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THE TREES OF THE MANGROVE SWAMP COMMUNITY OF SAN SALVADOR ISLAND, THE BAHAMAS AND THEIR "SUCCESSION" PATTERNS.

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INTRODUCTION

The Mangrove Swamp Plant Subcommunity derives its name from the red mangrove, *Rhizophora mangle* (Correll and Correll 1982). This community consists of a swamp forest that occurs generally along the borders of many tropical shores where wave action is not intense and mud and plant debris are deposited (Chapman 1976). Sheltered habitats have been reported to be essential for mangrove development (Davis 1940). On exposed coasts mangroves are localized in the lee of other coastal landforms. The plants of the mangrove community are considered to be halophytes that are well adapted to salt water and fluctuations of sea level. Specifically, on San Salvador Island, the Mangrove Swamp Subcommunity lines the inland salt water lakes as well as the tidal basin called Pigeon Creek, located on the southeastern part of the island (Smith 1982).

The typical trees associated with the mangrove swamp on San Salvador are red mangrove, black mangrove, white mangrove, and buttonwood (Table 1). The understory vegetation identified with the mangrove areas are saltwort, sea purslane, rush grass, and glasswort (Table 2).

The Mangrove Swamp Communities have initially been viewed as a successional sequence in which a colonizing species starts at the shoreline and is replaced by a succession species, followed by another succession species until a climax species, from a terrestrial inland community, is reached (Davis 1940). The common example begins with the red mangrove, followed by the black mangrove, followed by white mangrove or buttonwood. Tomlinson (1986) does not consider the latter as a mangrove tree but a mangrove associate. Other authors have pointed out that mangrove trees are facultative halophytes growing where other species cannot grow. Black mangroves have been reported to grow in fresh water mud in a greenhouse environment (Chapman 1976). We find that buttonwood grows in great abundance in the mangle on San Salvador and therefore include this species among the mangrove trees of the Island. We will first describe and illustrate the mangrove species of San Salvador and then discuss our observed exceptions to the zonation and succession patterns as reported in the literature.

MANGROVE TREES OF SAN SALVADOR

The Red Mangrove

The red mangrove, *Rhizophora mangle*, is a shrub or tree that grows on San Salvador to a height of 6 meters. The name *Rhizophora* in

TABLE 1. THE MANGROVE TREES ASSOCIATED WITH THE MANGROVE SWAMP ON SAN SALVADOR ISLAND.

COMMON NAME	SPECIES	FAMILY
RED MANGROVE	*Rhizophora mangle* L.	RHIZOPHORACEAE (Mangrove Family)
BLACK MANGROVE	*Avicennia germinans* (L.)L.	AVICENNIACEAE (Black Mangrove Family)
WHITE MANGROVE	*Laguncularia racemosa* (L.) Gaertin. f.	COMBRETACEAE (White Mangrove Family)
BUTTONWOOD	*Conocarpus erectus* L. *Conocarpus erectus* L. var. *sericeus* Griseb.	COMBRETACEAE (White Mangrove Family)

TABLE 2. SOME UNDERSTORY VEGETATION ASSOCIATED WITH THE MANGROVE AREAS ON SAN SALVADOR ISLAND.

COMMON NAME	SPECIES	FAMILY
SALTWORT	*Batis maritima* L.	BATACEAE (Saltwort Family)
SEA PURSLANE	*Sesuvium portulacastrum* L.	AIZOACEAE (Carpet Weed Family)
RUSH WEED	*Sporobolus virginicus* L. Knuth	GRAMINEAE (Grass Family)
GLASSWORT	*Salicornia virginica* L.	CHENOPODIACEAE (Goosefoot Family)

Greek means "root bearing" and the species name *mangle* is the Arawak Indian name for swamp. The plants are distinguished by their large adventitious aerial roots found protruding from their trunks (Figs. 1 and 2). These prop roots often form a tangled network of impenetrable thickets (Fig. 2). The root system serves as a stabilizer against shifting sediments and also as a means of aeration.

The leaves are opposite on the twig with petioles up to 2 cm long continuing into the leaves as a stout midrib (Figs. 3 and 4). Each petiole has a prominent stipule 2.5-4 cm long, which leaves a prominent stipule scar at the base of the leaf. The leaf blade is entire and leathery, being deep green above and paler beneath.

The flowers occur in a group of 2-3 and are located on a stalk (peduncle) 1-4 cm long. These stalks protrude just above the leaf insertion on the stem. Both male and female reproductive structures are found within each flower. The solitary seed within each fruit develops on the parent tree (vivipary, Figs. 3 and 4). The radical (embryonic root) of the embryo may be observed protruding from the "fruit" while still attached to the twig. The embryonic leaves (cotyledons) remain attached to the "fruit" as a collar when the tip of the shoot containing the first seedling leaves (plumule end, Fig. 5) pulls out of the "fruit" and falls off the parent plant. The seedlings are weighted to fall into the water with the large primary root down. In shallow water this allows the seedling to quickly anchor in the mud ready to produce a new plant (Fig. 6). In deeper water, the seedlings are adapted to floating long distances in the sea, allowing rooting to occur when the seedling is carried to an area of shallow water in a protected environment.

The red mangroves are believed to be the major land builders (Fig. 2) on many of the Bahamian Islands (Correll and Correll 1982), as well as along the shoreline of the Florida Coast. The roots form a base for deposits of silt and other materials carried by the tides, such as accumulating detritus from the recycling of fallen leaves. It is hypothesized that in this way, land is built up which is gradually invaded by other vegetation. Red mangrove roots also provide breeding areas and nurseries for many species of animals that live in the sea (Correll and Correll 1982).

The Black Mangrove

The black mangrove, *Avicennia germinans*, is a shrub or tree which is distinguished by its horizontal roots which produce numerous rigidly erect blunt branches called pneumatophores that emerge above the soil surface and may extend to 30 cm long (Fig. 7).

The leaves are opposite with a petiole to about 2.5 cm long. There are no stipules associated with the petioles. The leaf blades are entire and usually grayish and hairy beneath. The inflorescence is either in the axil of the leaf or terminal on the twig. The sessile flowers are arranged on an elongated rachis (spike), which ranges to 6 cm long. The fruit usually produces only 1 seed. As in the red mangrove, the black mangrove embryo development is also viviparous.

The White Mangrove

The white mangrove, *Laguncularia racemosa*, is a shrub or tree with opposite leaves (Fig. 8) that have stout red petioles to 2 cm long. The petioles bear a pair of large salt glands near the leaf blade. The blade is entire and the bottom bears minute glands along the periphery. The

Fig. 1.
Red mangrove prop roots advancing into inland lake and forming a tangled network.

Fig. 2. Red mangrove population along the east shore of Pigeon Creek.

Fig. 3. Red mangrove tree with leathery leaves and viviparous fruit (arrow).

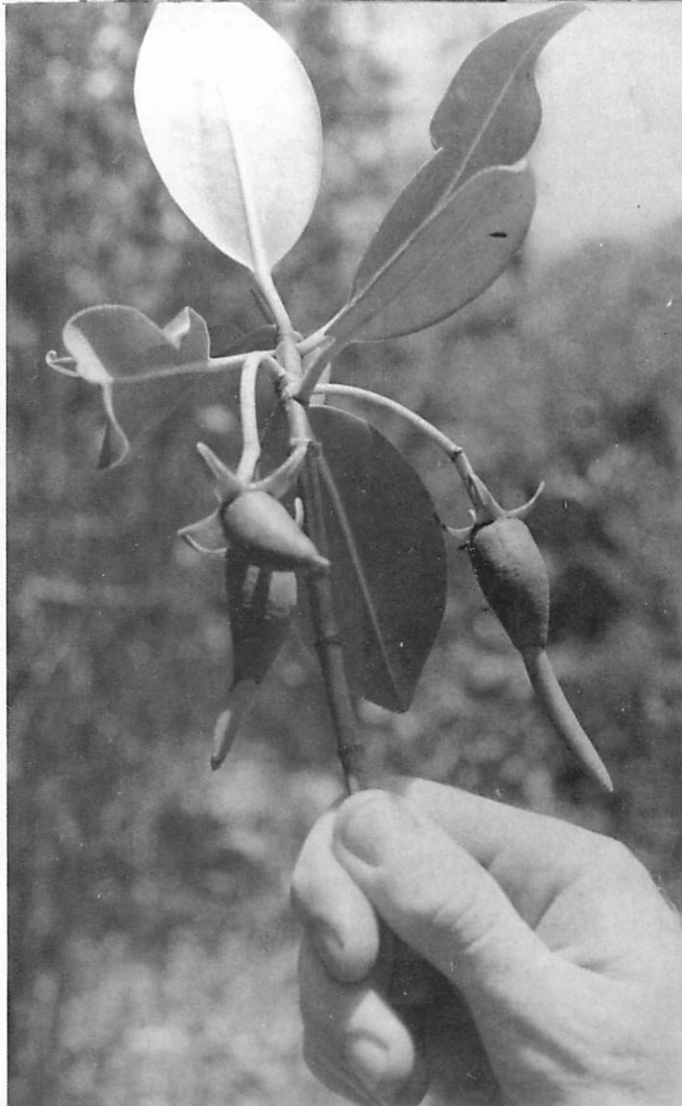

Fig. 4. Close up of red mangrove depicting opposite leaves with stout midribs and viviparous fruit.

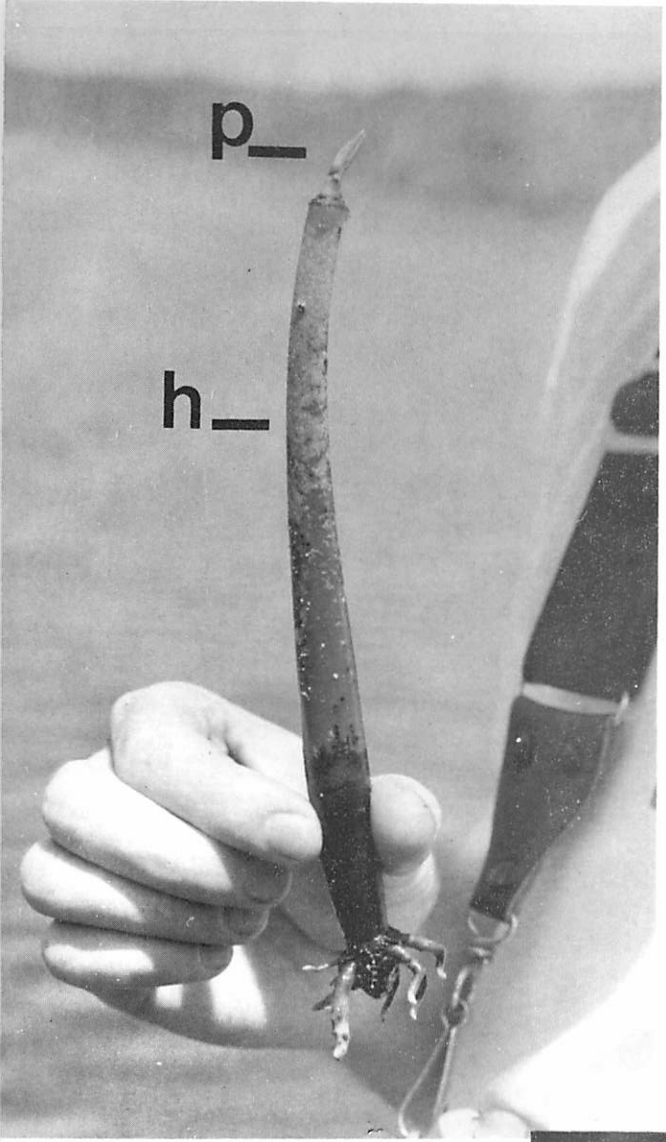

Fig. 5. Seedling of red mangrove showing first seeding leaves called the plumule (p). Note the elongated hypocotyl (h) and the seedling roots protruding from the primary root (radicle).

Fig. 6. Two stages in seedling development of red mangrove, following seedling anchorage in the substrate.

Fig. 7. Habit of black mangrove with large, erect, above ground root branches called pneumatophores.

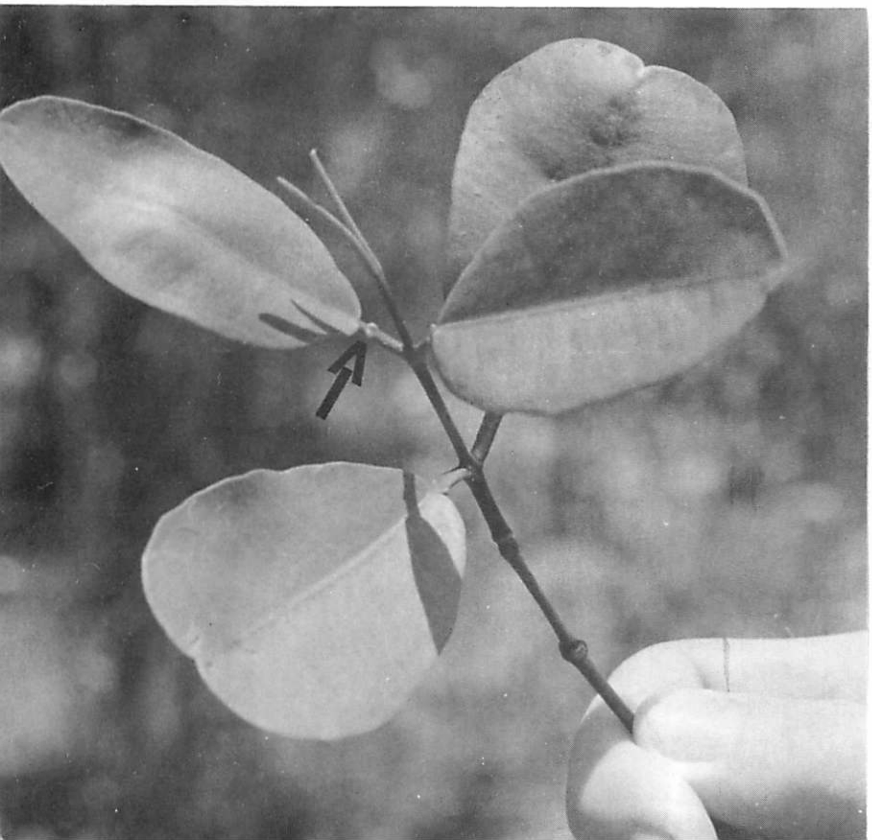

Fig. 8. Twig of white mangrove depicting opposite leaves and large salt glands (arrow) on petiole near leaf blade.

inflorescence is found in the axil of the leaf as a spike 3-6 cm long (Fig. 9). The flowers are sessile on the raceme. The solitary seed is found to germinate within the indehiscent drupe.

The Buttonwood

The buttonwood, *Conocarpus erectus*, is a shrub or tree having alternate leaves with petioles to about 1.5 cm long (Fig. 10). The petioles have 2 salt glands near the base of leathery blade. The flowers are stalked in heads on racemes 3-5 cm long. The fruit is a 2 winged drupe 4-7 mm long.

Plants having usually larger leaves with a soft silky hairy covering have been segregated as var. *sericeus* Griseb.

MANGROVE SUCCESSION

Zonation of species parallel to the shore has been widely identified on mangrove shorelines of the tropics (Chapman 1976). Zonation studies first made on mangroves were interpreted as one species preparing the way for another. The mangrove community, hence, is referred to as a halosere; that is, a series of ecological communities succeeding one another in the biotic development of an area. Typically, mangrove areas have been illustrated to demonstrate zonation as a series of different species from open water landward (Davis 1940). Therefore, zonation on mangrove shorelines has been interpreted to reflect temporal succession of those species.

More recently, however, researchers have theorized that the recognition of zonation need not imply succession of species but may reflect plant response to some factor varying normal to the coast such as salinity or frequency of tidal inundation (Woodroffe 1983).

We observed zonation of the various mangrove trees on San Salvador but, in addition, noted many exceptions to the reported (Davis 1940, Tomlinson 1986) succession patterns. The various mangrove species on San Salvador were observed to grow throughout the normal mangrove tidal range, from the shore of inland lakes or tidal basins landward. For example, at one small inland lake area, designated as Reckley Hill Pond, we observed that not only was red mangrove growing along the shore but also buttowood was found the same distance from the shore line. At Little Lake we observed that black mangrove and buttonwood were growing the same distance from shoreline but were not preceeded by red mangrove shoreward. We also observed this phenomonon with red and black mangrove at upper Pigeon Creek. Tomlinson (1986) confirms this discrepency by his statement that, "Perhaps there is no more confusing or controversial topic in mangrove ecology than succession."

In a study conducted in New Guinea, Johnstone (1983) reported that "many mangrove species can and do grow anywhere in the mangle from the seaward to the landward fringe". He hypothesized that "because of this ability of many mangrove species to grow anywhere within the normal tidal range, zonation can only be due to competition (modified or not by the environment)". Johnstone (1983) also suggested that the succession mechanism is not sequential replacement but competition, modulated by environmental factors such as nutrient pools, organic content of the soil, and temperature range.

Rabinowitz (1978b) studied competition among four mangrove species in the Panama mangrove swamp. By planting seedlings of the different mangrove species in their own zones, as well as in zones of 3 additional species, she found that there was no single habitat in which seedling growth was greater for all mangroves studied. In cases where departures from equal growth occured, mangrove seedlings generally showed superior growth in a foreign habitat over that in their parents' habitat.

In order to test the hypothesis that nutrient pools may or may not affect the ability of one species to compete where another would not, we collected soil samples, along the shoreline and landward, in the areas where red, black, and white mangroves and buttonwood were growing. Using Hach and LaMotte Soil Test Kits and Cornell soil procedures (Greweling and Peech 1965), preliminary analyses were made for two nutrient pools; nitrogen, in the forms of ammonia (NH_3), nitrate (NO_3^-) and nitrite (NO_2^-); and phosporous in the form of phosphate (PO_4^{-3}).

RESULTS

In May of 1986, the first preliminary study of soil nutrients was made on San Salvador Island at two mangrove sites (Table 3). Tests for ammonia, nitrate and phosphate were conducted using a Hach Soil Analysis Kit. The analysis from soil collected at Reckley Hill Pond indicated a possible trend of an increase in ammonia

Fig. 9. White mangrove with spiked influoresence in axil of leaves. Note sessile flowers on raceme.

Fig.10. Buttonwood showing flowers in stalked heads ("buttons").

TABLE 3. SOIL ANALYSES FROM TWO MANGROVE SITES ON SAN SALVADOR ISLAND, BAHAMAS.

COLLECTION SITES	AMMONIA NH_3*	NITRATE NO_3^-*	PHOSPHATE PO_4^{-3}*
RECKLEY HILL POND (5/4/1986)			
ALONG SHORE (red mangrove, buttonwood, sea purslane, salicornia)	345, 260	8	180, 165
ALONG SHORE 25 ft. from water (red mangrove, buttonwood, white mangrove)	445, 375	10	45, 15
LANDWARD -DRY SITE (white mangrove, red mangrove, bay marigold, sandspur)	525, 450	0	135, 180
LITTLE LAKE (5/8/1986)			
UNDER BUTTONWOOD 20 ft. from water	310, 345	10-12	15, 45
UNDER BLACK MANGROVE 35 ft. from water	370, 340	2-5	75, 45

*Analyses done on San Salvador Island immediately after collecting and drying soil, using Hach Soil Test Kits; values in lbs/Acre.

concentration landward. We could not identify any trends in ammonia concentration at the Little Lake sites. At Reckley Hill Pond there appeared to be a decrease in nitrate concentration from the shoreline landward. We could not detect a trend in phosphate concentrations at either site.

In May of 1987, soil samples were taken from Little Lake and Pigeon Creek. Again, using the Hach kit, we tested the soil for ammonia, nitrate, and phosphate (Tables 4 and 5). The Hach analyses for ammonia, at Little Lake (Table 4) were lower in absolute values than the results obtained in the 1986 study (Table 3). We again did not detect any trend in concentration difference from the various collection sites. The results for nitrate do not show any evidence (as indicated previously) for a decrease in concentration from the shoreline landward. The results for phosphate show definite concentration differences, however, no apparent pattern is evident.

At the Pigeon Creek site, definite zonation can be observed for mangrove species. The soil analysis for ammonia (Table 5) indicates a difference in concentration of this nutrient, however, there does not seem to be a trend in concentration from shore to land. The concentration of nitrate (Table 5) appears to be very low and no specific trends were obvious. There appears to be a decrease in phosphate concentration in samples from shoreline toward land (Table 5). We decided to reanalyze the soil using a different test method. Initial reanalysis was done using a La Motte Soil Analysis Kit. With this method we could retest for ammonia and phosphate but not for nitrate. This kit only analyzes for nitrite. We detected few differences, among the samples, using this soil analysis technique (Tables 6 and 7).

We therefore decided to use the Cornell test methods for soil analysis. With this method we retested for all three nutrients previously tested by the Hach method. Results appear in Tables 8 and 9. Although the absolute values differ, when the data for the three separate tests are compared, the lack of great differences from site to site are consistent. There were apparently no general trends, in the concentrations of these nutrients, that could be observed from one location to another.

DISCUSSION

Our preliminary results do not confirm the idea that a succession mechanism is modulated by different concentrations of nutrient pools of ammonia, nitrate, or phosphate. We lean toward

TABLE 4. SOIL ANALYSES FROM LITTLE LAKE SAN SALVADOR ISLAND, BAHAMAS

COLLECTION SITES	AMMONIA NH_3*	NITRATE NO_3^{-}*	PHOSPHATE PO_4^{-3}*
LITTLE LAKE (5/11/1987)			
ALONG SHORE 90 ft. N of pier 3 ft. from water	130, 160	0	80, 30
ALONG SHORE 225 ft. N of pier 9 ft. from water	145, 205	11	30, 23
START OF RED MANGROVE WITH RUSH GRASS 225 ft. N of pier 24 ft. from water	140, 200	14	14, 5
UNDER RED MANGROVE & BUTTONWOOD 150 ft. N of pier 24 ft. from water	130, 210	0	0, 0
RED & BLACK MANGROVE 150 ft. N of pier 24 ft. from water	105, 180	0	10, 0
BLACK MANGROVE TREE LINE 90 ft. N of pier 24 ft. from water	85, 135	18	5, 3
UNDER BLACK MANGROVE 90 ft. N of pier 45 ft. from water	120, 185	0	38, 30

*Analyses done using Hach Soil Test Kits; values in lbs/Acre.

TABLE 5. SOIL ANALYSES FROM PIGEON CREEK, SAN SALVADOR ISLAND, BAHAMAS

COLLECTION SITES	AMMONIA NH_3*	NITRATE NO_3^{-}*	PHOSPHATE PO_4^{-3}*
PIGEON CREEK (5/18/1987)			
SOUTH OF VILLAGE WHERE ROAD IS CLOSE TO SHORE UNDER RED MANGROVES 3 ft. from water	210, 190	0, 0	40
SOUTH OF VILLAGE WHERE ROAD IS CLOSE TO SHORE IN BLACK MANGROVES (REDS END AT 10 ft.) 15 ft. from water	380, 365	20, 17	30, 25
BLACK MANGROVE TREE LINE 25 ft. S of pier 50 ft. from front of Red Mangroves in a clearing with palm trees	165, 300	0, 0	15

*Analyses done using Hach soil Test Kits; values in lbs/Acre.

TABLE 6. SOIL ANALYSES FROM LITTLE LAKE, SAN SALVADOR ISLAND, BAHAMAS

COLLECTION SITES	AMMONIA NH_3*	NITRITE NO_2^{-}*	PHOSPHATE PO_4^{-3}*
LITTLE LAKE (5/11/1987)			
ALONG SHORE 90 ft. N of pier 3 ft. from water	<<10	<2	100-150
ALONG SHORE 225 ft. N of pier 9 ft. from water	<<10	<2	100-150
START OF RED MANGROVE WITH RUSH GRASS 225 ft. N of pier 24 ft. from water	<10	<<2	200
UNDER RED MANGROVE & BUTTONWOOD 150 ft. N of pier 24 ft. from water	<<10	<<2	100-150
RED & BLACK MANGROVE 150 ft. N of pier 24 ft. from water	<10	<<2	100-150
BLACK MANGROVE TREE LINE 90 ft. N of pier 24 ft. from water	<<10	<<2	150-200
UNDER BLACK MANGROVE 90 ft. N of pier 45 ft. from water	<<10	<<2	150-200

*Analyses done using LaMotte Soil Test Kits; values in lbs/Acre.

TABLE 7. SOIL ANALYSES FROM PIGEON CREEK, SAN SALVADOR ISLAND, BAHAMAS

COLLECTION SITES	AMMONIA NH_3*	NITRITE NO_2^{-}*	PHOSPHATE PO_4^{-3}*
PIGEON CREEK (5/18/1987)			
SOUTH OF VILLAGE WHERE ROAD IS CLOSE TO SHORE UNDER RED MANGROVES 3 ft. from water	<10	2	150-200
SOUTH OF VILLAGE WHERE ROAD IS CLOSE TO SHORE IN BLACK MANGROVES (REDS END AT 10 ft.) 15 ft. from water	<10	2	100-150
BLACK MANGROVE TREE LINE 25 ft. S of pier 50 ft. from front of Red Mangroves in a clearing with palm trees	<10	2	200

*Analyses done using LaMotte Soil Test Kits; values in lbs/Acre.

TABLE 8. SOIL ANALYSES FROM LITTLE LAKE, SAN SALVADOR ISLAND, BAHAMAS

COLLECTION SITES	AMMONIA NH_3*	NITRATE NO_3^{-}*	PHOSPHATE PO_4^{-3}*
LITTLE LAKE (5/11/1987)			
ALONG SHORE 90 ft. N of pier 3 ft. from water	50, 36	63, 12	10, 6
ALONG SHORE 225 ft. N of pier 9 ft. from water	60, 42	43, 45	40, 0
START OF RED MANGROVE WITH RUSH GRASS 225 ft. N of pier 24 ft. from water	74, 68	33, 52	35, 4
UNDER RED MANGROVE & BUTTONWOOD 150 ft. N of pier 24 ft. from water	60, 52	25, 12	23, 6
RED & BLACK MANGROVE 150 ft. N of pier 24 ft. from water	60, 54	15, 37	27, 6
BLACK MANGROVE TREE LINE 90 ft. N of pier 24 ft. from water	40, 40	32, 33	21, 0
UNDER BLACK MANGROVE 90 ft. N of pier 45 ft. from water	60, 54	12, 9	45, 0

*Analyses done using Cornell Test Methods; values in lbs/Acre.

TABLE 9. SOIL ANALYSES FROM PIGEON CREEK, SAN SALVADOR ISLAND, BAHAMAS

COLLECTION SITES	AMMONIA NH_3*	NITRATE NO_3^{-}*	PHOSPHATE PO_4^{-3}*
PIGEON CREEK (5/18/1987)			
SOUTH OF VILLAGE WHERE ROAD IS CLOSE TO SHORE UNDER RED MANGROVES 3 ft. from water	114, 58	16, 4	9, 8
SOUTH OF VILLAGE WHERE ROAD IS CLOSE TO SHORE IN BLACK MANGROVES (REDS END AT 10ft.) 15 ft. from water	80, 68	27, 55	7, 6
BLACK MANGROVE TREE LINE 25 ft. S of pier 50 ft. from front of Red Mangroves in a clearing with palm trees	62, 58	20, 20	9, 8

the conclusions of Rabinowitz (1978b) that "physiological differences among species are insufficient to account entirely for the zonation tendencies". In areas where we do observe zonation there is a typical ocean environment where extreme tidal changes occur. If, as is suggested by Lugo and Snedaker (1974), zonation is a "result of all the external sources acting on a locality," then the concentration of soil nutrients may not be considered a factor without examining other external sources such as salinity, temperature, and tidal influence. In addition, the morphology and anatomy of the roots of these various mangrove species may play an important role in their ability to survive in the various habitats. The soil environments of mangrove plants are typically anaerobic due to flooding (Gill and Tomlinson 1975). Therefore, roots growing in such an environment require a ready source of oxygen to allow respiration and nutrient absorption to occur. The aerial roots of the red mangrove have only about 5% gas space before penetration into the soil, compared with 50% gas space after soil penetration (Gill and Tomlinson 1975). In the black mangrove, the length of the aerial roots (pneumatophores) were reported to be in proportion to the depth of flooding (Gill and Tomlinson 1975). In areas of frequent flooding, such as in a tidal basin, these morphological and anatomical features may be a source for the causes of zonation in addition to the factor of dispersal by propagule size as suggested by Rabinowitz (1978a and b). We intend to further this study by investigating salinity and tidal inundation in typical versus atypical zonation areas.

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DEDICATION

This paper is dedicated to the memory of Deborah Rabinowitz, whose committment, open mindedness, and insights into the study of mangrove ecology shall continue to inspire current and future researches in the mangle.

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