AN ANALYSIS OF MANGROVE FORESTS ALONG THE GAMBIA RIVER ESTUARY: IMPLICATIONS FOR THE MANAGEMENT OF ESTUARINE RESOURCES

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SUMMARY AND CONCLUSIONS

- Mangroves along the Gambia River estuary cover an area of 60,000 to 70,000 ha with approximately 12% of this total occurring above the proposed barrage at Balingho.
- Most of the mangroves in the meso- and oligohaline sections of the estuary represent riverine forests inhabited by Rhizophora racemosa, R. harisonii, R. mangle, and Avicennia africana. Inland of these forests are basin mangroves dominated by the latter two species. In the higher salinity areas of the river, and up in the larger bolons, fringe and scrub mangrove forests are more common.
- The riverine and basin forests are dominated by trees >20 m, while forests in higher salinity areas have less structure and are generally <7 m.
- Based on forest structure statistics of the mangroves of The Gambia, the following litter productivity rates (t dry mass·ha^{-1}·yr^{-1}) were estimated for categories based on tree height: Rhizophora (>20 m) = 18.8; Rhizophora (7-20 m) = 10.4; Avicennia (>7 m) = 11.6; Avicennia plus Rhizophora (<7 m) = 4.0.
- Ratios of litter export to litter productivity were estimated based on results of other studies that have demonstrated the following relationship between the magnitude of detritus export and tidal amplitude: riverine forests = 0.94; fringe forest = 0.5; and basin forests = 0.2. Ratios used for mangroves in The Gambia were 0.75 for Rhizophora >20 m and 7 - 20 m in height, and 0.5 for Avicennia >7 m and Avicennia plus Rhizophora <7 m tall.

- Personal observations of minimum leaf litter accumulation in the riverine and basin mangrove forest of The Gambia substantiate the use of ratios above 0.5 for these forests.
- Based on these estimates of litter productivity and export to litter productivity ratios, detritus export was 289 $gC \cdot m^{-2} \cdot yr^{-1}$. Total export for mangroves along the Gambia River estuary was 181,040 $tC \cdot yr^{-1}$ with 40,080 $tC \cdot yr^{-1}$ occurring above the barrage and 140,960 $tC \cdot yr^{-1}$ below the barrage.
- Organic carbon inputs to the Gambia River estuary from phytoplankton net productivity was estimated at 14,782 $tC \cdot yr^{-1}$ based on $^{14}CO_2$ uptake studies in 1983.
- Organic carbon inputs to the Gambia River estuary from river discharge at Goulombo is equal to 15,960 $tC \cdot yr^{-1}$.
- Total organic carbon loading to the Gambia River estuary is 211,782 $tC \cdot yr^{-1}$, of which about 85% was contributed by allochthonous inputs from mangroves.
- The nonconservative behavior of nitrate, phosphate, and total suspended solids in bolons suggests that mangrove forests are a sink for these constituents. Such trapping mechanisms are occurring where the concentrations of these constituents in estuarine waters are high.
- The food web associated with mangrove bolons are representative of other mangrove ecosystems. There are four levels of the food chain with detritus serving as a major energy source: detritivores, mixed trophic level, middle carnivores, and higher carnivores.
- Fish that were associated with the mangrove food chains in the bolons constituted nearly 51.5% of the total catch of the artisanal fishery from

Banjul to Kaur in 1983. In the upper river, from Kaur to Fatuto, nearly 30% of the annual catch is represented by Tilapia, which is a detritivore found in mangrove bolons. Collectively, these trophic levels of the mangrove food chain represent 40% of the grand total catch of fish for the Gambia River estuary.

- Mangroves in The Gambia can be classified as existing in a very dry life zone, and are thus very susceptible to slight changes in hydrology. Therefore the present decline and death of mangrove trees along the Gambia River estuary can be attributed to the decline in precipitation over the last decade.
- The proposed barrage at Balingho will increase the salinity of typically meso- to oligohaline waters of the estuary to hypersalinity levels. Rhizophora racemosa and R. harisonii are very susceptible to salinities >15°/$_{oo}$ and will not tolerate the change in conditions due to the barrage.
- The proposed barrage at Balingho will also create a freshwater impoundment upriver with a water level at + 1.7 m GD. This high level of stagnant water will result in a loss of mangrove trees with heights >7 m in the area above the barrage due to drowning of their root systems.
- These losses of mangroves above and below the barrage will result in a loss of nearly 147,920 $tC \cdot yr^{-1}$ of detritus to the estuary. This decline is equivalent to 82% of the organic matter inputs to the estuary that are presently supporting a detritus-based fishery.
- Mangrove forests of The Gambia provide a vital natural resource to the artisanal fishery of the Gambia River estuary.

INTRODUCTION

The management of forested wetlands has received considerable attention in the last 15 years because of increased human exploitation of these wetlands as a forest resource, while at the same time natural resource managers have become more cognizant of the importance of these plant communities to the ecology of adjacent aquatic ecosystems. In the intertidal zone of the tropics, forested wetlands or mangroves are a resource in the form of a variety of forestry products and as an important component of estuarine ecosystems. The exploitation of mangroves for forestry products includes saw timber, building material, fence posts, fuelwood, tanins, and charcoal. In some areas of the world, such as Malaysia, these forests are managed for sustained yield to provide these resources. Mangroves have also been acknowledged as contributing to the productivity of coastal ecosystems by providing detritus to various levels of estuarine food chains (Heald 1969, W. E. Odum 1971, Twilley 1982, Twilley 1985). They are also important in the nutrient and sediment dynamics of estuaries as well as contributing to erosion and flood control in coastal areas.

Because of these two important roles of mangrove ecosystems as forests and estuarine resources, human manipulations of estuarine ecosystems that may alter or destroy these forests should be carefully evaluated to understand their potential impact on the entire estuarine basin. In the Gambia River estuary, located in West Africa, a salt barrage is proposed in the oligohaline region (Balingho), which will alter the hydrology and salt distribution of this tropical estuary. This report is an analysis of the mangrove forests in this estuary, and of the potential impact of this barrage to estuarine resources associated with these forested wetlands. This report is supplemented with

observations made in the field during a trip from 29 June to 2 July 1984 along the Gambia River estuary from Banjul to Georgetown (Appendix A).

STUDY AREA

The Gambia River estuary is located approximately 13°N latitude along the west coast of Africa (Fig. 1). The climate in this area is defined as Sub-Guinean within the Tropical Sudanese zone (Richard-Molard 1949) and as tropical semi-dry modified to tropical semi-wet nearer the sea. The climate is dominated by alternating dry Harmattan air mass, which originates in the Sahara, and southwesterly monsoon of humid oceanic air. As a result, there are distinct wet and dry seasons with the former season occurring from June to October (Fig. 2). Rainfall varies considerably from year to year in quantity (mean of about 1,140 mm) and distribution; the highest precipitation is usually in August. Due to Sahel drought, which has lasted through the 1970s, rainfall in the basin has followed a negative slope ($m = -19.9$ mm·yr^{-1}) for the last 23 yr of record (Arid Lands Information Center 1981) (Fig. 3). Rainfall occurs in high intensity storms with more than 50% of rain accumulated at Bombey, Senegal, falling at an intensity >27 mm·hr^{-1}, and intensities >100 mm·hr^{-1} are not uncommon (Jones and Wild 1975).

The difference in maximum and minimum monthly mean air temperatures during the year are only about 3.8°C for coastal locations, compared to 5.5°C at Kaur and 7.6°C at Basse which are more than 175 km from the mouth of the Gambia River estuary. The mean annual average of maximum and minimum air temperatures also increases inland from 25.1°C at Cape St. Mary and 25.5°C at Yundum, to 28.4°C at Kaur and 28.1°C at Basse (Fig. 2). These high annual air temperatures result in evapotranspiration rates (based on Penman method) ranging from 4.8 to 15.0 mm·d^{-1}, with higher rates occurring in April and May during the dry season.

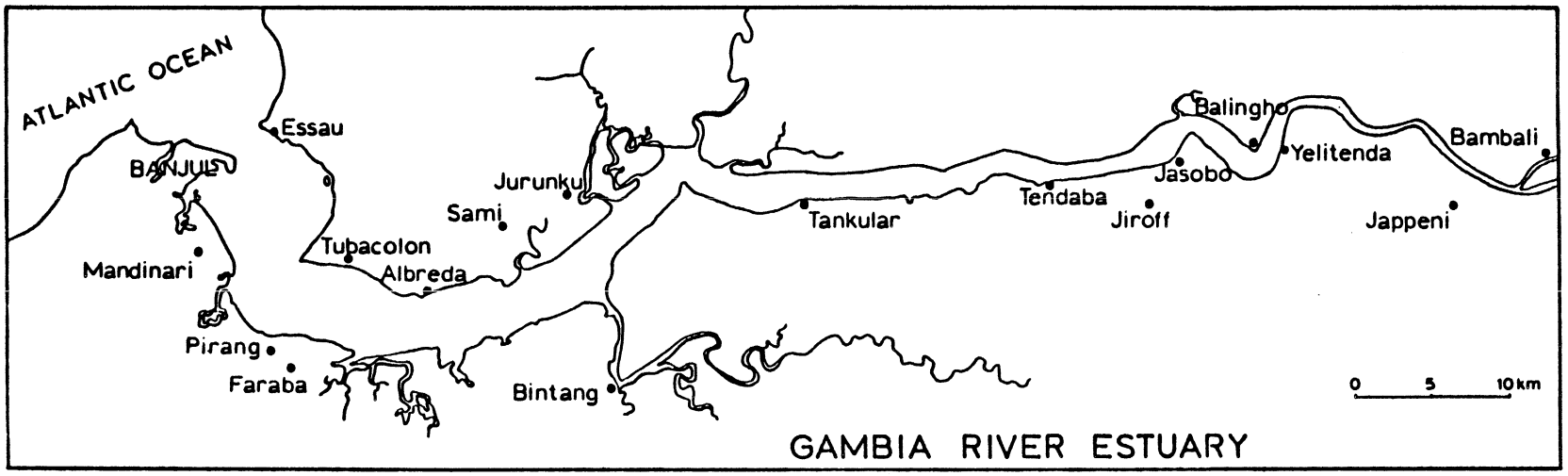

FIG. 1. Location of the Gambia River estuary in The Gambia, West Africa.

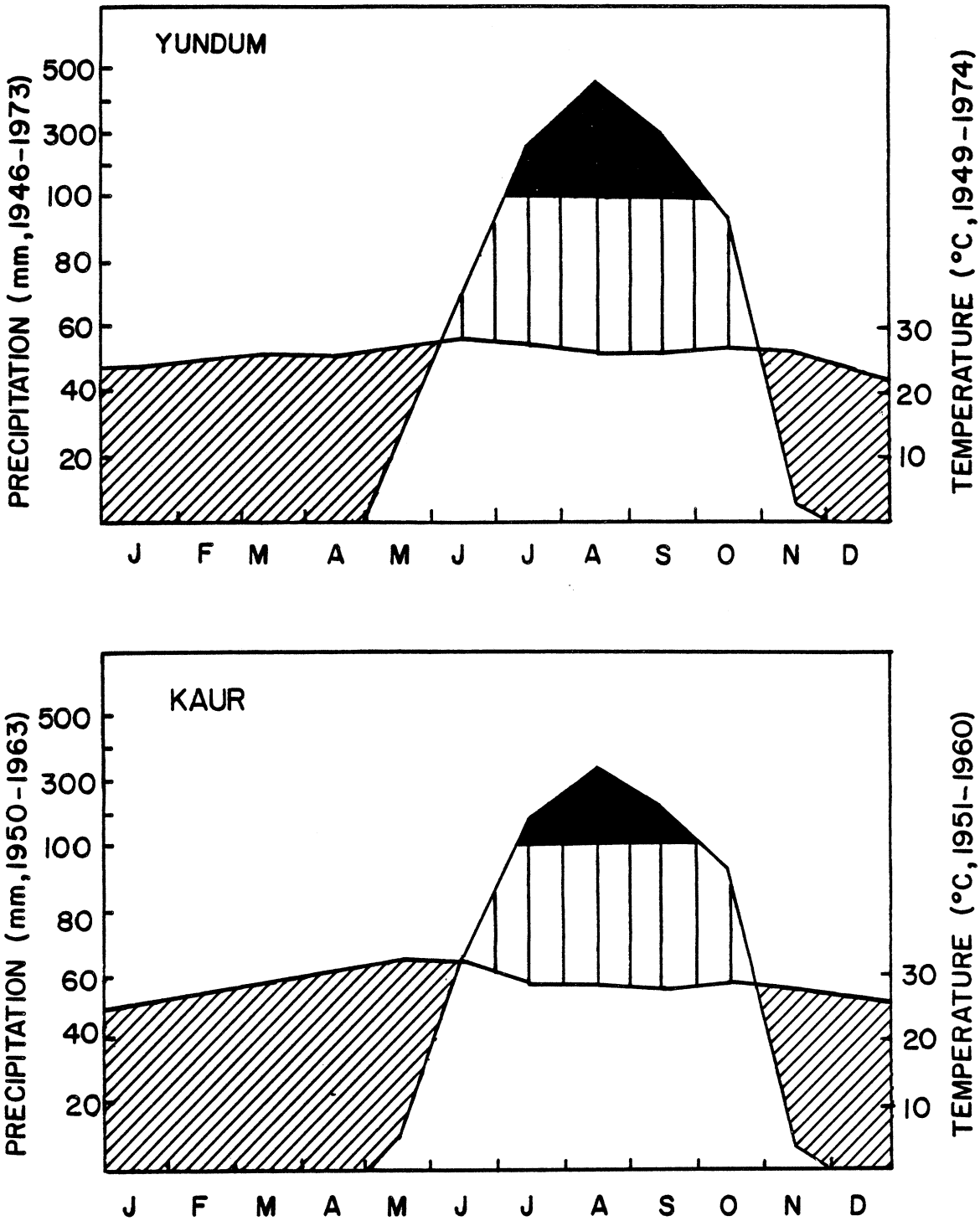

FIG. 2. Climatic diagrams of air temperature and precipitation for Yundum (near the mouth of the estuary) and Kaur (184 km upriver). Solid areas represent the rainy season, vertical lines the period when rainfall exceeds evaporation, and the dotted area the period when evaporation exceeds rainfall. The years of record are in parentheses following the label.

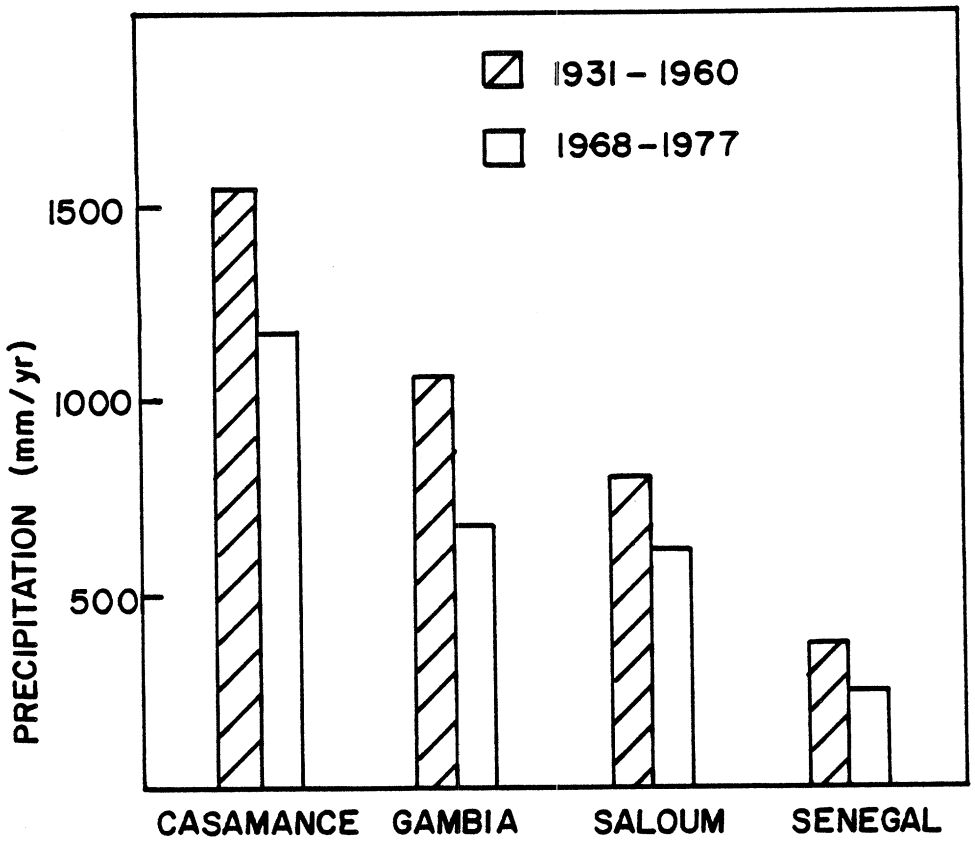

FIG. 3. Change in precipitation along the west coast of Africa from Saloum to Casamance by comparing annual totals from 1931 to 1960 to those from 1968 to 1977 (from Marius 1981).

The Gambia River originates in the moist evergreen forests of the Fouta d'Jallon plateau in the Guinean hinterland and flows 1,200 km to the Atlantic Ocean (Fig. 1). The total drainage area is 78,000 km^2 with moderate drainage gradient in Guinea (slope of 1-4%), low gradient in Senegal (slope of 0 - <1%), and virtually no slope over the last 500 km from Gouloumbo, Senegal, to Banjul. Collectively, the geology of the continental sub-basin consists of sedimentary formations (64%), metamorphics (20%), and intrusives (16%); a small band of Quaternary alluvium deposits border the Gambia River bed. Soil parent material is fine textured with little or no sand since the combined silt and clay fractions comprise more than 90% of the mineral material. These iron rich deposits are partially the products of laterite-rich uplands (Dunsmore et al. 1976). The high clay content, consisting of kaolinite with some silica, renders these soils resistant to infiltration.

Mean historical runoff is 231 mm or about 21% of precipitation. Annual mean discharge since 1953 has varied from 90-460 $m^3 \cdot s^{-1}$, with decreasing trend since 1970 as a result of the Sahel drought, and peak discharge occurs in early to mid September (Lesack et al. 1984). The transport of solutes by the Gambia River are classified as a river with low runoff (<5 $L \cdot s^{-1} \cdot km^{-2}$), warm (>15°C), and low relief. Runoff loss of Na, K, SO_4, N, and P from the Gambia River compared to precipitation loading rates unto the watershed are low, possibly reflecting the scarcity of essential nutrients in the watershed for upland plant communities (Lesack et al. 1984). The transport of particulate material also is very low and fits in better with high runoff rivers (>15 $L \cdot s^{-1} \cdot km^{-2}$) than low runoff rivers (Lesack et al. 1984). The export of particulate and total organic carbon is extremely low compared to rivers around the world (Schlesinger and Melack 1981, Meybeck 1982), with respective transport rates of 0.12 and 0.38 $t \cdot km^{-2} \cdot yr^{-1}$ (Lesack et al. 1984).

The Gambia River is tidal to Gouloumbo Bridge in Senegal, 526 km upstream from Banjul, during the dry season. As a consequence of low river discharge ($<5\ m^3 \cdot s^{-1}$), two sequential tides are able to penetrate the river at any one time. During this period, salinity normally reaches Carrols Wharf which is 219 km from the mouth. This was observed in July, 1983 (Fig. 4). United Nations Development Programme (1974) reported a salinity of 1.0°/oo at Kuntaur which is 248 km from Banjul. In wet season there is a rapid increase in river discharge ($>1{,}000\ m^3 \cdot s^{-1}$) and fresh water may be observed only 75 km from the mouth of the river (Herklots 1979). During October 1983, a salinity of <1°/oo was measured at 125 km upstream (Fig. 4). Thus the saltwater wedge may travel annually from about 100 km to 220 km upstream from the mouth of the estuary.

Tides in the Gambia River estuary are semidaily with unequal magnitude. The difference between mean high and low tide levels at Banjul is about 1.2 m (Fig. 5), with slightly lower tidal amplitude during the wet season. Mean high water during spring tides (Gambia Datum, GD) is +1.4 m at Banjul, compared to +1.7 m at Balingho and Kaur (188 km upriver) (Coode and Partners 1977). Extreme spring tides at Banjul are highest from August to October and may exceed +2.2 m GD.

THE BARRAGE

A salt-water barrage has been proposed at 1 km south of Yelitenda (Balingho) to provide a reservoir for rice irrigation, a barrier to tidal seawater, and a road crossing. The site is located at latitude 13° 25'N and longitude 15° 35'W and is 127 km from the mouth of the estuary. Salinity in this area may fluctuate from freshwater to about 16°/oo (Fig. 4), thus the use of the river for irrigation is strictly seasonal. Also, the extraction of fresh

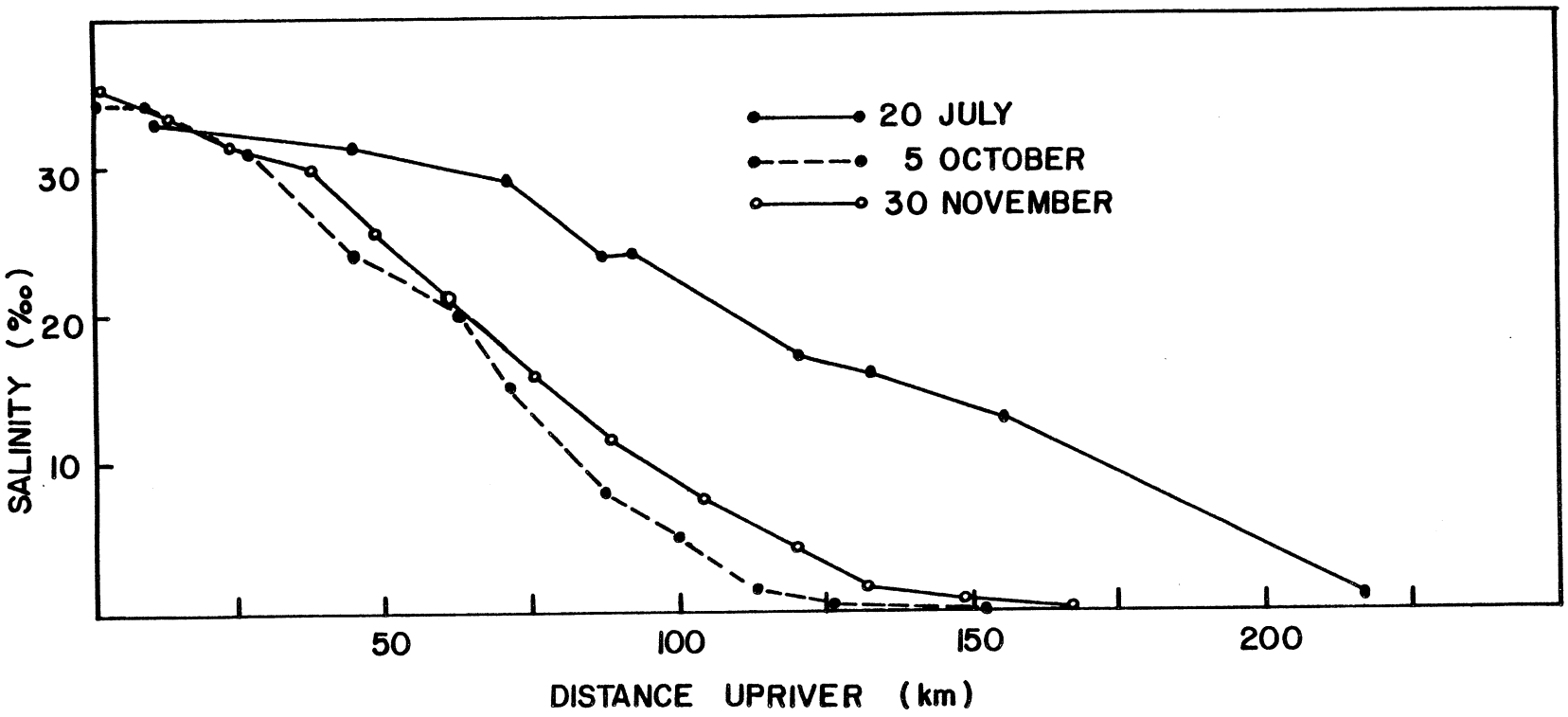

FIG. 4. Distribution of salinity along the Gambia River estuary during cruises in July, October, and November 1983 (Berry et al. 1985).

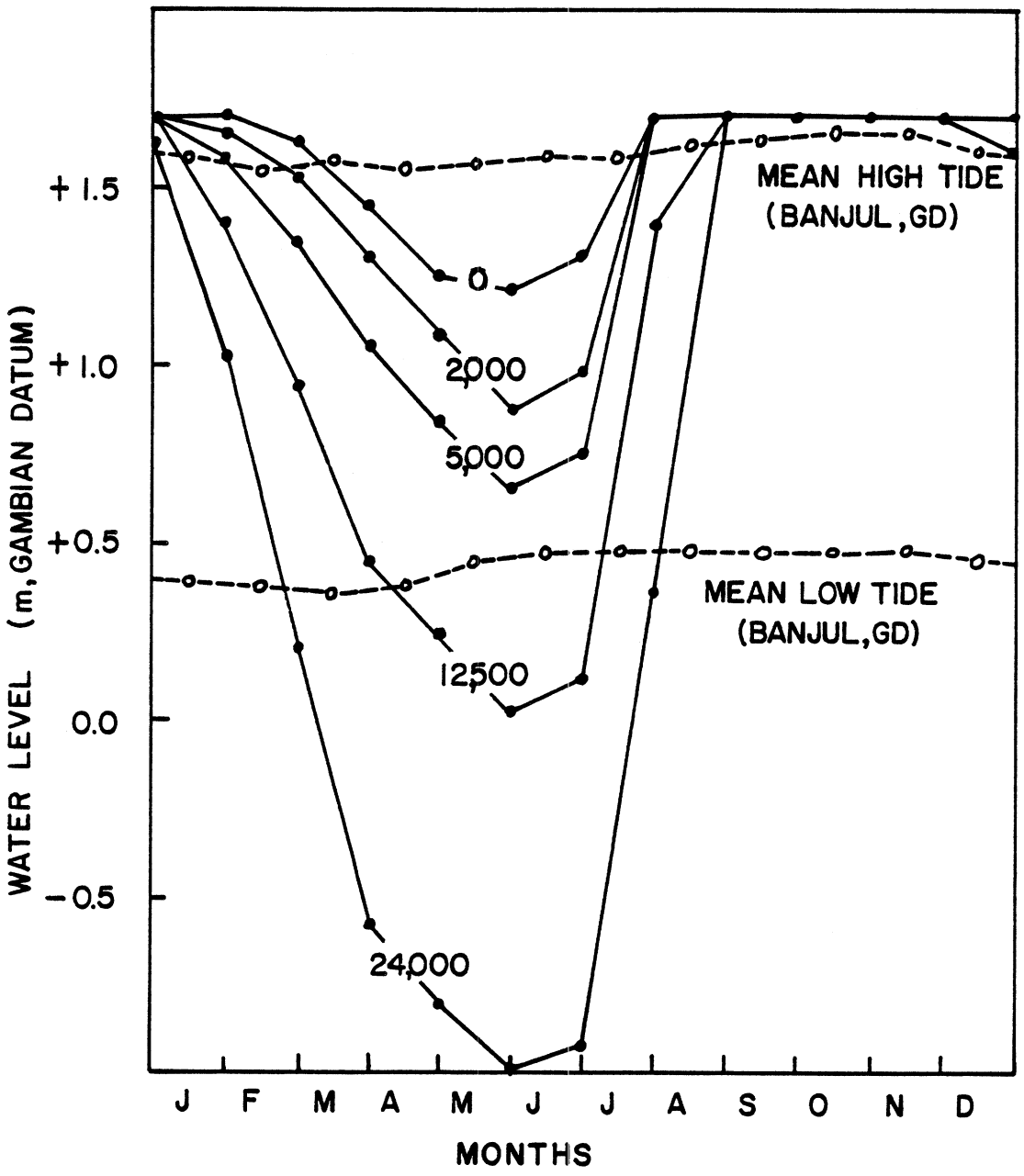

FIG. 5. Water levels in the Gambia River based on Gambia Datum including mean high and low tides at Banjul, and predictions of levels within the impoundment upriver from the barrage at different demands for irrigation based on areas (ha) cultivated with rice (from Coode and Partners 1977, Johnson 1978).

water at Kuntaur (231 km upriver) at a rate of 1 $m^3 \cdot s^{-1}$ during the dry season would move the saline mixing zone upriver by 1 km (Johnson 1978). The salt barrage is intended to prevent the upriver excursion of salinity which would eliminate irrigation in historically freshwater areas, and to provide a continuous source of water for rice fields in areas that originally could only farm rice during the rain season.

The barrage will be built such that maximum water level will be +1.70 m (GD), which is the approximate spring tide level in this area (Coode and Partners 1977). The original hydrologic budgets of water table fluctuations were based on irrigation demands for 24,000 ha of rice which would drop the water table to -1.02 m (GD) by the end of May (Coode and Partners 1977; Fig. 5). Water level changes based on different acreages of rice cultivation (Fig. 5) would range from a low of +1.2 m (GD) if no rice was irrigated to the extremely low levels estimated by Coode and Partners (1977) (calculated by Johnson 1978). In all of these scenarios, minimum water levels were observed at the end of May, and recovery of levels back to +1.70 m (GD) occurred by the end of August. The threshold acreage of rice at which minimum water levels would be below the natural tidal levels during May would be about 8,000 ha.

MANGROVE ANALYSIS

MANGROVE COMMUNITY TYPES

Lugo and Snedaker (1974) developed a classification scheme relating forest physiognomy and functional characteristics among mangroves with their hydrology and geomorphology. Six types of mangroves were identified (Fig. 6) that group environmental factors such as tidal hydrology, rainfall, soil texture, soil salinity, and juxtaposition to estuarine waters with the structure,

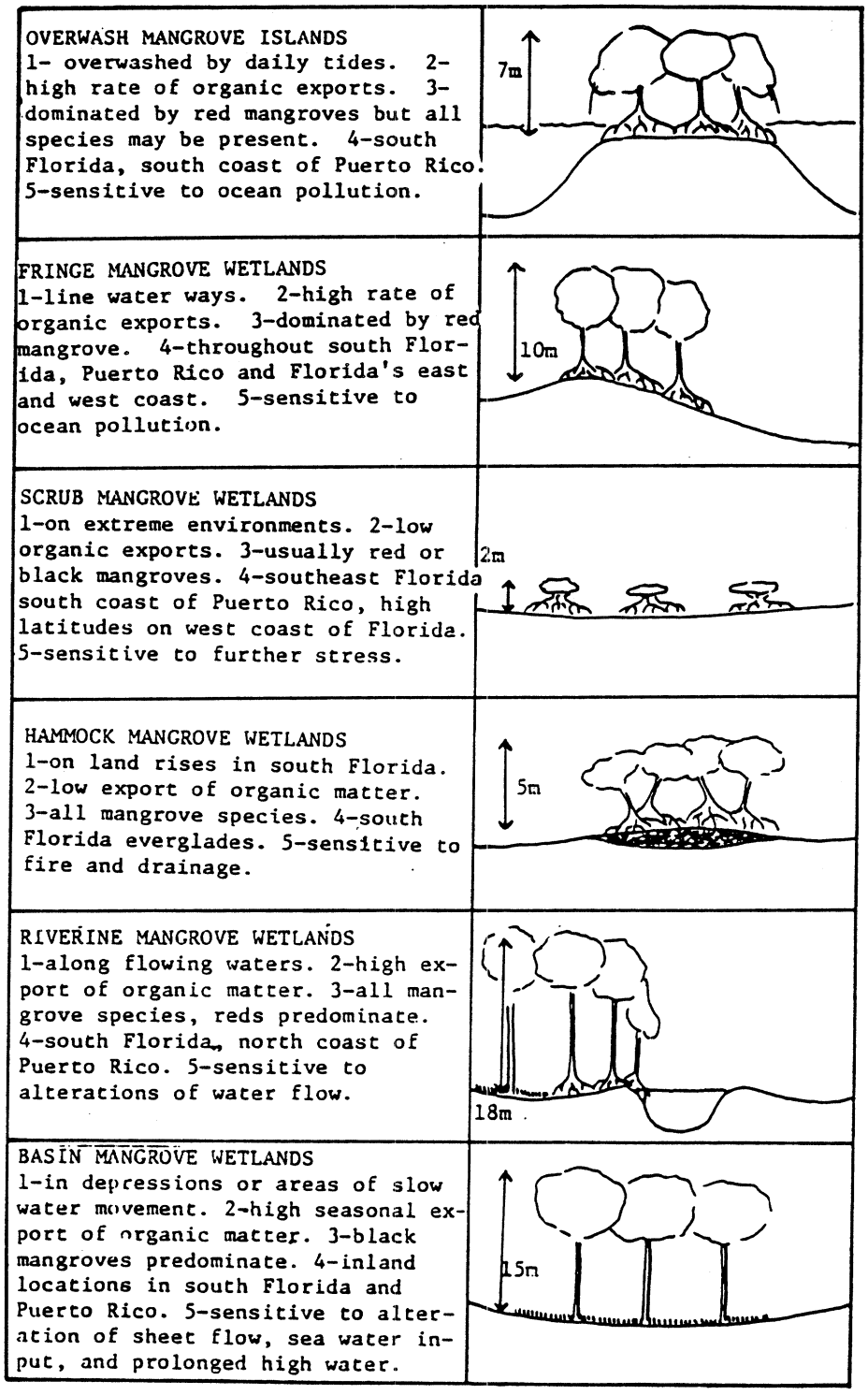

FIG. 6. The six mangrove community types from Lugo and Snedaker (1974).

productivity, and nutrient cycling characteristics of the forests. Although this classification system was based on surveys mostly from mangroves in the Americas, it has proven applicable to mangrove forests around the world; such is the case for West Africa.

The mangroves along the Gambia River estuary can be grouped into four of the mangrove types based on the scheme by Lugo and Snedaker (1974). The dominant type of mangrove along the Gambia River estuary is the riverine mangrove forest which occurs along most of its shoreline, except for near the mouth of the estuary and up in some adjacent bolons. These forests are inhabited by all three Rhizophora species found in this area and are characteristically greater than 10 m in height; they are most noticeable from Tendaba to Elephant Island. Inland of these riverine forests, which are inundated daily by tides, are basin mangrove wetlands which are dominated by Avicennia. These areas are infrequently flooded by tides (spring tides only) and consequently have a different soil texture and chemistry than the riverine forests.

At the mouth of the Gambia River estuary there are two types of mangroves. Fringe mangrove wetlands, dominated by Rhizophora mangle, occur along the shoreline of bays and lagoons that have fairly constant annual salinity. The tidal amplitude in this area is about 1.2 m, which would normally support forests with tree heights >10 m. Yet because of the high evapotranspiration rates characteristic of the Gambian climate, forests at the mouth of the Gambia River estuary have tree heights from 5-7 m. These fringe forests are very similar to those along the bays of south Florida, USA. In this same area, there are stands of scrub mangroves occurring more frequently along the more inland shorelines of the bays. Slight increases in the topography, due to storm deposits or more inland juxtaposition from the estuary, along a coastline with

such high evapotranspiration rates result in extreme soil salinity conditions. These scrub mangroves, dominated by Avicennia with minor occurrence of Rhizophora and Laguncularia, are usually <2 m tall.

SPECIES DISTRIBUTION AND ZONATION

Mangroves along the coast of Senegal and The Gambia are the most northern mangroves of the Atlantic type on the west coast of Africa located between 12° and 16°N latitude (Marius 1981). These mangroves extend over an area of 500,000 ha (most of the area is unvegetated tidal flats), half of which are in the estuary of the Casamance River and remainder in estuaries of the Gambia and Saloum rivers. In the Gambia River estuary, mangrove forests are comprised of six species including Rhizophora racemosa, R. harrisonii, R. mangle, Avicennia africana, Laguncularia racemosa, and Conocarpus erectus. Speciation of mangroves along West Africa is very similar to mangroves along the Atlantic coasts of the Americas, yet different to mangroves colonizing the east coast of Africa (Chapman 1976).

The typical distribution or zonation of these mangrove species along the shoreline of the Gambia River estuary is also similar to observations along the Americas' Atlantic coastline. In the mesohaline and oligohaline regions of the estuary, Rhizophora racemosa occupies a thin strip adjacent to the riverbank. This area of the intertidal zone is inundated twice daily by tides and is commonly associated with recent deposits of soft alluvium of high clay and silt mineral content. Yet these forests typically obtain tree heights greater than 20 m on an elaborate prop root system. Just inland of this fringe of R. racemosa is a stand of R. mangle which is also located in that portion of the intertidal zone flushed daily by tides. Mixed among both of these is R.

harrisonii. At the level of mean high water there is usually a mixture of R. mangle and Avicennia africana which is less frequently flooded by tides compared to the pure Rhizophora stands. This group of mangroves, from the monospecific strip of Rhizophora racemosa to the mixed stand of R. mangle and A. africana, constitutes the riverine mangrove forests.

Inland of the mixed R. mangle and Avicennia africana are normally monospecific stands of Avicennia which are located above mean high water levels. This vegetation band marks a distinct transition zone in vegetation and soil characteristics between the lower and upper intertidal areas. Associated with this zone is usually a sharp rise in soil salinity due to the infrequent nature of tidal inundation and high evapotranspiration rates (Fig. 7). This area of mangrove may be classified as basin mangrove wetland.

Soil salinity continues to increase inland of this mangrove zone which is indicated by a gradual decrease in tree height and density of A. africana as distance from the estuary inland increases (Fig. 7). The adjacent more inland zone is usually void of any vegetation due to hypersalinity (pH may drop but salinity is considered a key factor) and is referred to as bare tanne. Inland of this zone may be tannes vegetated with marsh plants including Sesuvium portulacastrum, Philoxerus vermicularis, Paspalum vaginatum, Eleocharis mutata, and Eleocharis carribea. This zone is referred to as a herbaceous tanne. These tannes represent the most inland extent of the intertidal zone. The sequence of these tannes (bare vs. herbaceous) may vary depending on topography which controls where precipitation and runoff may concentrate, resulting in slightly lower soil salinity. In many areas of the upper intertidal zone of The Gambia, the hydrology of this area has been modified by dikes built by humans for the production of rice.

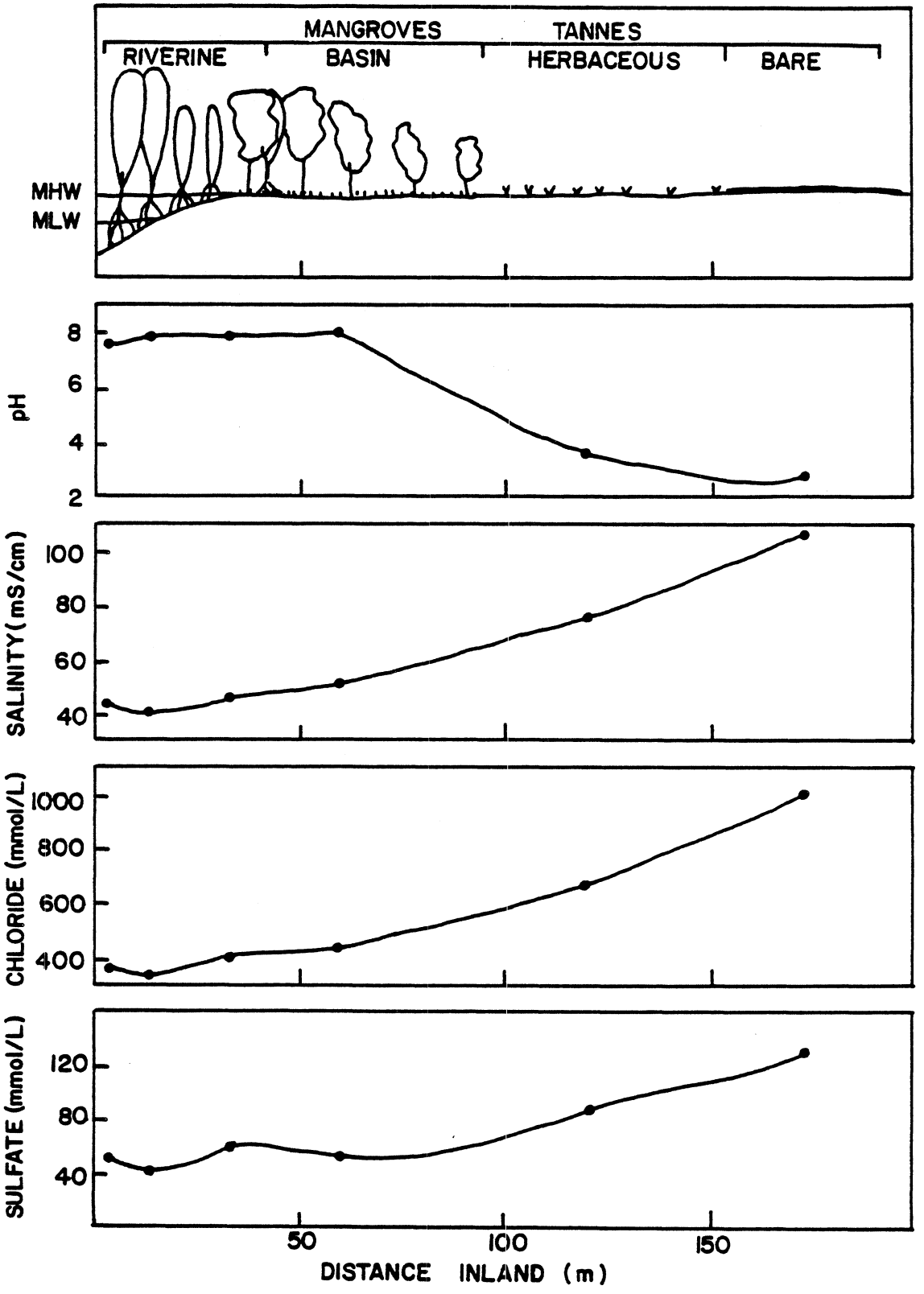

FIG. 7. Vegetation sequence of mangroves in the Gambia estuary including soil chemistry at 0.5 m depth at distances inland from the estuary.

This vegetation sequence varies considerably along the Gambia River estuary, most noticeably by the exclusion of the more inland mangrove associes. In many areas, only the fringe of the riverine mangroves is present, forming a thin strip of mangroves along the estuary. This sequence is not applicable to mangrove forests along the mouth of the estuary where monospecific stands of R. mangle form fringe mangrove wetlands along the bays. Also in this area are scrub mangroves dominated with Avicennia which have no apparent zonation pattern.

FOREST STRUCTURE

The diversity in structure of mangrove forests along the Gambia River estuary is demonstrated in Figure 8 by the change in tree heights along the longitudinal axis of the estuary. These data are personal observations (tree heights measured with clinometer) at sites along the estuary during July, 1984, and indicate higher forest structure in the mesohaline region of the estuary. Also apparent is that the higher structured forests are along the north bank of this estuary. This was most noticeable at about 150 km upriver at Bai Tenda and Elephant Island where tree heights on the north bank were 20-30 m compared to only 10 m on the south bank. As discussed above, mangroves at the mouth of the estuary were normally 5-7 m in the fringe forests and only 1 m in the scrub mangrove wetlands.

This diversity in forest structure is also reflected in a forestry survey of Rhizophora mangrove forest (>7 m tree height) along the Gambia River estuary (Forster 1983; Table 1). The complexity index (Holdridge et al. 1971), which uses the variables of tree density, basal area, species number, and tree height to determine forest structure of Rhizophora forests in this survey, ranged from

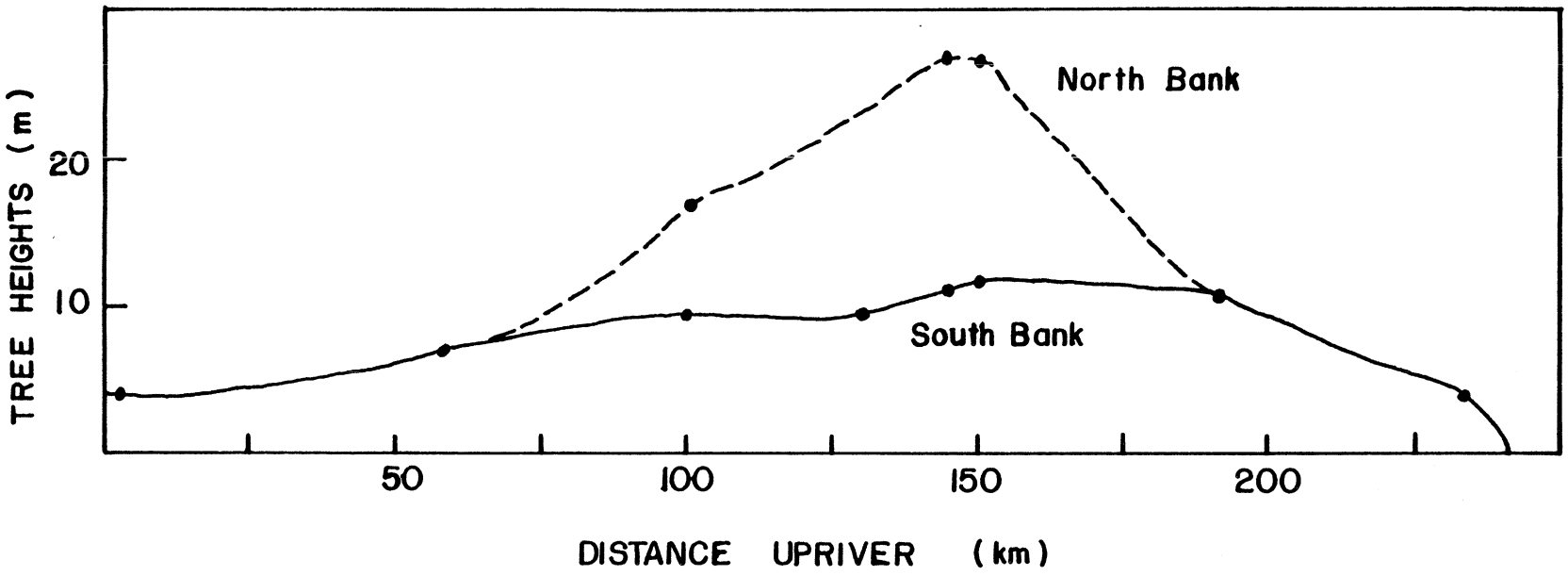

FIG. 8. Tree heights measured at sites along the Gambia River estuary.

TABLE 1. Structure of tall Rhizophora mangrove forest (>7 m) along the Gambia River estuary (from Forster 1983).

	Western Division	Lower River Division	North Bank and MacCarthy Island Division	Total
Area (ha)	4,692	4,291	5,461	14,980
Density (N/ha)	371	385	472	416
Basal Area (m^2/ha)	11.8	15.7	30.3	18.5
Mean Diam (cm)	20	23	23	24
Mean Height (m)	11	12	13	13
Total Volume (m^3/ha)	103.0	153.2	208.9	183.5
Damaged Trees* (% of density)	32.0	23.0	21.0	25
Dead Trees (% of volume)	21.0	19.0	8.0	22
Structural Index@	0.48	0.73	1.25	1.00
Complexity Index&	1.92	2.92	5.00	4.00

*including some signs of decay in the crown
@Structural Index = (Mean Height x Basal Area x Density) ÷ 1,000
&Complexity Index = (Mean Height x Basal Area x Density x Species No.) ÷ 1,000

1.92 to 5.00 with the lower number associated with the Western Division of the estuary (south bank near the mouth of estuary). The average index for the entire mangrove area along the Gambia estuary was 4.00.

Structural indexes of the mangrove forests above Yelitenda were calculated from Johnson (1978) using size class distributions of three categories of mangrove forests based on tree heights: Rhizophora, >20 m; Rhizophora, 7-20 m; and Avicennia, >7 m. Using the median diameter at breast height (dbh) for each 5-cm size class starting at 10-cm dbh, and the density of each respective size class, the basal area in a 1 ha stand of each mangrove category was determined (Table 2). Assumptions of tree height are given in Table 2 along with calculations of complexity index (Holdridge 1971). Complexity indexes ranged from 4.4 to 11.2, with the tall Rhizophora forests having the greater structure. These values are within a range of 2.3 - 72.0 for riverine mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica (Pool et al. 1977; Table 2). The most significant difference among these riverine mangrove forests is density, with forests along the Gambia estuary being less dense.

AREAL DISTRIBUTION

Estimates of aerial distribution of mangroves along the Gambia River estuary in Table 3 range from 45,000 ha (Giglioli and Thornton 1965) to 71,343 (Checchi and Co. 1981; from Johnson 1978 and Abell 1980). The most accurate estimates based on planimetry of aerial photos are by Rodriguez-Bejaram (personal communiation), Forster (1983), and Dunsmore et al. (1976) which range from 60,000 to 67,000 ha. Mangroves have been classified based on stand height (m) with 7 m the delineation between tall and short forests (Table 4). Checchi and Company (1981) used estimates above the proposed barrage at Balingho by Johnson

TABLE 2. Structural indexes (based on trees with dbh >10 cm) of mangroves in the Gambia River estuary compared with riverine mangrove forests in North and Central America.

	Tree Height	Density (no./0.1 ha	Basal Area (m^2/0.1 ha)	Complexity* Index	Reference
The Gambia (above Balingho)					
Rhizophora:	>20 m	39	2.86	11.2	Johnson 1978
Rhizophora:	7-20 m	56	1.38	4.4	"
Avicennia:	>7 m	34	3.31	6.7	"
Florida, USA					
Ten Thousand Island		60	2.17	2.3	Pool et al. 1977
Puerto Rico					
Vacia Talega		98	1.71	7.5	"
Mexico					
Roblitos		91	2.41	3.5	"
Isla La Palma		145	5.59	41.3	"
Rio de las Cañas		103	5.61	27.7	"
Costa Rica					
Moin		118	9.53	72.0	"
Boca Barranca		66	3.18	6.0	"

*Complexity Index = (Tree Height x Density x Basal Area x No. Species) ÷1000 (Holdridge et al. 1971)

TABLE 3. Estimates of mangrove distribution along the Gambia River estuary.

Mangrove Area (ha)	Reference
66,000	Brunt 1959
45,000	Giglioli and Thornton 1965
67,000	Dunsmore et al. 1976
71,343	Checchi and Co. 1981
66,900	Forster 1983

(1978) and estimates below the barrage by Abell (1980) to calculate mangrove distribution by stand height for Rhizophora and Avicennia for the Gambia estuary. Based on these estimates, nearly half the mangroves are >7 m (∿36,000 ha) and 10% (6,125 ha) are >20 m. However, Forster (1983) found that about 52,000 ha or 78% of the total coverage was <7 m. He states that these estimates are about double the estimates for short mangroves by Brunt (1959). Thus Brunt's value of about 30,000 ha of mangrove <7 m was similar to those figures presented by Checchi and Company (1981). These differences are extreme and further analyses are needed to correct the confusion. This is a very important statistic since the only estimates of litter productivity for the Gambia River estuary are based on stand height.

Another important statistic concerning mangrove cover is the areal distribution for the two dominant genuses of mangroves in this estuary, Rhizophora and Avicennia. Most of these forests are monospecific zones of each genus and follow a zonation pattern of Rhizophora inhabiting the fringe mangrove zone adjacent to estuarine waters, and Avicennia occurring inland of the fringe zone. This zonation pattern probably reflects some gradient in tidal hydrology (and

TABLE 4. Two estimates of the areal distribution of mangroves in the Gambia River estuary. Classification system uses tree heights (m).

Region	Classification <7 m	7-20 m	>20 m	Total	Reference
		Estimate I			
Below Barrage					Abell 1980
Rhizophora	11,880	18,330	2,520	32,730	
Avicennia	21,590	8,310	0	29,900	
Subtotal	33,470	26,640	2,520	62,630	
Above Barrage					Johnson 1978
Rhizophora	757	3,406	3,605	7,768	
Avicennia	237	708	0	945	
Subtotal	994	4,114	3,605	8,713	
Total Estuary					Checchi and Company 1981
Rhizophora	12,637	21,736	6,125	40,498	
Avicennia	21,827	9,018	0	30,845	
Total	34,464	30,754	6,125	71,343	
		Estimate II			
Western Division	16,800	4,700*		21,500	Forster 1983
Lower River Division	12,400	4,300		16,700	
North Bank Division	22,600	5,500		28,100	
McCarthy Is. Division	100	500		600	
Total Estuary	51,900	15,000		66,900	

*Trees >7 m

thus other soil characteristics such as salinity, hydrogen sulfide, etc.), which is significant to estimates of potential detritus export from these intertidal forests. Thus estimates of areal distribution of each genus may enable a prediction of detritus transport rates to the estuary. The only figures available are from Checchi and Company (1981) which estimate that 57% of total mangrove coverage, or 40,498 ha, are of the genus Rhizophora.

The impacted area of mangroves above the proposed barrage is 8,713 ha according to Johnson (1978) and 7,930 ha from Rodriquez-Bejarano (personal communication); and both estimates represent 12% of the total area according to figures from Checchi and Company (1981), or 13% based on figures for total mangrove cover by Forster (1983). The area above the barrage represents 59% of mangrove trees >20 m, yet only 3% of the trees <7 m inhabit this area indicating an unequal distribution of tree height along the salinity gradient.

Forster (1983) noted that their estimates for total mangrove cover were similar to those by Brunt (1959), indicating that a large-scale loss of mangrove forests may not be occurring. The two estimates do have large differences in the distribution of mangroves according to the 7 m demarcation in tree height as discussed above. Based on these differences, about half of the tall mangrove trees (>7 m) have been eliminated since 1959 and replaced by mangrove forests <7 m.

LITTER PRODUCTIVITY

Background

The purpose of studies on the production and decomposition of litter in forests is to better understand the role of litter dynamics in such ecosystem properties as nutrient cycling, succession, and stability (Bray and Gorham

1964). Litter dynamics have been extensively studied in terrestrial forests (Jenny et al. 1949, Brown 1980), while less work has been done on the production and turnover of litter in forested wetlands. Such information is particularly needed for intertidal forested wetlands, such as mangroves, in order to understand the coupling of these forests to the productivity of coastal fisheries. Other interests in the litter production of mangroves include the production of peat that occurs in many of these coastal swamps, and the optimization of managed forests for exploitations such as charcoal, posts, chip wood, and tanins.

Litter production values for mangrove forests worldwide range from 1.20 $t \cdot ha^{-1} \cdot yr^{-1}$ for scrub mangroves in south Florida to 23.4 $t \cdot ha^{-1} \cdot yr^{-1}$ for a 20-yr-old managed forest in Malaysia (Table 5). Grouping mangrove forests by the scheme of Lugo and Snedaker (1974) used in Table 5 separates mangroves into categories that represent forests with similar hydrography. There is a gradient in the frequency in tidal inundation from scrub to basin to fringe mangrove forests, and riverine mangroves are frequently inundated by freshnets from rivers as well as tides. It has been suggested by Pool et al. (1975) that litter production rates in mangroves are a function of water turnover within the forest, and the rank of the means of litter production in Table 5 (riverine > fringe > basin > scrub) supports this hypothesis.

An association between wetland hydrology and net primary production has been observed for a variety of wetland communities including Spartina marshes (DeLaune et al. 1979, Steever et al. 1976), Zizania aquatica (Whigham and Simpson 1977), and freshwater forested wetlands (Connor and Day 1976, Brown et al. 1979, Brown 1981, Brinson et al. 1981). Wharton and Brinson (1979) suggested that the production of alluvial swamps was dependent on water

TABLE 5. Summary of total litter fall rates for different types of mangrove forests.

Mangrove Type	Litter Fall ($t \cdot ha^{-1} \cdot yr^{-1}$)	Reference
Scrub Mangroves		
Turkey Pt., SE Florida, USA	2.71	Pool et al. 1975
Turkey Pt., SE Florida, USA	1.20	Snedaker and Brown 1981
Turkey Pt., SE Florida, USA	1.68	
Mean ± (SE)	1.86 (0.55)	
Basin Mangroves		
Monospecific		
Fort Myers, SW Florida, USA	3.51	Twilley et al. (in press)
Rookery Bay, SW Florida, USA	5.38	
Rookery Bay, SW Florida, USA	4.69	
Clam Bay, SW Florida, USA	5.79	Heald et al. 1979
S. Thailand	6.70	Christenson 1978
Mixed Forest		
Fort Myers, SW Florida, USA	8.68	Twilley et al. (in press)
Rookery Bay, SW Florida, USA	7.51	
Piñones, Puerto Rico	9.70	Pool et al. 1975
Turkey Pt., SE Florida, USA	7.50	Snedaker and Brown 1981
Mean ± (SE)	6.61 (0.70)	
Fringe and Overwash Mangroves		
Ten Thousand Is., Florida, USA	10.24	Snedaker and Brown 1981
Ten Thousand Is., Florida, USA	9.81	
Turkey Pt., SE Florida, USA	10.82	
Turkey Pt., SE Florida, USA	7.71	Pool et al. 1975
North River, Florida, USA	8.76	Heald 1969
Cieba, Puerto Rico	6.64	Pool et al. 1975
Mean ± (SE)	9.00 (0.72)	
Riverine Mangroves		
Ten Thousand Is., Florida, USA	10.66	Snedaker and Brown 1981
Ten Thousand Is., Florida, USA	11.73	
Chokolskee Bay, Florida, USA	11.75	Sell 1977
Chokolskee Bay, Florida, USA	11.83	
Gordon River, SW Florida, USA	14.43	
Gordon River, SW Florida, USA	9.09	
Vacia Talega, Puerto Rico	14.45	Pool et al. 1975
El Encanto River, Columbia	14.09	Hernández and Mullen 1979
Sungai Merbok Estuary, Malaysia	10.07	Ong et al. 1981
Matang Mangrove Forest, Malaysia	23.4	Ong et al. 1982
Mean ± (SE)	12.98 (1.01)	

movement, not only as a source of silts and clays, but also a supply of nutrients and aeration for optimal growth. Together with the trends observed for different groups of mangroves, these results for a variety of wetlands suggest that the chemical and kinetic properties of tides in intertidal environments may ultimately be expressed in the magnitude of litter and/or net primary production of the plant community.

The Gambia

There is no published information on the magnitude of litter productivity of mangroves along the Gambia River estuary. In order to evaluate the potential importance of these forests to estuarine resources, litter productivity is a very important index. This report estimates litter productivity of mangroves in the Gambia estuary using an association between forest structure and litter productivity based on information for mangrove forests in United States, Puerto Rico, and Costa Rica (Pool et al. 1975, Pool et al. 1977). An index of forest structure for eight sites in these three provinces was based on tree height (Ht), basal area (BA), and tree density (D) for 0.1 ha plots using the formula: (Ht x BA x D) 1,000. This is similar to Holdridge et al.'s (1971) complexity index, with the omission of the number of species present. Structural index (X) for each site (Pool et al. 1977) was positively correlated with the litter productivity estimates (Y) made at each site (Pool et al. 1975) (Fig. 9). The equation [$Y = 4.89(X) + 5.05$, $r^2 = 0.85$] results in a Y intercept of + 5.05 $t \cdot ha^{-1} \cdot yr^{-1}$. Such a high intercept is due to the fact that structural statistics were gathered only on trees with dbh >10 cm. Since all forestry statistics for mangroves in The Gambia are based on this dbh, this relationship was used.

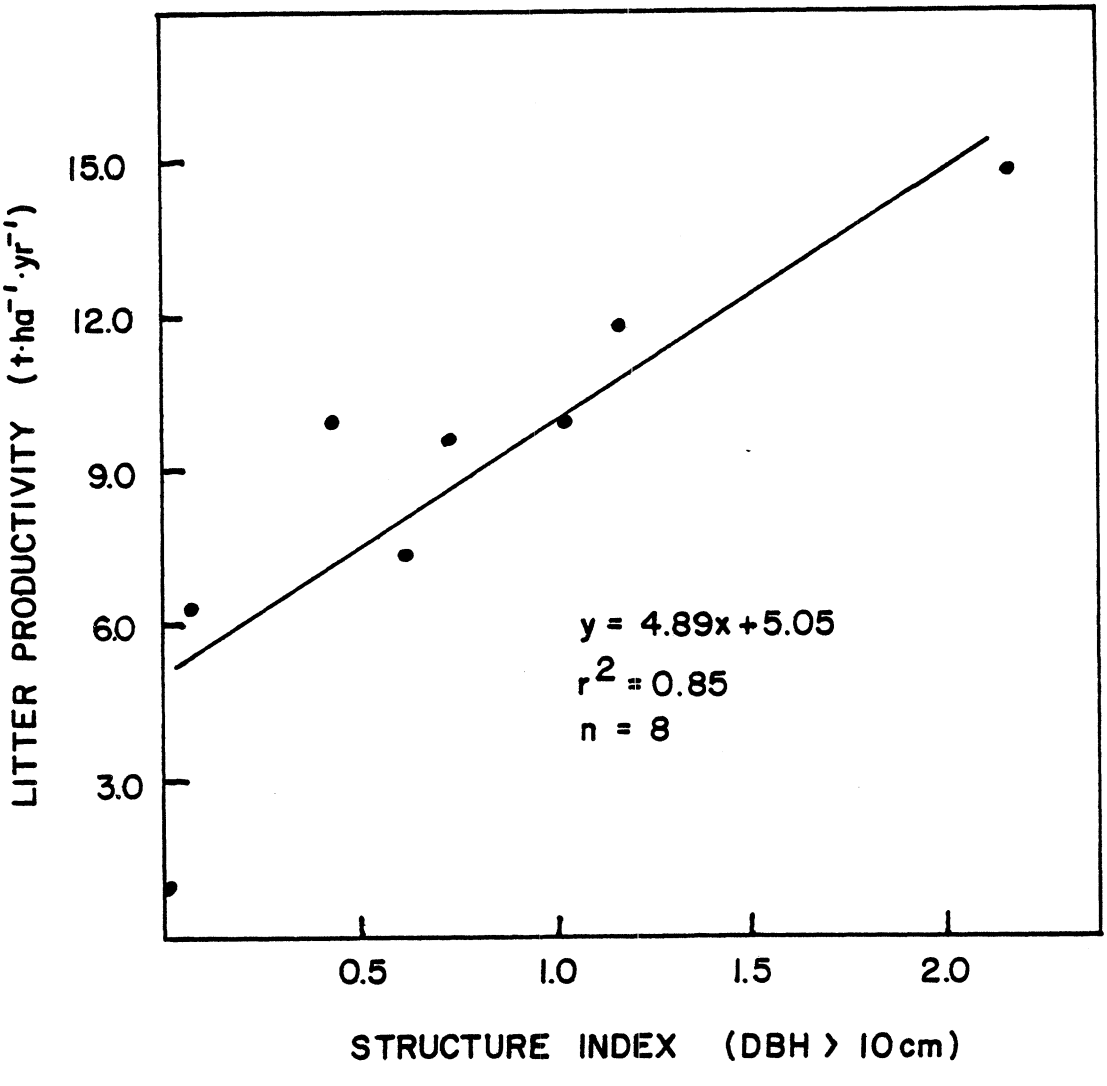

FIG. 9. Relationship among structural indexes of mangrove forests and their litter productivity estimates.

Using this relationship between forest structure and litter productivity, estimates of the productivity of mangroves along the Gambia River estuary were made based on previously discussed forest structure statistics (Table 6). The structural indexes for the four categories of mangrove forests (based on tree heights) used by Johnson (1978) are: Rhizophora trees >20 m = 2.81; Rhizophora trees 7-20 m = 1.09; Avicennia trees >7 m = 1.34; and Avicennia plus Rhizophora trees <7 m = no forestry statistics available. The resulting litter productivity estimates varied from 10.4 to 18.8 $t \cdot ha^{-1} \cdot yr^{-1}$, which are within the range for riverine mangroves listed in Table 5 (Twilley et al. in press). The litter productivity value for the forests with tree heights <7 m was based on a value for a mixed forest in South Florida that upon observation by the author was similar to the structure of these forests in The Gambia (Fort Myers, SW Florida, USA; See Table 5). This value is considered a conservative estimate.

The areal production of litter for mangrove forests above and below Balingho are calculated from areal distributions estimates of mangroves by Johnson (1978) and Abell (1980), respectively. The total production was 583,670 $t \cdot yr^{-1}$, of which 115,380 $t \cdot yr^{-1}$ (20%) occurred in the impacted area above the proposed barrage at Balingho (Table 6).

Estimates were also made of litter productivity of Rhizophora forests with tree heights >7 m in The Gambia using forestry statistics by Forster (1983). This category of forests produced 132,780 $t \cdot yr^{-1}$ of dry litter mass, most of which occurred in the North Bank and MacCarthy Division of The Gambia (Table 7).

TABLE 6. Estimates of litter production (dry mass) for the mangroves above and below Yelitenda based on information from Johnson (1978) and Abell (1980). Mangrove categories are based on species and tree heights (m).

Category	Structural Index	Production Estimate ($t \cdot ha^{-1} \cdot yr^{-1}$)	Area (ha)	Annual Production ($t \cdot yr^{-1} \times 10^3$)
Above Yelitenda				
Rhizophora: >20 m	2.81	18.8	3,605	67.77
Rhizophora: 7-20 m	1.09	10.4	3,406	35.42
Avicennia: >7 m	1.34	11.6	708	8.21
Avicennia plus Rhizophora: <7 m	NA	4.0	994	3.98
Subtotal			9,713	115.38
Below Yelitenda				
Rhizophora: >20 m	2.81	18.8	2,520	47.38
Rhizophora: 7-20 m	1.09	10.4	18,330	190.63
Avicennia: >7 m	1.34	11.6	8,310	96.40
Avicennia plus Rhizophora: <7 m	NA	4.0	33,470	133.88
Subtotal			62,630	468.29
Total			71,343	583.67

TABLE 7. Estimates of litter production (dry mass) for Rhizophora mangroves with tree heights >7 m based on data from Forster (1983).

Category	Structural* Index	Production Estimate ($t \cdot ha^{-1} \cdot yr^{-1}$)	Area (ha)	Annual Production ($t \cdot yr^{-1} \times 10^3$)
Western Division	0.48	7.4	4,692	34.72
Lower River Division	0.73	8.6	4,291	36.90
North Bank Division	1.25	11.2	5,461	61.16
MacCarthy Division	1.00	9.9		
Total			14,444	132.78

*Structural Index = (Basal Area x Tree Height x Density) ÷ 1000; based on 0.1 ha plots

EXCHANGE OF DETRITUS AND NUTRIENTS

Estuarine ecosystems are coupled to intertidal wetlands by tides that create a two-way flux of materials. Problems associated with the measurement of these tidal fluxes have resulted in a controversy surrounding the hypothesis that intertidal wetlands affect the productivity and nutrient cycles of estuarine waters (Teal 1962, Odum and de la Cruz 1963, de la Cruz 1965, Day et al. 1973, Haines 1977, Haines 1979, Nixon 1980, Odum 1980). Estimates of organic carbon export from intertidal wetlands range from 45% (Teal 1962, Axelrad et al. 1976, Roman 1981) to less than 1% (Heinle and Flemer 1976) of their net production, while other intertidal wetlands may import organic carbon (Woodwell et al. 1977). The present view is that the exchange of organic carbon in intertidal wetlands may be site specific depending on the geomorphology and tidal hydrology of the region (Mann 1975, Odum et al. 1979, Welsh et al. 1982). Mangroves represent nearly 75% of the intertidal vegetation in the tropics and

the exchange of detritus and nutrients with these forests may strongly influence the productivity of tropical coastal ecosystems.

Detritus

Background. Organic carbon export estimates for riverine and fringe mangroves represent rates for intertidal wetlands regularly inundated by tides. In an Australian riverine mangrove forest, particulate organic matter export was 420 $gC \cdot m^{-2} \cdot yr^{-1}$, which was about 94% of litter fall (Boto and Bunt 1981). Particulate detritus export from fringe mangroves in south Florida was estimated at 186 $gC \cdot m^{-2} \cdot yr^{-1}$, or only 42% of litter fall (Heald 1969). The tides in the riverine forest were 3 m/tide, for an annual tidal amplitude of about 2,190 m; compared to 0.5 m/tide in south Florida or 355 $m \cdot yr^{-1}$ in the fringe forest. Both of these export estimates are for leaf litter and particulate carbon export only, and do not include export of DOC to adjacent estuarine systems.

Total organic carbon export from infrequently flooded basin mangroves was 64 $gC \cdot m^{-2} \cdot yr^{-1}$ (Twilley 1985). The annual tidal amplitude inside the basin forests was only 12 m, and as a result only 22% of the litter fall inputs to the forest floor were exported (Twilley 1982). In forested wetlands with no tidal influence, TOC export was only about 6% of the litter production rate (Day et al. 1977, Mulholland 1981). These comparisons suggest that tides influence what proportion of litter produced in mangroves is exported, and that the magnitude of this organic carbon export from mangroves is directly related to the cumulative tidal amplitude within the forests (Fig. 10).

Nearly 75% of the TOC exported from the basin mangrove forests was dissolved organic carbon. DOC also dominated total organic carbon flux from intertidal marshes (Axelrad et al. 1976, Happ et al. 1977, Pendleton 1979, Roman

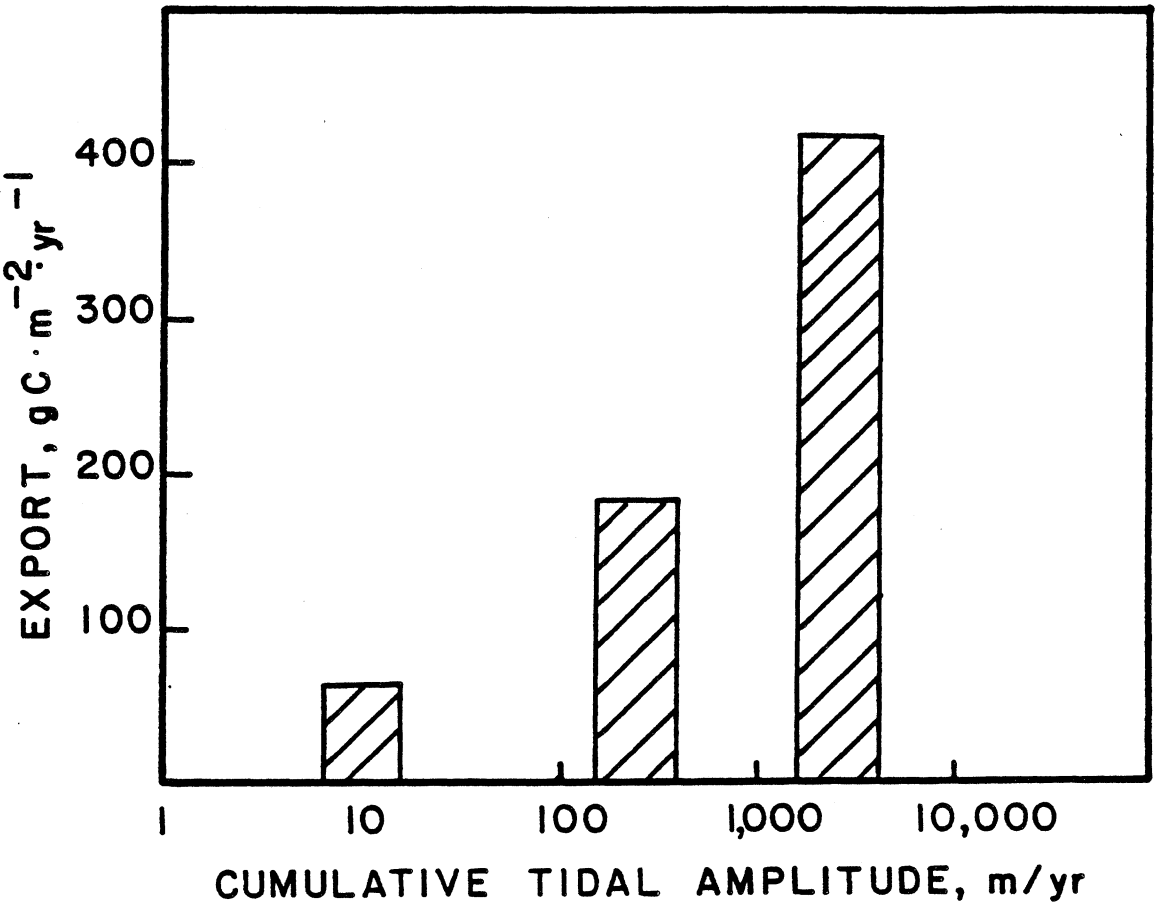

FIG. 10. Annual net export of organic carbon from mangrove forests in relation to the cumulative tidal amplitude per year in the forest. Export values (left to right) are for basin (Twilley 1985), fringe (Heald 1969), and riverine (Boto and Bunt 1981) mangroves.

1981), and more than 93% of the total organic carbon export from bottomland hardwood swamps (Mulholland and Kuenzler 1979). Mulholland and Kuenzler (1979) attributed higher DOC export from forested wetlands compared to uplands to higher water residence time in wetlands together with leaching of organic carbon from the litter. Leaching of DOC from mangrove leaf litter, particularly from black mangrove leaves, accounted for the initial high loss of leaf dry mass during decomposition (Twilley 1982), thus providing a source of DOC to the surface water of these forests. The effect of water residence time on DOC concentrations coincides with the observation in basin mangrove forests that these concentrations decreased during August and September when tidal frequency increased (Twilley 1985).

Rainfall also increases the export of DOC from basin mangroves, similar to results for salt marshes (Harris et al. 1980, Roman 1981). The inputs of organic carbon from the forest canopy to the surface water via stemflow and throughfall increased the DOC concentrations in the surface water. This mechanism, and probably others, account for DOC being the major form of organic carbon export from most intertidal wetlands, which has only been substantiated in recent studies. During the infancy of the "outwelling" concept of detritus flux from intertidal wetlands only particulate detritus was measured, thus grossly underestimating the potential contribution of organic carbon from these systems to estuarine waters.

Rates of organic carbon export from mangroves are dependent on the volume of tidal water inundating the forest each month, which may be influenced most by tidal frequency (Twilley et al. in press). As a result, export rates are usually seasonal in response to the seasonal rise in mean sea level (msl), with greatest quantities of export occurring from August to October and lowest values

from December to May for mangroves in South Florida. This supports the proposal by Kjerfve et al. (1978) that an increase in msl during the summer may influence material exchange in tidal creeks as a result of increased tidal inundation of wetlands along the southeastern coast of the USA.

The residence time of litter on the forest floor of mangroves is controlled by the relative influence of leaf decomposition and export. A comparison of the litter production, storage, and export characteristics of riverine (Boto and Bunt 1981), fringe (Heald 1969, Pool et al. 1975), and basin mangroves (Twilley et al. in press) summarizes the effect of these two factors on litter dynamics among mangrove forests (Fig. 11). The annual estimates of cumulative tidal amplitude in these three forest types is 2,190 m, 355 m, and 15 m, respectively. As discussed by Twilley (1985), the export of organic carbon from mangroves is associated with increased tidal influence, as may be litter production. Yet the two are not proportional, since litter production in the riverine forest is 1.7 times that of the basin forest, while the difference in litter export is 7.3 times higher in the riverine forest. As tidal influence within mangrove forests increases, leaf export dominates organic carbon export, and thus the ratio of organic carbon export to litter production increases. Such ratios are 0.94 in riverine forests (Boto and Bunt 1981) where leaf litter on the forest floor is negligible. Consequently, leaf decomposition rates for Rhizophora leaves are not proportional to residence times of litter in either fringe or riverine forests since most of the leaf litter is exported.

For basin mangrove forests, organic carbon export is only about 20% of the carbon input to the forest floor via litter fall (Twilley 1985), and litter standing crop ranges from 100 to 500 g dry mass$\cdot m^{-2}$. Although the seasonal standing crop values of litter decreased as tidal influence increased, this

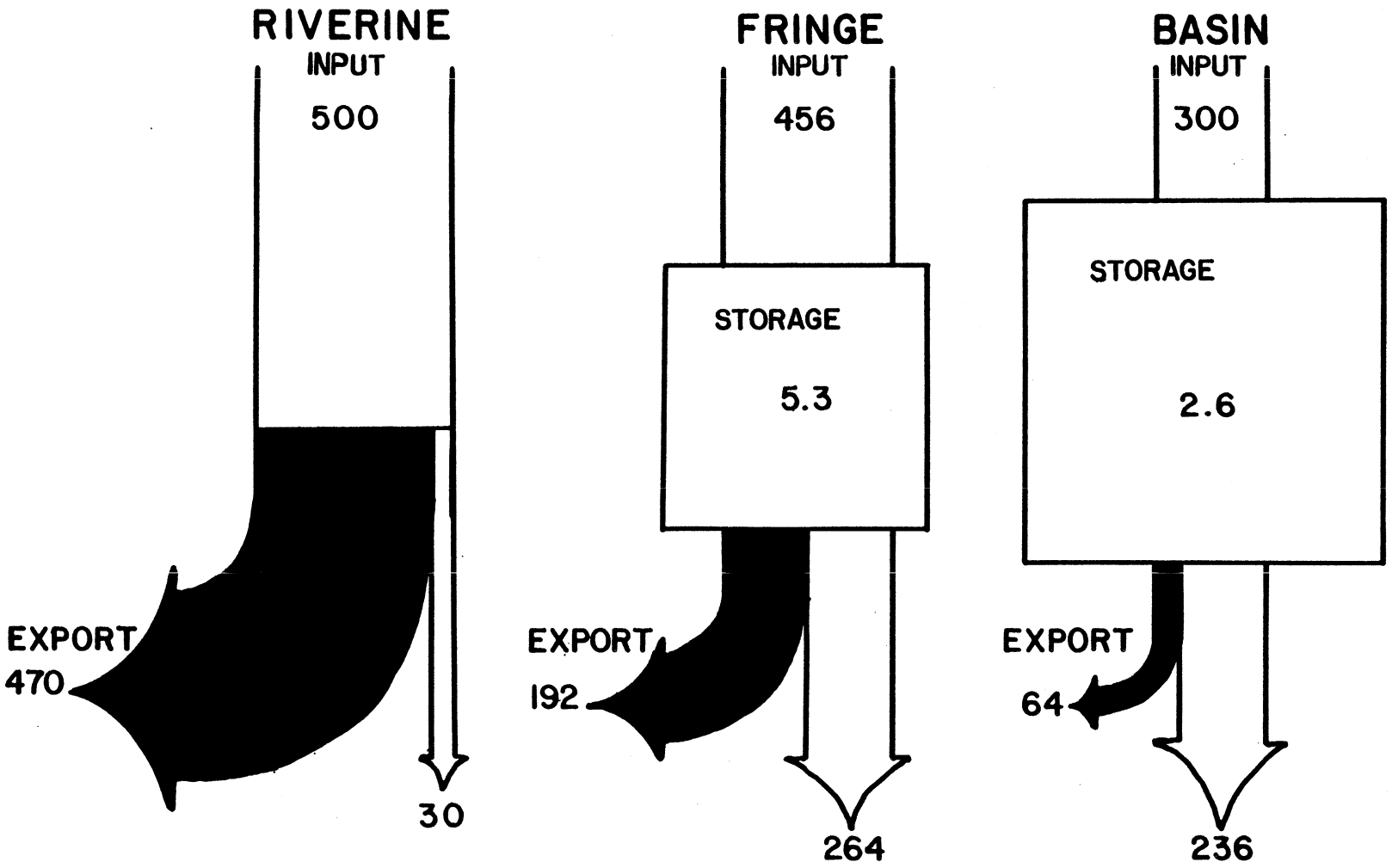

FIG. 11. Summary of organic carbon inputs (litter fall), storages (litter standing crop), and losses (export and other losses including decomposition and peat production) associated with the litter of a riverine (Boto and Bunt 1981), fringe (Heald 1969, Pool et al. 1975), and basin (Twilley et al. in press) mangrove forest. The litter fall and standing crop values for the basin forest are from Rookery Bay Forest 1 based on area weighed results for the mixed and monospecific zones. Storages are in $gC \cdot m^{-2}$ and flows in $gC \cdot m^{-2} \cdot yr^{-1}$.

response can be explained by the effects of hydrology on leaf decomposition (Twilley et al. in press). Export of leaves from basin mangroves was negligible during the summer (Twilley 1985) when minimum litter values were observed.

The residence times of leaf litter in basin mangroves vary from 0.13 to 0.51 yr (Table 8). Leaf litter residence times for monospecific basin forests at Rookery Bay are similar to values for riverine forests, which indicates that under some conditions the relative influence of export and decomposition on litter dynamics may be equal. However, as indicated in Figure 11, the short residence time of leaf litter in riverine systems represents a loss from the system, while leaf fragmentation in basin forests results in the formation of peat deposits which are characteristic of these inland forests (Davis 1943). The organic carbon content of alluvial mangrove soils are only 4-5% (dry mass) (Hesse 1961, Giglioli and Thornton 1965), compared to about 20% for basin mangrove forests (Coultas 1978, Twilley 1982).

The Gambia. Estimates of detritus export from mangroves along the Gambia River estuary were based on litter productivity values calculated above, and on assumptions of the percentage of this litter that is exported annually. As previously discussed, these export:production ratios for litter are strongly influenced by tidal hydrology, and range from 0.20 for basin mangrove forests to 0.94 for riverine mangroves. Based on these considerations, and a tidal amplitude of 1.2 m in the riverine forests of the Gambia estuary, an E:P ratio of 0.75 was applied to forests in the intertidal zone flushed daily by tides (Rhizophora >20 m and Rhizophora 7-20 m). Avicennia forests and mixed forests of Rhizophora and Avicennia inhabit more inland areas of the intertidal zone and thus E:P ratios of 0.5 were applied to these sites. Based on these E:P ratios

TABLE 8. Estimates of detritus export as dry mass and as carbon from mangroves along the Gambia River estuary. Mangrove categories are based on species and tree heights (m).

Category	Litter Production: Per Area ($t \cdot ha^{-1} \cdot yr^{-1}$)	Litter Production: Total ($t \cdot yr^{-1} \times 10^3$)	E:P* Ratio	Export: Dry Mass ($t \cdot yr^{-1} \times 10^3$)	Export: Carbon** ($t \cdot yr^{-1} \times 10^3$)
Above Yelitenda					
Rhizophora: >20 m	18.8	67.77	0.75	50.83	24.40
Rhizophora: 7-20 m	10.4	35.42	0.75	26.57	12.75
Avicennia: >7 m	11.6	8.21	0.50	4.11	1.97
Avicennia plus Rhizophora: <7 m	4.0	3.98	0.50	1.99	0.96
Subtotal		115.38		83.50	40.08
Below Yelitenda					
Rhizophora: >20 m	18.8	47.38	0.75	35.54	17.06
Rhizophora: 7-20 m	10.4	190.63	0.75	142.97	68.63
Avicennia: >7 m	11.6	96.40	0.50	48.20	23.14
Avicennia plus Rhizophora: <7 m	4.0	133.88	0.50	66.94	32.13
Subtotal		468.29		293.65	140.96
Total		583.67		377.15	181.04

*Ratio of export to litter production in these mangrove groups according to Twilley et al. (in press)

**Assuming carbon concentration of 48% per gram dry mass (Twilley 1982)

and litter productivity estimates for each category of forests, the export of detritus from mangroves of the Gambia River estuary was calculated for areas above and below Balingho (Table 8). Litter dry mass is usually about 48% carbon (Twilley 1982); from this assumption estimates of organic carbon export from these riverine mangroves were made. Total export was 181,040 $tC \cdot yr^{-1}$, of which 40,080 $t \cdot yr^{-1}$ (22%) occurred from above Balingho. Based on a total area of mangroves along the Gambia River estuary (Johnson 1978, Abell 1980; equals 71,343 ha), detritus export is estimated at 289 g $C \cdot m^{-2} \cdot yr^{-1}$ (per m^2 of mangrove).

Cumulative tidal amplitude in the mangroves of the Gambia estuary is 876 $m \cdot yr^{-1}$ (1.2 m amplitude x $2 \cdot day^{-1}$ x 365 $d \cdot yr^{-1}$). Using the relationship between tidal hydrology and detritus export in Figure 10, the magnitude for export from mangroves of the Gambia estuary should range from 200 to 400 $gC \cdot m^{-2} \cdot yr^{-1}$. The estimate above based on litter production and export to production ratios falls within this range.

Annual patterns in precipitation and levels of spring high tides (Fig. 12) indicate that detritus export would be maximum from July to October.

Nutrients

Introduction. Intertidal forested wetlands may function as either a source or a sink of nutrients to estuarine waters. Nixon (1980) argued that the paradigm in ecology that wetlands are a nutrient sink contradicts the "outwelling" concept of marshes proposed by Odum (1980). Yet in his review, Nixon (1980) summarized that the "outwelling" of detritus from marshes may be about 100 gC $m^{-2} \cdot yr^{-1}$, less than previously estimated, while both the net flux of nitrogen and phosphorus may be from coastal waters into the marsh. Thus in-

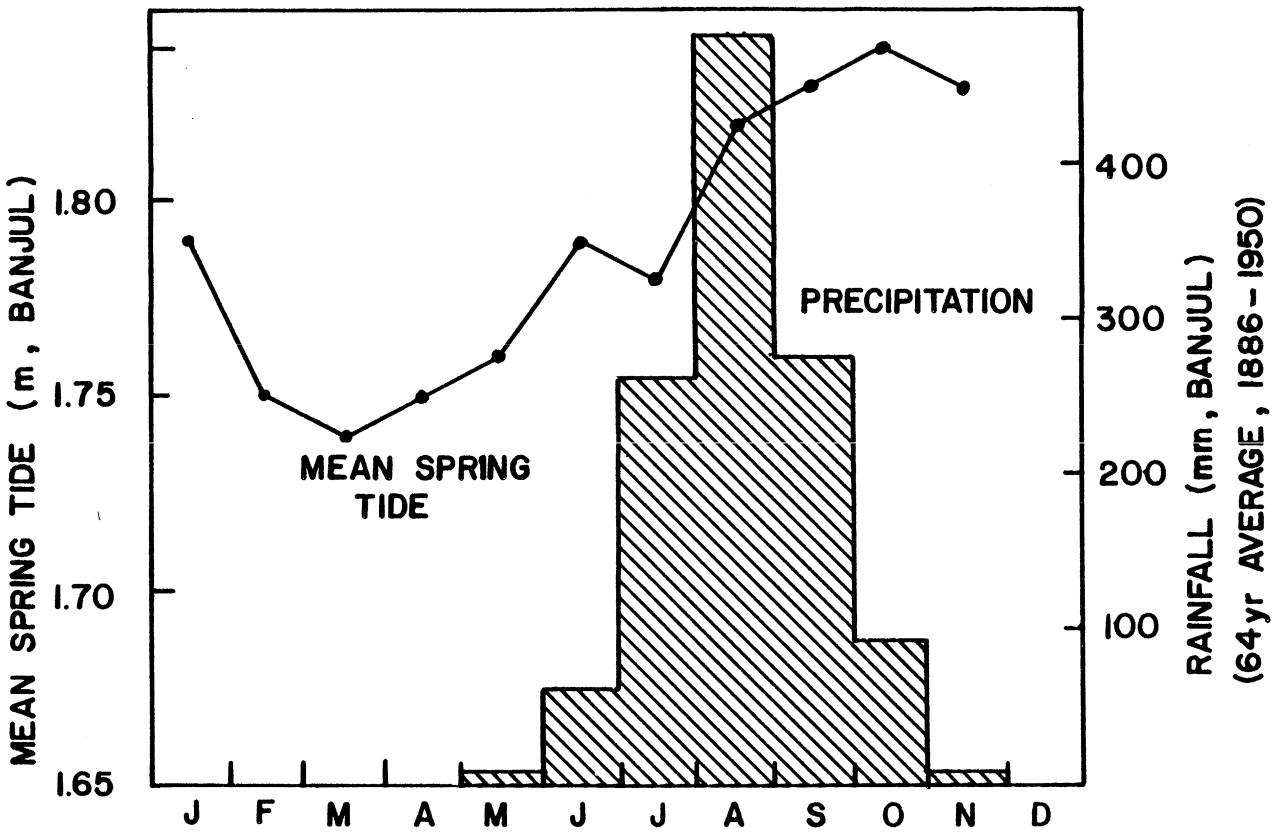

FIG. 12. Annual patterns of precipitation and tidal heights of spring tides (Gambia Ports Authority 1983) in the Gambia River estuary.

tertidal wetlands may be able to function both as a source of detritus and a sink of nutrients in estuarine ecosystems. However, as discussed above for detritus flow, the function of a system as sink or source of nutrients is probably dependent on site-specific characteristics such as regional hydrology and geomorphology (Odum et al. 1979).

The net flux of nutrients among intertidal wetlands and coastal waters may depend on the transformations of nutrients among inorganic and organic forms, and the fate of these forms of nutrients in the marsh. Two major mechanisms associated with the loss of nutrients within the marsh are burial of organic and inorganic materials, and gaseous exchange with the atmosphere.

Burial is associated with the accumulation of organic matter from plant material that remains in the marsh following losses due to decomposition and export. Recently it has been demonstrated that the belowground biomass of intertidal wetlands may be more productive than aboveground structures, and thus represents a large potential source of organic matter for the accumulation of peat. Nutrients assimilated by the biomass during the growing season are lost from the system via burial of this plant detritus deep into the sediments.

Sediments entering the marsh from adjacent estuarine waters may also be transporting nutrients adsorbed to their surfaces, and these particles are deposited and buried in the peat of intertidal wetlands. These adsorption mechanisms are also associated with organic matter within the marsh, and have been shown to be important in the accumulation of metals in marsh systems. Thus nutrient sinks via burial may result from the absorption and adsorption of nutrients entering intertidal wetlands from either coastal waters and/or upland runoff.

For carbon, sulfur, and nitrogen, the net exchange of nutrients with the atmosphere may be paramount to understanding the source or sink characteristic of an intertidal wetland. Since nitrogen is most often indicated as potentially limiting primary production of estuarine ecosystems, we will emphasize its atmospheric cycle in this discussion. Large pools of organic material and bacterial biomass in the top decimeter of the marsh surface result in a high demand for electron acceptors. Denitrification is a collection of processes by which nitrate (NO_3^-) is utilized as an electron acceptor and nitrogen is converted to either N_2O or N_2. The latter form of nitrogen gas may be the dominant product of denitrification in marine and estuarine intertidal wetlands. Since N_2 is highly insoluble and so little of it is recycled by nitrogen fixation, denitrification represents a potential loss of nitrogen from the system. Denitrification rates are dependent on the supply of nitrate, thus nitrification rates ($NH_4^+ \rightarrow NO_3^-$) and/or the input of NO_3 from estuarine waters and/or upland runoff, strongly influence the magnitude of this nitrogen sink in intertidal wetlands.

The magnitude of nutrient loss via burial and atmospheric exchange relative to the recycling of nutrients within the wetland, along with the net exchange of nutrients with estuarine waters at the wetland boundary, will determine the function of these systems as a nutrient source or sink in estuarine ecosystems.

The Gambia. Sources and sinks of nutrients in the Gambia River estuary were evaluated using mixing diagrams of dissolved nutrients during October and November 1983 (Berry et al. 1985). Concentrations of nitrogen, phosphorus, and total suspended solid were determined on samples collected along longitudinal transects of the estuary as well as along the Bai Tenda bolon during cruises

aboard the R/V Laurentian. Mixing diagrams are plots of salinity along the "X" axis and the nutrient concentrations along the "Y" axis. A straight line between the two end members is called the theoretical dilution line and represents concentrations based on dilution along the salinity gradient. Variation from this theoretical line represents concentrations that result from processes that cause either a sink (below the theoretical line) or source (about the theoretical line) of that nutrient along the estuarine axis (see Liss 1976 for discussion).

Dilution plots of nitrate along the Gambia River estuary indicate a source of this nutrient occurs in the oligohaline regions of the estuary during October. This source of nitrate is due to nitrification in the water column as indicated by a decrease in ammonium concentrations and a sag in the percentage of saturated dissolved oxygen in this upper region of the estuary. Nitrate concentrations reached nearly 300 $\mu g \cdot L^{-1}$ near Elephant Island about 200 km from the estuary mouth (Fig. 13). By November, the source of nitrate in low salinity waters was diminished with peak concentrations of only 225 $\mu g \cdot L^{-1}$ (Fig. 13). This dilution plot also indicates that a process resulting in a nitrate sink may be occurring further down the estuary. Phosphate also is being produced along the estuary in October and November, particularly in the mesohaline areas where concentrations may reach 25 $\mu g \cdot L^{-1}$. Dilution plots of total suspended solids indicate that the estuary retains a major portion of the sediment load within the system. Sediment deposition was most noticeable in the oligohaline areas where concentrations decreased from 100 to about 25 $mg \cdot L^{-1}$.

Mixing diagrams were also used to evaluate the net flow of nutrient exchange in the mangrove bolons (Fig. 14). Changes in nutrient concentration at a station during a tide may only reflect the movement of nutrients in a parcel of

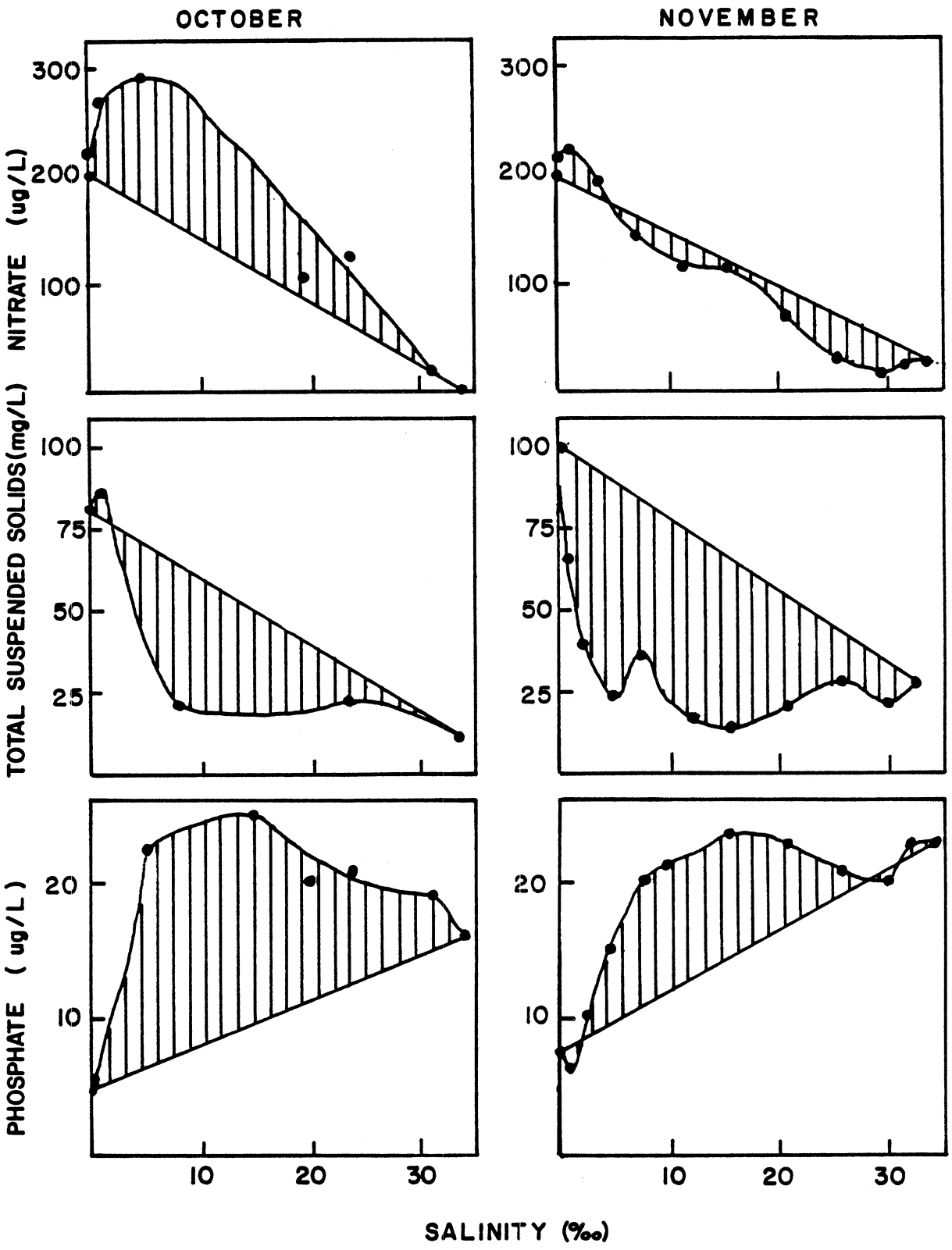

FIG. 13. Mixing diagrams for nitrate, total suspended solids, and phosphate along the Gambia River estuary during October and November, 1983.

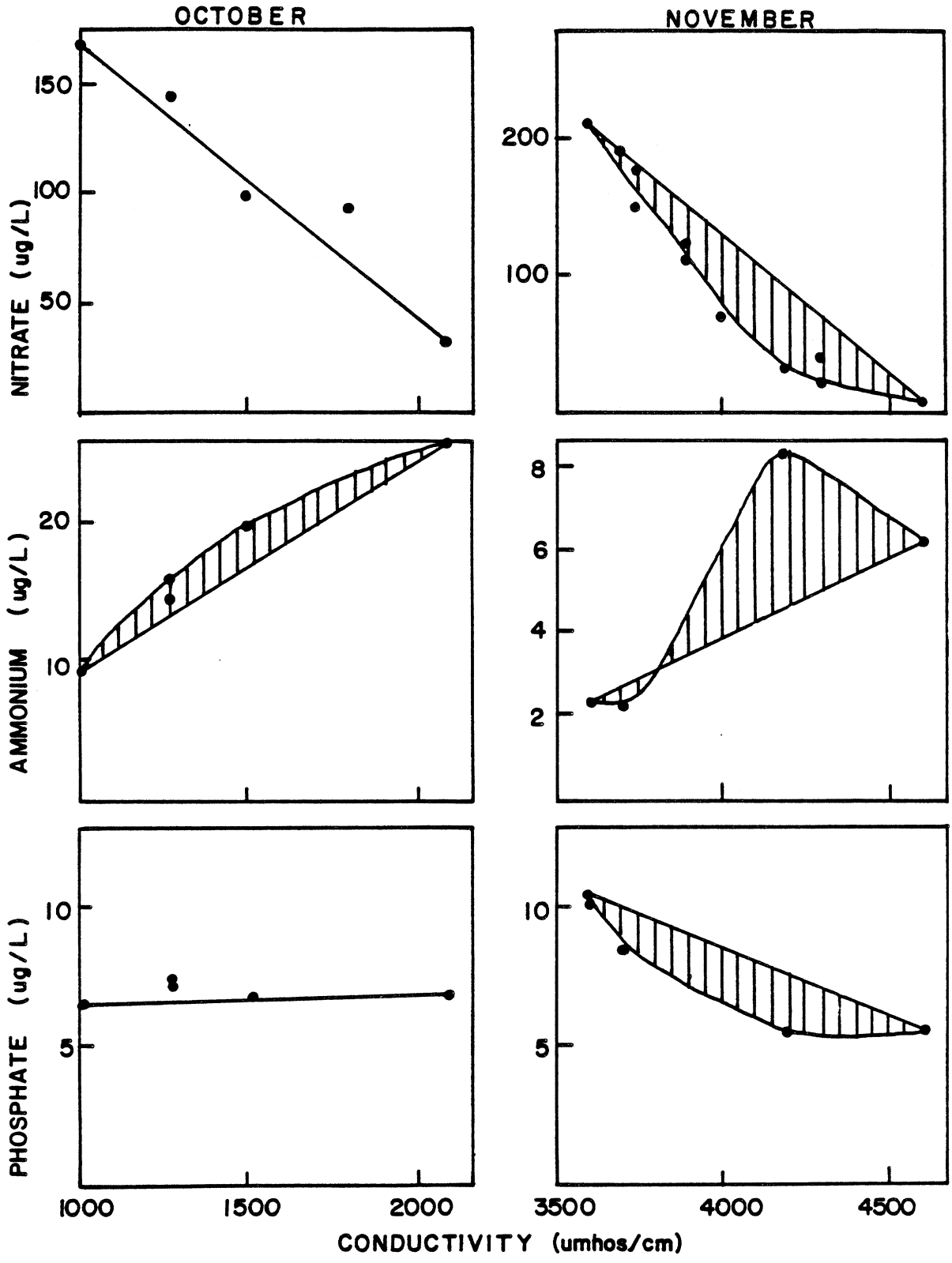

FIG. 14. Mixing diagrams for nitrate, ammonium, and phosphate along the Bai Tenda bolon in the Gambia River estuary during October and November, 1983.

water and not any net change due to processes within the bolon. Evapotranspiration causes higher salinities (conductivities) in the headwaters of a mangrove bolon, thus salt can be used as a tracer of water exchanging with mangroves during a tide. Using conductivity and nutrient concentrations of water at five stations in the Bai Tenda bolon during ebb tides, dilution plots were made to evaluate the fate of these nutrients in the bolons. Negative slopes were observed for nitrate and phosphate indicating that concentrations of these nutrients are much higher in the estuary than in the bolon headwaters. This was particularly evident for nitrate that varied from 210 $\mu g \cdot L^{-1}$ at the mouth of a bolon to about 10 $\mu g \cdot L^{-1}$ in the mangroves. For both these nutrients, dilution plots indicate that concentration may be only attributed to dilution during October; yet during November, a sink for both nutrients was observed along the bolon. A loss of suspended solids was also observed within the bolons with deposition occurring in the headwaters. In contrast to these parameters, diagrams of ammonium indicated that this reduced form of nitrogen was being produced within the mangroves, probably a result of high mineralization rates associated with these organic soils.

These dilution plots suggest that mangroves along the Gambia River serve as a nutrient sink for nitrate and phosphate, and trap total suspended material from estuarine waters. These three parameters have peak concentrations along the mesohaline and oligohaline regions of the estuary where mangrove forests are most prominent. Nitrate may be utilized in the sediments of these plant communities as an electron acceptor (denitrification) and phosphate may be adsorbed by sediments or organic material. Mangroves have been recognized as contributing to the stabilization of shorelines by accumulating riverborne sediments. However, these functions are only suggested by the data analysis

presented, and the role of these forested ecosystems in nitrogen, phosphorus, and sediment budgets of the Gambia River ecosystem awaits more complete investigation.

ALLOCHTHONOUS ORGANIC MATTER

Background

There are three major sources of organic matter utilized by secondary consumers in estuaries: autochthonous production from phytoplankton and benthic autotrophs (algae and seagrasses), allochthonous detritus from upland watersheds (riverine input), and finally allochthonous detritus from intertidal wetlands. Collectively, these pools of organic matter support the high consumption of energy characteristic of estuarine ecosystems. Many economically important fisheries, such as shrimp, use the estuary for a nursery consuming large quantities of food during their most active stages of growth. Thus, the sources of organic matter in estuaries must be sustained in order to maintain these high rates of secondary productivity.

Much controversy has existed over the relative importance of these three sources of organic matter in estuarine ecosystems. Salt marshes were established as the major source of detritus sustaining secondary production in estuarine waters based on their high net primary production and detritus export rates (Teal 1962). Turner (1977) has also demonstrated the relationship between fishery yields in some coastal waters (kg of shrimp harvested) to the amount of marsh land in the area. However, Haines (1977, 1979) has argued that detritus from phytoplankton and riverine sources may be more important than marsh detritus in estuaries. She found that the del ^{13}C ratio of detritus in estuaries reflected the C-3 autotrophic pathway of phytoplankton and forested

wetlands rather than the C-4 mechanism associated with saltmarsh net production. Other investigators using del ^{13}C data have observed a diversity of ratios implicating all three sources of nutrition for secondary consumers depending on which source of detritus was most available (Macko and Zieman 1983). Sources of detritus can vary considerably among estuaries and are related to the geomorphological, hydrological, and physical characteristics of the system (Mann 1975, Odum et al. 1979, Welsh et al. 1982).

The importance of a source of detritus in an estuary may thus be related to its contribution to the organic matter pool within the system. In south Florida, Macko and Zieman (1983) concluded from del ^{13}C ratios that the major source of nutrition for penaeid shrimp in Rookery Bay was mangrove detritus. Based on a budget of autochthonous and allochthonous inputs of organic matter to this estuary, Twilley (1982) also concluded that mangrove detritus was a major source of energy for secondary productivity in this system. Since detritivores are basically nonselective in acquiring their food, compared to herbivores, their dependence on a specific source of detritus may be related to its availability. Thus a budget of the relative sources of organic matter from autochthonous net production, river discharge, and mangrove export to the pool of organic matter in the Gambia estuary may reflect the importance of these sources of detritus to the fisheries of this system.

The Gambia

The annual net production of phytoplankton of the Gambia estuary was estimated from data collected on four cruises on the R/V Laurentian (Healey et al. 1985). The estuary was divided into three segments (Lower - Banjul to Mootah Point; Middle - Mootah Point to Kauntaur; Upper - Kauntaur to Goulombo)

and net production was measured at four times during the year within each segment using ^{14}C uptake in light and dark BOD bottles incubated at various depths at each station. Net production was converted to a daily per m^2 rate by integrating production with depth and assuming a production period of 9 $h \cdot d^{-1}$. Mean net productivity ranged from 0.7 to 152.9 mg C $\cdot m^{-2} \cdot d^{-1}$ for the estuary, and these minimum and maximum rates occurred in the mid-estuary stations (Table 9). There was no consistent seasonality with minimum and maximum rates, except that lower rates in the mid and upper estuary stations were associated with higher sediment load during high river discharge. Annual net production was 20.45, 25.54, and 10.55 $gC \cdot m^{-2} \cdot yr^{-1}$ at the lower, middle, and upper estuary stations of the Gambia River (Table 9).

Based on these rates, and the areal dimensions of each segment, net primary productivity of the Gambia estuary was estimated at 14,782 $tC \cdot yr^{-1}$ (Table 9). Nearly 57% of this total occurred from Banjul to Mootah Point. Riverine input of organic carbon to the Gambia River estuary at Goulombo is estimated at 15,960 $tC \cdot yr^{-1}$ (Lesack et al. 1984). Allochthonous inputs of organic carbon from mangrove wetlands along the Gambia estuary were estimated at 181,040 $tC \cdot yr^{-1}$ (Table 10). Thus, the total amount of organic carbon available for secondary production within the Gambia River estuary annually is about 211,782 tC (Table 10). Of this total, about 85.5% is contributed by the mangrove forests, while phytoplanktonic and riverine sources account for about 7% each. There are no estimates for benthic net production from algae and/or seagrasses, yet this is probably minimal due to the high turbidity of this system.

Estimates for phytoplankton and riverine inputs are based on actual organic carbon measurements. Inputs of detritus from mangroves are based on estimates of litter fall and export:litter production ratios (these export ratios are

TABLE 9. Seasonal and annual estimates of net primary productivity (^{14}C uptake) of phytoplankton in the Gambia River estuary. (Lower = Banjul to Mootah Point; Middle = Mootah Point to Kauntaur; Upper = Kauntaur to Goulombo).

Description	Lower	Middle	Upper	Sum
	Seasonal Rates (mg $C \cdot m^{-2} \cdot d^{-1}$)			
August	52.2	121.5	62.3	
October	78.0	0.7	12.7	
December	64.0	2.5	13.5	
March	30.3	152.9	26.5	
		Annual Rates		
Per m^2 ($gC \cdot m^{-2} \cdot yr^{-1}$)	20.45	25.54	10.55	21.42
Per segment ($tC \cdot yr^{-1}$)	8,405	5,849	528	14,782

TABLE 10. Estimates of annual inputs of total organic carbon to the Gambia River estuary (Banjul to Goulombo) from net primary primary production of phytoplankton, riverine discharge, and mangrove export.

Source	TOC Inputs (tC/yr)	Reference
Phytoplankton	14,782	Healey et al. 1985
Gambia River	15,960	Lesack et al. 1984
Mangroves	181,040	This study
Total	211,782	

based on tidal amplitude). The estimates of detritus export from mangroves along the Gambia River estuary are within the range for mangroves under similar tidal amplitude. Even if these estimates are off by 50% (90,520 $tC \cdot yr^{-1}$), mangrove detritus would still represent nearly 75% of the total organic carbon pool available for secondary productivity.

MANGROVES AND FISHERIES

Introduction

One of the most important assets of estuaries as a natural resource to humans is their function as a nursery for a diverse group of fisheries. Numerous species of fish and crustaceans utilize estuaries during the juvenile stages of their development following spawning in either coastal or freshwater systems. Estuaries are productive nurseries because they provide an adequate supply of food, have a diversity of environmental conditions (including salintiy and temperature), and maintain habitat protection from predation. Best management practices for estuaries should include optimization for all three of these characteristics, yet scientific understanding is lacking in establishing key linkages between these parameters and secondary productivity of estuarine ecosystems.

A key linkage that has received some scientific investigation is between the types of food webs associated with the input of organic matter to an estuary. In a profile of mangrove communities of South Florida, Odum et al. (1982) summarized a plethora of studies documenting the diverse fauna associated with these productive ecosystems. They concluded that a continuum of mangrove communities from freshwater to marine environments serves as a nursery for numerous species of estuarine-dependent fishes that are spawned offshore

including striped mullet, gray snapper, sheepshead, spotted sea trout, red drum, and silver perch. The relative importance of mangroves may vary along this continuum depending on the ability of other estuarine primary producers such as seagrasses and phytoplankton communities to inhabit the area. In the Fakahatchee Stand of riverine mangroves of South Florida, Carter et al. (1973) ranked the mangrove-fringed bays as the most important nursery grounds among the habitats available for fisheries. Odum et al. (1979) established that within these types of riverine mangrove systems, leaf material and associated microflora were the foundation of a detritus food chain that supported a mixed trophic level of herbivores, carnivores, and omnivores. This mixed trophic level included amphipods, shrimp, polychaetes, crabs, molluscs, and a few fish, which supported middle and higher level carnivores, many of which were economically important fisheries. Thus a linkage among mangrove productivity, detritus food webs, and estuarine food chains was documented.

A more quantitative linkage between the productivities of intertidal wetlands and fisheries would establish the magnitude of the impact of wetland destruction to estuarine productivity. Turner (1977) calculated a relationship between shrimp landings ($kg \cdot yr^{-1}$) to the areal coverage of intertidal vegetation for northeastern Gulf of Mexico and on a more regional scale in Louisiana. Macnae (1974) was less successful in establishing a similar type of model between the harvests of prawn shrimp and mangrove coverage because of insufficient statistics, yet for the few examples listed there was a positive trend between these two variables. Although detailed quantitative models of detritus food chains are still lacking, surveys and studies such as that by Odum et al. (1979) establish that for estuaries to continue their function as nurseries, they must provide a large source of food to support the recruitment of juveniles into these areas.

The Gambia

Food webs associated with mangrove bolons along the Gambia River estuary are described in a list of invertebrates (Appendix B) and fish (Appendix C) sampled in these intertidal ecosystems. Detritus-consuming invertebrates are dominated by snails (Tympantonus fuscatus var. fuscatus) and crabs (Sesarma huzardi) that inhabit the muds of bolons. Both penaeid (Penaeus duorarum) and prawn shrimp (Nematopalaeron hastafus) consume mangrove detritus suspended in the water column. These detritivores, plus a group of fish including three species of Tilapia (Tilapia sp., T. occidentalis, and T. heudeloti) and two others (Liza falcipinnis and Pellonula vorax), constitute the basic linkage between mangrove litter production and complex food webs in the Gambia River estuary. Through this group of organisms energy from these productive forests may be transfered to a hierarchy of consumers that collectively represent the secondary productivity of this estuary.

A description of a food web in the Gambia estuary was developed from information on the gut contents of fish inhabiting the Bai Tenda bolon (Table 11). From this information the fish were arranged into four groups representing a hierarchy of trophic levels as used by Odum et al. (1979) for the mangrove system in south Florida, USA: detrivores, mixed trophic level, middle carnivores, and higher carnivores. The detritivores were listed above and include fish with only detritus material within their guts. The mixed trophic level was dominated by Chrysycthys nigrodigitalis and C. furcatus, and their stomachs also included detritus along with representatives of other trophic levels (e.g., crabs, shrimp, fish). The guts of middle consumers had only representatives of the middle hierarchy of the food web such as molluscs, crabs, and shrimp, and were dominated by Polydactylus quadrifilis and Bostrychus

TABLE 11. Listing of fish sampled in the Bai Tenda bolon of the Gambia River estuary and the frequency of the type of material found in their guts.

	Detritus	Seed, Grain	Vascular Plants	Insects	Molluscs	Snails	Shrimps	Crab	Fish	Total
DETRITIVORES										
Tilapia sp.	2	-	-	-	-	-	-	-	-	2
Liza falcipinnis	15	-	-	-	-	-	-	-	-	15
Tilapia occidentalis	5	-	-	-	-	-	-	-	-	5
Pellonula vorax	1	-	-	-	-	-	-	-	-	1
Tilapia headeloti	17	-	-	-	-	-	-	-	-	17
MIXED TROPHIC LEVEL										
Chrysychthys nigrodigitatus	73	15	1	3	4	1	9	31	12	149
Chrysichthys furcatus	8	1	-	-	-	-	4	11	4	29
Fonticulus elongatus	4	-	-	-	-	-	2	-	1	7
Pythonichthys marcrurus	2	-	-	-	-	-	-	2	-	4
Psettias sebae	3	-	-	-	-	-	-	-	2	5
MIDDLE CARNIVORES										
Plectorhynchus macrolepsis	-	-	-	-	-	-	1	1	-	2
Polydactylus quadrifilis	-	-	-	-	-	-	2	2	-	4
Elops senegalensis	-	-	-	-	-	-	1	-	-	1
Schilbe mystus	-	-	-	1	-	-	-	-	-	1
Bostrychus africanus	-	-	-	-	1	-	-	-	-	1
HIGHER CARNIVORES										
Hemichromis bimaculatus	-	-	-	-	-	-	-	2	5	7
Hemichromis fasciatus	-	-	-	-	-	-	-	-	7	7
Hepsetus odoe	-	-	-	-	-	-	-	-	12	12
Strongylura senegalensis	-	-	-	-	-	-	-	-	1	1
Hydrocynus brevis	-	-	-	-	-	-	-	-	1	1

africanus (Table 11). The higher carnivores had only fish in their guts and included Hemichromis fasciatus and Hepsetus odoe.

The potential importance of this mangrove food web to the local economy may be evaluated using catch statistics of the artisanal river fishery for July 1982 - June 1983 (R. Moll, personal communication). Catches of Kujeli (Polydactylus quadratilis), Catfish (Chrysichthys nigrodigitalis and C. furcatus), and Jotor (Fonticulus elongatus) constituted nearly 51.5% of the total catch of the artisanal fishery from Banjul to Kaur. Diets of the latter two groups represent mixed trophic levels with significant amounts of detritus, while Kajeli are middle carnivores feeding on shrimp and crab. In the upper river, from Kaur to Fatuto, nearly 30% of the annual catch is represented by Tilapia, which is a detritivore found in mangrove bolons. The three species of Talapia found in the bolon all had only detritus in their guts (Table 11). Collectively, these trophic levels of the mangrove food chain represent 40% of the grand total catch of fish for the Gambia River estuary.

MANGROVES AND ESTUARINE RESOURCES

MANGROVE STRESS

An increase in the mortality of mangroves along the Gambia River estuary has been noticed over the past several years. Dead mangrove trees are particularly evident along the more inland areas of the intertidal zone in bolons that extend several km from the main body of the estuary, e.g., Bintang bolon. According to Johnson (1978), patches of dead trees could not be detected in aerial photographs taken in January and February 1972, and that most of the impact was associated with trees <7 m in height. An understanding of what stress or stressors may be causing this increased mortality is needed in order

to discuss the impact of further changes in the ecology of the Gambia River basin. Two scenerios discussed below have been proposed as the cause of increased tree mortality of the mangrove forests - disease and drought.

Disease

Teas and McEwan (1982) cited a gall disease, simlar to one caused by a fungus [Cylindrocaroen didymum (Hartig) Wallenw] in Florida, as responsible for mass mortality of Rhizophora sp. in the Gambia River estuary. Trees >20 m tall were most susceptible and galls were widespread throughout the mangroves along this estuary. Based on this evidence, Checchi and Company (1981) predicted that within 3-5 years there would be a mass loss of Rhizophora along the river, suggesting that present harvesting should be undertaken immediately to utilize what is presently left of this natural resource.

Jimenez et al. (1984) suggested that galls are common among mangrove forests as a normal occurrence in forest development. By comparing several forests, they summarized that abnormal tree mortality by gall disease would require infestation of more than 25% of stems per ha. Since older trees are more susceptible to the fungus, infestation may represent a higher percentage of total basal area of the forest. Even in cases where there were abnormal infestations of the gall in mangrove forests, it was suspected that some other stress had increased the susceptibility of the forest to this disease.

In The Gambia, dead trees comprise less than 15% of the total mangrove area according to a recent report by Forster (1983). This percent is well within the natural range for tree mortality among mangrove forests (Jiminez et al. 1984), indicating that there is not a mass mortality phenomenon occurring in mangrove forests along the Gambia River.

Drought

Intertidal wetland forests do not fall into the classification of world life zones or plant formations by L.R. Holdridge (1967; Fig. 15). These life zones are based on available precipitation, evapotranspiration, and mean temperature (biotemperature). Thus, the structure of plant communities can generally be described in relation to the net availability of water (precipitation - evapotransporation), as well as to temperature. Yet intertidal plant communities have the advantage of obtaining water from several sources other than just precipitation; these include groundwater flow, river flooding, and/or tidal inundation. In The Gambia, where water loss by evapotranspiration is high relative to precipitation, the high tidal amplitude and riverine discharge of the Gambia River basin subsidize the high demand for water from high annual mean temperatures (26°C). Thus these forests are able to generate structure uncharacteristic of the very dry life zone in which they exist. The ability of mangrove forest structure to be independent of those characteristics for a particular life zone was also evident for forests in Florida, Puerto Rico, Mexico, and Costa Rica (Pool et al. 1977). In this survey by Pool et al. (1977), mangrove forests with the second and fourth highest complexity index occurred in tropical dry forest life zones; these forests had more structure than those mangrove forests occurring in moist tropical life zones.

Yet these life zone characteristics do emphasize a key point concerning the ecology of mangrove forests in arid environments - that they are very susceptible to slight changes in hydrology. For mangrove forests in arid life zones, small shifts in precipitation patterns become very noticeable in mangrove forest structure (Cintrón et al. 1978). Cyclic patterns in mangrove forest succession and structure have been documented for arid environments of Puerto

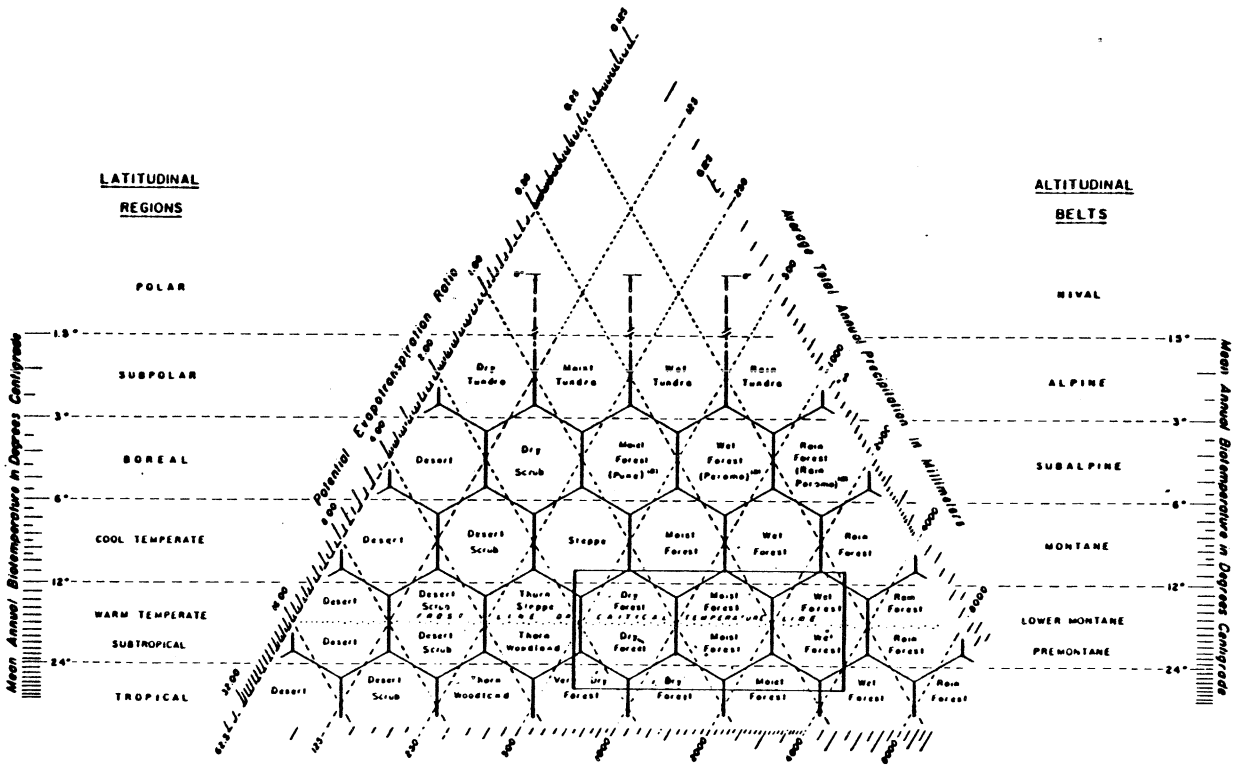

FIG. 15. Diagram for the classification of world life zones or plant formations by Holdridge et al. (1971). The rectangular box indicates zones for mangroves as described by Pool et al. (1977).

Rico in relation to cyclic patterns in rainfall (Cintrón et al. 1978). Similar observations have been made for mangroves in south Florida (Davis and Hilsenbeck 1974). In all of these cases, a reduction in rainfall resulted in increased soil salinity which resulted in an increase in tree mortality. This increased mortality resulted in vegetation shifts from forests to "tannes" or "salinas" (areas within the intertidal zone void of vegetation) that expanded at the expense of the area previously colonized by mangroves.

The cyclic nature of these shifts in mangrove forest structure observed in Puerto Rico results from changes in soil salinity stress which influences tree mortality and areal coverage. Increased rainfall (sometimes in the form of a hurricane) stimulates regeneration of forests within unvegetated "tannes" with pioneer mangrove species such as Rhizophora. The mechanisms associated with this flip/flop control of hydrology on mangrove forest structure is demonstrated in the model of mangrove ecosystem in Figure 16. The tank which depicts soil water (diagrams use energy language characters as in H. T. Odum 1971) has inputs and losses of water as discussed above. Since transpiration is so high, the turnover time of the tank is low and thus changes in inputs quickly result in increases in salinity which translate to stress on the mangrove forest. Cintrón et al. (1978) suggested that management of mangroves in dry forest life zones should account for this cyclic phenomenon by maintaining buffer zones for the expansion of mangroves during "wet" years. Also, tree mortality should be accepted as a natural process in these forests, and thus short-term observations should be placed in the perspective of the cyclic nature of these systems.

These observations by Cintrón et al. (1978) are very applicable to the mangrove forests of The Gambia which are also located in an arid life zone. Marius (1981) has documented the change in mangroves along the Saloum, the

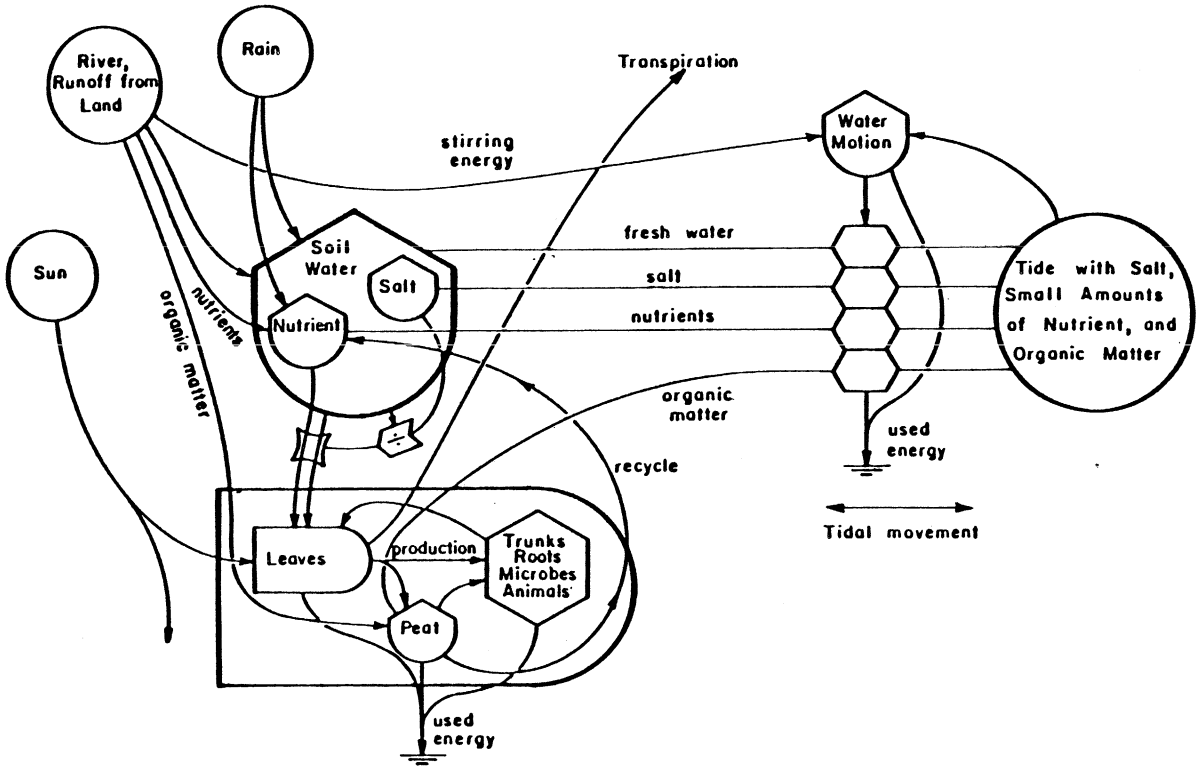

FIG. 16. A model of energy flow in mangrove ecosystems from Cintrón et al. (1978) using symbols from H.T. Odum (1971).

Gambia, and Casamance estuaries in the last decade due to the increased drought conditions in this region. Data collected by Marius (1981) from 1971 to 1978 for a mangrove forest in Senegal (Fig. 17) indicate that vegetation shifts have resulted in a decline of mangrove forest cover due to the expansion of inland "tannes." Intertidal areas vegetated by Rhizophora and Avicennia during 1971 were areas of dead trees in 1974, and by 1978 these areas were bare land. Soil water properties of these areas also changed: salinity of areas once vegetated by mangroves increased from 60 $ms \cdot cm^{-1}$ in 1971 to 150 $ms \cdot cm^{-1}$ by 1978, and pH of soil water in these areas declined from about 7 to <5. The levels of both of these properties (salinity and pH) shifted to values characteristic of vegetated and unvegetated "tannes," and are the result of a decrease in rainfall in the region (Marius 1981, see Fig. 3 of this report). Decreases in precipitation inputs to the soil water compartment result in changes in many soil water properties such as salinity, pH, hydrogen sulfide content, and concentration of other potentially toxic constituents; thus the exact mechanism causing the decline in vegetation is not known. However, this phenomenon is identical to those described by Cintrón et al. (1978) for other mangroves in arid environments and demonstrates the sensitive nature of these forests to changes in hydrology.

IMPACT OF PROPOSED DEVELOPMENT

Justification for the proposed salt barrage at Balingho on the Gambia River estuary is based on controlling water levels and salt distribution in the river in order to increase agricultural production in the region. The restriction of salt water at Balingho will result in an increase in salinities in an area of the estuary that was formerly mesohaline. The lack of any freshwater flow to

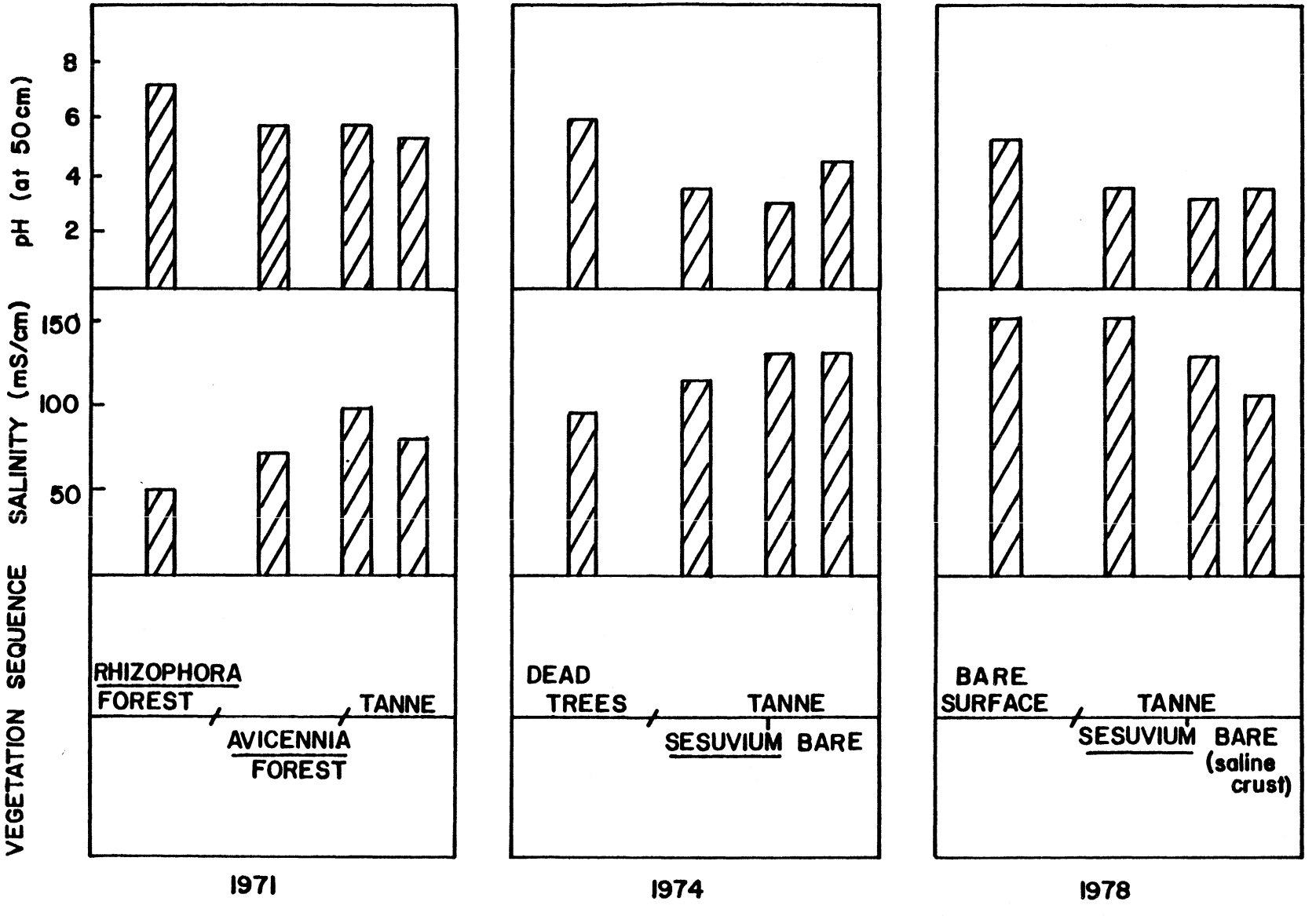

FIG. 17. Changes in pH and salinity of soil water and vegetation cover along a transect in the intertidal zone of an estuary in Senegal from 1971 to 1978 based on data from Marius (1981).

modulate the salinity of this region will drastically change the character of this region of the estuary. Estuaries need fresh water in order to be estuaries. The impoundment of fresh water by the proposed dam at Balingho will result in the formation of a marine ecosystem downstream.

The encroachment of higher salinity water into this mesohaline region of the Gambia estuary and the cessation of a seasonal freshet during the rain season will have deleterious effects on mangrove ecosystems. As explained above, mangrove forests that exist in arid environments are very susceptible to changes in hydrology. Many mangroves in dry forest life zones are able to develop into highly structured forests, but only with the subsidy of some periodic "washout" by fresh water; such is the case for the mangroves in the Balingho region of the Gambia River estuary. Even under present conditions, the effects of increased stress as a result of a decline in precipitation can be observed in mangrove forests in this area. The encroachment of "tannes" into areas previously colonized by mangroves is evident in the Bintang bolon and has been documented for estuaries in Senegal (Marius 1981). The "whispey" appearance of the tips of tree limbs in the canopy of Rhizophora >20 m tall is particularly common at Yelitenda. This aberrant formation in mangrove trees results from the lack of water transpiring to the canopy due to increased salinity of water in the soil (S. Snedaker, personal communication). Increased salinity and a decline in riverine freshwater flow will only exacerbate these two phenomenon. The tall (>7 m) Rhizophora and Avicennia trees will die and the total area of mangrove cover will decline soon after the barrage is built. This impact below the barrage includes 29,160 ha of mangroves (trees >7 m) which represents an estimated 334.41 x 10^3 $t \cdot yr^{-1}$ of dry mass from litter fall (from Table 6). Based on estimates of detritus export from these forests, that is

equivalent to a loss of 109.9 $t \cdot yr^{-1}$ x 10^3 of organic carbon from the estuary below the proposed barrage at Balingho.

Water levels above the barrage will be maintained at +1.70 m GD and salt water penetration will be prohibited thus forming an expansive freshwater impoundment in this region of the Gambia River. Evidence from studies on the effects of impoundments on mangroves varies as to which species are more susceptible to constant flooding; yet personal observation of impoundments in South Florida, USA, suggests that responses are specific to the magnitude and time interval of the change. Rhizophora can exist under flooded conditions only if the water level does not entirely cover the lenticels on their prop roots. Avicennia have root modifications called pneumatophores for transporting air to roots in an anaerobic environment. These pneumatophores are able to adapt to increasing water levels by elongation; for instance pneumatophores of Avicennia trees in the Mosquito Lagoon impoundment in Florida, USA, has pneumatophores that are 3 feet long. If the water level change occurs before pneumatophores can adapt, then these "root breathing" organs will be inundated and the trees will die.

As previously discussed (see Fig. 5), water levels will be maintained at +1.7 m GD from July to December, and depending on the acreage of rice cultivation, the water levels will drop from +1.2 m (0 ha of cultivation) to -1.0 m GD (24,000 ha of cultivation) during the dry season. For 6 months of the year water levels will be above high tide level (at Banjul) and only at rice cultivation of 8,000 ha will water levels drop to normal low tide levels. Since the duration of these water level changes will be much longer than the normal diel frequency of tides, it is anticipated that the root system of existing mangrove forests will not be able to adapt to this impoundment. Mangrove forests with

much less structure may survive and the areas abandoned by the death of the larger trees will most likely be colonized by less productive marsh species rather than mangroves since the impoundment will be fresh water. A conservative impact of mangrove loss along the Gambia River above the barrage includes trees >7 m which represents 7,719 ha of forests (from Table 4). This is equivalent to about 111.4 x 10^3 t dry mass /yr of litter in the watershed, which is equal to a loss of about 39.12 x 10^3 $tC \cdot yr^{-1}$ of allochthonous organic carbon to the estuary. Since tidal amplitude will be nonexistant in the impoundment, which is the key mechanism for the transport of organic carbon from wetlands, this estimate of the decline in allochthonous organic carbon import to the river above Balingho is a gross underestimate.

Together, the loss of allochthonous organic carbon to the Gambia River estuary below and above Balingho as a result of the proposed barrage equals 147.92 x 10^3 $tC \cdot yr^{-1}$. This loss is equivalent to 82% of the present estimate of total detritus input from mangroves to the estuary. Since inputs of organic carbon from phytoplankton and riverine discharge are so low, this decline in allochthonous detritus from mangroves represents nearly 70% of the total inputs of organic matter to this system. This loss of organic matter to an estuary that presently supports a diverse detritus food chain could have a negative impact on the fisheries of the Gambia estuary. The productivity of mangroves is coupled to the estuary and this energy is transferred along a food web that produces a source of protein for the people of The Gambia. Thus the loss of this mangrove productivity in the form of decreased detritus flow into the Gambia estuary as a consequence of the barrage should be evaluated against the gain in agricultural production that may be provided in the region. As suggested by this study, the mangroves of The Gambia may be a vital national

resource to the artisanal fisheries of this estuary. With better utilization of this fishery by the Gambian government, these forests could contribute more significantly to the local economy as a natural resource, rather than as forestry products or freshwater impoundments as presently proposed.

REFERENCES

Abell, T.M. 1980. Letter to R.J. McEwan, 28 May 1980. Overseas Development Administration, Land Resources Development Center. Surbiton, Surrey. England.

Arid Lands Information Center. 1981. Draft environmental profile on The Gambia. University of Arizona. Tucson, Arizona. National Park Service contract No. CX-0001-0-0003. 85 pp.

Axelrad, D.M., K.A. Moore, and M.E. Bender. 1976. Nitrogen, phosphorus, and carbon flux in Chesapeake Bay marshes. Virginia Water Research Center. Bull. 79, Virginia Polytechnical Institute, Blacksburg, Virginia.

Berry, T.D., R.A. Moll, and G.L. Krausse. 1985. Physical and chemical environment of the Gambia River, West Africa, 1983-1984. International Programs Report No. 9, Great Lakes and Marine Waters Center, The University of Michigan, Ann Arbor, Michigan.

Boto, K.G., and J.S. Bunt. 1981. Tidal export of particulate organic matter from a Northern Australian mangrove system. Estuarine, Coastal and Shelf Science 13:247-255.

Bray, J.R., and E. Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101-157.

Brinson, M.M., A.E. Lugo, and S. Brown. 1981. Primary productivity, decomposition, and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics 12:123-161.

Brown, S. 1980. Rates of organic matter accumulation and litter production in tropical forest ecosystems, pp. 118-139. In The role of tropical forests on the world carbon cycle. (Ed. S. Brown, A.E. Lugo, and B. Liegel), Symposium held at Institute of Tropical Forestry, Rio Piedras, Puerto Rico. U.S. Department of Energy, CONF-800350.

Brown, S. 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. Ecological Monographs 51:403-427.

Brown, S., M.M. Brinson, and A.E. Lugo. 1979. Structure and function of riparian wetlands, pp. 17-31. In Strategies for protection and management of floodplain wetlands and other riparian ecosystems. Symposium Proceedings, U.S. Department of Agriculture. GTR-WO-12.

Brunt, M. 1959. The Gambia land use and vegetation survey. Proc. 3rd Int. Afr. Soils Conf. Dalaba 1:389-394.

Carter, M.R., L.A. Burns, T.R. Cavainder, K.R. Dugger, P.L. Fore, D.E. Hicks, H.L. Revells, and A.W. Schmidt. 1973. Ecosystem analysis of the Big Cypress Swamp and estuaries. U.S. Environ. Prot. Agency, Region 4, Atlanta, Ga. EPA 904/9-74-002.

Chapman, V.J. 1976. Mangrove Vegetation. J. Cramer, Germany.

Checchi and Company. 1981. Mangrove feasibility study. Gambia Forestry Project No. 635-0205. Final Report. Washington, D.C.

Christenson, B. 1978. Biomass and primary production of Rhizophora apiculata BL. in a mangrove in southern Thailand. Aquatic Botany 4:43-52.

Cintrón, G., A.E. Lugo, D.J. Pool, and G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. Biotropica 10:110-121.

Connor, W.H., and J.W. Day, Jr. 1976. Productivity and composition of a bald cypress-water tupelo site and bottomland hardwood site in a Louisiana swamp. American Journal of Botany 63:1354-1364.

Coode and Partners. 1977. The Gambia barrage study. Final Report. 20 Station Road, South Norwood, London, UK.

Coultas, C.L. 1978. The soils of the intertidal zone of Rookery Bay, Florida. Soil Science Society of America 42:111-115.

Davis, G.E., and C.E. Hilsenbeck. 1974. The effects of watershed management on the Shark River Slough-Whitewater Bay estuary of Everglades National Park, Florida. Draft Report, Everglades National Park. Homestead, Florida. 16 pp.

Davis, J.H., Jr. 1943. The natural features of southern Florida. Geological Survey Bulletin No. 25. Department of Conservation, Tallahassee, Florida.

Day, J.W., Jr., W.G. Smith, P.R. Wagner, and W.C. Stowe. 1973. Community structure and carbon budget of a salt marsh and shallow bay estuarine system in Louisiana. Center for Wetland Resources, Louisiana State University, Baton Rouge. Public. No. LSU-SG-72-04.

Day, J.W., Jr., T.J. Butler, and W.H. Connor. 1977. Production and nutrient export studies in a cypress swamp and lake system in Louisiana, pp. 255-269. In M. Wiley (ed.), Estuarine Processes, Vol. 2. Academic Press, N.Y.

de la Cruz, A.A. 1965. A study of particulate organic detritus in a Georgia salt marsh estuarine ecosystem. Ph.D. thesis. Univ. of Georgia, Athens, Georgia.

DeLaune, R.D., R.J. Buresh, and W.H. Patrick, Jr. 1979. Relationship of soil properties to standing crop biomass of Spartina alterniflora in a Louisiana marsh. Estuarine and Coastal Marine Science 8:477-487.

Dunsmore, J., A.R. Blan, G. Lowe, D. Moffatt, I. Anderson, and J. Williams. 1976. The agricultural development of the Gambia: An agricultural environmental and socio-economic analysis. LRD 22.

Forster, H. 1983. Evaluation of the national forest inventory of the Gambia. German Agency for Technical Cooperation, Ltd. Report No. 10.

Gambia Ports Authority. 1983. Tide tables for Banjul 1983. Banjul, The Gambia.

Giglioli, M.E.C., and I. Thornton. 1965. The mangrove swamps of Keneba, lower Gambia River basin. I. Description notes on the climate, mangrove swamps and the physical composition of their soils. Journal of Applied Ecology 2:81-103.

Haines, E.B. 1977. The origin of detritus in Georgia salt marsh estuaries. Oikos 29:254-260.

Haines, E.B. 1979. Interactions between Georgia salt marshes and coastal waters: A changing paradigm, pp. 35-46. In R.J. Livingston (ed.), Ecological Processes in Coastal and Marine Systems. Marine Science Volume 10, Plenum Press, N.Y.

Happ, G., J.G. Gosselink, and J.W. Day, Jr. 1977. The seasonal distribution of organic carbon in a Louisiana estuary. Estuarine, Coastal and Marine Science 5:695-705.

Harris, R.C., B.W. Ribelin, and C. Dreyer. 1980. Sources and variability of suspended particulates and organic carbon in a salt marsh estuary, pp. 371-384. In P. Hamilton and K.B. Macdonald (eds.), Estuarine and Wetland Processes with Emphasis on Modeling. Marine Science Volume 11, Plenum Press, N.Y.

Heald, E.J. 1969. The production of organic detritus in a south Florida estuary. Ph.D. dissertation, University of Miami, Coral Gables.

Heald, E.J., M.A. Roessler, and G.L. Beardsley. 1979. Litter production in a southwest Florida black mangrove community, pp. 24-32. In Proceedings of the Florida Anti-Mosquito Association 50th Meeting, April 22-25, 1979.

Healey, M.J., R.A. Moll, and D. Page. 1985. Plankton assemblages of the Gambia River, West Africa. International Programs Report No. 10, Great Lakes and Marine Waters Center, The University of Michigan, Ann Arbor, Michigan.

Heinle, D.R., and D.A. Flemer. 1976. Flows of materials between poorly flooded tidal marshes and an estuary. Marine Biology 35:359-373.

Herklots, P.G. 1979. The Gambia second phase rural development programme. Annex 4. Irrigation developoment. Consultancy Report, UK Overseas Development Administration.

Hernández, A., and K. Mullen. 1979. Productividad primaria neta en un manglar del pacifico Colombiano. Memorias del Simposium sobre Pacifico Colombiano. Universidad del Valle. Cali-Colombia. S.A.

Hesse, P.R. 1961. Some differences between the soils of Rhizophora and Avicennia mangrove swamps in Sierra Leone. Plant Soil 14:335-346.

Holdridge, L.R. 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica. 206 pp.

Holdridge, L.R., W.C. Grenke, W.H. Hatheway, T. Liang, and J.A. Tosi, Jr. 1971. Forest Environments in Tropical Life Zones. Pergamon Press, New York.

Jenny, H. S.P. Gessel, and F.T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Science 68:419-432.

Jimenez, J.A., A.E. Lugo, and G. Cintrón. 1984. Tree mortality in mangrove forests. Unpublished manuscript. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

Johnson, M.S. 1978. Inventory of mangroves above the proposed Gambia River barrage at Yelitenda, The Gambia. Land Resources Development Center, Project Report 54. Surbiton, Surrey, England.

Jones, M.J., and A. Wild. 1975. Soils of the West African Savanna. Commonwealth Agricultural Bureaux. 246 pp.

Kjerfve, B., J.E. Greer, and R.L. Crout. 1978. Low frequency response of estuarine sea level to non-local forcing, pp. 497-513. In M.L. Wiley (ed.), Estuarine Interactions. Academic Press, New York.

Lesack, L.F., R.E. Hecky, and J.M. Melack. 1984. Transport of carbon, nitrogen, phosphorus, and major solutes in the Gambia River, West Africa. Limnology and Oceanography 29:816-830.

Liss, P.S. 1976. Conservative and non-conservative behavior of dissolved constituents during estuarine mixing, pp. 93-130. In J.D. Burton and P.S. Liss (eds.), Estuarine Chemistry. Academic Press, New York.

Lugo, A.E., and S.C. Snedaker. 1974. The ecology of mangroves. Annual Review of Ecology and Systematics 5:39-64.

Macko, S.A., and J. Zieman. 1983. Stable isotope composition and amino acid analysis of estuarine plant litter undergoing decomposition. Estuarine Research Federation Biennual Meeting, Virginia Beach.

Macnae, W. 1974. Mangrove forests and fisheries. FAO/UNDP Indian Ocean Programme. IOFC/DEV/7434.

Mann, K.H. 1975. Relationship between morphometry and biological functioning in three coastal inlets of Nova Scotia, pp. 634-644. In L.E. Cronin (ed.), Estuarine Research. Volume 1. Academic Press, New York.

Marius, C. 1981. Acid sulphate soils of the mangrove area of Senegal and Gambia. In H. Dost and N. van Breeman (eds), Proceedings of the Bangkok Symposium on Acid-Sulphate Soils. I.L.R.I. publication 31, The Netherlands.

Meybeck, M. 1982. Carbon, nitrogen, and phosphorus transport by world rivers. American Journal of Science 282:401-450.

Mulholland, P.J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecological Monographs 51:307-322.

Mulholland, P.J., and E.J. Kuenzler. 1979. Organic carbon export from upland and forested wetland watersheds. Limnology and Oceanography 24:960-966.

Nixon, S.W. 1980. Between coastal marshes and coastal waters -- a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry, pp. 437-525. In P. Hamilton and K.B. MacDonald (eds.), Estuarine and Wetland Processes with Emphasis on Modeling. Plenum Press, N.Y.

Odum, E.P. 1980. The status of three ecosystem-level hypotheses regarding salt marsh estuaries: tidal subsidy, outwelling, and detritus-based food chains, pp. 485-495. In V.S. Kennedy (ed.), Estuarine Perspectives. Academic Press, Inc. N.Y.

Odum, E.P., and A.A. de la Cruz. 1963. Detritus as a major component of ecosystems. A.I.B.S. Bulletin No. 13:39-40.

Odum, H.T. 1971. Environment, Power, and Society. John Wiley and Sons, N.Y.

Odum, W.E. 1971. Pathways of energy flow in a south Florida estuary. Sea Grant Bulletin No. 7, Univ. of Miami Sea Grant Program.

Odum, W.E., J.S. Fisher, and J.C. Pickral. 1979. Factors controlling the flux of particulate organic carbon from estuarine wetlands, pp. 69-80. In R.J. Livingston (ed.), Ecological Processes in Coastal and Marine Systems. Marine Science Volume 10, Plenum Press, N.Y.

Odum, W.E., C.C. McIvor, and T.J. Smith, III. 1982. The ecology of the mangroves of south Florida: A community profile. Fish and Wildlife Service/Office of Biological Services, Washington, D.C. FWS/OBS-81/24.

Ong, J.E., W.K. Gong, and C.H. Wong. 1981. Ecological monitoring of the Sungai Merbok estuarine mangrove ecosystem. School of Biological Sciences, Universiti Sains Malaysia, Penang, Malaysia.

Ong, J.E., W.K. Gong, and C.H. Wong. 1982. Productivity and nutrient status of litter in a managed mangrove forest. Symposium on mangrove forest ecosystem productivity, BIOTROP-UNESCO, Bogor, Indonesia.

Pendleton, E. 1979. Tidal import and export of organic detritus and organisms in a North Carolina salt marsh creek system. Ph.D. dissertation, North Carolina State University, Raleigh.

Pool, D.J., A.E. Lugo, and S.C. Snedaker. 1975. Litter production in mangrove forests of southern Florida and Puerto Rico, pp. 213-237. In Proceedings of the International Symposium on Biology and Management of Mangroves (Ed. G.E. Walsh, S.C. Snedaker, and H.J. Teas). Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

Pool, D.J., S.C. Snedaker, and A.E. Lugo. 1977. Structure of mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica. Biotropica 9:195-212.

Richard-Molard, J. 1949. Afrique Occidentale Francaise. Paris. from Giglioli, M.E.C., and I. Thornton. 1965. The mangrove swamps of Keneba, lower Gambia River basin. I. Descriptive notes on the climate, the mangrove swamps, and the physical composition of their soil. J. of Applied Ecology 2:81-103.

Roman, C.T. 1981. Detrital exchange processes of a Delaware salt marsh. Ph.D. dissertation. University of Delaware, Lewes, Delaware.

Schlesinger, W.H., and J.M. Melack. 1981. Transport of organic carbon in world's rivers. Tellus 33:172-187.

Sell, M.G., Jr. 1977. Modelling the response of mangrove ecosystems to herbicide spraying, hurricanes, nutrient enrichment and economic development. Ph.D. thesis. University of Florida, Gainesville, Florida.

Snedaker, S.C., and M.S. Brown. 1981. Water quality and mangrove ecosystem dynamics. Final Report to United States Environmental Protection Agency EPA-600/4-81-022. Gulf Breeze, Florida.

Steever, E.Z., R.S. Warren, and W.A. Niering. 1976. Tidal energy subsidy and standing crop production of Spartina alterniflora. Estuarine Coastal and Marine Science 4:473-478.

Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.

Teas, H.J., and R.J. McEwan. 1982. An epidemic dieback gall disease of Rhizophora mangroves in the Gambia, West Africa. Plant Disease 66:522-523.

Turner, R.E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106(5): 411-416.

Twilley, R.R. 1982. Litter dynamics and organic carbon exchange in black mangrove (Avicennia germinans) basin forests in a southwest Florida estuary. Ph.D. dissertation. University of Florida, Gainesville.

Twilley, R.R. 1985. The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. Estuarine, Coastal and Shelf Science 20: 543-557.

Twilley, R.R., A.E. Lugo, and C. Patterson-Zucca. Production, standing crop, and decomposition of litter in basin mangrove forests in Southwest Florida. Ecology: in press.

United Nations Development Programme. 1974. Hydrological and topographical studies on The Gambia River Basin. Final report, 5. Reading, England: Howard Humphreys and Sons, for UNDP.

Welsh, B.L., R.B. Whitlatch, and W.F. Bohlen. 1982. Relationship between physical characteristics and organic carbon sources as a basis for comparing estuaries in southern New England, pp. 53-67. In V.S. Kennedy (ed.), Estuarine Comparisons. Academic Press, N.Y.

Wharton, C.H., and M.M. Brinson. 1979. Characteristics of southeastern river systems. Strategies for protection and management of floodplain wetlands and other riparian ecosystems, pp. 32-40. In Symposium Proceedings, U.S. Department of Agriculture, Washington, D.C. GTR-WO-12.

Whigham, D., and R.L. Simpson. 1977. Growth, mortality and biomass partitioning in freshwater tidal wetland populations of wild rice (Zizania aquatica var. aquatica). Bulletin Torrey Botanical Club 104:347-351.

Woodwell, G.M., D.E. Whitney, C.A.S. Hall, and R.A. Houghton. 1977. The Flax Pond ecosystem study: exchanges of carbon in water between a salt marsh and Long Island Sound. Limnology and Oceanography 22:833-838.

APPENDIX A. List of sites visited along the Gambia River estuary during June, 1984.

Site	Distance Upriver (km)
Oyster Bolon	0
Lamin Island	5
Bintang	60
Duntu Malang Bolon	100
Tendaba Camp	100
Yelitenda	129
Bai Tenda	145
Elephant Island	150
Jessadi Wharf Town	192
Kudung Tenda	235
Pasari Island	235
Georgetown	291

APPENDIX B. List of invertebrates collected in mangrove bolons along the Gambia River estuary.

Mollusca

Tympantonus fuscatus var. *fuscatus*
Neritina adansoniana

Crustacea

Penaeid Shrimps
Parapenaeopsis atlantica
Penaeus duorarum

Prawn Shrimp
Nematopalaemon hastatus

Caridean Shrimp
Paleomonetes sp.

Mud Crabs
Sesarma huzardi
Sesarma elegans
Panopeus africanus

Blue Crabs
Callinectus pallidus
Callinectus amnicola
Callinectus marginatus

APPENDIX C. List of fish species caught in the Bai Tenda bolon along the Gambia River estuary during 1983.

Aplocheilichthys normani
Bostrychus africanus
Chrysichthys furcatus
Chrysychthys nigrodigitatus
Cynoglossus senegalensis
Elops lacerta
Elops senegalensis
Fonticulus elongatus
Hemichromis bimaculatus
Hemichromis fasciatus
Hepsetus odoe
Hydrocynus brevis
Hyporhamphus picarti
Ilisha africana
Liza falcipinnis
Pellonula vorax
Plectorhynchus macrolepis
Polydactylus quadrifilis
Pomadasys jubellini
Porogobius schlegeli
Psettias sebae
Pseudotolithus senegalensis
Pythonichthys marcrurns
Schilbe mystus
Strongylura senegalensis
Synodontis gambiensis
Tilapia brevimanus
Tilapia hendeloti
Tilapia occidentalis
Tilapia rheophila
Tilapia sp.
Trachinotus falcatus