

Soil Characteristics and Vegetation Structure in a Heavily Deteriorated Mangrove Forest in the Caribbean Coast of Colombia¹

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ABSTRACT

Mass mortality and biomass of mangrove trees are related to soil factors in the Caribbean Coast of Colombia. Soil properties measured were particle size distribution, bulk density, organic matter, total nitrogen, total phosphorus, pH, redox potential, salinity, and extractable nitrogen (NO_2 , NO_3 , NH_4) and phosphorus (PO_4). Sampling was performed at three locations along two 50 m transects at each site. Soil nutrient concentrations of either exchangeable nitrogen or phosphorus were comparable to other reported values. Redox potentials (E_h) were variable probably due to microtopographic conditions and to the amount of water and organic matter present in the soil. Hydrogen potentials (pH) are within the range reported as normal for mangrove soils. Locations with highest biomass had an average soil salinity of 35 with a range of 20 to 53. Sites with dead or dwarfed vegetation had an average soil salinity of 74 and minimum and maximum values observed were 52 and 100 respectively. Statistical analysis exhibited temporal and spatial differences in soil salinity and suggest that this parameter is most correlated to the development and distribution of mangrove vegetation in the area indicating that basal area and biomass volume are inversely correlated with soil salinity.

Key words: Ciénaga Grande de Santa Marta; Caribbean coast of Colombia; mangrove mortality; soil hypersalinization; vegetation attributes

WORLDWIDE, MASSIVE MANGROVE MORTALITIES HAVE BEEN DOCUMENTED for Gambia, Puerto Rico, Australia, and Colombia with causes ranging from natural (hurricanes, tsunamis, frosts) to man-induced (hydrological regime alterations: diversion of riverine and terrestrial runoff, dredging) (Breen & Hill 1969, Jiménez & Lugo 1985, Jiménez *et al.* 1985, Botero 1990, Smith *et al.* 1994). Cintrón *et al.* (1978) reported rapid increases in mangrove tree mortality beyond a soil salinity threshold of about 65 in Puerto Rico. Massive mortalities due to chronic flooding of mangroves in the Kosi Estuary system and in Puerto Rico have been reported by Breen and Hill (1969) and Jiménez *et al.* (1985).

The region known as Ciénaga Grande de Santa Marta is part of the exterior delta of the Magdalena River and is the largest estuarine lagoonal complex in Colombia. It is located in a very arid zone, with an annual water deficit of 1031 mm/yr because evapotranspiration largely exceeds precipitation (CETIH 1978). The lagoonal complex is surrounded almost entirely by mangrove forests which covered 52,000 ha until approximately 1960 (González 1989) (Fig.

1). At this time, the mangrove started to die massively as a consequence of man-induced alterations in riverine and marine exchange of water in the system. A road, constructed in 1956, interrupted all natural connections between the lagoon and the sea except the Boca de la Barra. Since approximately 1975 the canals that brought fresh water from the Magdalena River into the system started to be diked. Recently, five artificial and indirect connections (box culverts) have been constructed to re-establish, at least partially, some connection with the ocean. Fresh water is received only in the eastern flank of the system, from rivers flowing from the Sierra Nevada de Santa Marta which is the highest coastal mountain in the world (5800 m elev.).

Aerophotographic records of the area (González 1988) show that mangrove mortality by 1987 had affected approximately 16,460 ha, 30 percent of the total forested wetland area. The rate of mangrove loss increased substantially from 174.5 ha/yr between 1956 and 1968, to 826.5 ha between 1968 and 1987. A recent (1993) SPOT 3 satellite image of the area shows 21,778 ha of dead mangrove, meaning that in 6 years mangrove mortality increased to 886 ha/yr or 2.4 ha/d (Fig. 2). The most pronounced recent mortality has occurred

¹ Received 7 January 1996; revision accepted 18 September 1996.

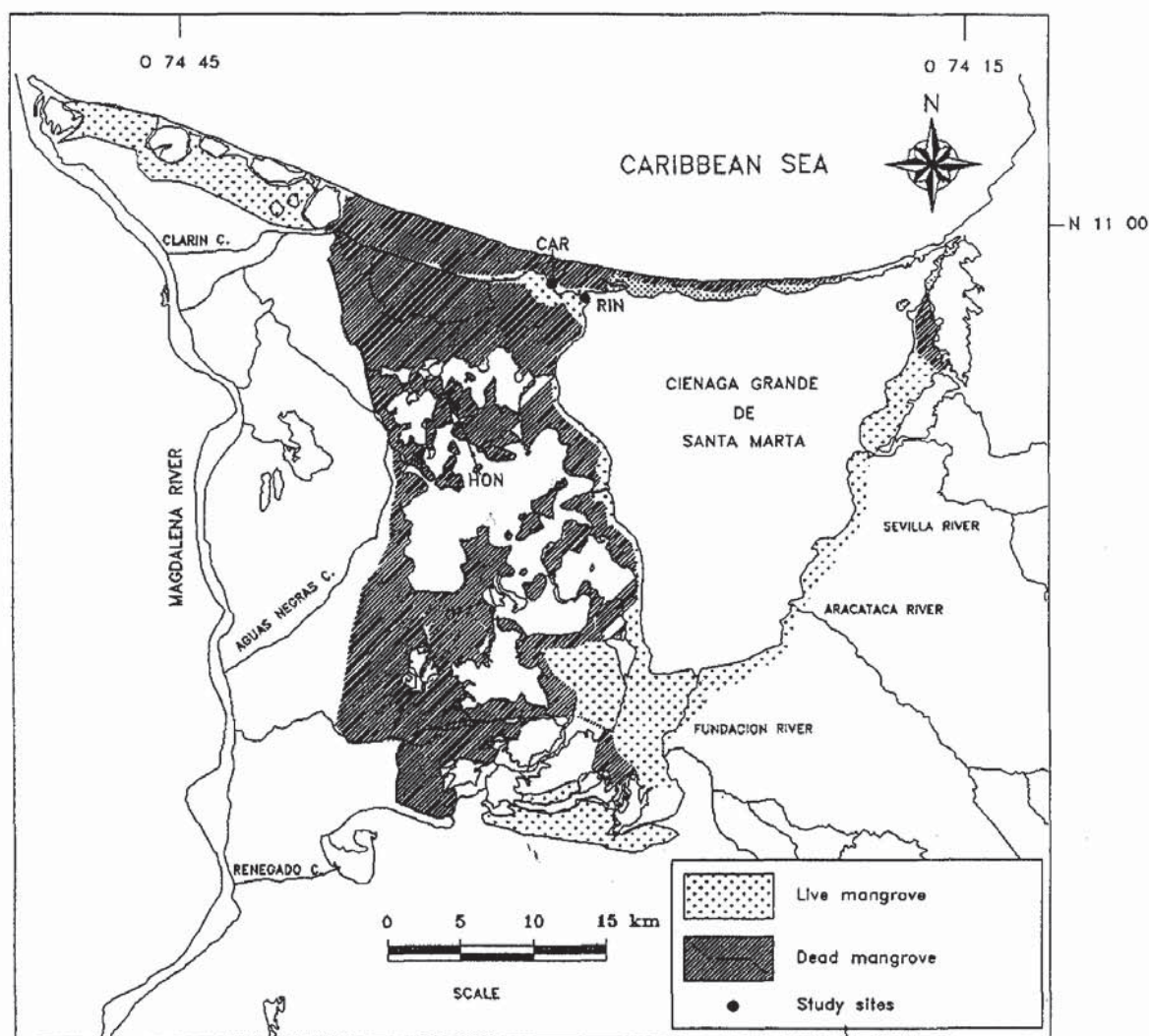


FIGURE 1. Ciénaga Grande de Santa Marta region indicating dead and alive mangrove zones as well as location of study sites, Rinconada (RIN), Carevaca (CAR), and Caño Hondo (HON).

mainly in the western and south-western part of the system (Fig. 1).

There are many factors that control the productivity, structure, and mortality patterns of mangroves, including climate, geomorphology, tidal range, freshwater input, intensity and frequency of runoff and flushing, and soil or substrate characteristics (Boto & Wellington 1984, Jiménez & Lugo 1985, Twilley 1988). Preliminary fieldwork and observations in the area lead us to hypothesize that soil hypersalinization is strongly correlated with the massive mangrove die-off (Sánchez 1988, Botero & Botero 1989, Botero 1990). However, the decreased exchange of fresh and sea water in the system may change other soil factors such as nutrients, redox potentials, pH, and organic matter content that are equally important for mangrove

growth (Boto 1982, Hutchings & Saenger 1987). The absence of extended periods of flooding, owing to the interruption of the communications with the Magdalena River and to the arid conditions of the area, preclude us from considering this, as a possible cause for the die-off. We present an analysis of some of the main edaphic factors of mangrove swamps, to determine, preliminarily, if other factors besides salinity, could be also correlated to the catastrophic die-off and lack of regeneration of mangrove vegetation in this tropical lagoon/delta complex. We did not measure sulfide concentrations in the mangrove soils owing to logistical constraints. However, no strong sulfide odor was apparent in either our study sites or in other sites of the area that we have visited periodically for a 5–6 year period.

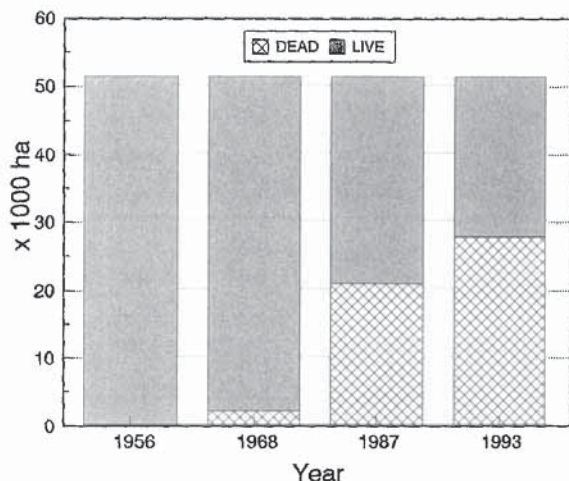


FIGURE 2. Dead and live mangrove coverage in the region of Ciénaga Grande de Santa Marta as determined from aerophotographic and SPOT 3 satellite images (taken from M. Hubele, PROCINAGA, unpublished report on the analysis of a SPOT 3 Satellite image of the Ciénaga Grande de Santa Marta).

MATERIALS AND METHODS

STUDY SITES.—Based on preliminary field observations and on the apparent condition of the mangrove vegetation, three sampling stations were selected in which soil variables were analyzed and vegetation structure studied from May 1990 to February 1991. Site RIN represents live and apparently healthy mangroves, *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* in relatively good condition. According to Lugo and Snedaker's (1974) physiographic classification of mangroves, this forest belongs to a basin type. The forest floor, with an uneven topography and small, permanent pools, is densely covered with pneumatophores. A conspicuous water flow between the lagoon and the forest floor was observed during the major rainy season and high tide. Site HON represents an almost completely dead mangrove stand with a narrow belt of live *R. mangle* and *A. germinans* fringing the creek. Here, the forest floor is soft and organic with a low topographic level that allows frequent water exchange with the creek. According to Lugo and Snedaker's (1974) classification, this site is a basin forest. Site CAR represents a dead mangrove stand (basin type) with a narrow belt of poorly developed trees of *A. germinans* fringing the channel or creek, followed by a sand flat with dead trees. More inland, there are sparse shrubs of *A. germinans* with diameters at breast height (DBH) smaller than 2.5 cm. The topographic level at the creek's edge is about 25 cm

above mean tide level and acts as a barrier to water flow between the creek and the forest floor.

SOIL CHARACTERISTICS.—Two 50 m transects 10 m apart and perpendicular to the lagoon or creek edge were established at each site. Sampling points were marked at 10 m intervals along the transects. For determinations of total organic carbon, total nitrogen and phosphorus, grain size and bulk density, surface (0–20 cm) soil samples were taken only once, at the beginning of the study. Organic matter content was determined by oven-drying the samples to constant weight and later ashing at 550°C for 24 h. Bulk density was determined from the volume of water displaced by a sample of wet soil according to Allen *et al.* (1974) and expressed as weight of dry soil per volume. Grain size, total nitrogen and total phosphorus were analyzed by wet sieving, Kjeldahl and P_2O_5 in ashes according to Baver (1956), Bremner (1965), and Jackson (1958), respectively. Other soil variables including pH, redox potential, and extractable nitrates, nitrites, ammonium, and phosphates were measured during three different climatic seasons: (1) Long dry from December to April (LD); (2) long rainy from October to November (LR); (3) short dry from July to August (SD). Samples were collected at 5 cm and 40 cm at the ten points of each site. Soil cores of approximately 5.5 cm in diameter and 60 cm long were sampled and analyzed for extracted nutrients and redox potentials (measured directly by insertion of a combined Schott Gerate Pt/SCE electrode). pH was measured in the field with a glass electrode of a Schott Gerate pH meter inserted into the pore water collected in holes dug adjacent to the sampling points. Soil subsamples for nutrient analysis were taken from the core and placed in 25 ml plastic vials which were sealed and refrigerated. In the laboratory, nutrients were extracted from the soil following the methods of Boto and Wellington (1984) and analyzed according to standard colorimetric methods (APHA, 1975). For seasonal soil salinity measurements, a WTW conductivity meter electrode was introduced into the pore water collected in holes dug adjacent to the soil sampling points. Conductivity readings were expressed in the Practical Salinity Scale according to Unesco (1985).

VEGETATION ATTRIBUTES.—To quantify forest structure and biomass, five 100 m² plots were located along both transects adding up a total of 1000 m²/site. Soil was sampled in the center of each 100 m². In each plot, tree height and DBH were re-

corded for all the trees with DBH equal to or larger than 2.5 cm. Tree height was measured with a RANGING 120 optimizer and DBH with a diameter tape. These measurements were used to calculate basal area and absolute density according to Schaeffer-Novelli and Cintron (1986) for each station. The volume of the live mangrove biomass was estimated by multiplying basal area times tree height and adding the individual tree volumes of each plot.

Vegetation variables and those soil variables measured only once during the study period were analyzed with a one-way ANOVA when assumptions were met, and with non-parametric methods when, after transformations, they were not. With soil variables measured during the three climatic seasons, a repeated-measures analysis of variance was performed, following Moser *et al.* (1990) and Gurevitch and Chester (1986), using seasons as the factor of repeated measures and testing differences among sites with the sums of the values of the three seasons obtained for each point.

Simple soil-vegetation correlations were calculated using the vegetation value from each of the 30 plots (10 from each site) and the value for each soil variable in the respective point (located within the plot); for those variables assessed during the three climatic seasons the data were averaged for each point.

RESULTS

SOIL TEXTURE AND CLASSIFICATION.—The soils of sites 1 (RIN) and 3 (CAR) are made up of fine mineral silts down to about 60 cm depth and contain large quantities of root material. Owing to their mineral content (between 3–38%) and to the flooding conditions they are subjected to, they are classified as Fluvaquents. The soils of site 2 (HON) are mainly organic (46–70% organic matter) with 94 percent of particles > 0.062 mm made up mostly of fine roots or root particles. They are classified as Histosols, specifically Tropofibrists.

SOIL BULK DENSITY.—Bulk density of the top 40 cm sections of soil was similar in sites RIN and CAR (Table 1). Bulk density at these two sites was significantly higher than in site 2 (HON) which was only 0.176 g/cm³ (Table 1), owing to the high organic matter content of the soil at this site.

SOIL pH.—In general, average soil pH was slightly acid (6.53) ranging from 5.8 to 6.85 (Fig. 3). Average pH was highest in HON for the three cli-

TABLE 1. Basic soil properties measured in May 1990. Values followed by different letters within the same column are significantly different ($P < 0.05$). Paired comparisons: Tukey for bulk density (BD), organic matter (OM) and total nitrogen (N_t), Mann-Whitney for total phosphorus (P_t). In parentheses ± 1 SE.

Variable Site	BD g/cm ³	OM percent	N_t percent	P_t percent
RIN	0.742a (0.071)	14.26b (2.74)	0.37b (0.05)	0.15a (0.01)
CAR	0.742a (0.072)	16.42b (2.12)	0.41b (0.04)	0.09b (0.01)
HON	0.176b (0.014)	57.05a (1.54)	1.25a (0.05)	0.12b (0.02)

matic seasons (Fig. 3). No correlation was found between pH and forest live basal area.

SOIL REDOX POTENTIAL (E_h).—Average E_h values were relatively low (between 175 and –150 mV) for all sites and seasons, but not all soils were reduced at all times (Fig. 3). Mean values lower than –60 mV were observed only during the rainy season in HON. Significantly lower E_h values were found in HON while CAR and RIN did not show significant differences between them. There was no correlation between E_h and forest live basal area.

SOIL SALINITY.—Salinities ranged from 19.8–53.5 at RIN, 40.2–103 at CAR, and 34.4–93.1 at HON (Fig. 4). There were significant differences among sites ($F = 136.38$, $P < 0.0001$). Highest salinities at all sites occurred during the long dry season and lowest values during the long rainy season. Salinity was inversely correlated with forest live basal area ($r = -0.79$, $N = 27$, $P < 0.001$). Total mangrove biomass volume and average salinity per site are presented in Fig. 5 and show a decrease in biomass with increasing soil salinity. Figure 6 shows soil salinity data obtained during the two years prior to this study (1988–1990) at RIN and CAR. In CAR (dead mangrove site) average soil salinity was 90 and was higher than 100 for seven months of the year. The live mangrove site (RIN) showed an average soil salinity of 35 and values were never higher than 50.

AMMONIUM.—Pore water concentrations of ammonium varied from 0.26–14.56 $\mu\text{g}/\text{cm}^3$ at HON, 0.62–21.83 $\mu\text{g}/\text{cm}^3$ at CAR and 0.91–25.17 $\mu\text{g}/\text{cm}^3$ at RIN (Fig. 7). Highest average concentrations were found in CAR and lowest in HON ($F = 20.50$ $P < 0.0001$) and differences between RIN and HON were not significant (Tu-

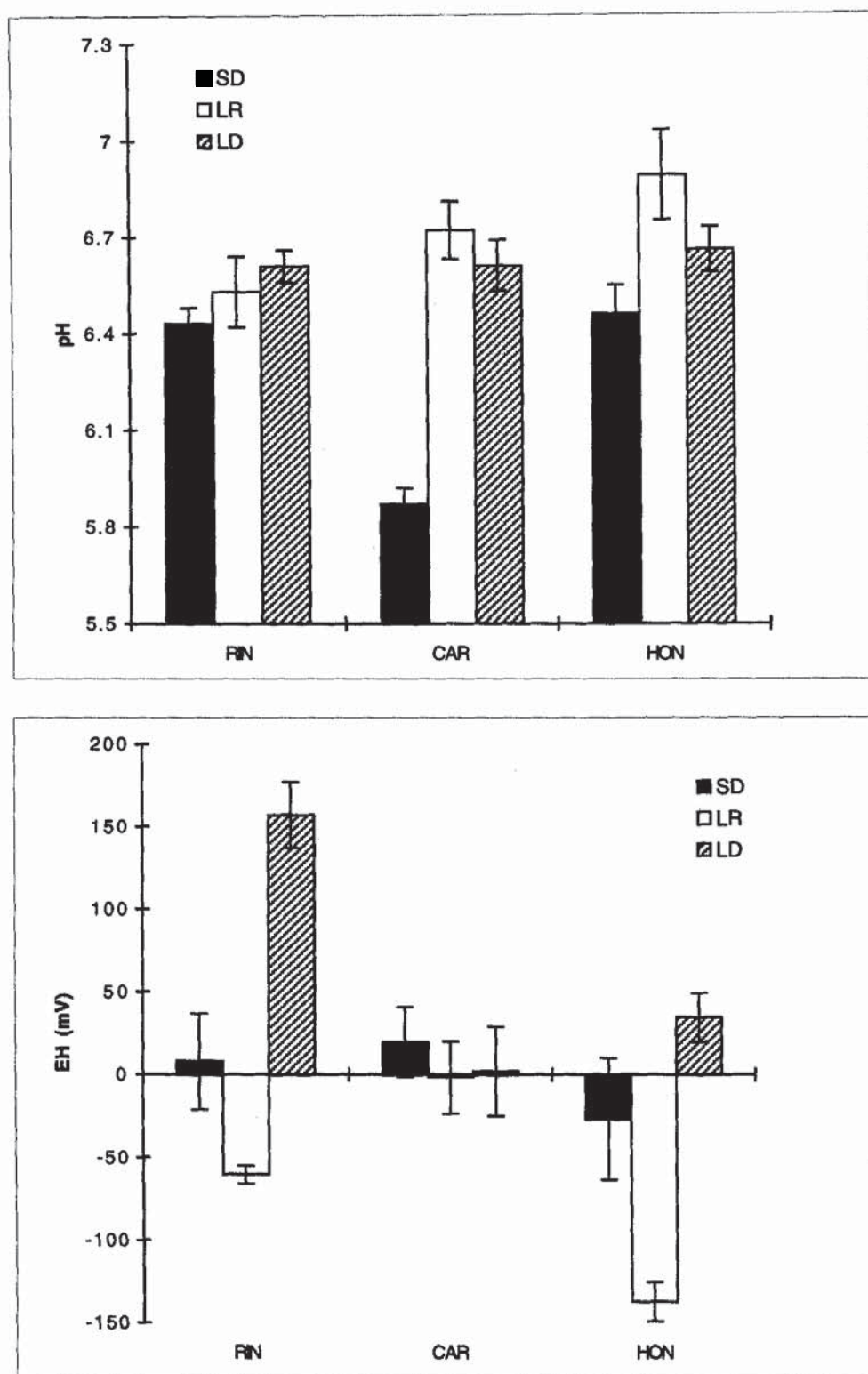


FIGURE 3. Average values of soil pH and E_h at the study sites RIN, CAR and HON during the three different climatic seasons long dry (LD), short dry (SD), and long rainy (LR). Bars represent standard errors.

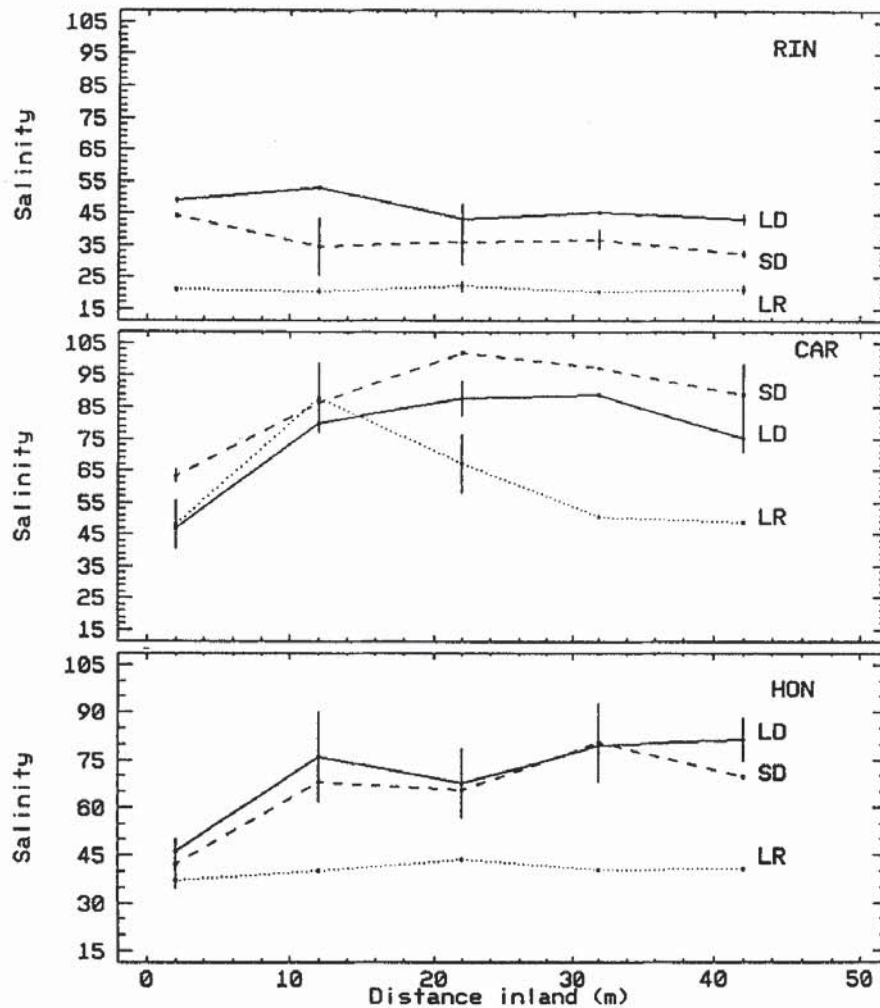


FIGURE 4. Soil salinity profiles of each study site during the three climatic seasons, long dry (LD), short dry (SD), and long rainy (LR).

key Test $P > 0.05$). Ammonium concentrations did not show any significant correlation with forest live basal area.

NITRATES PLUS NITRITES.—Concentrations of these nutrients were extremely low in all three sites varying from 0.03–11.36 $\mu\text{g}/\text{cm}^3$ at RIN, 0.07–8.26 $\mu\text{g}/\text{cm}^3$ at CAR, and 0.05–5.23 $\mu\text{g}/\text{cm}^3$ at HON (Fig. 7). As with ammonium, highest average concentrations were found in CAR and lowest in HON and differences between RIN and HON were not significant. No correlation was found between these forms of inorganic nitrogen and forest live basal area.

PHOSPHATE.—Concentration of this nutrient varied from 0.40–80.50 $\mu\text{g}/\text{cm}^3$ at RIN, 0.05–37.41 $\mu\text{g}/\text{cm}^3$ at CAR, and 0.69–10.79 $\mu\text{g}/\text{cm}^3$ at HON (Fig. 7). Highest average concentrations were

found in RIN and these were significantly different (Tukey Test, $P < 0.05$) from those at CAR and HON. No significant relation was found between this inorganic nutrient and forest live basal area.

TOTAL NITROGEN (N_t) AND PHOSPHORUS (P_t).—Site 1 (RIN) had the highest concentration of P_t (0.15% of dry weight) and lowest N_t (0.37% of dry weight) while site 3 (CAR) had the lowest P_t (0.09% dry weight) and site 2 (HON) the highest N_t (1.25% dry weight) (Table 1). A significant correlation was found between P_t and forest live basal area ($r = 0.63$, $N = 29$, $P < 0.01$), but no correlation was found between N_t and forest live basal area.

In summary, soils of RIN had the finest texture, lowest organic matter content, highest E_h , lowest salinities, and highest phosphorus concen-

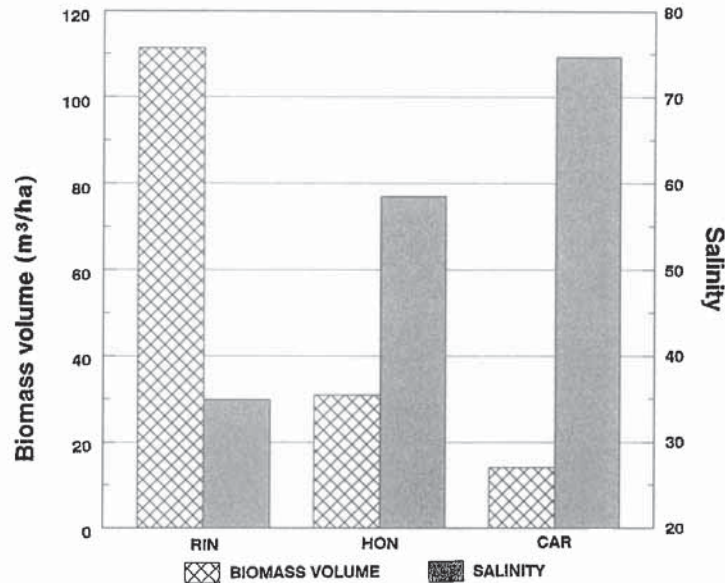


FIGURE 5. Total mangrove biomass volume and average soil salinity at the study sites RIN, CAR, and HON.

trations, both exchangeable and total. Nitrogen concentrations, both extractable and total, were lower than in CAR and not significantly different from those found at HON. CAR soils had significantly lower phosphate and total phosphorus concentrations than RIN and the highest soil salinities. HON soils are mainly organic and had the highest total nitrogen concentrations, lowest E_h , and intermediate salinity values.

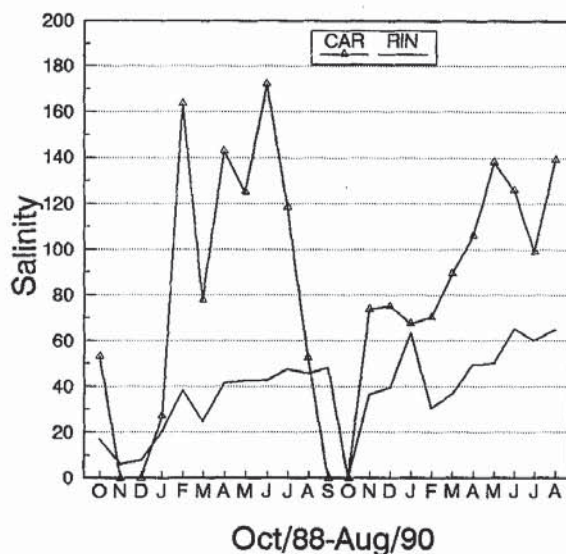


FIGURE 6. Average monthly soil salinity at study sites RIN and CAR during the period October 1988–August 1990.

VEGETATION ATTRIBUTES.—Table 2 presents the vegetation attributes of the three stations studied and the significance of the differences among stations. Site 1 (RIN) had the highest forest biomass volume (111.3 m³/ha), basal area (12.1 m²/ha), density (1810 trees/ha), and Holdridge's complexity index (CI, 4.16). Sites HON and CAR had vegetation only in the fringe (5–10 m) of the creek with basal areas of 2.4 and 2.9 m²/ha, biomass volume of 30.9 and 14.0 m³/ha, and tree densities of 400 and 340 trees/ha, respectively. Although site 2 (HON) had more vigorous trees than site 3 (CAR), there is no vegetation nor apparent regeneration in the inland areas of the forest as observed at CAR. However, DBH measurements of dead trees show values as high as 62.2 cm at CAR and 34.5 cm at HON. Correlation analysis between soil factors and certain vegetation attributes in our study area indicate that basal area and biomass volume are directly correlated to total phosphorus concentrations and inversely correlated with soil salinity.

DISCUSSION

Mangrove trees are found on a wide variety of substrates including mud, silt, peat, sand, and even rock and coral shingle provided there are sufficient crevices for root attachment. However according to Butler *et al.* (1977) and Galloway (1982), mangrove ecosystems appear to be well developed only on muds and fine-grained sand. Our study sites have soils mainly with a fine mineral silt compo-

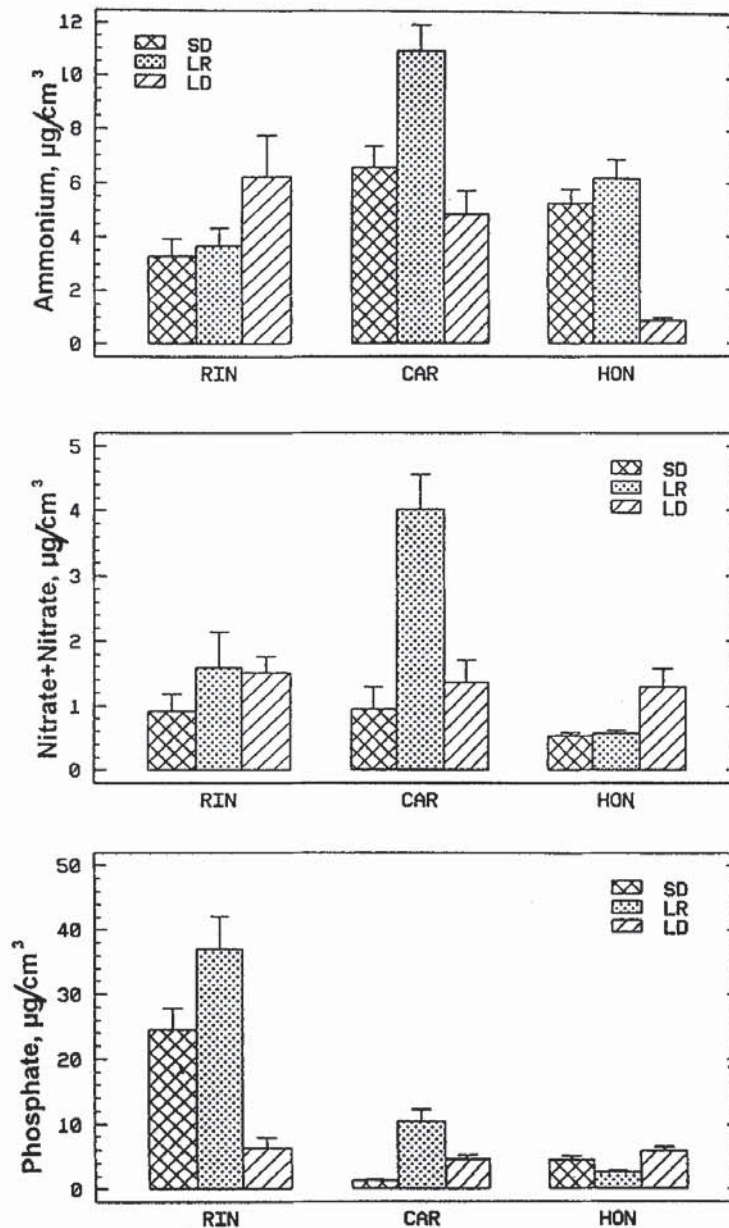


FIGURE 7. Average values of soil available nutrients at the different study sites during the three climatic seasons, long dry (LD), short dry (SD), and long rainy (LR). Bars represent standard errors.

sition except for HON where organic matter in the form of peat is predominant. This formation of peat may be a consequence of slow decomposition processes and of accumulation due to reduced water exchange. This large organic matter content probably influences other soil factors such as pH, redox potential, nutrient concentration, and water retention (Neue 1985).

Water dynamics between the forest floor and the creeks, together with microtopographic differences in the forest floor and with the vegetation

itself, influence the nutritional status, salinity, pH, redox potential, and other sediment characteristics (Thom 1967). In RIN, a lower topographic level favors the almost permanent exchange of water from the lagoon to the forest floor resulting in lower salinity values and higher phosphate concentrations.

Extreme climatic conditions of the study area are responsible for the occurrence of significant interactions between climatic season and sampling sites for all physico-chemical parameters measured

TABLE 2. *Mangrove attributes at the three study sites. Values followed by different letters within the same row are significantly different (Tukey test for basal area, biomass volume, diameter breast height (DBH), Mann-Whitney test for density). In parentheses ± 1 SE.*

Site Variable	RIN	CAR	HON
Basal area (m ² /ha)	12.08a (2.23)	2.16b (1.48)	2.93b (2.10)
Biomass volume (m ³ /ha)	113.30a (23.72)	14.02b (8.43)	30.29b (26.98)
DBH (cm)	7.39a (0.42)	7.84a (0.77)	7.58a (0.96)
Height (m)	7.91a (0.96)	5.53b (0.30)	6.03b (0.48)
Density (trees/ha)	1810a (273)	340b (227)	400b (246)

in the mangrove soils. The hydrological, geomorphological, and microclimatic characteristics of each sampling site determined differential effects on the soils of the area.

A comparison with E_h values measured in other healthy mangrove soils (Boto & Wellington 1984) indicates that this parameter is not limiting vegetation regrowth in our study area or causing the massive die-off. Values at some of our dead study sites are higher than in the mangrove soils with live trees probably due to the fact that the soils are poorly flooded and remain dry most of the year.

Soil pH values in the study area are within the range considered normal (Pannier & Pannier 1974) for mangrove soils. Therefore it is unlikely that this factor is affecting negatively the mangrove vegetation of the area.

Even though the soils of the three study sites showed differences in their nutritional status, there does not seem to be a nitrogen deficiency in any of the sites. Extractable nitrogen was virtually all in the ammonium form and this is consistent with the relatively low E_h values found. Lowest values of total nitrogen were measured in RIN, which is the site that showed the best vegetational state. Inorganic nitrogen concentrations for mangrove soils of our study sites are well within the range of values reported for healthy mangroves (Heese 1961, Boto 1983, Boto & Wellington 1984, Boon & Cain 1988). Highest concentrations of ammonium, and nitrate plus nitrite in CAR, could be an indication of high decomposition and mineralization rates of the large amount of dead organic matter and of low assimilation due to the fact that most of the vegetation is dead. Accordingly, the lower concen-

trations of inorganic nitrogen in RIN could be due to assimilation processes of the live vegetation at this site. Boto and Wellington (1984) indicated that ammonium depletion in mangrove soils accompanied an increase in tree growth. Low redox potentials in HON could be inhibiting decomposition and mineralization processes, to some point, and thus explain the low ammonium and nitrates plus nitrite concentrations found in spite of the large amount of dead organic matter present.

Inorganic phosphorus and total phosphorus availability does not seem to be limited in RIN, being higher than in other mangrove soils (Boto 1983, Boto & Wellington 1984). Even though statistical analysis did not show a significant correlation between inorganic phosphorus and live basal area, there does seem to be a deficiency of this nutrient in CAR and HON where vegetation development is poor. Phosphate levels are known to depend mostly on riverine sources (Spencer 1956, Boto 1982) and these two sites are rather isolated from these, CAR owing to its high topographic level and HON to its geographic location. On the other hand, phosphate levels did show some relationship, although not statistically significant, with live basal area of the mangrove vegetation (Fig. 8).

In an arid climate such as the one of the study area, mangrove ecosystems depend largely on riverine and tidal flows for the maintenance of adequate soil conditions. Alteration or interruption of these natural floods will most likely result in a deterioration of the mangrove vegetation. Field observations of dead mangrove trees over 10 m in height and with DBH as high as 62.2 cm suggest that with predisturbance environmental conditions forests in the area were well developed. The most vigorous live mangrove trees (as defined by larger DBH, taller trees and thus greater aerial biomass and live basal area) were found in places with lower salinities and higher phosphate concentrations (Figs. 5, 8) that is in RIN and along the edges of creeks. In CAR and HON, the increase in salinity gradient was accompanied by a drastic reduction of vegetation biomass (Fig. 5). Since HON shows lower salinity values than CAR but its vegetation is in a worse state, it could be hypothesized that a combination of effects resulting from hypersalinity, low redox potentials, and low phosphorus levels, both exchangeable and total, is responsible for the state of these mangroves. Similar observations, regarding salinity gradients and vegetation structure in arid climates have been made by Pool *et al.* (1977), Cintrón *et al.* (1978, 1980), and Soto and Jiménez (1982).

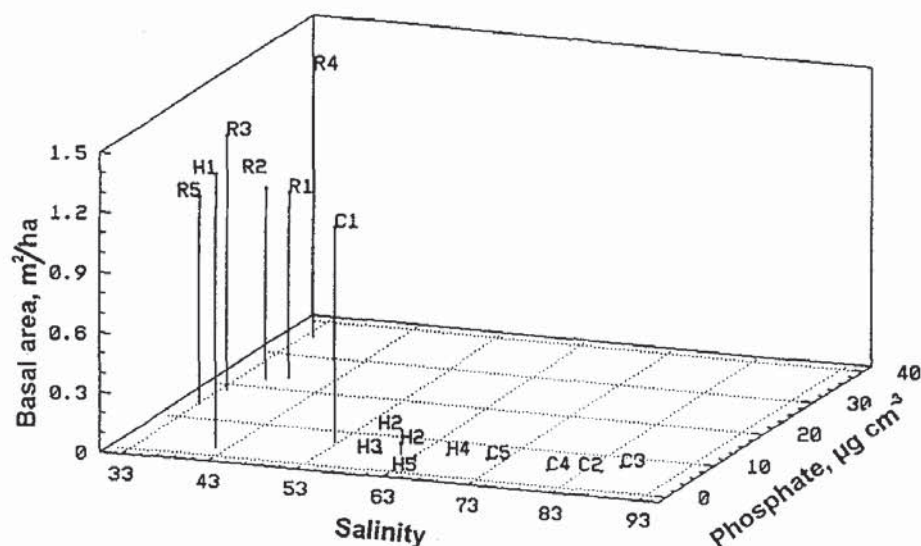


FIGURE 8. Live basal area at the sampling plots as related to soil salinity and phosphate concentration.

Brown (1981) found that the increases in primary productivity from scrub to riverine freshwater forested wetlands was explained by the increasing phosphorus inflows to the forest. In mangrove forests any relationship between indices of community structure and phosphorus soil concentration must take into account salinity and its effect on vegetation structure. Fig. 8 shows how both factors are influencing mangrove basal areas in our study area.

Clearly, the extreme hypersaline conditions found in HON and CAR cannot support the growth of mangrove species, not even *Avicennia germinans*. Since the mangrove die-off started almost twenty years ago, we cannot say for sure that the present soil conditions are equal to those that originated the die-off. However, since the die-off still continues, especially towards the southwestern

section of the region as riverine water flows are further interrupted, we can assume with a reasonable certainty that what started 20 years ago is a similar process to the one occurring presently. Qualitative observations by the authors for more than eight years indicate that when high precipitation levels occur (every 5–7 yr), soil salinity decreases and new mangrove seedlings appear. When dry conditions return, salinities increase again and most of the settled seedlings die.

In conclusion, the analysis of edaphic factors in our study area, of their relationship to vegetation structure and a comparison with the few historical data available on soil salinity, points to the fact that the extreme high salinity of the soil is the environmental factor most strongly correlated with the present state of deterioration of the mangrove forest in the area.

LITERATURE CITED

- ALLEN, S. E., H. M. GRIMSHAW, J. A. PARKINSON AND C. QUARMBY. 1974. Chemical analysis of ecological materials. First edition. Blackwell Scientific Publications, Oxford, England, 368 pp.
- APHA. 1975. Standard methods for examination of water and waste water. 14th Edition. American Public Health Association, American Water Works Association, Water Pollution Control Federation, Washington, D.C. 1193 pp.
- BAVER, L. D. 1956. Soil physics. Third edition, John Wiley & Sons, New York, New York.
- BOON, P. I. AND S. CAIN. 1988. Nitrogen cycling in salt marsh and mangrove sediments at Western Port, Victoria, Australia. *Aust. J. Mar. Freshwat. Res.* 39: 607–623.
- BOTERO, J. E. Y L. BOTERO. 1989. Problemática del sistema Ciénaga Grande de Santa Marta. En: Colombia y el agua: tres aspectos. Bogotá. *Fescol* 5: 11–28.
- BOTERO, L. 1990. Massive mangrove mortality on the Caribbean Coast of Colombia. *Vida Silvestre Neotropical* 2(2): 77–78.
- BOTO, K. G. 1982. Nutrient and organic fluxes in mangroves. In B. F. Clough (Ed.), *Mangrove ecosystems in*

- Australia—structure, function and management, pp. 239–259. Proc. Aust. Nat. mangrove workshop AIMS. AIMS with ANU Press, Canberra, Australia.
- . 1983. Nutrient status and other soil factors affecting mangrove productivity in north-east Australia. *Wetlands (Australia)* 3: 45–50.
- , AND J. T. WELLINGTON. 1984. Soil characteristics and nutrient status in a northern Australian mangrove forest. *Estuaries* 7(1): 61–69.
- BREEN, C. M. AND B. J. HILL. 1969. A mass mortality of mangroves in the Kosi Estuary. *Trans. Roy. Soc. S. Afr.* 38(3): 285–303.
- BREMNER, J. M. 1965. Methods of soil analysis. In C. A. Black (Ed.). American Society of Agronomy, Madison, Wisconsin.
- BROWN, S. 1981. A comparison of the structure, primary productivity and transpiration of cypress ecosystems in Florida. *Ecol. Monogr.* 51: 403–427.
- BUTLER, A. J., A. M. DEPER, S. C. MCKILLUP AND D. P. THOMAS. 1977. Distribution and sediments of mangrove forests in South Australia. *Trans. Roy. Soc. S. Aust.* 101: 35–44.
- CETIH. 1978. Diagnóstico sobre el comportamiento hídrico de la Ciénaga Grande de Santa Marta. Informe final. Universidad de los Andes-INDERENA, Bogotá, Colombia.
- CINTRÓN, G., A. E. LUGO, D. J. POOL AND G. MORRIS. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10(2): 110–121.
- , C. GOENAGA, Y J. GONZÁLEZ-LIBOY. 1980. Ecología del manglar en una zona árida: exposición al oleaje y estructura del manglar. *Boletín Instituto Oceanográfico de São Paulo* 29(2): 113–127.
- GALLOWAY, R. W. 1982. Distribution and physiographic patterns of Australian mangroves. In B. F. Clough (Ed.). *Mangrove ecosystems in Australia—structure, function and management*, pp. 31–54. Proc. Aust. Nat. Mangrove workshop AIMS. AIMS with ANU Press, Canberra, Australia.
- GONZÁLEZ, E. 1989. Cambios ocurridos en la cobertura del manglar de la Ciénaga Grande de Santa Marta durante los años 1956 a 1987. Informe presentado a COLCIENCIAS-INVEMAR, 25 pp.
- GUREVITCH, J., AND S. T. CHESTER, JR. 1986. Analysis of repeated measures experiments. *Ecology* 67(1): 251–255.
- HESSE, P. R. 1961. Decomposition of organic matter in a mangrove swamp soil. *Plant Soil* 14: 249–263.
- HUTCHINGS, P. AND P. SAENDER. 1987. *Ecology of mangroves*. University of Queensland Press, London, Brisbane, Australia.
- JACKSON, M. L. 1958. *Soil chemical analysis*. Prentice Hall, Englewood Cliffs, New Jersey.
- JIMÉNEZ, J. A. AND A. LUGO. 1985. Tree mortality in mangrove forests. *Biotropica* 17(3): 177–185.
- , R. MARTÍNEZ AND L. ENCARNACIÓN. 1985. Massive tree mortality in a Puerto Rican mangrove forest. *Caribb. J. Sci.* 21(1–2): 75–78.
- LUGO, A. E., AND S. C. SNEDAKER. 1974. The ecology of mangroves. *Annu. Rev. Ecol. Syst.* 5:39–63.
- MOSER, E. B., A. M. SAKTON AND S. R. PEKESHI. 1990. Repeated measures analysis of variance: application to tree research. *Can. J. For. Res.* 20: 524–535.
- NEUE, H. U. 1985. Organic matter dynamics in wetland soils. In (Ed.). *Wetland soils: characterization, classification and utilization*, pp. 109–122. International Rice Research Institute, Los Baños, Laguna, Philippines.
- PANNIER, F. Y R. F. PANNIER. 1974. *Manglares: Un enfoque ecofisiológico*. Anales Instituto de Biología de México Serie Botánica 45: 51–57.
- POOL, J. D., S. C. SNEDAKER AND A. E. LUGO. 1977. Structure of mangrove forests in Florida, Puerto Rico, México and Costa Rica. *Biotropica* 9(3): 195–212.
- SÁNCHEZ, P. H. 1988. Hacia la salvación del Parque Nacional Isla de Salamanca. *Trianea (Acta Científica Técnica, INDERENA)* 2: 505–527.
- SCHAEFFER-NOVELLI, Y. Y G. CINTRÓN. 1986. *Guía para estudio de áreas de manguezal*. Caribbean ecological research. São Paulo, Brazil. 150 pp.
- SMITH III, T. J., M. B. ROBBLEE, H. R. WANLESS, AND T. W. DOYLE. 1994. Mangroves, hurricanes and lightning strikes. *Bioscience* 44(4): 256–262.
- SOTO, R. Y J. JIMÉNEZ. 1982. Análisis fisonómico estructural del manglar de Puerto Soley, La Cruz, Guanacaste, Costa Rica. *Rev. Biol. Trop.* 30(2): 161–168.
- SPENCER, R. 1956. Studies in Australian estuarine hydrology. II. The Swan River. *Aust. J. Mar. Freshwat. Res.* 7: 193–253.
- THOM, B. C. 1967. Mangrove ecology and deltaic geomorphology: Tabasco, México. *J. Ecol.* 55: 301–343.
- TWILLEY, R. 1988. Coupling of mangroves to the productivity of estuarine and coastal waters. In B. O. Jansson (Ed.). *Coastal-offshore ecosystem interactions*, pp. 155–180. Springer-Verlag, Berlin, Germany.
- UNESCO. 1985. The international system of units (SI) in oceanography, UNESCO Technical papers No. 45, IAPSO Pub. Sci. No. 32, Paris, France.