

"CEER-M.128 NUTRIENT CYCLING BY THE RED MANGROVE, RHIZOPHORA MANGLE L., IN JOYUDA LAGOON ON THE WEST COAST OF PUERTO RICO, CENTER FOR ENERGY AND ENVIRONMENT RESEARCH

NUTRIENT CYCLING BY THE RED MANGROVE, RHIZOPHORA MANGLE L., IN JOYUDA LAGOON ON THE WEST COAST OF PUERTO RICO. By Edwin Allen Levine. This work was partially supported by The Marine Ecology Division of the Center for Energy and Environment Research, University of Puerto Rico, Mayaguez MS Thesis, Marine Sciences, RUM-UPR (1981)

ABSTRACT

La Laguna Joyuda represents a nearly closed ecosystem, excellent for study purposes. The present study examines the flow rates of nutrients between the mangrove community and the lagoon. Through sampling, experiments, transects, chemical analysis, and the comparison of aerial photographs, the nitrogen cycle in this system is documented. It was found that the residence time of nitrogen in the lagoon water is short; the biomass of mangroves is approximately 720 tons; the renewal rate of nitrogen is 15.9 tons per year; the return rate of nitrogen to the lagoon is 1.92 tons per year; and the growth rate of the mangroves is approximately 1,960 square meters per year or 2.97 tons nitrogen per year. Recommendations for subsequent studies are presented.

ARE THE MANGROVES

Our lives intertwined hopeful, helpless we are the mangroves, graciously hooking tapestry of roots on the coast of a tropical strand. 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

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The knowledge given to this project is invaluable. Also, to my loving wife Judy, for all of her understanding and inspiration, and to my parents, without whom all this would never have been possible.

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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.

The text with corrections:

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 Pagen 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. Garcia (1961) 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 bioluminescence 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 (*).

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

Lopez and Teas (1978) have developed a model for determining the cycling of trace metals in mangroves. With proper modification, this model has been applied to this study of nutrient cycling in the mangrove-lagoon ecosystem. The model consists of a sequence of discrete 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, the 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 has 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. Similarly, 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 roots 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 shrubs ranging from 3 to 5 cm in diameter.

Each type of tree compartment (leaves, etc.) was stored in separate plastic bags to make up samples that

"Composites were taken over the forest. ANT samples were oven-dried at 70% 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 Millipore (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 determinations in a Technicon Autoanalyzer 11 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.

For estimates of litter production, the model of Pool, et al. (1975) was followed. Eight baskets of known area (0.108 m²) were placed at intervals among the fringe mangroves. The baskets, with small holes in the bottom to allow rainwater 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 due to decay. Samples were dried to a constant weight."

The kinetics in the uptake of ammonium displayed by the mangrove seedlings were studied. The decay rate of *Avicennia marina* 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 (0.45 μ) 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,

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 m² 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/m²/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 (gw), 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/m² and 945 gdw/m² 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/m²/day total litter and 2.56 gdw/m²/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/m²/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 26 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 TOTAL LEAF

Date | Wet | Dry | Wet | Dry

4/27 | 332 | 205 | 13188 | 51

... | ... | ... | ... | ...

... | ... | ... | ... | ...

... | ... | ... | ... | ...

... | ... | ... | ... | ...

The text seems to be a series of data tables and descriptions for scientific study. However, the information is not well-organized or coherent. Here's my attempt to make it more readable:

Table 1:

560192 26373 to 206 133 170
 nas 18386 ne 63
 reno 9 a 51
 we 146 Bh 3 62
 2nn moon 986 38 13683.

a) 5708 ae 123 13585 76 333 261 208 147

TOTAL 3881 1812 2023 1005
 MEAN 2719 1672
 STANDARD DEVIATION 18 60

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
ape	104	2	7	237	
sm	36	19	0	4	89
6/08	1	70	34	Fy	219 13
no	133	20	83	326	
ens	83	5a	57	37	230
ano	96	160	n	2	3B
rom	2	37	°	34	164
nas	83	38	4	30	156
yeno	67	36	°	"	10
we	82	5	8	28	123
2n7	ma	3	3	30	v0
ae	a4	5	n	22	an
5/08	ne	v	3	48	ve0 76

Total: 1339 708 35 361
 g/m²/yr = 1919 (total litter) and 945 (leaf litter)
 g/m²/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 4: Percent dry weight of total sample by compartment.

TABLE 4

Date	Leaves	Seedlings	Twigs	Miscellaneous
a	3	a	10	3
sm	6	2	°	6
6/08	a	2	6	10
ms	38	4	8	6
ans	36	2	25	18
sno	2%	46	20	6

10m 86 23 ° 2
as 3 2 3 9
weno 86 20 ° 1“
wis ° 4 6 2
zn 62 2 n 25
ane 70 3 9 8
5/08 6 0 1 26
m6 ry 7 19 2

Total Collection 49 26 2 3
Mean 33 23 ° 6
Standard deviation 4 6 8 8

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

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.

26 of the total: miscellaneous items ranged from 2 to 25%, and were 13% of the total.

The totals 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, accounting for 68 to 86% of the total litter produced. Wood-fall ranged from 3 to 15%, and miscellaneous items ranged from 8 to 21%. Goulter and Allaway (1979), working in Australia with *Avicenia 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 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...

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

8/13 23 1 7 1 0 0 1 Tom ° 6 1 8 6 sree

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), with the mean being 2.8 gdw/m²/day. Heald (1971) found leaf-fall to average about 1.3 g/m²/day in May, and Pool et al. (1975) found mean rates of leaf-fall are fairly constant for all mangrove forests studied (overall mean = 2.2 g/m²/day, SD = 1.06). Only during the three seedling peaks previously mentioned, leaves were 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 the amount of rain and leaf-fall at the 0.01 significance level, $r = 0.07$ (Scheffler, 1979). As can be seen in Figure 9, precipitation peaked in both 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, $r = 2.609$ (Scheffler, 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

STATION 4 5 6 7 8 8 8 9 8 6

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./m²/day).

30 Standard deviation 128.0 726.8/357.9 21.9 10.5

Figure 8. Graphic representation of total litter-fall.

Leaf litter-fall per square meter per collection period, all values in grams dry weight.

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

33. 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.

34. Goulter and Allaway (1979) also found that occasional storms coincided with increased litter-fall. They state that the

Productivity is high, but 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 watersheds (Pool, et al., 1975).

The 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 average, leaves contained 31 percent more water during the wet season than during the dry season; seedlings contained 22 percent more; wood contained 36 percent more; 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 is also different.

Table 8 shows the percentage water content of leaves and total litter. The comparison between wet (more than 6 inches precipitation per month) and dry (less than 6 inches precipitation per month)

seasons are presented. All weights are in grams.

Table 9 shows the 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 are presented. All weights are in grams.

Table 9: Sand Dune Wood Seedlings Dry/Wet Water Content

Dry Months	Wet Months	Dry/Wet Ratio	Water Content (%)
427	22/27	2	50
6/08	26/30	13	
53/97	45	-	50
5/36	88	26/200	83
43/55	2	-	68
7k	-	54/69	2
127	26	758	-
0.3/1	66	2/87	49
3/4	25	297	45
46	-	-	277
43	8	-	40
vr	43	-	-
16	ya	33	38
8/10	20	76	50
5/08	-	50	13
20	45	-	3975
28	1/52	-	-
Hean	aye	34	34
Standard deviation	18/24	23	34

This data reflects 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. Various researchers have discussed the role of plant detritus in different ecosystems such as salt marshes, estuaries, woodlands, lakes, rivers, and mangrove forests. 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.

In order to clarify the terms used in this work, the following definitions, sourced 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. Therefore, "debris" is roughly equivalent to the term "litter", which is commonly used to describe decaying plant material in more fully terrestrial communities.

"Detritus" is debris that has been fragmented to the point where individual particle size does not exceed 2 or 3 mm in its smallest dimension. The primary 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 ongoing degradation processes which cause a reduction in the size of a debris fragment until its component parts can no longer be considered particulate. At this stage, it enters the vague realm of "colloidal" or "dissolved organic" material, which plays a crucial role in detrital food chains.

A decrease in size does not necessarily result in a decline in energy content; as Odum and de la Cruz (1967) demonstrated, a reduction in particle size is accompanied by enrichment and an increase in metabolic activity as a result of adsorbed microbiota.

The ability of decomposing litter to retain and hold nitrogen 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 the 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 considerable number of bacteria that were found to thrive in this environment. This indicates the high potential value of this primary source of organic matter in supporting the complex flora and fauna of coastal waters.

'As Darnell (1967) 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 lagoon 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 found in other studies, it is important to note that the conditions in each study were different.

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

Date 8/01 - 10/11 (data not shown)'

Also, we can see in Table 10 that the grams of the dry weight remaining are as follows: 100, 92, 83, 80, 62, 62, 62, 10, 10, 0, 12.

Figure 10. The decay rate of *Rhizophora* mangrove leaves in Joyude Lagoon water. The percent scale represents the amount of litter remaining compared to the starting dry weight.

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

As per Heald (1971), for red mangrove leaves in brackish water in Florida, the two slopes of the regression lines were not significantly different at the 99% confidence level ($p < 0.01$, $t = 0.11$) using the Student t-test (Zar, 1974). The graph of the decay rate (Fig. 10) during the "winter" months (October-February) showed the slowest decay rates. The temperature of the environment might 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 that on average, 5.1 percent of the leaf was 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 due to biological actions rather than 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.

This indicates 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 what naturally occurs 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 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% R). 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.

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

1. Marine		
2. Mangrove		
Leaves	1.06	
Branches	0.61	0.36
Trunk	0.49	
Main Root	0.68	0.36
Feeding Root		
Fibrous Root	1.20	
Pneumatophores	0.70	0.62
Aerial Root		
Dead Leaves	1.23	
Fruit	1.60	0.65

Seedlings 0.74

Flowers

Table 12. Nitrogen production by Vitter 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 (*Sadicornis* sp.--1.57, *Eustypius* sp.--1.82, *Arecia* sp.--2.59, Pan 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 entire lagoon would contain approximately 67.1 kg of nitrogen per hectare per year (Table 12).

With there being 47.61 hectares of mangrove surrounding Joyuda Lagoon (Carvajal, et al., 1980), this yields approximately 3,195 kg of 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 6. 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).

Figure 12. Nutrient content of Joyuda Lagoon water, in $\mu\text{g-at/liter}$, during each sampling period. Circles, o, represent mean value for sampling period.

The text appears to include a mix of technical information and what could be part of a data table. Some of the text is also unclear, possibly due to typographical errors or incorrect formatting. Here is a cleaned up version of the readable parts:

"Bars represent the range of concentrations found in each sampling period. Non-detectable nutrient levels are represented by ND. Points plotted with an 'x' represent unusually high readings thought to be due to experimental error, and these are disregarded from all calculations. Limit of detection: P09 = 0.03 $\mu\text{g-at/l}$, Titer OZ = 0.015 NO; 0.08 $\mu\text{g-at/l}$, Titer Myf = 0.1 $\mu\text{g-at/t}$ Titer.

Table 13. Ammonium concentrations ($\mu\text{g-at NH}_4\text{-N/liter}$) 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. Nitrate concentrations ($\mu\text{g-at H}_05\text{-N/liter}$) 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."

The rest of the text appears to be part of data tables or lists, but it's unclear due to formatting issues and possible typographical errors. If you could provide more context or a clearer version of the text, I would be better able to assist you.

The text is largely nonsensical and cannot be fixed. However, the coherent parts can be rewritten as follows:

Table 15. Nitrite concentrations ($\mu\text{g-at NO}_2\text{-N/Titer}$) in Joyuda Lagoon water, on each collection date, at each station. Samples on 7/16 were 211 below the limit of detection.

Table 16. Phosphate concentrations ($\mu\text{g-at PO}_4\text{-P/liter}$) in Joyuda Lagoon water, on each collection date, at each station. A concentration marked with an (*) was questionable, and therefore not included in the calculation of the mean. On dates marked non-detectable, 21 samples were below the limit of detection.

There is an approximately constant proportion of 15:1 (N:P, by atoms) by phytoplankton as they grow, and 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).

When analyzing the nutrient data for Joyuda Lagoon water, assuming the Redfield ratio holds for mangroves, it appears that phosphorus 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 (Vatiele, et al., 1978; Patrick and Delaune, 1976; and Foneroy, 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 were within values reported for other coastal areas. Analysis of water samples from the canal connecting the mid-lagoon,

Table 17. Comparison of nutrient concentrations in water. All values in micrograms per liter.

Table 17. 0.6-1.7 Walsh, 1967. Hawaiian mangrove swamp, 1.0-1.5 Carpenter, et al., 1969. Chesapeake Bay, Maryland. 0-25 9 10 0-8 Valiela, et al., 1978. Great Sippewissett Marsh, Massachusetts. Jackson, 1977, California, Nicholas, 1967. Mexico. Kuenzler, et al., 1979, Pamlico River, N.C. Naiman and Sibert, 1978, British Columbia. This study. Joyuda Lagoon, Puerto Rico.

The lagoon and the ocean, and the ocean revealed higher nutrient concentrations in the lagoon. (micrograms per liter) 15 No\$po,? Ocean 133.818 0.3 Canal 29° 7.8 2.6 0.5 We 8.2 6.0 2.2 0.8 In October 1978, 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.

The prime argument for their conservation is 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. In areas where nutrients are available but not in great excess, communities of intermediate stability develop. However, where nutrients are in short supply and 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 Joyude 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 Jayuda Lagoon should be very stable. The calculated mean nutrient concentrations for the entire study period are: 3.05 ug-at MHf-N/1; 1.15 ug-at NO5-N/1; 0.23 ug-at NO§-N/1; and 0.73 ug-at PO“?=P/1.

INTERSTITIAL WATER

The purpose of sampling the interstitial water within the shore of Joyude 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, defined by Manheim (1976), are 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 Gusnica, 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

The adapter (A) is attached to a plastic tube (PT) which threads through the cap (C), and galvanized pipe (GP) and attaches to a collecting jar (C2) that is connected to a portable vacuum pump (PVP). The cap (C) is held in place by three hex set screws (i). 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 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 database. 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 spatial heterogeneity. They suggest 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...

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

We continue with oxygen donors; 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 is crucial as 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 high-nutrient areas compared to low-nutrient areas. Montgomery, et al. (1979), quoting from Byrnes, et al. (1972), indicated that in lakes, the flux in NH₄-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 that 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 Bitlen, 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, HPO₄²⁻ and HPO₄³⁻ 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 O₂, and correspondingly low O_p, 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

The sampler, which takes about one week to equilibrate with the interstitial water, has a sample size of 4. Zimmermann, et al. (1978) describe a sampler made of PVC that requires 48 hours to equilibrate. Price, et al. (1979) use a sampler which requires one sampler for each depth sampled. Makerson (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

1. Uptake Mechanisms

For the sake of simplicity, the processes involved in the 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) discusses the uptake of phosphorous; and Shaked and Sanin (1973) describe 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 free space is negatively charged and absorbs 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 are usually exposed to high salt concentrations. Such limitation may take place at the surface of epidermal cells, cortical cells, or at the endodermis. The 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 that 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

Reasons. The preferential assimilation of ammonium over nitrate has been observed in many algae. It is now referred to as a "nearly universal" phenomenon (Kuenzler, et al, 199). 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 also show a preference for ammonium. 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 the limitation in the rate of reduction of nitrite to ammonium. However, when ammonium is provided, protein synthesis is the rate limiting step, resulting in the accumulation of amino acids and inhibition of nitrate and nitrite uptake.

It has been concluded that the interaction represents an energy-saving adaptation that allows 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 the highest concentration level in the pore water surrounding mangrove roots. Experiment T 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 dinoflagellates (Muscatine and O'Evia, 1978).

IV. Role of the Soft Norris (1979) suggests that edaphic factors, possibly an oxygen deficiency, a metabolic poison such as hydrogen sulfide, or competition from other ion carriers, might inhibit nitrogen uptake in the marsh.

The text should be revised as follows:

The way to increase the Michaelis-Menten half-saturation constant (K_s) for uptake is suggested. It is also proposed 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. The 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 the root hairs (Itai, 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 (Weisel, 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 a progressively diminishing slope is expected, and found, when the rate of ion uptake is plotted versus the ion content in soil. Essentially, 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).

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, competitive inhibition with nitrate carriers is thought to occur when different ions of the same charge compete for the same binding site on a carrier. This affects the uptake kinetics by increasing the K_s . 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

cause 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 resulted in 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

Yoshi, et al.

(1975) found distinct seasonal changes in the ionic composition of mangroves. Chapman (1962) indicated seasonal differences in respiration rates for medium and mature seedlings of *Avicennia marina*. He believes this drift in respiration rate with season may well be due to the increase in atmospheric (ambient) temperature, engendering 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, V_{max} , is temperature sensitive, while the efficiency of uptake, K_s , 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 time

(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...

The text appears to be a combination of scientific findings and data tables, with several spelling and formatting errors. Here's a corrected version:

A Michaelis-Menten hyperbola is based on the equation $V_{max} + \frac{V_0 S}{K_s}$ where V is the uptake rate, V_{max} is the maximum uptake rate, S is the concentration of the nutrient, and K_s is the half-saturation constant (the value of S when $V = V_{max}/2$) (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. V_{max} was estimated algebraically from the reciprocal of the original intercept. K_s was calculated as the product of V_{max} and the slope.

Table 20: Results of mangrove ammonium uptake experiments. Ammonium concentrations in $\mu\text{g-at NH}_4\text{-N/liter}$.

Table 20: Continued.

Table 21: Values for uptake velocity, V , in $\mu\text{g-at/liter/hour}$, and ammonium concentration, S , in $\mu\text{g-at NH}_4\text{-N/liter}$.

Figure 14: Ammonium uptake ($\mu\text{g-at NH}_4\text{-N/liter}$) per hour by ten mangrove seedlings. All experimental values shown are for uptake in light.

Figure 15: Mangrove nutrient uptake experiment 1. 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.

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

Page 85: 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, are unlikely since a control consisting of a beaker of seawater enriched with ammonium chloride showed only a slight change in ammonium levels. Experiments I and II were carried out for 28 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, overnight. The seedlings were transferred to a fresh nutrient solution, and the sampling began. 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 V_{max} and K_s .

Table 22

Time	Exp. 1	Exp. II	Exp. III
0	0.32	0.03	1.00
1-2	0.63	0.08	0.83
2-3	0.71	0.08	3.33
3-4	3.33	0.08	0.77
4-5	0.23	0.08	1.67
5-6	0.83	0.05	1.00

Regression Line = $y=0.26+12.11x$

$V_{max} = 0.26$

$V_{max} = 3.85 \text{ ug-at N/liter/hour}$

$K_s = \text{stope-}V_{max} \text{ ks} = 12.11-3.85 \text{ Ks} = 46.62 \text{ ug-at Nig-N/Viter}$

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 1 for the 24 hour period. From the 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.

1. 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 Nif-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 15N (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 Nif-N/liter.

Spartina (Better known as Seagrass): 453-216

Rhizophora mangle: 46.6

TABLE 23

Reference Vmax 0.003-0.036 3.85 Morris, 1979 Morris, 1979 Morris, 1979 Norris, 1979 Kuenzler, et al. 1979 Dugdate, 1976 This study, 1980

Organisms compete for limiting nutrients (Dugdale, 1976). The Ks for Rhizophora mangle found in this study was 46.6 ug-at NH-N/liter. This compares closely with that for Spartina (57 ug-at NH-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 was 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 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 all

Figure 18, Simplified model of nitrogen flow in Joyuda Lagoon (modified after Lugo, et al., 1978, and Odum, 1972). Nitrogen concentration of lagoon water plus interstitial water estimated to 2 meters. K_y = rate of mangrove nitrogen uptake. 2 = mangrove

Biomass surrounding Joyuda Lagoon. K_p = rate of mangrove litter-fall. The mangrove litter surrounding the lagoon. The rate of mangrove decomposition.

This compartment is 0.3 tonnes. The rate of nitrogen uptake by mangroves ($k_y = 15.9$ 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 (Colley, et al., 1962). This formula yields a value of 720 tonnes N for standing crop. Subtracting the rate of litter-fall, K_y , from the rate of uptake, K_y , gives a growth rate of 10.7 tonnes 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 m² 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 discrepancy may lie in the assumption, by this author, that mangrove trees assimilate nitrogen at the same rate as mangrove seedlings. It may be that in reality fully developed trees take up nitrogen 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 (1881) calculated a mean growth rate of 33 m per year for mangroves colonizing Enrique Reef south of

La Parguera, Puerto Rico. As this is an unprotected area that's more sensitive to disturbances such as hurricanes and fluctuating ocean nutrient concentrations, a slower rate is to be expected. The extrapolated amount of mangrove debris surrounding the lagoon, specifically compartment 3, is estimated to be 3.36 tonnes N. This is being gradually degraded and returned to the lagoon at a rate of 1.92 tonnes N per year (K_3).

K3 was calculated assuming that half of the mangrove debris falls on land and the other half over water. The rate of mangrove decomposition in water, found in this study, and the rate of 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 the Joyuda Lagoon. Any changes, such as mining or development in the surrounding area, can thus be assessed. In the past, there have been reports of fish kills in the lagoon (Pagén and Austin, 1970 and Erdman, 1963). With the information presented in this study, potential causes of future such catastrophes may be detected.

The 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 these 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 groundwater, 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 quantified.

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