$-N/l; and 0.23 ug·at PO_4^{-3}-P/l.

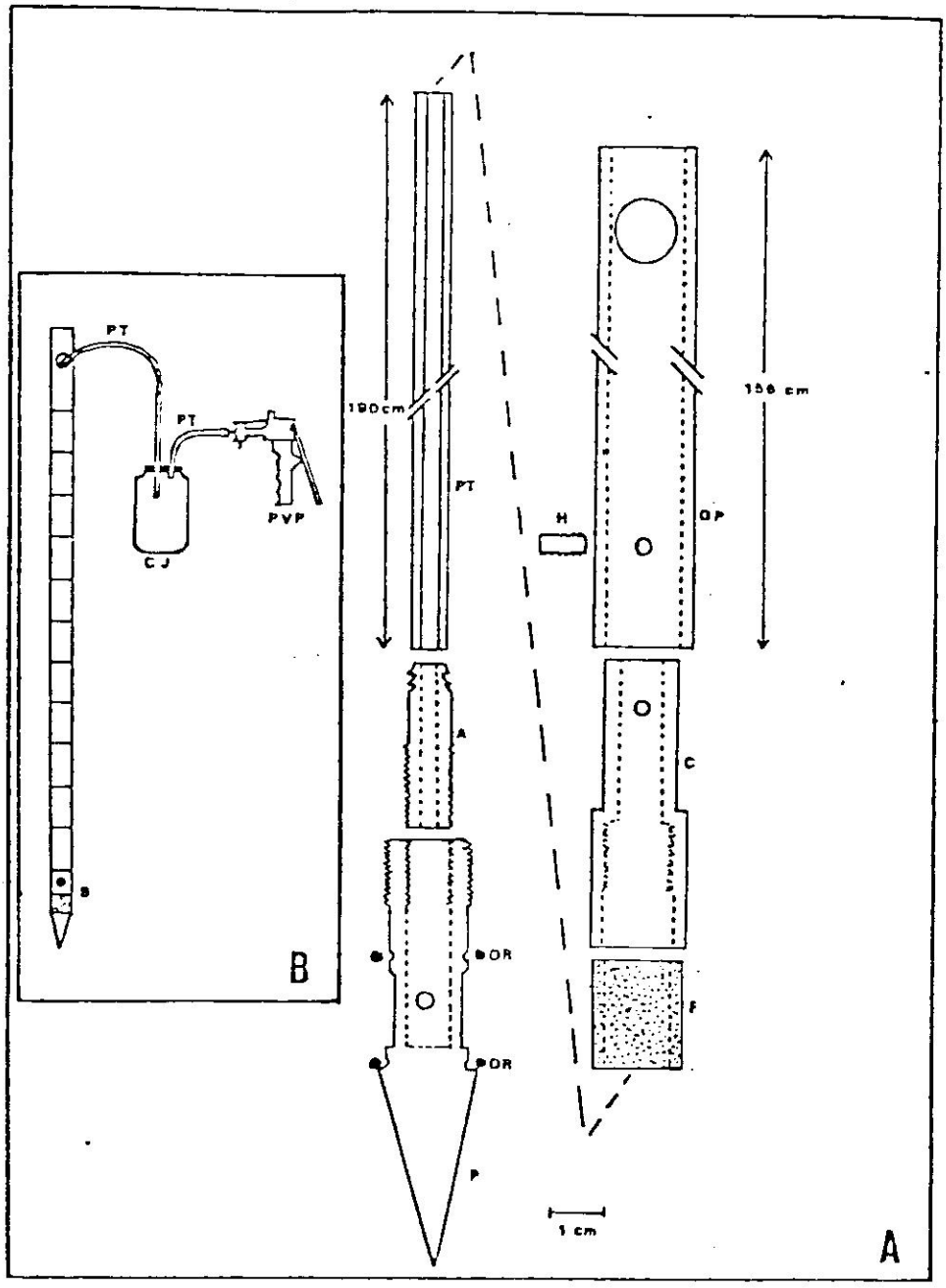
INTERSTITIAL WATER

The purpose of sampling the interstitial water within the shore of Joyuda Lagoon was to establish concentrations of the nutrients concerned in this study in the compartment where the bulk of mangrove nutrient uptake occurs. Interstitial waters are defined by Manheim (1976) as the aqueous solutes that occupy the pore space between particles in rocks and sediment. Their composition reflects the nature of the original fluids buried with the sediments, fluid-particle reactions, and migration of fluids and dissolved components by convection and diffusion.

With this end in mind, an interstitial water sampler was designed and constructed by this investigator at the Interex factory in Guánica, Puerto Rico.

The sampler (Fig. 13) consists of a galvanized pipe (GP), fitted with a stainless steel point (P), onto which a bronze sintered filter (F) has been machined to fit between two O-rings (OR) on the point. The point section is connected to an adapter (A) to which a plastic tube (PT) is attached, this threads through the cap (C), and galvanized pipe (GP) and attaches to a collecting jar (CJ) which is connected to a portable vacuum pump (PVP). The cap (C) is held in place by three hex set screws (H). The sampler is used by setting it in the sediment to the desired depth, measured on the 10 centimeter scale engraved on the galvanized pipe. A vacuum is then applied and a water

Figure 13. Diagramatic representation of interstitial water sampler used in this study. Abbreviations explained in text.


PT
PT
PVP
CJ
S
B
190cm
PT
H
OP
156 cm
A
C
OR
OR
F
P
1 cm
A

sample is withdrawn from the sediment into the collecting jar.

Unfortunately, the fouling of the sintered filter by fine sediments precluded the collection of further interstitial water samples, resulting in an incomplete data base. However, one complete profile was obtained. The results of its analyses are presented in Table 18, and compared with other interstitial values in Table 19.

As can be seen in Table 19, interstitial nutrient concentrations have been found to encompass a wide range.

Montgomery, et al. (1979) found high variability of nutrient levels within a one meter square plot of a subtidal mud flat in Florida. These variations were partitioned into four major sources: the variability due to the samplers; the variability due to analytical technique; the variation due to sampling in the field; and the variation due to spacial heterogeneity. They suggest that the possibility arises that the chemical character of the organic matter and biological activity on the organic matter are responsible for the particular nutrient profiles.

Considerable variability of the concentration of nutrient elements in interstitial water was also found by Manheim (1976). He states the following major reactions occurring in approximately the following sequence, many of them being mediated by bacterial or enzymatic agencies, are responsible for particular nutrient profiles: (1) oxidation of organic matter by molecular oxygen; (2) anaerobic oxidation of organic matter using nitrate, nitrite, or metal oxides as oxygen donors; (3) anaerobic oxidation of organic matter using sulfate as an oxygen

Table 18. Nutrient concentrations in interstitial water at station 8. All nutrient values are in ug-at/liter. Depths were measured from the sediment-water interface. Surface samples were taken from the water surface. The date of sampling was 18 May, 1980.

Table 18

Depth (cm)	NH_4^+	NO_3^-	NO_2^-	PO_4^{-3}
surface	6.28	1.0	0.2	below detection
20	21.6	1.0	0.15	0.9
50	26.8	0.9	0.15	1.0
80	13.3	0.8	0.15	1.0
110	26.8	0.7	0.15	2.3

Table 19. Comparison of interstitial water nutrient concentrations.

All values in ug·at/liter.

Table 19

PO_4^{-3}	NO_3^-	NO_2^-	NH_4^+	Reference and Comments
8.2	----	----	----	Nicholas, 1967. 1.2 meters depth, Mexico.
60-300	----	----	----	Hesslein, 1976. 0-35 cm depth in Hudson River sediments.
----	0-200	----	----	Vanderborght and Billen, 1975. 0-15 cm depth in an artificial lagoon in Belgium.
0-120	2.08	----	0-1200	Price, et al., 1979. 0-10 cm depth in a mixed seagrass bed, Fla.
0-1.4	----	----	0-9	Martens, et al., 1979. 0-100 cm depth in Long Island Sound.
1-10	----	----	62-150	Montgomery, et al., 1979. 5-40 cm depth in a Fla. mud flat.
0.2-3.5	----	----	2-33	Manheim, 1976. 50-1500 cm depth in terrigenous sediments, Bering Sea.
0.9-2.3	0.7-1	0.15-0.2	22-27	This study, 1980. 20-110 cm depth, Joyuda Lagoon, P. R.

donor; and (4) fermentation and methane synthesis in the absence of sulfate.

The availability of nutrient solutes in pore water depends upon the concentration gradients and electrical potential gradients (Manahan, 1979). Nitrogen containing organics are composed of nitrogen bound to humus, amino acids, and amino sugars. In most soils, over 90 percent of the nitrogen content is organic. This organic nitrogen is primarily the product of the biodegradation of dead plants and animals. It is eventually hydrolyzed to ammonium, which can be oxidized to nitrate by natural processes in the soil (Manahan, 1979). Unlike potassium and phosphorous, nitrogen is not a significant product of mineral weathering. Soil humus serves as a reservoir of nitrogen required by plants (Manahan, 1979).

Samples of interstitial water seeping into holes dug by Onuf, et al. (1977) next to red mangrove roots at low tide confirmed that levels of ammonium more than an order of magnitude higher extended to the roots in higher—compared to low—nutrient areas.

Montgomery, et al. (1979) quoting from Byrnes, et al. (1972), indicated that in lakes the flux in NH_4^+-N will proceed from interstitial water to lake water with the 0 to 4 centimeter sediment layer providing the immediate source of nitrogen. Sediment from 5 to 16 centimeters provides a long term source of ammonium nitrogen.

Manahan (1979) found ammonium ions are strongly bound to soils due to their positive charge. Because nitrate (an anion) is not strongly bound to soil, it is readily carried through soil formations by

water. A major means of nitrogen loss in flooded soils and swamp sediments is the nitrification/denitrification process. However, nitrogen loss could be minimized or inhibited by other chemical characteristics of organic soils, specifically tannins and hydrogen sulfide (Kimball and Teas, 1975), which abound in the mangrove environment.

Nitrogen-fixation was found by Kimball and Teas (1975) consistently in the surface sediments and soil profiles of five mangrove communities studied. The principle nitrogen-fixation in these soils was anaerobic, probably bacterial; additional fixation which occurs in the surface layers is likely attributed to blue-green algae and photosynthetic bacteria. Fixation in anoxic sediments in the dark is generally attributed to heterotrophic bacteria. Rates of nitrogen-fixation generally decrease with depth.

Vertical concentration profiles of nitrate and nitrite in interstitial water of sediments in the Sluice Dock (an artificial lagoon) in Belgium shows a maximum at a few centimeters depth where sediments are sandy and poor in organic matter, while in muddy organic rich sediments, nitrate is lower in interstitial water than in the overlying water, and decreases rapidly with depth (Vanderborght and Billen, 1975). This second circumstance was found to be the case in Joyuda Lagoon.

Phosphorous compounds are composed of phosphate esters, inositol phosphate (phytic acids), and phospholipids, and are a source of plant phosphate. In the pH range that is present in most soils, $H_2PO_4^-$ and $HPO_4^=$ are the predominant orthophosphate species (Manahan, 1979). Martens, et al. (1978) believe that phosphate removal at depth is caused

by authigenic mineral formation.

In the presence of active decomposition, with high values for free CO_2 and correspondingly low O_2, the calcareous matter in the sediment acts as a regulatory mechanism in controlling the pH of interstitial water, so that the pH of this water is not greatly different from that of seawater (Hedgpeth, 1957).

Emery, et al. (1957) states that the salinity of interstitial water is dependent on that of the overlying water and thus in an estuarine environment can be much higher or much lower than normal seawater. There is only slow interchange between the interstitial water and the overlying water. Because the salinity of the interstitial water is subject to a smaller range and variation than the overlying water, it provides a fairly stable environment for burrowing organisms and for the roots of plants.

According to Lugo and Cintrón (1975) regardless of surface water salinity, soil interstitial salinities were high in all mangrove communities studied in Puerto Rico and Haiti.

Though the sampler constructed for this study proved inadequate for the fine sediments encountered in Joyuda Lagoon, it has proved very useful for sampling areas of coarser sediments.

In comparison with other interstitial water samplers in the literature, the sampler described in this study appears superior to most for sampling sandy sediments, in its ease of use, amount of sample able to be drawn, and time involved in sampling.

Hesslein (1976) describes a dialysis membrane interstitial water

sampler which takes about one week to equilibrate with the interstitial water and the sample size is 4 ml. Zimmermann, et al. (1978) describe a sampler made of PVC and requires 48 hours to equilibrate. Price, et al. (1979) use a sampler which requires one sampler for each depth sampled. Makemson (1972) used a fragile glass volumetric pipette for interstitial water sampling of a sandy beach. Besides these devices, the older methods of pore water collection were sediment corers (Murray, 1977), and sediment squeezers (Reeburgh, 1967), which produce very small samples from very large amounts of sediment.

Montgomery, et al. (1979) discuss how temperature, oxygen, and carbon dioxide affect the concentrations of nutrients in sediment pore water collected using sediment squeezers. They further state the need for inert conditions while collecting, storing, and analyzing anoxic pore water samples. This is in agreement with the findings of Manheim (1976), who writes that interstitial water samples should be in a state which is as close as possible to their in situ condition.

NUTRIENT UPTAKE

I. Uptake Mechanisms

For the sake of simplicity, the processes involved in movement of ions are divided into nonmetabolic (passive) and metabolic (active) ones. Muscatine and D'Elia (1978) describe ammonium uptake by corals in these terms; D'Elia (1979) the uptake of phosphorous; and Shaked and Banin (1973) the uptake of nitrate by plants in saline environments.

When ions are transported into a cell as a result of electrochemical potential differences, the process is called passive or nonmetabolic uptake. Rates of ion uptake by such a process are linearly correlated with the external concentration of the ions, and are only very little affected by temperature change (Waisel, 1972).

Nonmetabolic uptake starts with the entry of an ion into the free space of a root. The free space is defined as the volume of tissue which is available for free diffusion. Cell walls are considered the major component of the free space; they are negatively charged and adsorb cations. Beyond the cell wall is a membrane which is selective and its properties determine the quality and quantity of the moving ions. Limitation of ion transport by a selective barrier is critical for plants which usually are exposed to high salt concentrations. Such limitation may take place at the surface of epidermal cells, cortical cells, or at the endodermis. Uptake of ions into the osmotic space against an electrochemical potential gradient requires an expenditure of

metabolic energy and, therefore, a normal supply of oxygen and metabolites (Waisel, 1972).

The rates of such active uptake are generally temperature-dependent, although the uptake of cations is affected less by temperature than of anions (Waisel, 1972).

When plotted against time, ion uptake in most plant species investigated so far is expressed by a saturation type curve. Such a curve indicates that the uptake capacity of plants is limited. Limitation may result in three cases: (a) saturation of a limited number of intracellular stationary binding sites, and formation of an exchange equilibrium; (b) saturation of the attachment sites on a dynamic transport pump; and (c) reduction of the uptake rate (Waisel, 1972).

II. Effects of Light

The uptake rate of ammonium was greatest during periods of light and lower in the dark. Light enhanced uptake of ammonium by coral symbionts has been described by Muscatine and D'Elia (1978); enhancement of both nitrate and ammonium uptake by phytoplankton, especially the latter, by Kuenzler, et al. (1979); and phosphate enhanced absorption in eelgrass described by McRoy and Barsdate (1970).

The reason for this light enhanced uptake by autotrophs is that the energy required for the functioning of permeases must come directly or indirectly from that captured by chlorophyll (Dugdale, 1976).

III. Ammonium

Ammonium was used in the experimental medium as the limiting

nutrient for several reasons. Preferential assimilation of ammonium over nitrate has been observed for so many algae that it is now referred to as a "nearly universal" phenomenon (Kuenzler, et al., 1979). Patrick and Delaune (1976) and Morris (1979) found that *Spartina* absorbed ammonium-nitrogen at a greater maximum rate and with greater efficiency than nitrate-nitrogen. Dugdale (1976) found phytoplankton ammonium preference and McCarthy, et al. (1977) state eight other references with similar observations.

It is believed that the ammonium preference is related to the fact that nitrate utilization requires an energy expenditure for both induction of the nitrate reductase enzyme system and for the chemical reduction of nitrate to ammonium. The amino acid pool remains low during growth on nitrate because of limitation in the rate of reduction of nitrite to ammonium. When ammonium is provided, however, protein synthesis is the rate limiting step, resulting in accumulation of amino acids and inhibition of nitrate and nitrite uptake. It has been concluded that the interaction represents an energy-saving adaption that permits cells to grow in a nitrogen-limited environment. In these environments, the cell is able to take advantage of a variety of nitrogen forms, some of which are present sporadically (Kuenzler, et al., 1979).

Other reasons for the use of ammonium are the relative ease of testing, and that ammonium was the nutrient at highest concentration level in the pore water surrounding mangrove roots. Experiment I was begun at ammonium concentrations approximating those found in the field.

Ammonium uptake has also been linked with increases in the rate of photosynthesis and excretion of labeled photosynthate in coral symbionts and dinoflagelates (Muscatine and D'Elia, 1978).

IV. Role of the Soil

Morris (1979) suggests that edaphic factors, possibly an oxygen deficiency, of a metabolic poison such as hydrogen sulfide, or competition from other ion carriers, might inhibit nitrogen uptake in the marsh in such a way as to increase the Michaelis-Menten half-saturation constant (Ks) for uptake. He also suggests that a gradient for such environmental factors could account for gradients in morphology and productivity in communities of *Spartina alterniflora*. Such gradients in mangrove swamp areas may also be responsible for the characteristic zonation of tree species encountered.

Movement of ions to root surfaces may take place by gradual exchange reactions. Since this is a relatively slow process, a region of low ion content is gradually formed near the root surface. The radius of the cylinder of depleted soil thus formed approximates the length of fine root hairs (Waisel, 1972). Root hairs are known to be the major participants in nutrient absorption in all plants (McRoy and Barsdate, 1970). Consequently, further uptake of ions by roots is limited by the rate of their supply from the bulk of the soil to the root surface. Such a supply of ions depends on two processes: ion diffusion and mass flow (Waisel, 1972).

In soil solutions the relationship between activity and concentration are further complicated by the presence of negatively-charged,

adsorbing clay surfaces and by ionic equilibria with insoluble or sparingly-soluble salts (Shaked and Banin, 1973).

Generally, a curved relationship with progressively diminishing slope is expected, and found, when the rate of ion uptake is plotted versus the ion content in soil. In essence, this is due to the fact that the rate limiting factor for the overall uptake process is shifting from being the ion content when this content is low to being the quantity of "carriers" in the plant cell membrane when ion content is high. Thus, in all cases where ion content is low, the rate of uptake is essentially proportional to it (Shaked and Banin, 1973).

V. Carrier Competition

A number of researchers have discussed carrier competition by ions in the uptake process (Waisel, 1972; Shaked and Banin, 1973; Joshi, et al., 1975; and Morris, 1979). Other cations compete with ammonium, and other anions with nitrate carriers. Competitive inhibition is thought to occur when different ions of like charge compete for the same binding site on a carrier, and this affects the uptake kinetics by increasing the Ks. Increased salinity impairs the uptake of inorganic nitrogen (Morris, 1979).

VI. Oxygen

Regarding the uptake process, aeration affects membrane permeability as well as the metabolic uptake mechanism. Thus, lack of oxygen and a high carbon dioxide content in the root medium causes roots to be leaky (Waisel, 1972). Research has shown that it is the concentration

of oxygen that is important in determining the rate of uptake, not simply its presence or absence (Morris, 1979).

VII. Uptake and Growth

Nutrient uptake and plant growth are separate processes that are coupled through various mechanisms including feedback control of uptake. Under steady-state conditions specific uptake and specific growth rates must be equal; during transient phases these rates may differ. With nutrient limited growth, the specific growth rate is controlled by the uptake of the limiting nutrient through the permease system. Under internally or non-nutrient controlled growth, the uptake is controlled to the level required for cell synthesis (Dugdale, 1976).

Evidence of nutrient supply limiting production is available from growth trials where fertilizers have been applied to a forest area and have given increased growth. The difficulty of correlating tree growth and nutrient status of the soil may be attributed to various causes, for instance, difficulty in sampling forest soils adequately because of their heterogeneity, compensating interactions between different nutrients and failure to express soil nutrient content on a soil volume basis or making allowance for differences in tree root distribution and nutrient uptake ability. Estimates of soil nutrients also vary according to the analytical procedure followed (Ovington, 1965).

VIII. Seasonal Variations

Joshi, et al. (1975) found distinct seasonal changes in ionic composition of mangroves. Chapman (1962) indicated seasonal differences

in respiration rates for medium and mature seedlings of *Rhizophora mangle*. He believes this drift in respiration rate with season may well be due to the increase in atmospheric (ambient) temperature, engendering a greater metabolic activity.

In agreement with these conclusions are Morris (1979) and Kuenzler, et al. (1979). The former found the optimum temperature for nitrogen uptake by *Spartina* is apparently greater than 24°C, and the maximum rate of nutrient uptake, Vmax, is temperature sensitive, while the efficiency of uptake, Ks, remains unchanged. The latter found nitrate and ammonium uptake rates for Pamlico plankton increased with increased temperature, at least in the range of 10 to 13°C, and concluded there must be some temperature or range of temperatures at which the uptake rates would be maximum.

It is felt by this author that the same should apply to mangrove uptake rates in Joyuda Lagoon. The seasonal fluctuations must occur, with yearly averages being approximated by this study.

MANGROVE UPTAKE

The first phase of the nutrient cycle through mangroves is uptake. Several experiments were performed using red mangrove seedlings grown in containers of seawater, at different nutrient concentration levels, to determine their rate of uptake. The rate of ammonium disappearance from solutions of known starting concentrations was measured as a function of time.

The data of nutrient uptake versus time was plotted and a curve was fitted to the data visually. Regression lines were calculated and concentration values at sampling times were then extrapolated from this line (Tables 20 and 21, Figs. 14 and 15). Uptake rates (V) were calculated from the concentration change over the sampling time interval. This was plotted against mean ammonium-nitrogen concentration (S) between samples (Fig. 16). The resulting curve of V versus S was then treated as a Michaelis-Menten hyperbola based on the equation

$$V = \frac{Vmax \cdot S}{Ks + S}$$

where V is the uptake rate, Vmax the maximum uptake rate, S the concentration of the nutrient, and Ks the half-saturation constant (the value of S when V = Vmax/2)(Muscatine and D'Elia, 1978).

Data were then transformed by plotting 1/V versus 1/S and a least-square linear regression was performed yielding a Lineweaver-Burk plot. Vmax was estimated algebraically from the reciprocal of the ordinal intercept. Ks was calculated as the product of Vmax and the slope

Table 20. Results of mangrove ammonium uptake experiments. Ammonium concentrations in ug.at NH_4^+-N/liter.

TABLE 20

Hour					
Exp. I					
0	32	26	31.3	26	31.3
1	31	26.5	28.2	28	30.9
2	33	27	26.6	29	31.8
3	32.5	28	25.2	30	30.4
4	31.5	28	24.9	20	28.5
5	30	28	20.6	30	28.1
6	27.5	28	19.4	29	28.1
12	27	27	18.9	27	29.0
18	27	27	13.8	27	25.3
24	35	29	13.4	30	30.7
Exp. II					
0	27	27	10.8	28	10.8
1	30.5	27	9.8	28	11.0
2	29.5	27	8.6	28.5	10.9
3	29	28	8.3	28.5	11.1
4	29	28	7.0	29	11.2
5	28	28	6.4	29	11.0
6	28	27	5.4	28	11.5
12	25.5	26	4.2	26	12.3
18	24.5	25	2.7	25	12.2
24	26	29	1.3	29.5	13.0
Exp. III					
0	33.5	25	4.9	25	4.9
1	33	26	4.0	27	5.0
2	31	26	3.8	28	4.9
3	29.5	27	3.6	29	5.1
4	30	27	3.3	29	5.3
5	29	27	3.0	29	5.4
6	28	27	2.8	28	5.2

Table 21. Values for uptake velocity, V, in ug·at/liter/hour, and ammonium concentration, S, in ug·at NH_4^+-N/liter.

TABLE 21

	Time	V	S
Exp. I	0-1	3.1	29.8
	1-2	1.6	27.4
	2-3	1.4	25.9
	3-4	0.3	25.1
	4-5	4.3	22.8
	5-6	1.2	20.0
Exp. II	0-1	1.0	10.3
	1-2	1.2	9.2
	2-3	0.3	8.5
	3-4	1.3	7.7
	4-5	0.6	6.7
	5-6	1.0	5.9
Exp. III	0-1	0.9	4.5
	1-2	0.2	3.9
	2-3	0.2	3.7
	3-4	0.3	3.5
	4-5	0.3	3.2
	5-6	0.2	2.9

Figure 14. Ammonium uptake (ug·at NH_4^+-N/liter) per hour by ten mangrove seedlings. All experimental values shown are for uptake in light.

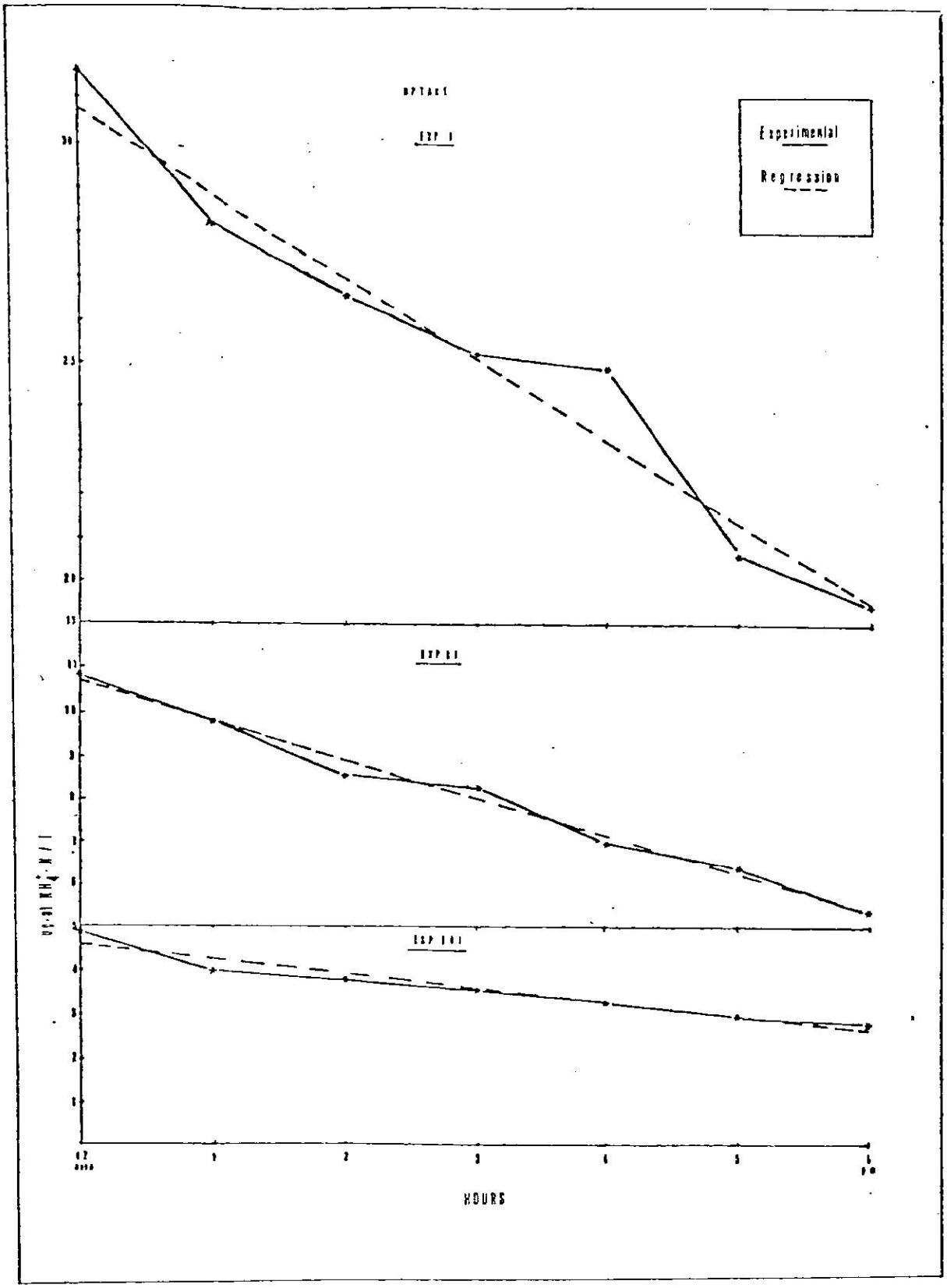

Experimental
Regression
HOURS

Figure 15. Mangrove nutrient uptake experiment I. Shown are both light and dark uptake rates for a 24 hour period. Also shown are the control NH_4 concentrations, and the corresponding calculated regression lines.

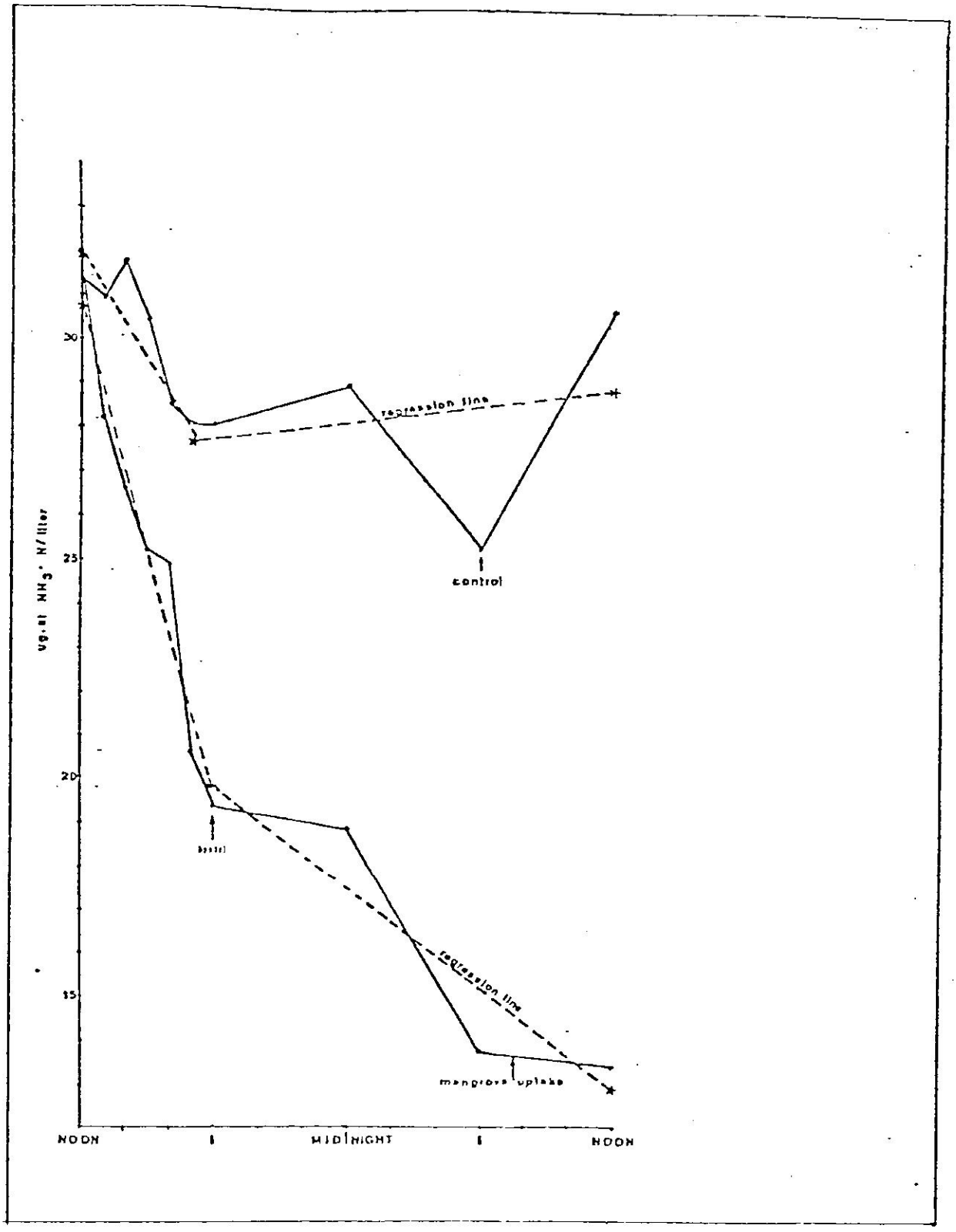
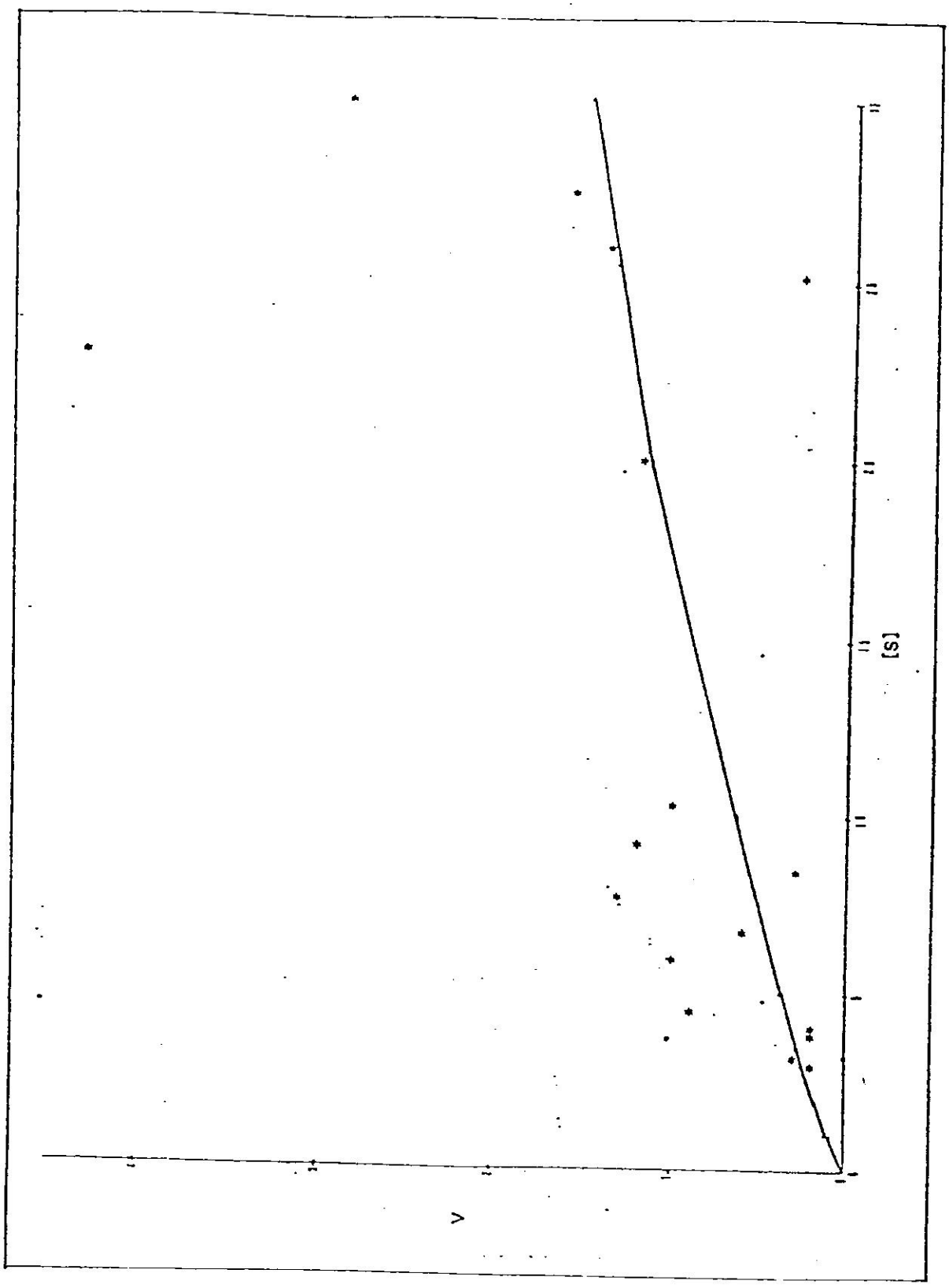

ug.at NH3 - N/liter
30
25
20
15
regression line
control
basal
regression line
mangrove uptake
NOON
MIDNIGHT
NOON

Figure 16. Plot of Michaelis-Menten uptake for mangrove seedlings. Initial velocity, V, versus substrate concentration, S.


[S]
V

of the regression line (Segal, 1968)(Table 22, Fig. 17).

Removal of ammonium must have been due to uptake by mangrove seedlings rather than exchange with the atmosphere, adsorption to the walls of the container, or significant bacterial uptake, since a control consisting of a beaker of seawater enriched with ammonium chloride showed only slight change in ammonium levels.

Experiments I and II were carried out for 24 hours. Experiment III was run for 6 hours. All experiments began at noon. The mangrove seedlings used had well developed root hairs. Prior to commencing an experiment the seedlings were allowed to acclimate in a nutrient solution, of the same concentration as the experiment, over night. The seedlings were transferred to a fresh nutrient solution, and the sampling begun. Chapman (1962) found that red mangrove seedlings in respiration studies reached a steady-state in less than 5 hours.

Since the experiments were performed in a closed system (where roots were protected from light) several factors may influence fluxes over prolonged experiments. These factors include bacterial growth in the medium, nutritional stress to the experimental organism, oxygen stress, and accumulation of noxious metabolites (D'Elia, 1977). Therefore, incubations did not exceed 24 hours.

The results of the uptake experiments are presented in Tables 20 and 21 and Figures 14 and 15, which also show graphically the calculated regression lines. In Figure 14 only the first 6 hours of the experiment are plotted to show uptake during the light period, when maximum rates were observed. During the 24 hour studies, after sunset the rate of

Table 22. Inverse values of uptake velocity, 1/V, and ammonium concentration, 1/S, used for the Lineweaver-Burk plot. Regression equation and calculations for Vmax and Ks.

TABLE 22

Time	Exp. I		Exp. II		Exp. III	
	1/V	1/S	1/V	1/S	1/V	1/S
0-1	0.32	0.03	1.00	0.10	1.11	0.22
1-2	0.63	0.04	0.83	0.11	5.00	0.26
2-3	0.71	0.04	3.33	0.12	5.00	0.27
3-4	3.33	0.04	0.77	0.13	3.33	0.29
4-5	0.23	0.04	1.67	0.15	3.33	0.31
5-6	0.83	0.05	1.00	0.17	5.00	0.34

Regression line = $y=0.26+12.11\ x$

$1/Vmax = 0.26$

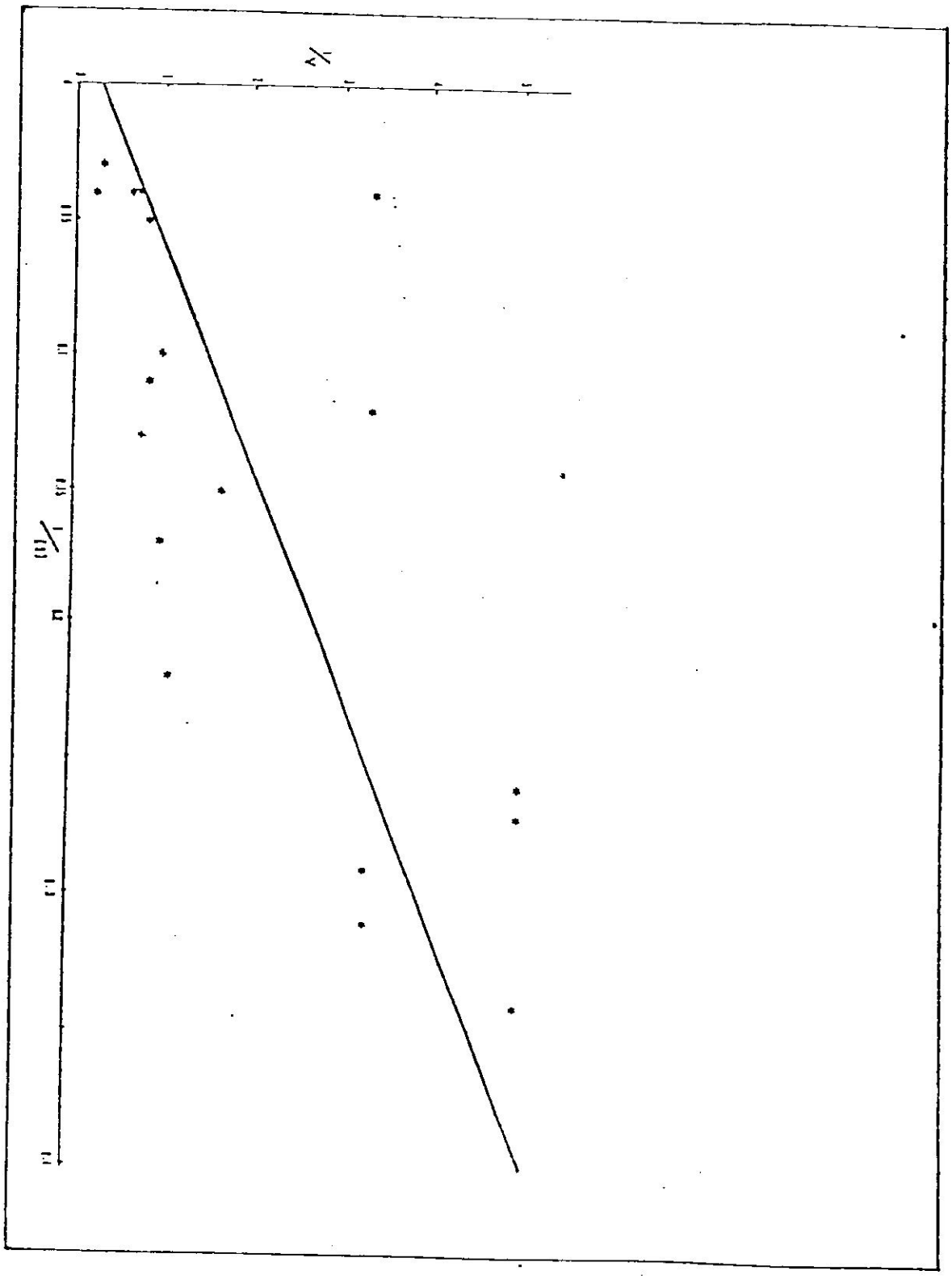
$Vmax = 3.85$ ug-at NH_4^+-N/liter/hour

Ks = slope·Vmax

$Ks = 12.11-3.85$

Ks = 46.62 ug-at NH_4^+-N/liter

Figure 17. Lineweaver-burk plot of inverse uptake velocity, 1/V, versus inverse concentration, 1/S, with mathematical regression line.



uptake decreased dramatically, but was never zero. This is demonstrated in Figure 15, which shows the results of experiment I for the 24 hour period.

From comparison of the slopes in Figure 14 it can be seen that as the concentration of ammonium in the medium decreased uptake rates also decreased.

I. Michaelis-Menten Kinetics

In the plot of uptake, V, versus ammonium concentration, S, the uptake curve yields a rectangular hyperbolic shape which indicates that the uptake rate became concentration independent at higher concentrations which is characteristic of Michaelis-Menten uptake kinetics (D'Elia, 1977).

Converting the data from the uptake curve of V versus S to a Lineweaver-Burk plot of 1/V versus 1/S (Table 22 and Fig. 17), we are able to arrive at Vmax and Ks as previously discussed. Table 23 is a comparison of Ks and Vmax values for different plants. Concentrations have all been converted to ug·at NH_4^+-N/liter.

Confirmation of the applicability of the Michaelis-Menten expression to the uptake of inorganic nitrogen by marine phytoplankton has been obtained for cultures in laboratory and for natural populations through shipboard experimentation. The data for the kinetic constants, Vmax and Ks, of natural populations have been obtained primarily with tracer ^{15}N (Dugdale, 1976).

The constant, Ks, is a measure of the affinity of the permeases for the substrate and thus an important indicator of the ability of an

Table 23. Comparison of Ks and Vmax values for ammonium for different types of plants. Values in ug·at NH_4^+-N/liter.

TABLE 23

Plant	Ks	Vmax	Reference
Spartina alterniflora	57	----	Morris. 1979
Carex aqualitis (Sedge grass)	153-218	----	Morris. 1979
Maize	295	----	Morris. 1979
Ryegrass	720	----	Morris. 1979
Phytoplankton	9-27	----	Kuenzler, et al. 1979
Phytoplankton	0-1.3	0.003-0.036	Dugdale. 1976
Rhizophora mangle	46.6	3.85	This study. 1980

organism to compete for limiting nutrients (Dugdale, 1976). The Ks for *Rhizophora mangle* found in this study was 46.6 ug-at NH_4^+-N/liter. This compares closely with that for *Spartina alterniflora* (57 ug-at NH_4^+-N/liter, Morris, 1979), another marsh plant.

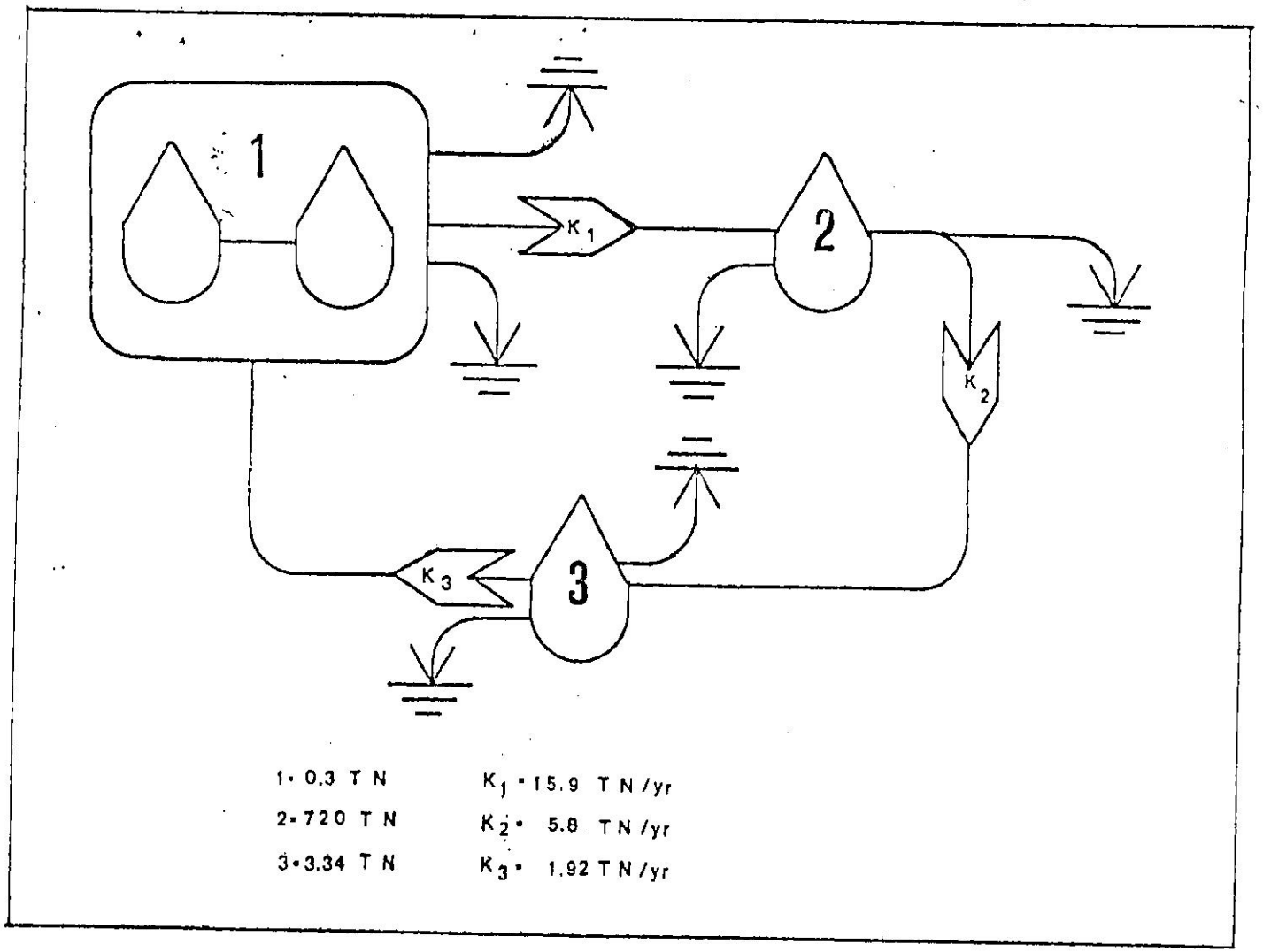
CONCLUSION

The goal of this study was to define the fluxes and storage of nutrients, in particular nitrogen, as it cycles through the mangroves fringing Joyuda Lagoon and the lagoon water. Toward this end, initial identification of the major compartments investigated and quantification of compartment magnitude and rates of flow between compartments have been defined (Fig. 18).

The compartments were arrived at through a modification of the model by Lugo, et al. (1976). Simplifying their model to the needs of this study provided the following: compartment 1 represents passive nutrient storage by the water phase of the lagoon; compartment 2 represents nutrients stored in the mangrove biomass surrounding the lagoon; and compartment 3 represents the nutrients stored in the form of mangrove debris around the lagoon. Major pathways of nutrient fluxes between compartments were defined as follows: the rate of nutrient uptake from compartment 1 to 2 is shown by K_1; the rate of litter-fall from compartment 2 to 3 is represented by K_2; and the rate of decomposition of litter from compartment 3 back to compartment 1 is shown by K_3.

Due to the difficulty in quantitating separately the interstitial water and the lagoonal water, they have been combined to form compartment 1. Since mangroves feed both interstitially (Zuberer and Silver, 1975) and directly from the lagoon (Clough and Attiwill, 1975) this combination appears reasonable. The calculated sum of nitrogen for

Figure 18. Simplified model of nitrogen flow in Joyuda Lagoon (modified after Lugo, et al., 1976, and Odum, 1972). 1 = nitrogen concentration of lagoon water plus interstitial water estimated to 2 meters. K_1 = rate of mangrove nitrogen uptake. 2 = mangrove biomass surrounding Joyuda Lagoon. K_2 = rate of mangrove litter-fall. 3 = mangrove litter surrounding lagoon. K_3 = rate of mangrove decomposition.


1
2
3
K1
K2
K3
1 • 0.3 T N
2 • 720 T N
3 • 3.34 T N
K1 • 15.9 T N/yr
K2 • 5.8 T N/yr
K3 • 1.92 T N/yr

this compartment is 0.3 tonnes. The rate of nitrogen uptake by mangroves (K_1 = 15.9 tonnes N per year) yields a short residence time for this nutrient.

The standing crop (biomass) of mangroves surrounding Joyuda Lagoon, compartment 2, has been calculated by multiplying the area covered by mangroves times the weight per unit area (Golley, et al., 1962). This formula yields a value of 720 tonnes N for standing crop.

Subtracting the rate of litter-fall, K_2, from the rate of uptake, K_1, gives a growth rate of 10.1 tonnes N per year. This is in close agreement with growth rates measured from aerial photographs. By accurately tracing onto high quality paper the actual area covered by mangroves in the photographs, then cutting out and weighing the paper and converting this weight by multiplying it by the weight of a known area taken from the scale, the difference in area is thus attainable (Shapiro, personal communication). This value is in turn multiplied by the mangrove biomass per unit area and then times the percentage nitrogen per unit biomass to yield the nitrogen content. From this technique the growth rate was found to be 1,960 m^2 per year or 2.97 tonnes N per year. This method was used as an independent check of the modeling approach, the result being about one-third that calculated by modeling.

One reason for this discrepency may lie in the assumption, by this author, that mangrove trees assimilate N at the same rate as mangrove seedlings. The case may be that in reality fully developed trees take up N at about one-third the rate of seedlings. This remains to be investigated. However, the fact that the results are within an order of

magnitude of each other shows the model to be fairly accurate.

Armstrong (1981) calculated a mean growth rate of 338 m^2 per year for mangroves colonizing Enrique Reef south of La Parguera, Puerto Rico. Since this is an unprotected area more sensitive to perturbations from hurricanes and lower ocean nutrient concentrations, this slower rate is to be expected.

The extrapolated amount of mangrove debris surrounding the lagoon, compartment 3, is 3.34 tonnes N. This is being degraded and returned to the lagoon at a rate of 1.92 tonnes N per year (K_3). K_3 was calculated with the assumption that one half of mangrove debris falls over land and one half over water. The rate of mangrove decomposition in water found in this study and that for decomposition on land reported by Heald (1971) were combined and used here.

This survey provides a baseline study of the nutrient levels in and around Joyuda Lagoon. Effects of change, for example mining or development, in the area surrounding the lagoon may thus be assessed. In the past, fish kills have been reported in the lagoon (Pagán and Austin, 1970 and Erdman, 1963). With the information presented in this study possible causes of such future catastrophies may be detected. Possible use of the lagoon for aquaculture has been discussed. The model will be useful in estimating fishery yields for the lagoon and the adjoining ocean area.

Although the present investigation provides a useful measure of the general magnitude of compartments and flow rates it is recognized that other compartments and exchange pathways do exist, the importance

of which must be assessed to provide a more accurate view of this system. For example, the amount of yearly export from the lagoon into the ocean, the amount of nutrients lost to mineralization and uptake by other organisms living in and around the lagoon. Also, sources of nutrient inputs into the lagoon such as ground water, precipitation, runoff, and miscellaneous sources (i.e. guano, decay of dead animals and other plants, etc.) as well as nitrogen fixation by microorganisms attached to mangrove roots need to be quantitated.

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