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The Mangrove Vegetation of the Atlantic Coast of Africa - A Review

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> "In every ... direction you will see the apparently endless walls of mangrove, unvarying in colour, unvarying in form, unvarying in height, save from perspective. Beneath and between you and them lie the rotting mud waters of Bonny River, and away up and down river, miles of rotting mud waters fringed with walls of rotting mud mangrove-swamp."
>
> Mary Kingsley (1897)

Introduction

The mangroves of West Africa are reasonably well-described floristically and ecologically, albeit in a widely scattered literature (Jackson, 1985), and they have recently been reviewed from a functional perspective (John and Lawson, 1990). However, a wider review of the mangrove vegetation along the entire Atlantic coast of Africa is justified to put these systems into a continental perspective and, thus, provide a basis for a regional comparison with the mangroves of the Atlantic coast of the Americas and elsewhere.

In terms of what are generally regarded as mangroves (Barth, 1982; Saenger *et al.,* 1983; Tomlinson, 1986), there are only six indigenous and one introduced woody species on the Atlantic coast of Africa (Wilcox, 1985). Clearly, this is a species-poor tropical plant assemblage, even if the associated species are considered. Apart from the intrinsic interest in such an ecosystem, questions as to the underlying causes of this impoverishment should provide some insights into the general understanding of mangrove systems.

Present Mangrove Setting

The Atlantic coast of Africa (from Gibraltar to the Cape of Good Hope) is approximately 14,040km long and it ranges from 36°N to a latitude of 35°S (fig. 1). Not surprisingly, it provides a large variety of coastal types in a range of climatic settings.

Ocean Currents & Tidal Characteristics

Several major ocean currents influence the western coast of Africa (Longhurst, 1962). Two cold currents, the Canary Current in the northern hemisphere and the Benguela Current in the southern hemisphere, move towards the equator squeezing, as it were, the region of warm water on the coast into a narrower belt than would be expected from a consideration of latitude alone (Lawson, 1966). As they approach the equator, these two currents turn westward and are then known as the North and South Equatorial currents respectively. Between them, the warmer Counter Equatorial current flows in the opposite direction towards the coast, moving northwards during the northern winter. Like the Counter Equatorial current, the Guinea current flows in an easterly direction travelling along the length of the Guinea coast and turning south in the Bay of Bonny, joining the westward flowing South Equatorial current (fig. 2).

Another feature of importance is the phenomenon of 'upwelling' of cold water which takes place along the coastline of the Gulf of Guinea. This causes short-term temperature drops and brings increased nutrients to the surface in June-August. Its influence is pronounced from western Nigeria to Côte d'Ivoire but it is much reduced west of there.

Tides on the Atlantic coast of Africa are of the semi-diurnal type with ranges that are locally variable but generally small (Table 1). Atlantic swells are ubiquitous along most of the unprotected western coast of Africa and, consequently, it is only in semi-enclosed bays and in lagoons and estuaries, that conditions can be described as sheltered. As the amplitude of the waves often exceeds the range of the tides, wave action is relatively more important in determining the presence and vertical extent of mangrove vegetation on the open shoreline. In estuaries and lagoons, highly variable hydrodynamic conditions prevail and it is difficult to generalize.

Rainfall & Temperature

Ombrothermic diagrams, after Walter and Lieth (1960), are shown (fig. 3) for sixteen climatic stations from western Africa. These diagrams clearly indicate that much of the western coast of Africa is uniformly mild to warm throughout the year but that there are large differences in total annual rainfall. In the north, coastal Mauritania and northern Senegal are arid (9-11 dry months) while similar conditions prevail in the south, largely as a result of the cold offshore watermasses.

In between these arid zones is situated the humid tropical zone with very high rainfalls in Guinea, Guinea-Bissau and Liberia as well as the head of the Gulf of Guinea (Nigeria, Cameroon, Equatorial Guinea and Gabon). The areas between the humid zones have an annual rainfall between 1000-2000mm punctuated by two short dry periods (Côte d'Ivoire, Ghana, Togo and Benin).

It should be noted, however, that along the entire coastline, maximal rainfall generally coincides with the warmer months. Unlike many mangrove coastlines elsewhere, cyclone activity is absent on the Atlantic coast of Africa (Anthony, 1989).

Geomorphology, Physiography and Hydrology

According to Lang and Paradis (1977; 1984), the last glaciation around 18,000 y. BP resulted in a lowering of sealevels of about 100-150m along the entire Gulf of Guinea coastline. Beginning around 10,000 y. BP, sea level rose again due to the melting of the glaciers, and reached a new maximum between 6,500 and 4,500 y. BP during the Nouakchottian transgression (Anthony, 1989). All valleys and river mouths were flooded in Senegal, Gambia, Guinea, Côte d'Ivoire and Gabon, forming rias still common today. Many interdunal areas in Mauritania and elsewhere were also flooded (up to 250km inland) and occupied by dense vegetation as a result of the humid conditions which accompanied this transgression (Faure and Hebrard, 1977; Elouard, 1968; Gowthorpe and Lamarche, 1993).

The Nouakchottian transgression also left sand deposits considerable distances inland, many of which still exist today and comprise the landward margins of the coastal plains as, for example, in Côte d'Ivoire, Ghana, Benin, Sao Tome and Angola.

Towards the end of the Nouakchottian transgression, between 4,800-4,200 y. BP, a north-south (along the Senegal to Guinea coast) and an east-west (along the Gulf of Guinea) littoral drift became established which gradually caused littoral sand-barriers to close the gulfs and rias that had been formed. This phenomenon was progressive, starting in Mauritania (4,000 y. BP), then Senegal (3,900-3,200 y. BP) and subsequently in Guinea, Côte d'Ivoire and Benin. By 3000 y. BP, for example, the mouth of the Casamance in Senegal was transformed into a large lagoon where mangroves had become established. This sand-barrier formation was further consolidated by the small Taffolian regression of about 1m at around 3,000 y. BP. By about 2,000-1,500 y. BP the Atlantic coastline of Africa had largely developed its present configuration and the climate had reverted abruptly from a humid type to the modern semi-arid climate without any transitional stages (Delibrias *et al.,* 1976; Kalck, 1978; Barusseau *et al.,* 1986; Lezines, 1988). Over the last 1,500 years, sealevel fluctuations have been small and difficult to establish with certainty, although sealevel rises of between 1-3.4mm/y have been reported from this region (Verstraete, 1989; Emery and Aubrey, 1991).

As a consequence of these sealevel and climate changes, most of the mangrove vegetation has contracted significantly along the west coast of Africa, with the remnants along parts of the coastline (e.g. Senegal, Côte d'Ivoire, Ghana, Togo, Benin and western Nigeria) characteristically in 'physiographic refugias' i.e. semi-enclosed coastal lagoons or embayments, generally with constrained tidal exchange and with limited (and markedly seasonal) freshwater input. Additional 'physiographic refugias' can be recognized where offshore sandbanks (e.g. Guinea), coral communities (e.g. Limbé, Cameroon) or coral rubble banks (e.g. Liberia, Nigeria) may protect the shoreline from wave action which, in turn, allows frontal mangroves to develop.

However, there are also some large deltas on this coastline which constitute 'salinity refugias'. Mangroves are associated with these river deltas particularly the larger ones such as the Gambia, Volta, Niger, Rio Muni, Ogooué, and Zaire; these settings are characterized by more or less continuous freshwater input, free tidal exchange as well as the abundant deposition of alluvial sediments. These areas can be further subdivided into estuarine (polyhaline) or fluvial (mesohaline) areas depending on the prevailing salinity regime.

<u>Mangrove Types</u>

As already noted by Grewe in 1941, open shoreline (frontal) mangroves are rare along the Atlantic coast because of the absence of fringing reefs - and thus the high energy exposure at most locations. Given the coastal settings described above, it appears that four mangrove types can be recognized on this coastline (Table 2). From Cape Verde to Liberia the coast is notched by deep-branching estuaries with low-silted sandbanks. The coastline east of Liberia to the Nigerian-Cameroon border is low and lined with barrier islands which enclose lagoons stretching parallel to the beach. Behind these lagoons a number of rivers empty. Thus, from Mauritania to Liberia, mangroves are predominantly deltaic (estuarine and fluvial) or frontal (Anthony, 1989) while all mangroves in Benin are lagoonal as there are no deltas and the open shoreline is sandy and of relatively high energy (Gaillard *et al.,* 1982; Baglo, 1989). Along the Gulf of Guinea coast, mangroves are largely lagoonal although a few deltas (e.g. Mono and Volta Rivers) occur. In Nigeria, where there are 36 estuaries which may be bar-built (e.g. Lagos Lagoon), drowned river valleys (e.g. Kwa Ibo) and river deltas (e.g. Niger delta), mangroves are essentially estuarine (Amadi, 1991; Isebor, 1993).

These differing settings are also reflected in the breadth of mangrove vegetation along the coastlines as discussed under the 'Extent of Mangrove Vegetation' below.

Floristics

The early literature concerning the mangrove vegetation of the Atlantic coast of Africa failed to distinguish the three species of *Rhizophora* (e.g. Pellegrin, 1952) and it was not until Keay (1953) clarified this situation, that reliable floristic data became available for analysis.

As Breteler (1969) had suggested for the Atlantic *Rhizophoras,* Wilcox (1985) has indicated that *R. harrisonii* might be a hybrid of *R. racemosa* and *R. mangle.* This is supported by intermediate morphological features (such as lengths of peduncle and pedicels and the number of flowers in the inflorescence), the low viability of *R. harrisonii* pollen (Wilcox, 1985; Breteler,

1969) and the poor fruit set of this species (Keay, 1953; Savory, 1953; Breteler, 1969).

Avicennia germinans has a similarly long synonymy (including a period when it was considered as an endemic species - *A. africanum)* before it became generally accepted that there were no significant morphological differences between the American and African populations (Compère, 1963).

Given the current taxonomic status, there are six indigenous and one *(Nypa fruticans)* introduced species of mangroves on the African coast. The records of *Osbornia octodonta* for western Africa by Chapman (1977) and Barth (1982) are undoubtedly based on locality confusion. Even when associated species are added to this list (Table 3), only 12 families constitute this widespread vegetation type. All of these families have counterpart species or genera on the American Atlantic coasts and the majority have counterparts along the eastern coast of Africa.

Vegetational History

Based on pollen analysis of sediments from the Niger delta (Sowunmi, 1981; 1986), offshore cores (Rossignol-Strick and Duzer, 1979) and peat deposits (Michel and Assemien, 1970; Assemien, 1971), the extent and floristic composition of the mangrove vegetation of western Africa has altered dramatically in conjunction with changing climatic conditions and palaeo-sealevels.

During the Palaeocene (63-55 m.y. BP) when the proto-Atlantic was a narrow waterway and western Africa was experiencing a 'wet' phase, there was no mangrove vegetation in the Niger delta but extensive estuarine swamp communities dominated by *Nypa.* The earliest *Nypa* pollen are recorded from Brazil (Hutchings and Saenger, 1987) and this genus apparently evolved in, and spread throughout, the proto-Atlantic at this time.

This *Nypa* dominated swamp community remained during the Eocene when sealevels fell and drier conditions prevailed. Two additional genera of palms, *Mauritia* now confined to the Americas and *Kentia,* now only occurring in Australia and New Zealand, were also common members of these estuarine swamps of the Niger delta during this period.

Towards the end of the Eocene when seasonally dry conditions were widespread in the region, *Nypa, Mauritia* and *Kentia* declined in abundance and finally disappeared altogether in the early Miocene (24 m.y. BP) - incidentally at the same time *Nypa* disappeared from the fossil record of Venezuela. These disappearances coincided with the sudden and predominating appearance of *Rhizophora* throughout the region - a situation which, with minor fluctuations, remains to the present. Thus, during the Inchirian transgression (c. 35,000 y. BP) there was a peak in *Rhizophora* pollen, as again during the Nouakchottian transgression around 5,500 y. BP (Sowunmi, 1986).

Mangroves were widespread during the Nouakchottian transgression based on pollen (Assemien, 1969) and other fossils dated around 5,700 to 5,300 y. BP (Tastet, 1981; Lezines, 1988; Gowthorpe and Lamarche, 1993). The inland occurrence of *Avicennia germinans* (accompanied by such non-halophytes as *Cadaba farinosa, Dichrostachys glomerata* and *Adansonia digitata)* in Senegal are also apparently living relicts of these much more widespread mangrove communities (Trochain and Dulau, 1942).

As a consequence of the adverse sealevel and climatic changes since the last transgression, the mangrove vegetation has contracted significantly along the west coast of Africa in areal extent, with the remnants virtually confined to refugia such as lagoons, embayments and deltas.

These relatively recent events must also be considered in relation to those of the geological past: a number of the proto-Atlantic mangrove taxa have migrated out of the region (e.g. *Nypa, Mauritia and Kentia)* while only selected members of the Indo-Pacific mangrove flora were able to enter and survive in the proto-Atlantic before the Tethys Sea (Mediterranean) became unavailable as a migration route.

As mentioned earlier, at present there are only six indigenous species of mangroves on the Atlantic coast of Africa. This contrasts with the Atlantic coast of the Americas where there is an additional species of *Avicennia* (Table 4). This suggests that since the late Eocene (38 m.y. BP), when the proto-Atlantic was being invaded by Indo-Pacific mangrove species, there has been complete and differential segregation between the Atlantic African and the East African/Indo-Pacific mangrove flora. However, since the mid-Miocene (20-14 m.y. BP), when the Tethys Sea dispersal route was no longer open (although it still contained extensive *Avicennia* communities with Indo-Pacific affinity - Bessedik, 1981; 1985) and direct dispersal between America and Africa was apparently no longer possible, there has been speciation only in the genus *Avicennia* in America, but apparently not in *Rhizophora, Laguncularia* or *Conocarpus* on either coast (Keay, 1953; Tomlinson, 1986; Jimenez, 1987).

All of the indigenous species of the Atlantic coast of Africa are shared with the Atlantic and Pacific coasts of America. Obversely, there are no endemic mangroves *(sensu stricto)* on the Atlantic coast of Africa nor, for that matter, on the east coast of Africa where the mangrove flora consists simply of a subset of the Indo-Pacific species. In contrast, all other major mangrove regions have at least one or more endemic species (Table 4).

The absence of any endemic species suggests that the African mangrove flora is a relict flora which, in turn, is supported by the fossil record which indicates that during the late Eocene to early Miocene, a much richer mangrove flora was present including, amongst others, *Nypa, Mauritia* and *Pelliciera.* To that must be added that the mangrove vegetation of the Atlantic coast of Africa is in retreat from relatively recent climatic and sealevel changes. It also suggests that the conditions along this coastline were not conducive to trigger speciation in the taxa present and/or that continuous geneflow was maintained across the Atlantic - a point which is further discussed below.

Biogeography

The northern and southern limits of the main mangrove genera are shown in figure 3. *Avicennia* is recorded as far north as the île Tidra (19°50'N) in Mauritania (Naurois and Roux, 1965), in an archipelago now included in Le Parc National du Banc d'Arguin, established on 24 June 1976. The genus *Rhizophora* is reported to extend to a little north of Saint Louis in the delta of the Tiallakh River (16°11'N) in southern Mauritania (Naurois and Roux, 1965), although which of the three species is involved is not explicit. However, on the basis of the occurrence of only *R. racemosa* in southern Mauritania (Nicou, 1956; Adam, 1965), this record is almost certainly of *R. racemosa.* It should be noted, however, that the stands of *R. racemosa* reported by Adam (1965) from the île de Thiong, have been cleared by the local inhabitants in the last two decades (Gowthorpe and Lamarche, 1993).

While the exact extent of *Conocarpus erectus* is not recorded, Adam (1965) reported its presence together with *A. germinans and R. racemosa* on the île de Thiong (16°03'N) on the Mauritanian banks of the Senegal River. This probably comprises its northernmost occurrence. The northern limit of *Laguncularia racemosa* is uncertain although the records from the delta of the Senegal River (Nicou, 1956) apparently comprise its northern limit.

The southern limit of extensive mangrove vegetation is found in the Angolan estuary of the Rio Longa (10°18'S) although isolated occurrences of *A. germinans* occur slightly south of Lobito (12°20'S) (Gossweiler and Mendonça, 1939; see also partial English translation of this paper by Airy-Shaw, 1947). Gossweiler and Mendonça (1939) also indicate that *R. mangle* does not occur south of Lobito where its niche appears to be occupied by *L. racemosa, Scaevola plumieri* and *Suaeda.* However, as these authors did not distinguish the various species of *Rhizophora,* precisely which species comprises the southernmost record remains unresolved.

The most southerly record of *Conocarpus* in Angola is from Praia de Chiloanga (5°5'S) in the Cabinda Province of Angola (Gossweiler and Mendonça, 1939). However, Pynaert (1933) records it from the northern banks of the Rio Zaire (6°10'S) which appears to be the most southerly record. The southern limit of *L. racemosa* lies between Lobito and Moçâmedes (15°10'S).

Both the northern and southern limits of mangroves (fig. 2) coincide with the limits of arid regions (UNESCO, 1979) defined as: summer rainfall and winter drought, 12 months/year with <30mm rainfall, and a precipitation to potential evapotranspiration ratio (P/PEt) < 0.03. This suggests that, as found on other western coasts of continents (e.g. Australia - Saenger and

Moverley, 1985), mangrove distribution in western Africa is more limited by aridity rather than by temperature.

In order to determine the potential dispersal distance of mangroves along the west African coast, the data on the distribution of mangrove and associated species on the offshore islands in the Gulf of Guinea (fig. 4) have been collated (Table 5) and regressed against the island area (fig. 5) and the distance from the mainland and nearest landward island (fig. 6).

As expected, there is a more or less linear relationship with island area, suggesting that habitat availability is a significant factor. The analysis against distance suggests that the dispersal ability of mangroves under these equatorial conditions allows a dispersal distance of 350km from the mainland or 250km from another island. Given a dispersal longevity in Panama of 35 days for *Laguncularia,* 110 for *Avicennia* and around 300 for *Rhizophora* (Rabinowitz, 1978) and with current speeds in the Gulf of Guinea around 0.3m/sec, the dispersal distances obtained from this simplistic analysis seem realistic. In turn, however, these dispersal distances would preclude any continuous (and unassisted) geneflow across the Atlantic Ocean.

Despite the extensive dispersal distances of these mangroves, plant distribution along the western shorelines of Africa is not uniform but shows a degree of patchiness (Table 6). For example, *Rhizophora mangle* is absent in Côte d'Ivoire, Ghana and Benin and is only very rare with only a small stand of *R. mangle* known from the lagoon at Owendo (Lebigre, 1983) in Gabon.

In addition to their variable distribution along the coastline, variable distances have been recorded for mangrove penetration up river systems (Table 7), ranging from around 100km in Guinea-Bissau to less than 20km in Equatorial Guinea. These upriver distances probably reflect the seasonal differences in hydrology, with greater salinity intrusion during the dry season.

Extent of Mangrove Vegetation

Altogether, African mangrove vegetation covers 45,787km^2 of which 31,111km^2 is found along western African coastline, 3,315km^2 in Madagascar and 11,361km^2 in the remainder of eastern Africa. The best estimates of the areal extent of mangrove vegetation along the western coast of Africa are shown in Table 8, together with some demographic and economic indicators of the respective states.

These data show that Nigeria and Gabon contain the largest mangrove areas and comprise over 50% of the total area for the Atlantic coastline. When the ratio of total mangrove area to coastline length in each country is considered (fig. 7), the mean breadth of mangrove vegetation ranges from 12.3km in Nigeria to a matter of metres in Mauritania. More significantly, however, the data in figure 7 indicates that, based on the breadth of mangrove vegetation, five groups can be recognized as follows:

1. Nigeria
2. Guinea
3. Gambia, Guinea-Bissau, Cameroon, Gabon and Zaire,
4. Senegal, Sierra Leone
5. Mauritania, Liberia, Côte d'Ivoire, Ghana, Togo, Benin, Congo, Equatorial Guinea and Angola.

These groups, while artificial, clearly reflect the physiographic settings (described earlier) as well as the hydrological regimes of the regional mangrove communities. Consequently, these groups have been used for the regional descriptions below.

Regional Descriptions of Mangrove Vegetation

Group 1: NIGERIA

This region is characterized by the high rainfall and humid conditions associated with the Niger delta which dominates the 853km long shoreline of Nigeria. The Niger delta has developed from the interaction of the sediment-laden Niger and coastal processes, thereby creating beach-ridge barrier islands, a freshwater floodplain, and between these structures an extensive brackish mangrove swamp (Keay, 1953; Savory, 1953; Wilcox, 1985; Adegbehin, 1993; Ajao, 1993; Isebor and Awosika, 1993). However, extensive lagoonal systems also occur around Lagos in the west and estuarine systems characterize the coast between the Niger delta and the Cameroon border (Amadi, 1990).

In the lagoons and deltas, *Rhizophora racemosa* is the most abundant mangrove and *Avicennia germinans, R. harrisonii* and *R. mangle* are only sparsely present (Wilcox, 1985, CEC 1987; Isebor, 1993). In the estuaries, however, the mangrove communities may differ in species composition. Thus, in the Bonny estuary, *Nypa* is abundant near Port Harcourt but decreases in abundance towards the mouth where the mangroves rarely exceed 10-12m in height (Saenger, pers. obs.). Ukpong (1989; 1992) has described the mangrove communities of the Imo and Kwa Ibo Rivers in south-eastern Nigeria where there are approximately 196km^2 and 50km^2 of mangroves respectively. These communities are numerically dominated by *A. germinans* as shown in Table 9. Heights varied from 3-15m with *A. germinans* the tallest trees, particularly at the estuarine mouths. The abundance of *Nypa fruticans* in these plots indicates that, at least during the wet season, these areas are brackish to almost freshwater, while the dominance of *A. germinans* suggests that highly saline conditions occur during the dry season.

Using ordination analysis, Ukpong (1992) concluded that six community types can be distinguished, although each of the types is co-dominated by *A.*

germinans and, at least, one of the *Rhizophora* spp. Ukpong (1989; 1992) also investigated the relationship between the vegetation and the soil characteristics at rooting depth. Basal area of the trees, tree density and cover were negatively correlated with soil chloride content.

Group 2: GUINEA

This region is also characterized by a high rainfall (4125 mm/y in Conakry) but the coastal configuration is less suited to the formation of extensive deltas. Nevertheless, most mangroves are associated with deltas and rias although frontal mangroves also occur, sometimes associated with cheniers and/or beach ridges (Schnell, 1952; Jacques-Felix and Chezeau, 1960; Bertrand, 1991). Saltflats or 'tannes' occur widely and are associated with chenier plains - but not generally with beach-ridge areas.

Although Bertrand (1991) suggests that *R. mangle* is rare and only found at the mouths of some rivers e.g. Tabounsou and Rio Nunez, Jacques-Felix (1957) described it as widespread from the îles Tristâo in the north to the Sierra Leone border in the south.

Structural analysis (Table 10) of the littoral communities in the delta of the Soumba River (9°45'N) based on SPOT image 30-330 taken on 19 April 1986 (fig. 8) showed that, even in a high rainfall deltaic area, the mangrove vegetation is dominated by short (<7m high) formations and that tall (>15m high) mangroves occupy an area of around 6.4% of the littoral vegetation.

3. GAMBIA, GUINEA-BISSAU, CAMEROON, GABON AND ZAIRE,

The mangrove vegetation of this group is largely confined to estuaries with seasonally high rainfall and river flow which has led to considerable mudflat development.

In these regions, the rivers constitute 'salinity refugias'. For example, the Gambia River, with its relatively high and continuous freshwater input, acts as a brackish water system throughout the year although the position of the salt wedge shows considerable up- and down-river movement (Blasco, 1983; Healey *et al.,* 1988). In Zaire there are 226km^2 of mangroves associated with the mouth of the Zaire River (Pynaert, 1933; Delevoy, 1945; Robyns, 1950; Sayer *et al.,* 1992) but they do not extend north of the mouth except for one estuary (Darteville, 1950).

Throughout these areas, *R. racemosa* is the pioneer species, colonizing recently deposited alluvial soils up to the level of daily tidal flooding. It may also form tall gallery forests (e.g. along the lower Gambia River or in the Wouri Estuary) reaching a height of 40m and 1m trunk diameters (Pynaert, 1933; Boyé *et al.,* 1975; Blasco, 1983; Din, 1991). However, according to Lebigre (1983), *Rhizophora racemosa* can be classified into three formations in Gabon: a very tall form, such as at Pointe Pongwé, varying between 20-40m in height and resembling the gallery forests of Gambia while at the other extreme, there is a very small form, characteristic of the Rio Muni and Gabon estuary, often with a ground cover of *Paspalum vaginatum* or *Eleocharis* spp.

R. harrisonii occurs with *R. mangle* at the boundary between *Rhizophora* and *Avicennia* mangrove stands. Giglioli and Thornton (1965), however, found that at Keneba, in lower Gambia, *R. harrisonii* colonizes the fibrous clay recently vacated by *R. racemosa* and that *R. mangle* grows in the higher elevation, sandier soils where it is often intermixed with the waterward edge of the *Avicennia* zone. *R. harrisonii* is intermediate in size (3-6m in Cameroon) between *R. racemosa* and the small form of *R. mangle* found in West Africa. In Gabon, Lebigre (1983) described this species as mostly of the order of 2m in height but there are some tall *R. harrisoni* bordering the creeks and in forests abutting the upland areas. Soils are acid-sulphate but little different from those of *R. racemosa.*

R. mangle occurs in the drier and often more saline landward edge of the *Rhizophora* zone. *Avicennia* typically occurs on the higher elevation fibrous clay or sandier soils. *A. germinans* may vary in height from 7-20m in Gambia (Blasco, 1983), around 12m in Cameroon (Din, 1991) or up to ~30m with trunks around 1 m in diameter and virtually no understorey in Gabon (Lebigre, 1983). *Laguncularia racemosa* is uncommon but may form a shrub <3m high, generally co-occurring with low-growing *Rhizophora* or *Avicennia.*

Other mangrove associates commonly present include *Hibiscus tiliaceus, Conocarpus erectus, Carapa procera, Drepanocarpus lunatus, Dalbergia ecastaphyllum, Oxystigma mannii, Pandanus candelabrum, Phoenix reclinata, Pterocarpus* and *Acrostichum aureum* (Pynaert, 1933; Delevoy, 1945; Boyé *et al.,* 1975; Blasco, 1983; Lebigre, 1983; CEC 1987; Din, 1991; Appolinaire, 1993).

In Cameroon, *Nypa* has recently become distributed throughout the mangroves of the Wouri estuary (Saenger, pers. obs.) and Din (1991) records its presence at Pointe Olga.

Saltflats or 'tannes' occur throughout this region wherever there is a marked dry season. Giglioni and Thornton (1965) suggested that where evapotranspiration exceeds 1500mm per year, barren saltflats replace herbaceous halophytes. Although most saltflats are probably of human origin, particularly in the higher rainfall areas, Anthony (1989) has suggested that their extensive occurrence, notably north of the Guinea coast, must reflect, at least partly, a combination of a sealevel pulse in the last 1000 years (from a highstand of 1-1.5m to the present level) and climatic deterioration (i.e. increasing aridity).

The saltflats generally consist of clayey soils, which may be fairly acid, or more rarely of sandy soils (Lebigre, 1983). These areas generally have mangroves (often <1m high *Avicennia, Laguncularia* or *Conocarpus)* around their margins with patches of *Sesuvium portulacastrum* and sedges or grasses (such as *Paspalum vaginatum*). At their landward margins palms, *Hibiscus tiliaceus* or *Pandanus candelabrum* are commonly present.

Both in Cameroon and in Gabon, a freshwater swamp forest appears to be associated with the mangroves (Boyé *et al.,* 1975; Lebigre, 1983). This formation is generally saline but often flooded by rains due to poor drainage. *Rhizophora, Pandanus* and *Acrostichum aureum* are present, but also the following rainforest species: *Chrysobalanus ellipticus* (Rosaceae), *Manilkara lacera* (Sapotaceae) and *Syzigium guineense* (Myrtaceae).

Group 4: SENEGAL AND SIERRA LEONE

This mangrove group is transitional between the seasonally wet group (Group 3) and the dry-arid group (Group 5) discussed below. In these regions, the mangroves are predominantly deltaic but the more fluvial elements (such as the freshwater swamp forests) are absent.

Mangroves in Senegal are concentrated in two main areas, each typified by a particular river - the Casamance and the Saloum (Marius, 1984). Both these estuaries are 'inverse estuaries'. During the dry season, the salinity of the waters around the mangroves can be 2-3 times greater than that found in neighbouring seawater (Marius, 1981; 1984; Marius and Lucas, 1982). In Sierra Leone, approximately 80% of the total mangrove vegetation occurs in the estuaries of the Scarcies, Sierra Leone and Sherbo Rivers (Johnson and Johnson, 1993).

Tomlinson (1957) has described the mangroves of northern Sierra Leone, close to the border with Guinea while Gledhill (1963) has described those of Aberdeen Creek. At Aberdeen Creek, *R. racemosa* is rare (Gledhill, 1963) but *R. harrisonii* may be up to 5m, *R. mangle* up to 2m, *Laguncularia* to 4m, *Avicennia* to 5m and *Conocarpus* 2-3m.

As elsewhere in West Africa, *R. racemosa* generally occurs on newly deposited sediments fringing creeks and may be tall while the other species are all low (Thompson, 1945; Tomlinson, 1957; Jordan, 1963; 1964). The occurrence of *R. racemosa* on new deposits may be due to a high nutrient demand of this species or to the difficulty of the establishment of its seedlings in the fibrous soil. As *R. racemosa* matures, the soils invariably become highly fibrous while under the other species it is more variable (Hesse, 1961). Where shrubby growth of *Avicennia* occurs, it may be growing on fibrous soils after the initial colonizing *R. racemosa* has died or been removed.

Thompson (1945) has described mangroves in Sierra Leone as consisting exclusively of *Rhizophora* wherever marked freshwater seepage occurs. In contrast, *Avicennia* may co-occur with *Rhizophora* where freshwater seepage is absent.

It should also be noted that Adam (1958) reports the presence of the mangrove creeper *Brachypterys ovata* (Family Malpighiaceae) from Sierra Leone and Guinea (near Dubréka and Conakry). The restricted distribution of this species in West Africa, together with its widespread occurrence on the Atlantic coast of tropical America, suggests that this species may be a relatively recent introduction which requires further investigation.

Limited salt-marshes occur in Senegal and Sierra Leone with the following species: *Sesuvium portulacastrum, Paspalum vaginatum, Eleocharis caribaea, E. mutata, Sporobolus robustus, Philoxerus vermicularis* and *Scirpus maritimus* (Marius, 1979; Tomlinson, 1957).

Group 5. MAURITANIA, LIBERIA, COTE D'IVOIRE, GHANA, TOGO, BENIN, EQUATORIAL GUINEA, CONGO AND ANGOLA

This group represents the most dry-arid mangrove vegetation on the Atlantic coast of Africa, where the mangroves are confined to narrow fringes partially lining estuaries and coastal lagoons. Liberia clearly does not belong to this group on rainfall data alone but the virtual confinement of mangroves to deltas and the overall restricted area of mangroves in Liberia, has reduced the mean breadth of mangrove vegetation to that of other members of this group.

In Mauritania, remnant stands of mangroves have been described consisting only of *Avicennia germinans* (Naurois and Roux, 1965; Gowthorpe and Lamarche 1993).

Liberia does not have extensive wetlands along its coasts and most mangroves occur at river mouths with some lesser development of lagoonal communities (Kunkel, 1966). Thus, Adam (1970a) has described the lagoonal mangroves around Cape Palmas in south-eastern Liberia. These communities attain a height of around 3m and are dominated by *Conocarpus erectus* with only rare specimens of *Avicennia germinans* and *Rhizophora racemosa.* Thickets of the fern *Acrostichum aureum* are also common.

Near Buchanan on the central Liberian coast, estuarine mangroves occur (Adam 1970b). Although these may have once been dominated by *Rhizophora racemosa,* this species is locally absent due to felling. The remaining vegetation consists of stunted *Rhizophora harrisonii, Avicennia germinans* and *Conocarpus erectus* with thickets of *Acrostichum aureum. Laguncularia racemosa* was not observed.

Kunkel (1966) has described the mangrove-associated flora from Liberia and has interpreted its relationship in strictly successional terms. Whether the Liberian successional sequences are really applicable elsewhere is doubtful, particularly where the rate of sand movement and erosional mudflat deposition is lower than in Liberia.

In Côte d'Ivoire, the climatic variation along the coast is very slight and physiognomic/species differences must be non-climatic e.g. hydrological, geomorphological etc. Egnankou (1985) has subdivided the mangroves of Côte d'Ivoire into two groups: (1) Those from Assinie to Fresco (including lagunes Aby, Ebrié, Grand Lahou, and Potou as well as the Mé, Comoe, Bandama, Tagba Rivers all of which empty into the coastal lagoon system) These lagoonal mangroves are relatively depauperate and only around Abata to Mossou and around Grand Bassam, do they attain heights of around 20m. Only *R. racemosa, Avicennia* and *Conocarpus* occur with the best stands on River Mé. *R. racemosa* colonizes the front of the water. (2) The second group are the deltaic rivermouth systems associated with the Sassandra, Cavally, Niéro, San Pédro, Brimé, Dodo, Nichia and Tabou on the coast between Fresco and Bliéron. These are dominated by *A. germinans* and *R. racemosa.*

Paradis (1989) has described the mangrove communities of the lagoonal system around Fresco in detail, particularly the lagune Nyi. He described four zones as including (1) an *Avicennia* zone 15-18m high; (2) a *Rhizophora racemosa* zone 8-10m high; (3) a shrub zone of *Dalbergia* 4m high (mixed with *H. tiliaceus, Drepanocarpus* and *Acrostichum);* and (4) a *Paspalum vaginatum* grassland 0.8m high. Hédin (1933) has described the non-mangrove lagoonal vegetation around Grand Bassam.

Virtually all of the mangroves of the lagoonal system of Côte d'Ivoire have been hydrologically disturbed, particularly by the construction of the canal de Vridi, commenced in 1938 and completed in 1950 (Paradis, 1989). It is 2.7km long and provides a permanent opening to the lagoonal system where it did not previously exist - while the old mouth at Grand Bassam is now generally sanded up (Durand and Skubich, 1982; Durand and Chantraine, 1982).

The climate of Ghana is relatively dry and much of the coastal areas are dominated by savannah with occasional boababs *(Adansonia digitata).* Mangroves are confined to the lower reaches and delta of the Volta River and to the numerous coastal lagoons such as Keta, Korle and Kpeshie Lagoons (Kwei, 1977; CEC 1987; Amlalo, 1990).

Boughey (1957) has suggested that a clear distinction in terms of species composition could be made in Ghana with species of *Rhizophora* confined to open lagoons. Closed lagoons, characterized by elevated salinity during the dry season, support populations of the more salt-tolerant species including *Avicennia, Conocarpus, Laguncularia* and *Acrostichum.* This explanation is similar to that offered by Thompson (1945) for Sierra Leone, where *Rhizophora* and *Avicennia* occurred together wherever salinity became elevated due to the absence of freshwater seepage.

While such a distinction in the lagoonal setting is generally helpful, there are exceptions. For example, Korle Lagoon near Accra, has an artificially maintained connection to the sea but the mangroves are dominated by *Avicennia germinans* to the virtual exclusion of *Rhizophora.*

All mangroves in Benin are lagoonal as there are no active deltas and the open shoreline is sandy and of relatively high energy (Paradis, 1976; Baglo, 1989). *Rhizophora mangle* is absent in Benin which Blasco (1985) has suggested might be due to the irregular and hyposaline hydrological regime within the lagoonal system of Benin. *Laguncularia* and *R. harrisonii* are rare (Paradis and Adjanohoun, 1974; Blasco, 1985; Baglo, 1989).

Mangroves have virtually disappeared from Lac Nokoué due to the Cotonou barrage, and the general regional aridity. In Lac Ahémé there are only ~50ha left. Extending for 60km from Togbin to Grand Popo in the west, the coastal lagoon system contains the most important mangrove stands (Paradis, 1981). This lagoonal system is connected to the sea by a small opening which closes naturally, causing the Mono River (mean flow 500-1000m^3/sec) to flow inland to Lac Ahémé during the wet season. When flooding becomes extreme, local fishermen open a new connection. The mangroves of this lagoonal system consists of *Rhizophora* and *Avicennia* 5-6m high with occasional emergents up to 15m. At the back, *Laguncularia, Dalbergia, Drepanocarpus, Paspalum* and *Acrostichum aureum.*

Only at Azizahoue can trees still be found up to 25m in the coastal lagoon (CEC, 1987). At Adounko (3km east of Togbin) there is a small stand of *R. harrisonii* around 20m high while around Gbetou and île d'Ahoundji in Lac Ahémé, there are mixed stands of *Avicennia* and *Rhizophora* between 8-13m high (Paradis, 1981; Blasco, 1985).

There is one private mangrove plantation in the lagoon at Ahouandji, planted by a local fisherman to enhance his regular catch. Seedlings of *Rhizophora* were planted and these have been augmented by natural seedlings of *Avicennia* (Blasco, 1985).

In the lagoonal system of Togo, mangroves occur around the mouth of the Mono River and in its western tributaries, particularly the Vensi and Gbaga Rivers (Paradis, 1981; Akpagana, 1993). Formerly, they appear to have occurred further east as Grewe (1941) records mangroves in Kitta Lagoon and on the eastern shores of Lake Togo.

Mangroves are confined to estuaries in Equatorial Guinea with the following major areas: Ntem R. 18km^2; Mbia R. 1.5km^2; Ekuko R. 10km^2; Mbini 53km^2 Muni 65km^2 (Sayer *et al.,* 1992). Similarly, mangroves of Congo occur within estuaries and lagoons of the Atlantic coast (Camara, 1993). Mangrove communities are extensively developed in the Conkouati and Malonda lagoons but also occur in the estuaries of Noumbi, Loémé and Kouilou. According to Lebrun (1954), the mangroves are dominated by *Rhizophora racemosa* with *Avicennia, Conocarpus* and *Laguncularia* occurring respectively in order of frequency.

The most extensive stands in Angola are found in the Rio Lubinda (5°5'S), Cabinda, and in the Rio Zaire (6°10'S) where they appear to extend along the southern open coast. Other extensive mangrove communities occur at the mouths of the Chiluango, Loge and Cuanza Rivers with smaller outliers appearing southwards to Benguela. *R. racemosa* and *R. mangl*e can reach heights of up to 30m in the north of Angola (Huntley 1974), while south of Cuanza (9°15'S), *Rhizophora* is very short with heights of <1m (Gossweiler and Mendonça, 1939). *Avicennia* attains a height of 3-5m in the delta of the Rio Zaire but forms stunted formations further south (Gossweiler and Mendonça, 1939).

North of Cuanza, the landward margins of the mangroves are occupied by a littoral rainforest which appears to be similar to the freshwater swamp forests ('forêt inondee') described by Lebigre (1983) from Gabon with the following species in Angola (Gossweiler and Mendonça, 1939): *Chrysobalanus ellipticus, Drepanocarpus lunatus, Dalbergia ecastaphyllum, Pandanus, Annona palustris, Hibiscus tiliaceus, Erythroxylum emarginatum, Flagellaria indicum, Raphia* spp. and *Phoenix canariensis.*

Herbaceous halophyte species recorded from Angola (Gossweiler and Mendonça, 1939) include: *Arthrocnemum fruticosum, Arthrocnemum indicum, Arthrocnemum macrostachyum, Cyperus maritimus, Paspalum vaginatum, Sesuvium portulacastrum, Sporobolus robustus, Sporobolus virginicus* and *Suaeda fruticosa.*

Phenology

There are no systematic data on phenological events in mangroves from western Africa. The limited data on flowering of the various species at different localities (Table 11) have been compiled from incidental records in taxonomic or ecological accounts. These data indicate, however, that there are no clear trends of shifting flowering periods between north and south.

When the flowering records are arranged according to month for all locations combined (Table 12), the records indicate that slightly more than 60% of flowering occurs in the dry season, approximately from November to April north of the equator and May to October to the south. This finding is supported by Din (1991), who reported that flowering in Cameroon occurs predominantly during the dry season, i.e. mid-November to mid-March. Amobi (1974) also reports dry season flowering in the mangrove associates *Dalbergia ecastaphyllum, Drepanocarpus lunatus* and *Ormocarpum verrucosum.*

As with flowering, there are no systematic data on fruiting although Jackson (1964) provided data for seed-fall for one site in Nigeria. These data (Table 13) indicate that at Ikorodu in Western Nigeria, where the pronounced dry season extends from January to April, most species shed their propagules towards the end of the wet season and only *R. racemosa* and *H. tiliaceus* do so late in the dry season. However, the data are too scanty to indicate whether or not regional trends of shifting time patterns occur. However, when all of the available fruiting data are combined irrespective of locality (Table 14), mature fruit appear to be present predominantly during the wet period, i.e. May to October to the north of the equator, with slightly more than 60% of the records occurring in those months. This suggests that the time sequence described by Jackson (1964) occurs throughout the region.

It appears from the above that the principal mangrove species and their associates flower during the dry period of the year and fruit largely during the wet season. Given that all of the listed species have water-dispersed propagules and that they are either wind- or insect-pollinated, this phenological pattern is not surprising.

Physiology

There are virtually no physiological data available from West Africa on indigenous mangrove species and any associated flora. The only exception appears to be the osmotic data obtained by Walter and Steiner (1936) on their brief visit to Cameroon while returning from East Africa.

As a consequence, any physiological insights into West African mangrove systems have been derived by extrapolating North American data of shared mangrove species. While such extrapolations may be useful, they are based on the underlying assumption that the West African species do not differ physiologically from their North American analogues. While this assumption is based on the absence of any noticeable morphological difference, it has yet to be established that no physiological, biochemical or genetic differences exists. Comparative investigations into the biochemistry and genetics of Avicennia germinans from the Atlantic coasts of Africa and America are presently underway at ICIV, Toulouse in co-operation with the University of California (Berkeley).

Given that the mangrove populations on the two sides of the Atlantic have been separated for at least 10 million years with little likelihood of any significant geneflow between them, is it realistic to assume physiological, biochemical or genetic equivalence?

If anything, a re-examination of the original data of Walter and Steiner (1936) suggests that there are some physiological differences in the mangrove plants of the two sides of the Atlantic.

Walter and Steiner (1936) investigated the osmotic concentration of mangroves using a (then) newly developed refractometric technique. They simultaneously measured the chloride osmotic concentration in their samples. These measurements were carried out on a range of mangroves and associated species in Tanzania (East Africa) and Cameroon (West Africa) and they tabulated results obtained by the same technique from a range of mangrove species in Florida and the Caribbean.

These data have been summarized (fig. 9) and suggest that in the West African species, the total osmotic concentration directly varies with, and is accounted for, by the osmotic concentration due to chlorides. In contrast, the same species from either East Africa *(Terminalia catappa, Pandanus candelabrum, Phoenix reclinata, Acrostichum speciosum* and *Hibiscus tiliaceus)* or North America *(Rhizophora mangle, Avicennia germinans, Conocarpus erectus* and *Laguncularia racemosa)* showed that with increasing total osmotic concentration, no linear relationship with chloride concentration exist and that the chloride concentration could not explain the total osmotic concentration.

Given the current understanding of osmo-compensation in mangroves (Wyn Jones and Storey, 1981; Robinson and Jones, 1986), increasing osmotic concentration in the expressed cell sap is not accompanied by increased chloride but, rather, by a series of organic compounds such as glycinebetaine, choline-O-sulphate, choline-O-phosphate, proline and sorbitol. These osmo-compensators serve to maintain the osmotic concentration of the cell sap without increasing chloride concentrations which could adversely affect enzymes in the cytoplasm. What the West African mangrove data suggest is that the ability to osmo-compensate is less well-developed in the West African mangrove species in comparison with their analogues elsewhere. Because of the widespread occurrence of osmo-compensators in other mangrove regions, it appears that any lesser ability to be able to osmo-compensate is due to a secondary loss perhaps due to genedrift in remnant populations of West Africa.

The ecological implications of such a reduced ability to osmo-compensate in West African mangroves includes the pronounced confinement of mangroves to salinity refugia, and the susceptibility of mangrove communities to periods of aridity or increased saltwater incursion (such as might be expected with rapid sealevel rise).

Mangrove Zonation

In western Africa, mangrove zonation can only be recognized on a broadly generalized scale as clear zonation is absent at many sites (Din, 1991). Numerous irregularities in the vegetation exist because different species tend to establish on different microtopographic features and soil types. As a result, there appears to be a dynamic equilibrium with the vegetation constantly adjusting to the ever-changing estuarine landscape (Ukpong, 1992).

Nevertheless, *R. racemosa* is generally the predominant species on recently deposited, unconsolidated alluvium (Rosevear, 1947; Savory, 1953; Jacques-Felix, 1957; Jordan, 1964; Villiers, 1973; Marius, 1979; Lebigre, 1983; Egnankou, 1985; Din, 1991), often forming a monospecific zone. This monospecific zone is generally followed by a mixed *Rhizophora* zone, in which *R. racemosa, R. harrisonii* and *R. mangle* may co-occur, where the sediments are more consolidated but still inundated by the daily tides.

Above this level, where tidal inundation is reduced, an *Avicennia* zone generally occurs which may be monospecific, mixed with *Laguncularia* or *Conocarpus*, or interspersed with herbaceous halophytes with *Paspalum vaginatum* and/or *Sesuvium portulacastrum.* The more open *Avicennia* zone may gradually be replaced by *Paspalum vaginatum* or *Sesuvium portulacastrum* which, with further soil build-up, may result in vegetation-free saltflats (or 'tannes') in those areas inundated only by extreme spring tides each month. This characteristic seaward to landward sequence of species is illustrated (fig. 10) by data from Gabon (Villiers, 1973).

In contrast to zonation elsewhere (Snedaker, 1982), this sequence of species may not reflect intertidal gradients of waterlogging or salinity but may be due to varying soil preferences of the different species. For example, the prop roots of *R. racemosa* form a flying buttress structured base and below the surface of the soil, the roots immediately divide into innumerable hair-fine rootlets - supporting the tree by a thickly intertwined mat of roots (Attims and Cremers, 1967). This root mat is the source of *Rhizophora* peat deposits which, as Rosevear (1947) noted, may be so dense that it can be cut out in blocks, dried, and burned as peat fuel. With further growth of *R. racemosa,* the thick root mat gradually raises the soil surface which reduces the tidal flushing and may ultimately lead to the death of this species. Rosevear (1947) suggested that *R. racemosa* can only reach its optimal size where it starts growing on newly deposited soft mud. It may be that only one crop of the tall *R. racemosa* can grow at any one site before the root mat and elevation of the soil surface make the site unsuitable for a subsequent crop of this species (Rosevear, 1947; Jordan, 1964). Generally scrubby growth of *Rhizophora* follows tall *R. racemosa.*

R. harrisonii is often dominant in the middle areas of the *Rhizophora* zone. It does not compete with *R. racemosa* as a pioneer, apparently preferring the wetter, middle parts to the firmer and more peaty soil towards the inner limit (Savory, 1953). It rarely forms pure stands (Villiers, 1973).

Where it occurs, *R. mangle* is generally found on the drier, inner limit of the *Rhizophora* zone in western Africa although Lebigre (1989) records it only from one river mouth in Gabon. While it forms extensive pioneer forests of large trees in America, so far there are no confirmed reports of large trees of *R. mangle* in the mangroves of western Africa and Savory (1953) reported that, in Nigeria, this species grew only as a scrub up to 4 m high.

Savory (1953) first suggested that this difference in the distribution of the three species of *Rhizophora* lies in their different salt tolerances. Indeed, Chapman (1944) had shown that on the Jamaican shoreline, *R. mangle* had a high salt tolerance while *R. racemosa* has a lower salt tolerance. Thus, in Africa where seasonal freshwater inundation is common, *R. racemosa* is the dominant species and *R. mangle* is confined to higher land - which is less subject to flooding during the wet season with significantly higher salt concentrations during the dry seasons. On the other hand, Jordan (1963) has ascribed the distribution of this species to its inability to tolerate shade and, therefore, it is unable to compete with *R. racemosa.* It co-occurs with *Avicennia* (which has a more open canopy) and also grows in those areas (e.g. more landward and often sandier fringes) where *R. racemosa* does not occur.

Tomlinson (1957) noted that "the factors which control the distribution of the different species of vegetation are incompletely understood. It is usual to find *R. racemosa* fringing creeks in almost pure stands. *Avicennia nitida* is often found on slightly higher land away from the creek but seldom occurs as pure stands. The indications are that while *R. racemosa* makes good growth only on recently deposited heavy soils, *Avicennia* is particularly salt-tolerant and grows well on rather sandy soils in which there is marked accumulation of salt during the dry season, at the end of which salt crystals are commonly found on its leaves. The grasslands are still further removed from the creeks. The soils have a high proportion of sand, commonly about 70% at the surface, and are dry during the dry season."

In Nigeria, *A. germinans* cannot be considered as a frontal species but Rosevear (1947) described one such formation on Soden Island in the estuary of the Rio del Rey. Here *Avicennia* grows on sand, reaching heights of slightly over 30m with a clear bole length of 22m and girths up to 1.5m. On newly formed banks at the mouths of creeks opening into the sea numerous associations of *Laguncularia* bushes occurred, apparently as first colonists. Behind these, *Avicennia* was found. Rosevear (1947) concluded that "it seems possible that these two species may establish themselves on deposits which are predominantly sand from the sea rather than silt from the river, and that behind these barriers the normal slimy mangrove soil collects on which *Rhizophora* finds secure and favorable anchorage."

From his studies in Gabon, Lebigre (1983) also concluded that where rapid colonization was taking place, the pioneer species are *Laguncularia* and *Avicennia* but these are rapidly submerged or eliminated by *Rhizophora.* Similarly, Paradis (1979) has described *Laguncularia* and *Dalbergia* as 'opportunists' which characterize secondary successional stages in mangroves. As both are shade-intolerant and have abundant, widely dispersed seeds, these two species are able to rapidly colonize any gaps formed in the mangroves due to human disturbance. Particularly in the case of *Laguncularia,* this helps to explain the various accounts of its distribution in relation to the other species: for example, Rosevear (1947), Lebigre (1983) and Din (1991) describe *Laguncularia* as a pioneer species, colonizing newly deposited mudflats in the very frontal zone. Others describe it as occurring at the landward boundary of the mangroves where soils are better drained and of lower salinity; *Laguncularia* seems to be able to colonize virtually any unoccupied area in sheltered intertidal zones, becoming outcompeted or excluded by other species with denser canopies. Part of this wide ecological ability may be attributable to the abundant peg-root development (Jenik, 1970) that occurs in *Laguncularia* when growing on newly deposited muds.

Lebigre (1983) has additionally described the changes in zonation that were noted with increasing distance up-river in Gabon. Thus, near the mouth of the rivers, a zone of tall *R. racemosa* was noted, followed by a landward zone of *Avicennia.* In the mid-zone of the rivers, *R. harrisonii* predominated over *R. racemosa,* with well-developed *Avicennia* zones on their landward sides. Using air-photo interpretation, it was also noted that abundant salt-flats or 'tannes' characterized the mid-zones of rivers. Upper zones of rivers were characterized by the predominance of *R. racemosa* along the river banks, the absence of a landward *Avicennia* zone, and the direct transition from *R. racemosa* to a freshwater swamp forest (Lebigre, 1983). A similar transition, directly from *R. racemosa* to a freshwater swamp forest, has also been reported from Cameroon (Boyé *et al.,* 1975).

As discussed earlier, Kunkel (1966) has interpreted zonation in Liberian mangrove and associated vegetation in a strictly successional sense. This causative explanation has not been as prominently invoked in West Africa as it has been elsewhere and, as suggested by Snedaker (1982), is of doubtful general application.

Structure and Productivity

Only limited structural and productivity data have been collected from West African mangrove vegetation and one productivity estimate is available for *Paspalum vaginatum* saline grassland (Edwards and Ekundayo, 1982). The only biomass data for West African mangrove vegetation have been collected from the Saloum River (14°40'S) in Senegal (UNESCO, 1983; Diop and Bâ, 1993) using an allometric technique. Above-ground biomass of tall formations (mean height of 7.60m) was found to be 79t/ha while for medium formations (mean height of 5.64m), a biomass of 55t/ha was found (UNESCO, 1983). Diop and Bâ (1993) provide some structural data for the Saloum River site for which biomass estimates have been determined, together with slightly different estimates of biomass: they report an above-ground biomass of 60t/ha comprised of 52t/ha wood, 6.6t/ha leaves and 1.4t/ha buds together with a net primary productivity of 2,145kg/ha/y. Wood volume was estimated at 62m^3/ha (Diop and Bâ, 1993). These above-ground estimates of biomass conform with the worldwide trends (Saenger and Snedaker, 1993) of biomass in mangrove vegetation.

Blasco (1983) provides the following field estimates for biomass (wood volume) and productivity of Gambian mangroves: estuarine mangroves (<10m high) were estimated to have a standing stock of 50m^3/ha, with a primary productivity of 8t/ha/y; fluvial mangroves (>20m high) were estimated to have a standing stock of 150m^3/ha, and a primary productivity 15t/ha/y. While the wood volume estimates are similar to those measured in Senegal, the estimates of primary productivity are markedly higher. This is probably due to the greater height of the Gambian mangrove vegetation. For instance, the joint Gambian-German Forestry Project (quoted by Blasco, 1983) found the following structural distribution of mangrove vegetation in the Gambia catchment:

Community	Height (m)	Dominant	Area (ha)	%
Mangrove type I	>7	*Rhizophora*	15,312	23.1
Mangrove type II	<7	*Avicennia*	51,067	76.9

The percentage (23.1%) of mangroves >7m high does not differ greatly from the remotely sensed data from Guinea (Table 10), where mangroves of greater than 7m in height comprised 23.8% of the total mangrove area. However, with approximately a quarter of the mangroves in Gambia exceeding 7m in height and reaching up to 20-25m, higher primary productivity in comparison to Senegal is to be expected.

In terms of wood volume, the only other estimates are those of Pynaert (1933) for Zaire as follows: tall *Rhizophora* 500m^3/ha; other mangrove types 100-400m^3/ha. These estimates appear to be very high. On the other hand, in terms of the annual production of wood, Heske (1937) showed a mean annual increment (MAI) in mangroves on the Cameroon coast of 0.083m^3/ha/y compared with an MAI of 1.98m^3/ha/y for upland rainforest. These MAI estimates are very low when compared with MAI measurements elsewhere (e.g. 2-8m^3/ha/y for *Avicennia* in Bangladesh - Saenger and Siddiqi, 1993) and, with the high estimates for wood volume, suggest an improbably ancient age for these mangrove communities.

Other structural data are presented in Tables 9 and 15 for mangrove communities dominated by *Avicennia* and *Rhizophora* respectively. Both communities show a stem density of 384-492 stems/ha. Mean stem diameters (Table 15) for the *Rhizophora* dominated community varied from 8 to 31 cm while no data are available for the *Avicennia* dominated community (Table 9). However, Paradis (1989) has given the diameter distribution for *Avicennia* from 15-18m high stands at Fresco, Côte d'Ivoire, as follows:

∅ class (cm)	0-15	16-30	31-50	51-70	71-90	91-110	>110
No. of trees	23	10	7	12	7	7	1

While this undoubtedly represents an old, well-developed stand of *Avicennia,* there is the suggestion of a bimodal diameter distribution with a few very large old trees and more recent recruits in the <30cm diameter class.

Mangrove Fauna and Trophic/Functional Aspects

The mangrove vegetation of western Africa is intimately linked to the offshore coastal ecosystem (John and Lawson, 1990). Regularly influenced and disturbed by seasonal freshwater and diurnal tidal flooding, it exhibits features of an immature ecosystem, namely low species diversity and high productivity. The excess organic production is exploited by many marine species especially fishes and crustaceans that enter the mangrove environment as juveniles and return to the sea as adults for reproductive purposes.

The bacterially-mediated process by which this organic production becomes available for fish and crustaceans, has only been studied in the Gambia River. Healey *et al.* (1988) sampled the Gambia River during four different hydrologic seasons to determine selected microbial, nutrient, and physical parameters. The ranges of total bacterioplankton densities were similar to those of other tropical and temperate environments and the numbers of free bacteria remained similar over all seasons. However, the numbers of attached bacteria were greater during periods of high stream flows when suspended solids concentrations were higher. Consequently, heterotrophy overshadowed autotrophy in the river and bacterial abundance, distribution, and glucose uptake activity in this tropical floodplain river were greatly influenced by the annual flood. In turn, these data suggest that much of the organic material derived from the mangroves is broken down within the river and then flushed into nearshore waters with the annual flooding (Healey *et al.,* 1988).

Another linkage to the offshore coastal ecosystem is via the coastal waders which use many of the mangrove areas and coastal lagoons (Ntiamoa-Baidu, 1991). The significance of this linkage has only recently been recognized in West Africa with the identification of a series of potentially suitable sites for RAMSAR nomination in Côte d'Ivoire, Ghana and Benin (Schwarz, 1991).

Major Threats to Mangrove Vegetation

Prior to the colonial era, the mangrove vegetation of western Africa had little commercial significance although it had been traditionally exploited at the subsistence level. At the turn of the century, interest in the extraction of tan-bark from mangroves was stimulated by analyses which showed a generally high (10-30% per dry weight) tannin content (Drabble and Nierenstein, 1907; Drabble, 1908; Pynaert, 1933; Grewe, 1941) while in Guinea, the combined exploitation for tan-bark, telegraph poles and railway sleepers was advocated (Baillaud, 1904).

The first systematic exploitation of mangroves in western Africa, however, commenced at Manoka, Cameroon in 1919 when the 'Société Nationale du Cameroun' was granted logging concessions and built a timbermill (Hédin, 1928). Considerable quantities of *Rhizophora* timber were extracted, initially as railway sleepers but, subsequently, for barrel staves which were ultimately used to export palm oil. The data shows a sizeable export of *Rhizophora* timber (Table 16) but the proportion that this represents of the total timber extracted is no longer ascertainable.

Combined wood and tan-bark extraction also occurred in Cameroon, Gabon and Zaire but, in comparison with upland forest exploitation, it was relatively insignificant. Moreover, due to their somewhat lower tannin content, the mangroves of western Africa were spared the large-scale destruction that followed the intense tan-bark extraction in Mocambique, Tanzania and western Madagascar between 1905 to 1930 (Grewe, 1941).

As a result, the mangroves of western Africa represent a remnant system struggling against geological and climatic adversity but which has been spared the colonial over-exploitation that occurred elsewhere. Nevertheless, the demands of modern, post-colonial Africa, with its burgeoning population increasingly in urban centres, is making novel and threatening demands on these mangrove systems. These demands include extraction of products such as wood, often at levels which exceed sustainable levels; the use of mangrove lands for other productive (e.g. salt and/or rice production; aquaculture) or non-productive (e.g. foreshore and urban developments) activities; the accidental or deliberate discharge of wastes; and the alteration of hydrological regimes either through the upstream diversion of water by dam construction, or the altered influx of tidal waters through coastal erosion works or salt barrages.

Each of these threats are briefly reviewed below:

Domestic Firewood

The extraction of wood for domestic purposes as well as for salt production and fish smoking is common throughout West Africa (Adam, 1958; Kinako, 1977; Egnankou, 1985; Paradis, 1989; Bertrand, 1991). For example, Adam (1958) reported that 25-30m high *R. racemosa* are heavily exploited in Gambia and that much of the wood and bark is marketed through Dakar. Similarly, Paradis (1989) described from air-photo interpretation that between 1962-76, *Rhizophora racemosa* areas around Fresco in Côte d'Ivoire, have been reduced by about 80% due to firewood collecting and for tan-bark which is used to prolong the life of wood used for pirogues. As a consequence, extensive prairies of salt-tolerant grass *Paspalum vaginatum* have increased dramatically. In Guinea, annual estimates of mangrove wood consumption (Diallo, 1993) are: rural firewood 152,000t/y; urban firewood 54,000t/y; fish smoking 58,000t/y; and salt extraction 93,000t/y.

In Benin, domestic firewood usage is also high while additional demands result from "Acadja fishing", which is common in the lagoons and which requires additional mangrove wood for the stakes. The World Bank has estimated firewood consumption of Cotonou and Porto Novo as follows: 1984: 300,000m^3/y actual; 2000: 650,000m^3/y predicted; 2020: 1,400,000m^3/y predicted. Such demands as in Guinea or Benin cannot be met sustainably without large-scale mangrove afforestation.

In the Niger Delta, *R. racemosa* was heavily exploited for pitprops (e.g. at the Enugu coal mine, where 20,000m^3 was used - Ajao, 1993), for poles, for firewood and by the local fishermen for tanning their fishnets (Rosevear, 1947). The wood of *Avicennia* was rarely used although there is some localized use of the leaves for preparation of salt. However, present day exploitation is largely confined to domestic firewood and estimates of the standing volume of 283.2 x $10^6 m^3$ are considered to be capable of providing a sustainable timber yield of 0.6 to 1.6 x10^6 tonnes/y (Kinako, 1977).

Salt Production

Salt extraction from West African mangrove areas is widespread (Paradis, 1979; Vanden Berghen, 1984; Blasco, 1985; Bertrand, 1991). For example, in Benin, salt production is a traditional industry where the short dry season is not sufficient for solar extraction. To produce salt, the mangrove vegetation is removed in selected areas and the underlying soils are dug up to a depth of around 10cm to facilitate evaporation. After a few days, the upper crusts are raked and scraped and, finally, collected into heaps for processing. These soils are leached several times with the same water and the saline solution is then boiled to obtain crystallized salt (Blasco, 1985). The firewood requirement is met by the neighbouring mangroves. Hachimou (1993) has estimated that $1m^3$ of mangrove wood is required to produce 100kg of salt.

The environmental consequences of salt production in Benin, as in much of West Africa, include the formation of barren depressions in which the hydrological regime is modified; destruction of mangroves for firewood; compaction of the surface soil by repeated raking and trampling; and the creation of ecological conditions unsuitable for the recolonization by mangroves (Blasco 1985). Similarly, Paradis (1980) has suggested that where there are long dry seasons, bare salty areas are present and which may be extended (e.g. in Senegal and Gambia) by salt extraction. Even in more humid climates such as in Sierre Leone and Guinea, salt extraction has caused the formation of extensive denuded areas (Paradis, 1980; Bertrand, 1991).

Rice Cultivation

Using mangrove lands for the cultivation of rice is widespread in Gambia, Guinea, Guinea-Bissau, Senegal and Sierra Leone (Bertrand, 1991; Diallo, 1993). According to Simao (1993), the mangrove area in Guinea-Bissau has been halved due to ricefields and that the annual loss due to rice-growing was around 3,800ha/y between 1976 and 1990.

In less humid regions, rice cultivation is more restricted (e.g. in Côte d'Ivoire, rice cultivation occurs around Sassandra - Egnankou, 1985) but still encroaches on the more limited deltaic mangrove vegetation.

As many of the soils associated with mangroves have a high fibrous content, they often yield very low pH after drying out (Dent, 1947; Hart, *et al.,* 1963; Thornton and Giglioli, 1965). Extensive acid-sulphate soils (Table 17) have caused difficulties with cultivation of dryland rice varieties in most regions of West Africa (Dost, 1988).

Aquaculture

Aquaculture is not widespread in West Africa at present but it can be expected to increase in the near future. In those localities where aquaculture is already practised in mangrove areas, problems have been noted. For example, in Nigeria, aquaculture is being actively encouraged in mangrove areas (Wokoma and Ezenwa, 1982) even though problems of acidification and land degradation are associated with it (Ajao, 1993). Similarly at Makali, in northern Sierra Leone, problems have been noted with intense aquaculture in mangrove areas (Johnson and Johnson, 1993).

Dams and Barrages

Dams and barrages are a major threat to mangrove systems throughout West Africa through their disturbance to the hydrological and tidal regimes of the rivers and through the reduction of sediment supply to deltas. Major dams or barrages currently exist at Diama in Senegal (Bâ and Leung Tuck, 1989), on the Volta at Akossombo in Ghana (Ly, 1980) and at Nangbeto on the Mono River in Togo (CEC, 1987), at Cotonou in Benin, at Buyo in Côte d'Ivoire (Egnankou, 1985), and at Tchimbélé and Kinguélé on the Mbei River as well as at Poubara on the Ogooué River in Gabon. Sayer *et al.* (1992) report that more than 40 small anti-salt barrages have recently been built in Guinea-Bissau and there are other proposals currently under consideration (e.g. at Onitsja on the Niger River).

Bâ and Leung Tuck (1989) have described some of the adverse effects of the anti-salt barrage at Diama on the hydrology of the Senegal River and its estuarine system while others have described the ecological effects of the barrage on the Mono River (Akpagana, 1993). Nevertheless, the reduction in freshwater inflow to the deltas and estuaries of West Africa is likely to become more acute in the near future. Any increased salinity in the deltas is likely to add to the regional stresses due to decreasing rainfall over the last twenty or so years.

In Ghana, Ly (1980) found that the reduction of sediment supply via the Volta River initiated the onset of coastal erosion.

Oil Pollution

Although natural oil seeps have been reported from the mangroves of West Africa (Hutter, 1906), twenty-three out of 62 oilfields with some 1800 oil wells in the Niger Delta occur within the mangroves (CEC, 1987). Oil terminals are situated at Bonny, Brass and Kanuskiri while seismic lines (8,000km x 20-30m wide) and oil pipelines criss-cross the mangroves. Oils spills are common (Snowdon and Ekweozor, 1987) and the seismic lines have allowed saltwater intrusion into brackish and freshwater swamp areas, causing widespread mortality (Fagbami *et al.,* 1988).

The relatively minor oil spillage of 250 barrels of Nigerian crude into the Bonny estuary (Snowdon and Ekweozor, 1987) caused the oiling of mangrove prop roots and seedlings and resulted in partial defoliation and death of seedlings within a 500m^2 area.

An investigation into the causes of vegetation mortality over approximately 200 km^2 around the Tsekelewu Oil Field in the Niger delta was carried out (Fagbami *et al.,* 1988) using quantitative photo interpretation of black and white aerial photographs. Soil, surface and ground water samples were taken from the various zones for chemical analyses. Salt concentration decreased progressively landwards, with a marked increase at the saline-fresh water transitional zone where the greatest damage occurred. In the transitional saline-fresh water zone, all the vegetation including *A. germinans* was killed. The massive destruction was attributed to high salinity caused by salt water incursion from the sea as a result of seismic exploration.

In Gabon, petroleum exploration has left extensive systems of survey lines through the mangroves which have failed to revegetate since clearing (Lebigre, 1983; J. Fontes, pers. comm.). Similar effects from exploration activities have been reported from the mangroves in Angola (Huntley, 1974). Chronic oil spills have also been noted to have caused the degradation of Mvassa lagoon in the Congo (Camara, 1993) while the oil terminal in the Angolan enclave of Cabinda has been reported to affect the mangroves of Zaire (Sayer *et al.,* 1992).

Industrialization and Urbanization

The development of large urban centres with significant industrialization poses a number of threats to the mangrove vegetation. Thus, around Abidjan, Côte d'Ivoire, industrial pollution has adversely affected the coastal lagoons (e.g. Lagune Ebrié) and their associated mangroves (Carmouze and Caumette, 1985; Zabi, 1982). The decline in water quality has been magnified by sand-extraction from the coastal lagoon system (Egnankou, 1985).

Such effects on coastal lagoons are not confined to Côte d'Ivoire but occur, for example, in Ghana (Chemu and Korle lagoons - Biney, 1982), Benin and throughout Nigeria (Ajao and Fagade, 1990). In Gabon (Posso, 1993) reports pollution of the mangroves of the Como River due to the restaurants at Esterias Cape.

In Cameroon, the effects from Douala port extension, urban expansion, sand extraction and industrial pollution have caused damage to the mangroves of the Wouri estuary (Din 1991).

DDT Fishing

Fishing by the use of insecticides is illegal throughout the region but still widely practised, particularly in Côte d'Ivoire (Egnankou, 1985) and in Cameroon (Din 1991). While this activity causes little direct damage to the mangrove vegetation, its adverse effect on any aquatic fauna is likely to cause indirect effects on the vegetation.

Weed Invasion

Invasion and replacement of native mangrove by the mangrove palm *Nypa fruticans* also appears to be a local problem. Although known from the fossil record from throughout the Niger delta until 25 m.y. BP (Sowunmi, 1986), the present populations of *N. fruticans* were introduced to Calabar in 1906 and Oron in 1912 (Wilcox, 1985) from the Singapore Botanic Gardens. This species has spread throughout the Niger, Imo, Bonny and Cross Rivers since then. The spread has been slow but it is perceived to be accelerating over the last few years and it has now reached the Wouri Estuary in Cameroon where its dispersal is facilitated by local villagers who value its thatching properties (Din, 1991; Saenger, pers. obs.).

Introduced stands of *Nypa* have also recently been recorded from the Atlantic coast of Panama, where a similar spread is predicted (Duke, 1991).

Coastal Erosion

Coastal erosion is widespread in West Africa (Quelennec, 1987; Awosika *et al.,* 1993). However, in Nigeria the erosion of outer barrier beaches in the Niger delta poses the threat of extensive saltwater intrusion into mesohaline mangrove communities (Oyegun, 1990).

Management and Rehabilitation

Mangrove management and rehabilitation had some early supporters in West Africa. Already in 1909, Rivière described the plan to plant *Rhizophora* in Tunesia both to provide coastal protection and to produce tan-bark, as ".. véritable hérésie climatologique et culturale". That such mangrove planting was not feasible given the particular climatic conditions, had already been established by Rivière's own culture attempts in Algeria (Grewe 1941) and had already negated the proposal to stabilize the Suez canal banks with mangroves!

Similarly by 1911, demands were being made for the protection of mangroves and for the regulation of their exploitation around Douala in Cameroon, in order to safeguard their coastal protective function (Grewe, 1941). In Zaire, tannin extraction dates back to mangrove concessions granted in 1908 and these concessions included (i) riverine buffer zones to prevent erosion and siltation; (ii) concern over traditional user access to the mangroves; and (iii) a condition to replant extracted areas at 1000 seedlings/ha (Pynaert, 1933). The replanted mangroves were reported to have a stem diameter of 15cm after 15 years and to have become mature after 20-25 years (Pynaert, 1933).

Despite these early initiatives, mangrove management, conservation and rehabilitation is not generally well established in West Africa - although considerable variation exists in terms of management approaches. The management framework for each of the coastal states is briefly reviewed below:

Mauritania: Limited information on the management framework is available although the very limited mangrove relicts of Mauritania are contained within national parks (Table 18).

Senegal: A number of national parks containing mangroves have been established (Table 18) and these are managed by the National Park Directorate in the Ministry of Tourism and Nature Conservation. Non-national park areas are administered by the Direction des Eaux, Forêts et Chasses. The Saloum Delta National Park has also been listed as Biosphere Reserve and RAMSAR site since 1984. Nevertheless, mangroves in Senegal remain threatened by the extension of rice cultures and cutting for fuelwood (Diop and Bâ, 1993).

Gambia: A number of national parks containing mangroves have been established (Table 18) and are managed by the Wildlife Conservation Department. Attempts to develop sustainable commercial forestry are underway.

Guinea-Bissau: There is presently no mangrove management in Guinea-Bissau although a multidisciplinary coastal ecosystems study is presently underway and legislation for the conservation and management of mangroves is in preparation (Simao, 1993). A number of Ramsar Sites with mangroves exist (Table 18) and the Bijagos Archipelago (11.3°N, 16°W), with extensive mangrove areas has been proposed as a protected area but its status is uncertain. Other proposed reserves for mangroves include the Cacheu River and Cantanhez Forest (Sayer *et al.,* 1992).

Guinea: Concern over mangrove losses has been expressed and a forestry action plan (including mangroves) has been developed which according to Diallo (1993) should provide for sustainable use.

Liberia: No mangrove reserves have been established (Sayer *et al.,* 1993) and the mangroves remain under threat from wood exploitation.

Sierra Leone: Responsibility for mangrove vegetation is under the Ministry of Agriculture, Forestry and Fisheries (Johnson and Johnson, 1993). Extensive mangroves have been proposed for protection in the Bunce River area (8.50°N, 12.83°W).

Côte d'Ivoire: With the establishment in 1992 of a Direction de l'Environnement within the Ministère de l'Environnement, de la Construction et de l'Urbanisme, studies into the degradation of coastal lagoons are in progress. To date, however, there is no specific mangrove protection (Egnankou, 1993).

Ghana: Although possessing an Environment Protection Council since 1974 there are no mangrove reserves and there is no specific mangrove protection. However, management plans have been prepared for some specific wetland areas as RAMSAR sites (Sackey, 1993).

Togo: Responsibility for the mangroves falls within the Ministry of Environment and Tourism, specifically the Commission of Forests and Hunting, and the Commission of Flora (Akpagana, 1993). However, there are no existing specific measures for the management of mangroves.

Benin: Mangrove management is the responsibility of the Direction de l'Environnement, established in 1991 within the Ministère de l'Environnement, de l'Habitat et de l'Urbanisme. No official protective measures currently exist although a number of informal reserves have been identified. Two types of conservation areas are in use - those of religious significance e.g. the fetish-mangroves on the îlots des Avlékété and Mtogbodji, and at Kpétou (Blasco 1985; Baglo, 1989) where most exploitative activities are forbidden; and those controlled by local people where exploitative activities are regulated by the village chief.

The establishment of biosphere reserves has been in progress since 1981 and a mangrove replanting program has been in place since March 1987 as part of the Beninois-German Co-operative Program "de pêche lagunaire", involving 14 villages. In 1987, 12,000 propagules of *Rhizophora racemosa* were planted near Vekky Dogbodji in Lac Nokoué. Since then, planting was extended to Lac Ahémé and the coastal lagoon system with 121,000 propagules planted in 1988 and a further 250,000 in 1989. Cost of collection was 0,20FF per plant with the overall cost of planting estimated at $US360/ha (Baglo, 1989). Major problems with these new plantations include (i) prolonged freshwater inundation killing some of the seedlings; (ii) crab predation from *Goniopsis pelii;* and (iii) insect predation by the larvae of *Charaxes castor* (Nymphalidae).

Nigeria: A Federal Environmental Protection Agency was established in 1988 and, more recently, a National Coastal Management Authority has been proposed to regulate and manage all coastal resources. To date, no mangrove protection is in existence although the Cross River National Park contains some mangrove areas (Table 18). There exists a 247km^2 mangrove forest reserve but it is not worked regularly (CEC, 1987). The National Institute of Oceanography and Marine Resources (NIOMR) has recommended that a system of mangrove forest reserves be established to replenish trees that are unavoidably felled by coastal people. It was also suggested that the price of gas also needs to be reduced to an affordable level for coastal communities to reduce the use of mangroves for domestic cooking (Amadi, 1991).

Cameroon: The Ministry of Environment was established in 1992 but, at present, there is no legislation to control the management, utilisation or protection of mangroves (Appolinaire, 1993).

Equatorial Guinea: Limited information on the management framework is available but, according to Sayer *et al.* (1992), the mangroves have suffered little degradation although traditionally they have been exploited for firewood and building materials.

Gabon: Limited information on the management framework is available and, at present, there are no conservation reserves specifically for mangroves (Sayer et al., 1992). Three Ramsar sites (Table 18) contain some mangrove areas. However, except for around the immediate vicinity of the capital, the mangroves have suffered little degradation due to low population pressure.

Congo: Limited information on the management framework is available although at least one mangrove reserve (Conkouati Wildlife Reserve) has been established.

Zaire: Limited information on the management framework is available although a 100,000ha Mangrove Reserve (Table 18) was recently established in the Zaire River estuary. Mangrove utilisation leases in Zaire were granted as early as 1908 (Pynaert, 1933) by the Belgian colonial administration.

Angola: Limited information on the management framework is available although a large mangrove reserve (Parque Nacional da Qicama) with extensive mangroves has been in existence since 1957. With the unrest in the country, this reserve has been threatened by illegal grazing, cotton production, oil exploration and extraction as well as diamond prospecting (Huntley, 1974).

Major Data Gaps

The aim of this review was to assemble and evaluate existing information about the mangrove vegetation of the Atlantic coast of Africa and, in doing so, it has identified a number of areas where existing knowledge is extremely limited or lacking completely. By identifying those areas, this review might stimulate or encourage studies to fill those needs and thereby enhance the understanding of mangrove ecology on the African Atlantic coast and facilitate the conservation and management of these mangrove systems on a sustainable basis.

One of the obvious information gaps is the absence of detailed distributional and abundance data of mangrove species and their associates. Existing data has been summarised in Table 6 but inadequate data exist for several areas including Equatorial Guinea, Congo, Togo and Liberia.

With reliable distribution and abundance data, additional questions may be answered. For instance, why is *R. mangle* apprently absent from the drier coasts of Ghana, Côte d'Ivoire and Benin while present in Senegal? It is noteworthy that *R. mangle* occurs abundantly in Florida and Yucatan, Mexico with a similar rainfall to these West African areas. Are the West

African mangrove populations of this species less adapted to deal with high salinities as suggested by the data in figure 9?

In turn, such investigations may throw light on whether or not there has been some genetic differentiation between the mangrove species of the Atlantic coasts of Africa and America. Why do they appear not to have segregated, at least morphologically, during a separation of 10 million or so years? Has there been biochemical or physiological differentiation? More intriguingly, is there genetic leakage across the Atlantic?

At present, there is no systematic study of the phenology of the mangroves of the Atlantic coast of Africa; the summarized information has been extracted from herbarium data concerning individual specimens and from incidental observations. The absence of systematic data makes comparisons with the Americas difficult. More importantly, it is difficult to predict when flowers and fruits are available; this is particularly significant for ecological studies of those species (e.g. *Rhizophora)* where reliable species identification requires the presence of flowers and fruits.

Similarly, there are no litter fall data for the Atlantic coast of Africa and only very limited biomass data. While data for many of the individual species are available from the American Atlantic coast, the absence of these data from the African coast makes functional comparisons between the African mangroves and those of other areas difficult. Litter and wood productivity estimates are important respectively for quantifying the overall contributions made by mangroves to nearshore waters and for assessing the potential for commercial wood production from mangrove systems.

There appears to be little effort put into the establishment of sustainable forestry operations of the mangroves as have been developed in India, Bangladesh, Malaysia and Thailand. There is little doubt that at least the mangroves of Nigeria, Cameroon, Gabon and Equatorial Guinea could be exploited on a sustainable basis. Similarly, with the exception of Benin, there have been few attempts at mangrove afforestation not only to produce wood but to enhance the coastal stability of the coastal regions - as, for example, in Bangladesh (Saenger and Siddiqi, 1993). In the case of the Niger delta, efforts at developing a sustainable mangrove forestry industry would appear to be a prioroity.

From a management perspective, there have been relatively few hydrological studies on the effects of dams and barrages on the downstream mangrove vegetation. Such studies are vital not only for the continued functioning of the mangrove systems but also in terms of the supply of sediments to coastal areas - a factor already implicated in coastal erosion. Similarly, the likely effects on coastal erosion, particularly in relation to mangroves, need to be investigated.

Although the extent of acid-sulphate soils is reasonably well-known (Table 17), their pedogenesis is only now being understood. The role of mangrove vegetation in the genesis and development of acid-sulphate soils is still in need of further investigation (Feller *et al.,* 1989), particularly in view of the widespread and on-going conversion of mangrove soils to rice cultivation.

Finally, given the mangrove areas, the population pressures and the per capita gross national product (GNP) of the west African nations (Table 8), it would seem that any conservation initiatives would be most rewarding in Gabon, Congo, Cameroon and Senegal in that order. On the other hand, conservation initiatives appear to be most urgently needed in Guinea, Sierra Leone, Côte d'Ivoire, Benin, Nigeria, Cameroon and Equatorial Guinea.

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Table 1. Spring tidal ranges at a number of western African localities.

Location	Spring Tidal Range (m)
Cape Bimbia, Cameroon	0.80
Escravos, Nigeria	0.92
Pointe Olga, Cameroon	0.97
Takoradi, Ghana	1.23
Dakar, Senegal	1.26
Cotonou, Benin	1.30
Casamance, Senegal	1.40
Libreville, Gabon	1.50
Banjul, Gambia	1.68
Bonny, Nigeria	1.82
Caio, Guinea-Bissau	2.30
Freetown, Sierra Leone	2.58
Cachen, Guinea-Bissau	2.74
Calabar, Nigeria	3.07
Abidjan, Côte d'Ivoire	3.10
Conakry, Guinea	3.50
Monrovia, Liberia	3.60
Luanda, Angola	4.20
Babaque, Guinea-Bissau	4.24
Port Etienne, Mauritania	5.80

Based on various sources including Lawson (1966), Diop (1990) and the National Tidal Facility, Flinders University, South Australia.

Table 2. Geomorphological and hydrological settings of mangroves along the Atlantic coast of Africa.

	Frontal	Deltaic		Lagoonal
		Estuarine	Fluvial	
Mauritania	-	+	-	+
Senegal	-	+	-	-
Gambia	-	+	+	-
Guinea-Bissau	+	+	+	-
Guinea	+	+	+	-
Sierra Leone	+	+	+	-
Liberia	-	+	-	+
Côte d'Ivoire	-	+	-	+
Ghana	-	+	-	+
Togo	-	-	-	+
Benin	-	-	-	+
Nigeria	-	+	+	+
Cameroon	-	+	+	-
Equat. Guinea	-	+	+	-
Gabon	+	+	+	+
Congo	-	+	+	+
Zaire	?	+	+	?
Angola	+	+	+	-

+ present   - absent   ? insufficient data

Table 3. Listing of major families (with genera and species) of mangroves and significant mangrove associates on the Atlantic coasts of America and Africa and the eastern coast of Africa.

	Atlantic America	Atlantic Africa	Indian Ocean Africa
Avicenniaceae			
	Avicennia germinans	A. germinans	A. marina
	A. schaueriana	-	-
Rhizophoraceae			
	Rhizophora mangle	R. mangle	R. mucronata
	R. harrisonii	R. harrisonii	Bruguiera gymnorrhiza
	R. racemosa	R. racemosa	Ceriops tagal
Combretaceae			
	Laguncularia racemosa	L. racemosa	Lumnitzera racemosa
	Conocarpus erectus	C. erectus	-
Meliaceae			
	Carapa procera	C. procera	Xylocarpus granatum
	Carapa guyanensis	-	X. moluccensis
Sterculiaceae			
	-	-	Heritiera littoralis
Sonneratiaceae			
	-	-	Sonneratia alba
Malvaceae			
	Hibiscus tiliaceus	H. tiliaceus	H. tiliaceus
	Thespesia populnea	T. populnea	T. populnea
	-	-	T. acutiloba
Rosaceae			
	Chrysobalanus icaco	Chrysobalanus ellipticus	-
	-	C. orbicularis	-
Theaceae			
	Pelliciera rhizophoreae	-	-
Acrostichaceae			
	Acrostichum aureum	A. aureum	A. aureum
	A. danaefolium	-	A. speciosum
Lythraceae			
	-	-	Pemphis acidula
	-	-	Barringtonia racemosa
Palmeae			
	Mauritia flexuosa	Phoenix reclinata	P. reclinata
	-	P. canariensis	-
	Raphia taedigera	Raphia hookeri	-
	* Nypa fruticans	*Nypa fruticans	-
Fabaceae			
	Pterocarpus officinalis	P. santalinoides	-
	Drepanocarpus lunatus	D. lunatus	-
	Dalbergia ecastaphyllum	D. ecastaphyllum	Dalbergia spp.
	Mora oleifera	-	-
Pandanaceae			
	-	Pandanus candelabrum	-
Aizoaceae			
	Sesuvium portulacastrum	S. portulacastrum	S. portulacastrum
Poaceae			
	Sporobolus virginicus	S. virginicus	S. virginicus

* introduced species

Table 4: Endemic mangrove species of each of the major mangrove regions of the World.

Region	Endemic Mangrove Species
Pacific America:	A. bicolor
Atlantic America:	A. schaueriana
West Asia:	Sonneratia apetala, Heritiera fomes
South-East Asia:	A. alba, A. lanata, Bruguiera hainesii
North-East Asia:	Sonneratia hainanensis, Kandelia kandel
Australia & Pacific:	A. integra, Sonneratia lanceolata.

Table 5. Distribution of mangroves and associated species from the four islands in the Gulf of Guinea[a]

Species[b]	Fernando Po (= Bioko)	Principe	Sao Tomé	Annobon
A. germinans	+	+[c]	+	-
R. harrisonii	+	+	+	-
A. aureum	+	+	+	-
C. erectus	+	-	+	-
H. tiliaceus	+	-	+	-
C. procera	+	-	+	-
D. lunatus	+	+	-	-
P. candelabrum	+	+	-	-
R. racemosa	+	-	-	-
R. mangle	+	-	-	-
L. racemosa	+	-	-	-
P. reclinata	+	-	-	-
Chrysobalanus[d]	-	-	-	-
Area (km^2)	2,208	126	964	18
Max. Altitude (m)	2,850	948	2,024	655
Dist. to mainland (km)	32	215	235	340
Dist. to landward neighbour (km)	32	210	135	180
Number of Species	12	5	6	0

[a] based on data from Hutchinson *et al.,* 1954/72; Exell, 1945; 1973; Keay, 1953; Adams, 1957;

[b] *Thespesia populnea* has been omitted from this table as it has been widely planted in the towns on the islands;

[c] this unconfirmed record is based on a description for which no voucher specimen could be located (Exell, 1945);

[d] includes two species (see Table 3) both of which are present on the adjacent mainland (Wouri Estuary, Cameroon) but not recorded from any of the islands.

Table 6. Distribution of the mangrove species and associates along the Atlantic coast of Africa.

Location	Av	La	Co	Rr	Rm	Rh	Nf	Aa	Ht	Tp	Dl	Chr	Pc
Mauritania	x	-	r	r	-	-	-	-			x		x
Senegal	x	x	x	x	x	x	-	x			x		x
Gambia	x	x	x	x	x	x	-	x					
Guinea	x	x	x	x	x	x	-	x	x	x	x	x	
Guinea-Bissau	x	x	x	x	x	x	-					x	
Sierra Leone	x	x	x	x	x	x	-		x		x	x	
Liberia	x		x	x		x	-	x			x	x	x
Côte d'Ivoire	x	-	r	x	-	-	-	x	x		x	x	x
Ghana	x	x	x	x	-	x	-	x	x	x	x		x
Togo	x	-		x			-						
Benin	x	r	x	x	-	r	-	x	x	x	x	x	
Nigeria	x	x	x	x	x	x	x	x	x	x	x	x	x
Cameroon	x	x	x	x	x	x	x	x	x	x	x	x	x
Eq. Guinea	r			x									x
Gabon	x	x	x	x	x	x	-	x	x		x	x	x
Congo	x			x			-						
Zaire	x	r	x	x	x		-	x	x			x	x
Angola	x	x	x	x	x	x	-	x	x		x	x	x

x present; r rare; - definitely absent;

Compiled from numerous sources given individually under 'Regional Descriptions' below. Species abbreviations are as follows: Av Avicennia germinans; La Laguncularia racemosa; Co Conocarpus erectus; Rr Rhizophora racemosa; Rm Rhizophora mangle; Rh Rhizophora harrisonii; Nf Nypa fruticans; Aa Acrostichum aureum; Ht Hibiscus tiliaceus; Tp Thespesia populnea; Dl Drepanocarpus lanatus; Chr Chrysobalanus spp.; Pc Pandanus candelabrum.

Table 7. Upriver distances (km) reported for mangrove limits.

River	Distance upstream	Reference
Cacheu R., Guinea-Bissau	100	Sayer *et al.,* 1992
Saloum R., Senegal	70	Sayer *et al.,* 1992
Bonny R., Nigeria	70	Dublin-Green, 1990
Zaire R., Zaire	50	Delevoy, 1945
Wouri R., Cameroon	40	Boyé *et al.,* 1975
Muni R., Equatorial Guinea	17	Sayer *et al.,* 1992
Ntem R., Equatorial Guinea	15	Sayer *et al.,* 1992

Table 8. Areal extent of mangrove vegetation along the Atlantic coast of Africa together with selected demographic and economic indicators.

Country	Coastline Length	Population Density		Mangrove Area	Per Capita GNP
	(km)	(N/km^2)	(N/km)	(km^2)	(US$)
Mauritania	754	2.1	2,785	10	500
Senegal	531	37.4	13,559	1,853	710
Gambia	80	70.0	8,750	497	260
Guinea-Bissau	350	34.4	2,857	2,484	180
Guinea	320	27.3	20,938	2,963	480
Sierra Leone	402	54.3	9,701	1,838	240
Liberia	579	25.9	4,318	190	440
Côte d'Ivoire	515	35.5	21,942	150	730
Ghana	539	67.5	28,757	100	390
Togo	56	61.5	58,929	26	410
Benin	121	41.4	38,016	69	360
Nigeria	853	120.1	128,253	10,515	270
Cameroon	402	23.5	27,363	2,434	940
Equatorial Guinea	296	15.3	1,351	257	330
Gabon	885	4.8	1,356	6,129	3,220
Congo	169	5.7	11,243	120	1,010
Zaire	37	14.9	913,514	226	230
Angola	1,600	7.8	6,063	1,250	620

Based on various data sources including Saenger *et al.,* 1983; Hutchings and Saenger, 1987; Sayer *et al.,* 1992; Diop *et al.,* 1993.

Table 9. Structural analysis of plants >3m in height in forty-four 100m^2 quadrats from south-eastern Nigeria. (From Upkong, 1992).

Species	Frequency %	Rel. freq. %	Density (stems/ha)	Rel. dens. %	Cover %	Rel. cover %	I.V.
A. germinans	63.0	28.4	200	40.7	28.6	46.4	115.5
R. racemosa	41.4	18.7	98	20.0	10.4	16.9	55.6
R. mangle	44.0	19.9	68	13.8	10.0	16.3	50.0
R. harrisonii	24.4	11.0	40	8.1	3.8	6.2	25.3
N. fruticans	20.0	9.0	40	8.1	5.0	8.1	25.2
P. reclinata	14.8	6.8	25	5.1	2.3	3.7	15.6
P. candelabra	5.0	2.2	8	1.6	0.5	0.8	4.6
Triumfetta rhomboideae	5.0	2.2	8	1.6	0.5	0.8	4.6
Drepanocarpus lunatus	4.0	1.8	5	1.0	0.5	0.8	3.6
Total		100	492	100	61	100	300

Table 10. Structural composition of the littoral vegetation in the delta of the Soumba River, Guinea (derived from analysis of SPOT image 30-330 taken on 19 April 1986).

Community	Area (ha)	% littoral vegetation
Tall dense mangrove	402.1	6.4
Medium dense mangrove	856.7	13.6
Short dense mangrove	2269.2	36.1
Short sparse mangrove	1764.9	28.1
Saltflats & herblands	619.4	9.9
Riceponds	369.2	5.9
Total littoral vegetation	6281.5	100

Table 11. Flowering times of the principal mangrove species at various localities on the Atlantic coast of Africa.

Location	Av	La	Co	Rr	Rm	Rh
Senegal		1[1]	12-1[1]	1/5[6]	2[5]	1[5]
Gambia						5[6]
Guinea						5[6]
Sierra Leone		3-6[1]	3/12[1]	12-3[6]		3/6/10-11[6]
Liberia		7[1]		11-12[6]	7[6]	
Côte d'Ivoire	4[7]			10[5]/2[6]		
Ghana	5[7]	4[1]		7[6]		
Benin	3-6[3,4]	12[9]				
Nigeria	12-6[7,8]	12[1]	10[1]	2-11[6,8]	11[6]	11[6]
F. Po/S. Tome		11[1]				10[6]
Cameroon	1-2[2,]	11-12[2]	2-3[2]	12-2[2,6]		
Gabon				2[6]		1/8[6]
Congo				1[6]		
Angola				12[6]	6/11[6]	

Sources: [1] Hutchinson *et al.* 1954/72; [2] Din 1991; [3] Blasco 1985; [4] Baglo, 1989; [5] Assemien 1969; [6] Keay 1953; [7] Saenger pers. obs.; [8] Jackson 1964; [9] Paradis 1979

Species abbreviations are as follows: Av Avicennia germinans; La Laguncularia racemosa; Co Conocarpus erectus; Rr Rhizophora racemosa; Rm Rhizophora mangle; Rh Rhizophora harrisonii.

Table 12. Monthly distribution of flowering times recorded for mangroves and associated species divided between dry and wet season. (For sources see table 11).

Species	N	D	J	F	M	A	M	J	J	A	S	O
Avicennia germinans		+	+	+	+	+	+	+				
Rhizophora racemosa	+	+	+	+	+	+	+		+	+		+
Rhizophora harrisonii	+		+		+		+			+		+
Rhizophora mangle	+			+				+	+			
Laguncularia racemosa	+	+	+		+	+	+	+	+			
Conocarpus erectus		+	+	+	+							

Table 13: Seed-fall in mangroves and associated species at Ikoroda, Western Nigeria (from Jackson, 1964)

Species	Seed-fall
Avicennia germinans	October - January
Rhizophora racemosa	February - March
Hibiscus tiliaceus	March
Drepanocarpus lunatus	June - September
Dalbergia ecastaphyllum	June - December
Pterocarpus santalinoides	June - August
Ormocarpum verrucosum	May - December
Cynometra megalophylla	May

Table 14. Monthly distribution of fruiting times recorded for mangroves and associated species divided between dry and wet season. (For sources see table 11).

Species	N	D	J	F	M	A	M	J	J	A	S	O
Avicennia germinans	+	+	+									
Rhizophora racemosa	+	+		+	+	+				+	+	
Rhizophora harrisonii								+				
Rhizophora mangle	+						+	+	+		+	+
Drepanocarpus lunatus								+	+	+	+	
Dalbergia ecastaphyllum	+	+						+	+	+	+	+
Hibiscus tiliaceus					+							
Pterocarpus santalinoides								+	+	+		
Cynometra megalophylla							+					

Table 15. Structural data for the mangroves in the Wouri Estuary, Cameroon (from Din, 1991).

Species	Stems/ha	Basal Area (m^2/ha)	Mean ∅ (cm)	Freq (%)	Dom (%)	Dens (%)	Importance value (%)
R. racemosa	305	8.66	18	59.5	60.5	79.4	199.4
A. germinans	66	5.59	31	32.4	39.0	17.2	88.6
D. lunatus	13	0.07	8	8.1	0.5	3.4	12.0

Table 16. Export data for *Rhizophora* timber from the Wouri Estuary, Cameroon between 1919-37.

Year	tonnes
1919-26	30,000
1927	5,400
1928	no data
1929	5,600
1930	3,118
1931	1,249
1932	324
1933	373
1934	2,812
1935	1,333
1936	766
1937	553

From Hédin (1928) and the League of Nations, Annual Mandate Administration Reports quoted by Grewe (1941).

Table 17. Potential acid sulphate soils in West Africa (from Marius, 1984).

Country	km^2
Senegal	9,750
Gambia	3,750
Guinea-Bissau	11,750
Guinea	8,250
Sierra Leone	5,000
Liberia	1,250
Côte d'Ivoire	250
Ghana-Togo	1,500
Nigeria	15,500
Cameroon	2,500

Table 18. Existing and proposed protected areas containing some mangrove vegetation on the African Atlantic coast.

Country	Name	Status	Date	Area (km^2)
EXISTING				
Mauritania	Parc National du Banc d'Aguin	National Park	1976	11,730
		World Heritage Site	1989	
Senegal	Saloum Delta NP	National Park	1976	760
Senegal	Basse-Casamance NP	National Park	1970	50
Gambia	Gambia River NP	National Park	1978	25
Gambia	Kiang NP	National Park	1987	110
Gambia	Niume/Sine Saloum NP	National Park	1986	49
Guinea-Bissau	Cufada Lagoon	Ramsar Site	1990	391
Guinea-Bissau	Iles Tristao	Ramsar Site	1992	850
Guinea-Bissau	Konkouré	Ramsar Site	1992	900
Guinea-Bissau	Rio Kapatchez	Ramsar Site	1992	200
Guinea-Bissau	Rio Pongo	Ramsar Site	1992	300
Sierra Leone	Bonthe Mangrove Swamp	Nature Reserve	na	101
Sierra Leone	Sulima Mangrove Swamp	Nature Reserve	na	26
Sierra Leone	Bumpe Mangrove Swamp	Game Sanctuary	na	49
Ghana	Anlo-Keta Lagoon	Ramsar Site	1992	1,278
Ghana	Densu Delta	Ramsar Site	1992	46
Ghana	Muni Lagoon	Ramsar Site	1992	87
Ghana	Sakumo Lagoon	Ramsar Site	1992	13
Ghana	Songor Lagoon	Ramsar Site	1992	287
Nigeria	Cross River NP	National Park	1991	4,000
Gabon	Petit Loango	Ramsar Site	1986	4,800
Gabon	Setté Cama	Ramsar Site	1986	2,200
Gabon	Wongha-Wonghé	Ramsar Site	1986	3,800
Congo	Conkouati Wildlife Reserve	Nature Reserve	1980	1,443
Zaire	Zaire R. Mangrove Reserve	Nature Reserve	1992	1,000
Angola	Parque Nacional da Qicama	Game Reserve	1938	
		National Park	1957	9,960
PROPOSED				
Guinea-Bissau	Tarrafes NP	National Park	proposed	286
Guinea-Bissau	Bijagos Archipelago	status uncertain	proposed	na
Guinea-Bissau	Cacheu River	status uncertain	proposed	na
Guinea-Bissau	Cantanhez Forest	status uncertain	proposed	na
Liberia	Cape Mont Nature Reserve	Nature Reserve	proposed	na
Sierra Leone	Bunce River	status uncertain	proposed	na

Based on various data sources including Saenger *et al.,* 1983; Sayer *et al.,* 1992; Diop *et al.,* 1993; IUCN, 1994; and personal communications.

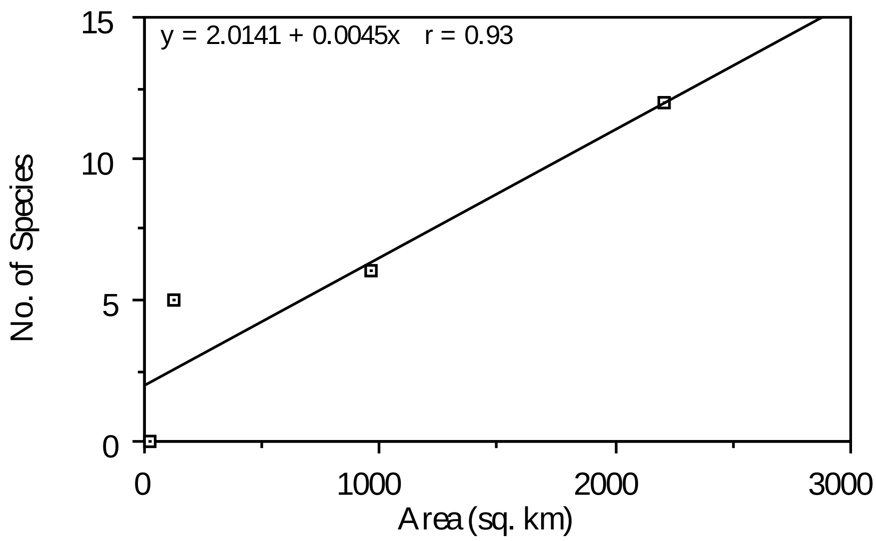

Fig. 5. Number of mangrove and associated species against the area of the Gulf of Guinea islands of Fernando Po, Principe, Sao Tomé and Annobon.

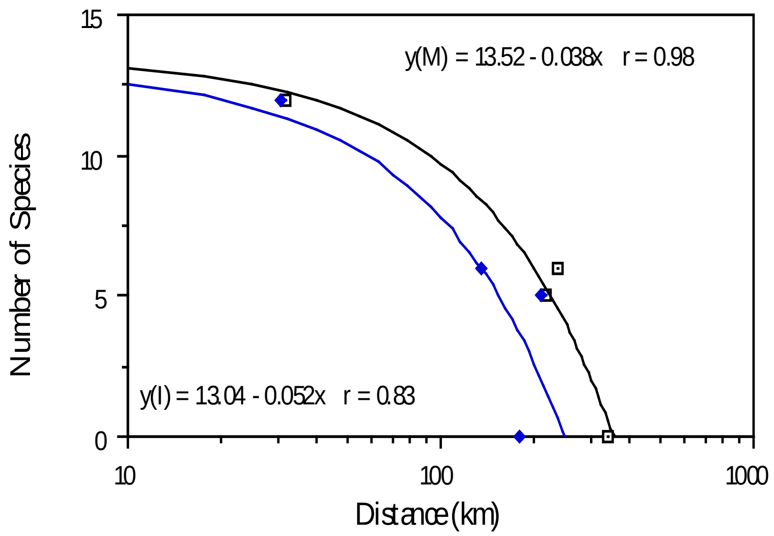

Fig. 6. Number of mangrove and associated species against the distance from the mainland - y(M) - and from the nearest landward island - y(I) - of the Gulf of Guinea islands of Fernando Po, Principe, Sao Tomé and Annobon.

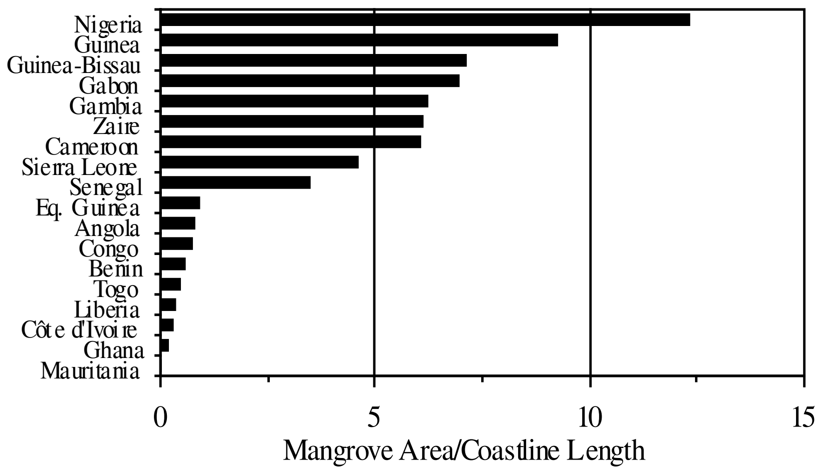

Fig. 7. Mean breadth of mangrove vegetation in West Africa, calculated from estimates of total mangrove area and length of coastline.

Legends for Plates

Plate 1. Dense stands of *Rhizophora racemosa* 10-12m high in the Wouri Estuary, Cameroon.

Plate 2. Dense stands of *Rhizophora racemosa* 10-12m high, forming a fringe on the coastal lagoon near Grand Lahou, Côte d'Ivoire.

Plate 3. Narrow waterway amongst the fringing *Rhizophora racemosa* of the coastal lagoon near Gran Lahou, Côte d'Ivoire.

Plate 4. Low stands of *Rhizophora mangle* in the Bonny River near Port Harcourt, Nigeria.

Plate 5. Mangrove vegetation of Sukoma Lagoon, near Tema, Ghana, dominated by *Avicennia germinans* up to 6m high.

Plate 6. Korle Lagoon, near Accra, Ghana, showing the degree of infilling due to sewage and stormwater inputs. Despite the continuously open connection with the ocean, the mangroves are dominated by *Avicennia germinans.*