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THE ECOLOGY OF MANGROVES

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INTRODUCTION

The Historical Perspective

Probably no other distinct plant community has attracted as much curiosity and scientific attention for as long as have the mangrove forests of the tropical and subtropical tidelands; a general bibliography would list some 1200 titles (L. Wilcox, personal communication). The first written account is reported by Bowman (7) from the Chronicle of Nearchus, dating back to the Greek mariners of 325 BC. The historical interest has been largely engendered by the unique adaptations (e.g. prop roots, pneumatophores, and viviparous seeds) of certain mangrove species and by their ubiquitous ability to function in a saline environment.

Unlike other terrestrial communities that can be lived in, managed, or exploited by man, mangroves offer only a few direct uses [tannin, construction timber, and charcoal (3, 69)], which may account for man's historical ambivalence concerning their value. This is revealed in the literature as attitudes that consider mangroves an academic curiosity at best, a nuisance at worst, and, in general, of little value to man and his works. In 1667, Du Terte (in 7) admonished travelers: "Wild boars and other savage beasts live in them . . . who lie in wait to surprise a person." Equally ominous were two Florida newspaper accounts[1] that reported "300 homes blackened" and "two men killed" by "mangrove root gas" in Miami, Florida. In 1938, Davis, whose mangrove research papers (17–20) are considered classics, referred to

[1]Respectively, the *Miami Herald,* Nov. 15, 1951, and the *Miami News,* Jul. 28, 1961.

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mangroves as "freaks" (16). And as late as 1969, Humm (in 67) considered a normally short-statured mangrove forest in south Florida to be "... a form of wasteland," a view consistent with the U.S.D.A. Soil Conservation Service's (25) omission of mangrove land from a classification based on "... relative suitability for crops, pastures, woodland, wildlife or other uses ..."

While many of the early writings cite the curious and unique nature of mangroves, Curtiss (in 7) in 1888 was probably the first to postulate broad ecological roles for mangroves, particularly in "building islands" and "extending shorelines." These roles were extensively studied and reported by Schimper (75) in 1903, and in 1925 by Warming (94), who laid the foundation for Davis's (17) illuminating studies in south Florida. These basic enquiries helped to create an attitude of benign neglect toward mangroves in the absence of economic value by suggesting that mangroves nonetheless might perform useful functions. In 1954, a citizen optimistically obtained an option to lease 16,800 acres of red mangrove (*Rhizophora mangle* L.) tidelands from the State of Florida[2] based on the nutritive value of the leaves as a livestock feed supplement (80). However, in recent years the increasing demand for waterfront property for residential and commercial development in Florida created a monetary value for mangrove land solely because of its coastal location.

In 1969, Heald (34) and W. Odum (67) released the results of their research documenting the dependence of south Florida's sport and commercial fisheries on the net production of red mangroves via a detrital energy flow pathway. Their work reaffirmed many earlier reports on the generic role of tidelands in the maintenance of estuaries (15, 44, 60, 61, 82) and catalyzed public initiatives to protect mangrove lands remaining outside of the public domain. This has proven to be a difficult task due to the legal questions dealing with the rights accruing to private ownership and the scientific questions dealing with the spatial definition of a red mangrove[3] community and what constitutes an impact therein.

In other areas of the world mangrove lands and the mangrove species have had, and are increasing in, economic importance for purposes other than real estate. Sierra Leone has focused considerable attention on the conversion and management of mangrove forests for rice production (see 23, 31–33, 35, 36, 40, 85, 86). Thailand (6) and Malaya (59, 95), where mangroves are valued for firewood, timber, and tanbark, are notable for their pioneering work in silvicultural practices. In the Marismas Nacionales on the west coast of Mexico, south of Mazatlan, migrating penaeid shrimp are trapped by brush weirs around mangrove forests and harvested under government regulation (D. Pool, personal communication). Philippine *Rhizophora* is a source of "bakawan," used by the Japanese in the manufacture of synthetic fabrics (56). The authors have observed similar, but undocumented, exten-

[2]The State of Florida claims ownership of tidelands below mean high water. Announcement of option to lease appeared in the *Miami Herald,* April 14, 1954.

[3]Black mangroves (*Avicennia germinans*) dominate in areas inland from the red mangroves and are only now being investigated with respect to their importance in estuarine food webs. The boundary between the two "communities" is not readily distinguishable in the field.

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sive utilization efforts in the tropical Americas, suggesting a pantropical economic importance of mangroves larger than might be surmised from the available literature. The defoliation of extensive mangrove areas in Viet Nam (87) has raised mordant questions concerning the socioeconomic implications of extensive herbicide utilization and has heightened interest in the ecological roles of mangrove tidelands (66). The background of a little-known but possibly substantial role of mangrove forests in the economy of this region lends a special urgency to the need for expansion of our knowledge of mangrove ecosystems.

The Ecosystem Approach

The long historical interest in mangroves has centered less on the interactions of man and mangroves than it has on the more tractable aspects of their physiology and general biology. These efforts have resulted in many valuable contributions too numerous to be reviewed individually in this paper. The reader is referred to the reference materials in Bowman (7), Chapman (12), Davis (17), Macnae (53, 54), Kuenzler (43), and Walter (93) for additional details. This review focuses on studies that have contributed to the conceptualization of mangroves and mangrove lands as components of larger regional coastal ecosystems. The analysis treats an ecosystem as a fully integrated, self-maintaining unit whose components, through their characteristic adaptations, contribute to the survival of the system.

The works of E. Odum (62) and H. Odum (65) set forth detailed discussions of ecosystem characteristics. Two kinds of systems can be distinguished: open and closed. Natural ecosystems are open systems with respect to both energy and matter, making the issue of ecosystem boundaries an academic question. Any natural area can be selected for study, as long as one is aware of the magnitude and quality of energy and matter exchange through the necessarily artificial boundaries that the investigator has selected. Depending upon the size of the system, its biological characteristics, and the kind of environment, the structure and functioning of the community within the area of study may or may not be sensitive to external influences and may or may not affect surrounding ecosystems in a significant way. This approach is particularly useful in the study of mangrove areas located at the interface between land and sea and thus influenced by both terrestrial and marine factors.

We have constructed a simple model (Figure 1) depicting the essential structural and functional attributes of mangrove ecosystems as well as the principal external energy sources and stresses that affect the system. The model is used here to orient the reader toward a general synthesis of the scientific literature discussed in this review. The model is composed of two mangrove compartments (above-ground structure and muds; the latter includes roots and aerobic and anaerobic processes); two external energy sources (the sun and upland runoff, which includes the contribution of rainfall); five mangrove processes (primary productivity, above-ground respiration, respiration of the muds, recycling of mineral nutrients, and the export of organic matter to estuaries or other contiguous ecosystems); and six potential stress factors (channelization, drainage, and siltation; hurricanes and herbicides;

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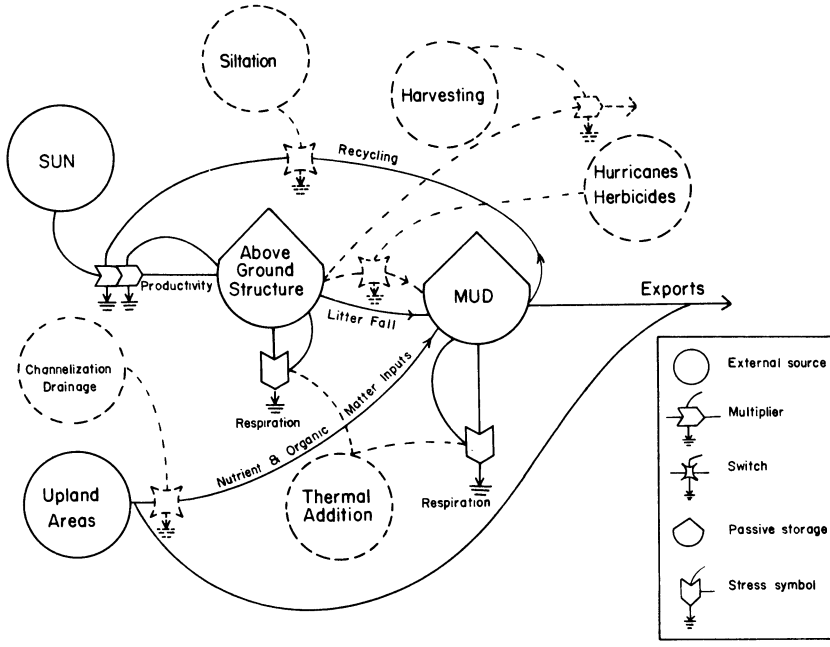

Figure 1 A simple energy model illustrating the major storages and flows in a mangrove ecosystem. Potential stresses are distinguished by dashed lines. In essence, the model is a series of differential equations graphically depicted using the ecological circuit language created by H. Odum (65).

and thermal loading). The basic mangrove ecosystem is depicted as two coupled storages (above-ground structure and muds) linked by the cycling of matter and powered by the interaction of sunlight and matter through photosynthesis. Each living storage is maintained by the respiration of the products of photosynthesis; the acceleration of respiration at elevated temperatures is shown with stress symbols. The export of materials is balanced by inputs from upland areas that can be modified by channelization and drainage. These activities stop the input flow into the mangrove system; the flow is diverted directly to downstream ecosystems. Litter fall normally occurs throughout the year, but hurricanes and herbicides are capable of turning a large portion of above-ground structure into detritus that may be exported or recycled in proportion to the viability of the remaining structure. Recycling can be stopped by such processes as siltation, which prevents the exchange of gases and mineral nutrients across the mud surface. Harvesting for utilitarian products (e.g. firewood, tanbark) is shown as a drain on the above-ground structure. The following discussions are oriented toward reviewing the mangrove literature within the context of the mangrove ecosystem so outlined.

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STRUCTURAL STUDIES OF MANGROVES

Classification

The term *mangrove* refers to two different concepts. First, it describes an ecological group of halophytic species belonging to some twelve genera in eight different families as distinguished by Waisel (90) and given below:

Avicenniaceae
- *Avicennia* sp.

Chenopodiaceae
- *Suaeda monoica*

Combretaceae
- *Laguncularia* sp.
- *Lumnitzera* sp.

Meliaceae
- *Conocarpus* sp.
- *Xylocarpus* sp.

Myrsinaceae
- *Aegiceras* sp.

Plumbaginaceae
- *Aegialitis* sp.

Rhizophoraceae
- *Rhizophora* sp.
- *Bruguiera* sp.
- *Ceriops* sp.

Sonneratiaceae
- *Sonneratia* sp.

The number and distribution of mangrove species is an interesting biogeographical problem, since fewer than 10 species are found in the New World tropics, while a total of 36 species has been reported for the Indo-West-Pacific region where mangroves attain their maximum development (54). Under certain conditions, succulents characteristic of xeric conditions grow in association with the mangrove species. In spite of this large taxonomic variability and geographic range, all mangroves exhibit marked similarities in physiological characteristics and morphological adaptations under similar environmental conditions.

In a second sense, the term mangrove refers to the complex of plant communities fringing sheltered tropical shores.[4] Schimper (75) defined *mangrove* to include the formation below the high tide mark. Consequently, he and many others have used the term *tidal forest* as a synonym for the mangrove forest. However, "true" mangroves may form only a part of the whole tidal zone; they may occur from far below the level of the lowest to above the level of the highest tides, or on coasts where there are no tides at all (17, 70).

ZONATION Most of the ecological literature on mangroves is concerned with the description of species composition and plant zonation. Macnae (54) reviewed the zonation schemes that had been proposed by several authors for the mangroves of the Indo-West-Pacific region. One was based on frequency of inundation, another on the salinity of the soil, and a third on the generic name of the dominant trees. Similar schemes have been applied to the mangroves of the New World by Davis (17) and de la Cruz (21), who compared the zonation of mangrove stands in the eastern and western hemispheres.

[4]Du, L. V. 1962. Ecology and silviculture of mangrove. Yale Univ. School of Forestry. Unpubl. mimeo. 28 pp.

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From these kinds of studies Davis (17), Watson (95), and others classified mangrove species as "pioneer" or "climax" species, inferring that each zone represents a stage in a succession leading via soil accumulation to a terrestrial forest (70). Another group of authors has put forward the view that zonation is a response of the mangrove ecosystem to external forces rather than a temporal sequence induced by the plants themselves. This concept of a steady state landscape as it applies to mangroves may be supported by the work of Thom (84) and Egler (24). Thom (84) has demonstrated that the zonation and structure of mangrove forests in Tabasco, Mexico are responsive to eustatic changes in sea level, and that mangrove zones can be viewed as steady state zones migrating toward or away from the sea, depending on its level. He postulated that mangrove zones were responsive to geomorphological changes in the regions where they grow. He considered substratum and water regime to be the important factors controlling zonation, and that each species, within its tolerance range to salinity, finds its place in the environmental gradient created by the regimes of substratum and water flow. According to Thom, salinity is simply a competition eliminator and not the determining factor in zonation. This agrees with the early work of Bowman (7) and Davis (17), who indicated that mangrove species were facultative saline species in both growth and physiology. Bowman thought, however, that salt was needed for optimum development.

Egler (24) calculated the age of Florida mangroves by assuming that the depth of the peat in mangrove areas keeps pace with changes in sea level. With a peat depth of 1.2 m and the sea level rising at a rate of 0.006 m/yr, he calculated the age of mangroves to be 6,500 yr. This age is in agreement with the geological history of the area (13).

Thus it appears plausible that the zonation of mangroves may not necessarily represent a successional sequence and that mangrove areas may not invariably accumulate soil. Instead, the "zonation" of mangroves may be a result of all the external sources acting on a locality. Perhaps in periods of decreasing tidal energy and lowering of the sea mangroves advance toward the sea, but when the flushing action of water is high or when the sea rises the zones migrate inland.

The distribution of animals within mangrove forests has been defined in terms of habitats in (29), and by Macnae (50, 53, 54) and Macnae & Kalk (55) in terms of environmental gradients within habitats. Macnae concluded that since animals show no marked zonation, but rather a preference for a particular type of habitat, the fauna is in reality fortuitously associated with mangroves. He found that the distribution of animals depends upon their resistance to water loss, their demand for protection from the sun, the level of the water table, the degree of consolidation of the soil, and the availability of microflora and microfauna or organic debris as a food source (55). Walsh (91) reported similar results for the mangrove forests of Hawaii, and held that the zonation of animals depends largely upon salinity differences, oxygen gradients, and the nature of the substratum.

PHYSIOGNOMY The delineation of successive monospecific mangrove zones (17) has been most successful where there is a steep topographic shoreline gradient, but not in large areas with very flat topographic slopes (e.g. 1 cm/km), as in much of

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the south Florida region. In south Florida the mangrove species (*R. mangle, A. germinans, Laguncularia racemosa,* and, occasionally, *Conocarpus erecta*) occur in varying mixtures in five major community types (79). The formation and physiognomy of these types appear to be strongly controlled by local patterns of tides and terrestrial surface drainage and they are distinguishable on these bases.

Fringe forest This forest type occurs along the fringes of protected shorelines and islands, and the mangrove species are distributed therein according to the zonation patterns described by Davis (17). The fringe forest is best defined along shorelines whose elevations are higher than mean high tide. The low velocities of the incoming and retreating tides and the dense, well-developed prop root system entrap all but the smallest organic debris. Due to the relatively open exposure along shorelines, the fringe forest is occasionally affected by strong winds, causing breakage and resulting in the accumulation of relatively large stocks of debris among the prop roots.

Riverine forest The "riverine" type designates the tall floodplain forests occurring along river and creek drainages. Although they are usually separated from the drainage way by a shallow berm, they are flushed by the daily tides. This forest type is often fronted by a fringe forest occupying the slope of the drainage way. During the summer wet season, water levels rise and salinity drops due to upland terrestrial runoff. The riverine type consists of relatively straight-trunked trees numerically dominated by *R. mangle* (with noticably few, short prop roots) and varying mixtures of *A. germinans* and *L. racemosa.* Low surface water flow velocities preclude scouring and redistribution of ground litter.

Overwash forest The smaller low islands and finger-like projections of larger land masses in shallow bays and estuaries are characterized by the *R. mangle* dominated "overwash forest" type. Their positions and alignments obstruct tidal flow and as a result this forest is overwashed at high tide. The incoming tidal velocities are high enough to carry with them any loose organic debris; the debris is dropped in the inner bays as the velocity decreases and is not returned to the overwash forest. The dense prop root system appears to be limited to the space defined by the ground surface and wet season (April through September) mean high water. The spatially-limited prop root system plus the absence of foliage below the canopy level give this forest type an appearance of a symmetrical and regular architecture when viewed from within.

Basin forest This forest type occurs in inland areas along drainage depressions channeling terrestrial runoff toward the coast. In the more coastal positions they receive the influence of the daily tides and are dominated by *R. mangle.* Traversing inland, the tidal influence lessens and the dominance becomes increasingly shared with *A. germinans* and *L. racemosa.* In this forest type all three species serve as hosts for vascular air plants of the Orchidaceae and Bromeliaceae. Beyond any tidal influence this physiognomic type grades into the strand community of the Everglades (see 13). A variant of the basin forest occurs as mangrove "hammocks" in

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southeast Dade and Monroe counties along the topographically flat coastal fringe. In terms of flora and physiognomy the hammock forest type is similar to the basin type but it occurs on ground that is slightly elevated (~5–10 cm) relative to surrounding areas, in contrast to the depressions associated with the basin type (Snedaker, unpublished). Both are associated with reducing environments and peat deposits, as are the fringe, riverine, and overwash forest types.

Dwarf forest This forest type is limited to the flat coastal fringe of south Florida and the Florida Keys. All four Florida mangrove species are present but the individual plants are less than 1.5 m tall. They are relatively old (40 years based on leaf scar counts) and exist in an environment lacking obvious external nutrient sources; community development may be nutrient limited (Snedaker, unpublished).

We have observed comparable forest types in similar environments in Mexico, Puerto Rico, Costa Rica, Panama, Ecuador, and in isolated areas in the Galapagos Islands.

The ubiquitous success of this classification scheme strengthens the importance of topographic control, through the governance of surface hydrology and tidal dynamics, in the distribution of mangrove species and physiognomic units (see 84). This five-unit classification scheme is intended by the authors as a supplement to, rather than a replacement of, the zonation patterns postulated in other works. Classical zonation is often visible at the ecotones between contiguous vegetation types; the emphasis here on causal mechanisms helps explain the differences among zonation schemes derived from studies in different parts of the world.

BIOMASS Many authors (28, 30, 72) demonstrated the utility of working with absolute measures of organic production as defined by standing-stock biomass. Not only do such data provide increasingly valuable means for making comparisons (72) among ecosystems, but they also provide a basis for evaluating world-wide productivity patterns (Golley & Leith, in 30). Biomass data require careful treatment, however, because turnover rates are also of importance to ecosystem comparisons, and biomass estimates tend to underestimate the impact of animal populations on ecosystem dynamics. A summary of the data available to us is presented in Table 1. The locations of several of the study sites are shown in Figure 2. The data for the mangroves of Florida are the most complete in terms of the number of forest types reported, but comparative root data are lacking.[5] The variability in the biomass data may be attributable to age, stand history, or structural differences as previously described. The ages of the forests are not reported, but possibly the larger biomass of the Panamanian forest is representative of an older forest protected from hurricane destruction. The forests in Florida had been influenced by a hurricane some 13 yr before the biomass-sampling harvest. The differences among the Florida mangrove-type estimates of biomass suggest that real variations exist among forest types. In comparison with other tropical forests (72), the biomass of mangrove forests is low.

[5]A good method for separating live versus dead roots in a consolidated peat matrix has not been worked out except for very small samples (28)

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Table 1 Mangrove forest biomass estimates. Data from Panama, Puerto Rico, Philippines, and Florida expressed as kilogram dry weight per hectare

Location Mangrove Type Reference	Panama[a] (28)	Puerto Rico[b] (29)	Philippines[c] (22)	Florida Overwash[d] (79)		Florida Riverine[e] (79)			Florida Fringe[e] (79)		Florida Scrub[f,i]	Florida Island[g] (79)	Florida Succession[h] (79)
Leaves	3550	7780	13,319	7263	6946	3810	9510	5934	5843	7037	712	4990	2215
Fruit & Flowers	21	—	—	20	236	148	0.4	28	210	131	—	78	—
Stems & Branches	—	12,740	—	—	—	16,770	27,670	17,000	19,120	18,550	3959	—	5908
Wood	159,209	27,960	24,346	70,380	70,480	62,850	133,660	40,960	65,150	109,960	—	18,090	—
Prop Roots	116,432	14,370	—	51,980	41,920	14,640	3060	22,270	27,200	17,190	3197	25,810	
Pneumatophores	—	—	8271	—	—	—	—	—	—	—	—	—	—
Subsurface Roots	189,761	49,970	—	—	—	—	—	—	—	—	—	8010	14,068
Litter	102,106	—	—	17,310	13,990	42,950	33,930	22,730	60,250	98,410	1140	—	323
Total Above-Ground Biomass Excluding Litter	279,212	62,850	45,936	129,643	119,582	98,218	173,900	86,192	117,523	152,868	7868	48,968	8123

[a] data from two 625 m^2 sample areas; stems and branches included in wood.
[b] data from two 25 m^2 sample areas using several sampling techniques.
[c] prop roots and pneumatophores included in wood.
[d] data from 25 m^2 sample areas; stems and branches included in wood.
[e] data from 25 m^2 sample areas.
[f] data from three 9 m^2 sample areas (Snedaker, unpublished data).
[g] single small tree on oyster bar; sample surface area described by crown.
[h] data from six 9 m^2 sample areas on dredged spoil bank; estimated age, 5 years.
[i] from S. C. Snedaker, unpublished manuscript.

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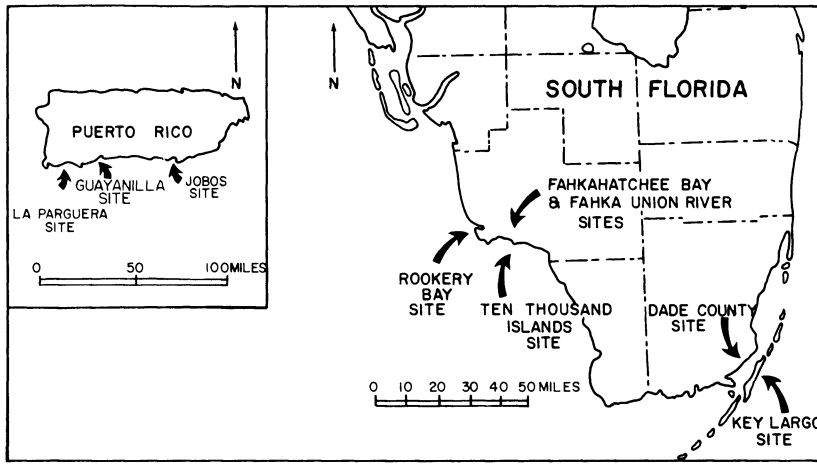

Figure 2 Location maps of mangrove ecology research sites in south Florida and Puerto Rico.

FUNCTIONAL STUDIES OF MANGROVES

Ecology has been defined as the study of the structure and function of nature (62), which in mangrove ecology has been oriented toward phytosociology and physiology. At the organizational level of the ecosystem, structural studies place emphasis on distribution and abundance of the major ecosystem components and functional studies search for an understanding of how these components are balanced and maintained through cycles of material and flows of energy. Unlike our knowledge of mangrove ecosystem structure, however, our understanding of mangrove ecosystem functioning has not yet benefited from a long history of the questioning and testing of emerging principles. This review represents the genesis of such an analysis of mangrove ecosystem function.

Cycling of Matter

The (open) cycles of matter transport in mangrove forests are driven by physical and biological factors that control the rate of import and export of inorganic and organic compounds. The physical factors include the daily tides, runoff, and rainfall. The biological processes of greatest significance to mineral cycling are leaf fall, decomposition, mineral uptake rates, and certain activities of the fauna. In Figure 1 we have subsumed mineral sources in overland runoff, rainfall, etc, into a general category of allochthonous inputs, primarily derived from the uplands. The decomposition process, which regenerates inorganic minerals from organic substrates, is incorporated by implication in the respiratory process in the muds. Animal activity was not shown in the diagram due to its low magnitude in terms of direct matter

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flow. However, animal populations have a significant influence on this ecosystem, especially insofar as they modify rates and patterns of materials transport. Some of these activities, and the synergy between physical and faunistic factors that governs ecosystem functioning, are explored in this text.

Gill & Tomlinson (26, 27), in their studies of the red mangrove in south Florida, found that flowering, fruit formation, leaf fall, and incremental growth occurred at measurable rates in all seasons. However, peak rates of leaf fall and growth were observed during summer months when air temperature and incident light were at their annual peaks. Similar results have been reported by Heald (34). In a two year study of litter fall at Rookery Bay and the Ten Thousand Islands (Figure 2), Snedaker & Lugo (79) found indications that leaf fall increases during dry periods. The timing of these events has a significant interaction with the hydrologic budget and the primary productivity of the forest community. Carter et al (10) in their studies of the Fahkahatchee Strand (Figure 2) in Florida found that absolute decreases in leaf fall followed drainage and entrained water stress. Apparently canopy thinning was a cause of significant reductions in evapotranspiration and an associated 40% reduction in the net primary productivity of the system.

Annual leaf fall rates for mangrove forests in Puerto Rico (La Parguera, Figure 2) and south Florida are remarkably constant (29, 34, 79). Only the scrub mangrove forest at the Dade County site (Figure 2) in south Florida (D. J. Pool, unpublished) deviates significantly from an annual mean leaf-fall rate of 2 $g/m^2 \cdot day$.[6] Leaf fall in this scrub forest may be a full order of magnitude less than in other mangrove stands. Litter production seems to be of crucial significance to the mangrove forest's ecological role as a component of a regional estuarine ecosystem. Golley et al (29) reported an export rate of particulate materials amounting to 2.27 g/m^2 of forested area per day. Heald (34), working in the Everglades Park area in Florida, estimated leaf and twig fall in a mangrove forest to be 2.4 $g/m^2 \cdot day$. In addition, his data indicate that on the average 40% of the detrital materials present in suspension in estuarine waters were of mangrove origin, and mangrove debris was the largest component of estuarine detrital materials throughout the year. Snedaker & Lugo (79) estimated an export of 0.5 $g/m^2 \cdot day$ or 25% of the leaf fall of a black-mangrove dominated (riverine) forest. In addition, during periods of high rainfall export was estimated to occur at a rate 20 times the rate of leaf fall.

Carter et al (10) summarized much of the information available on organic exports from various ecosystems and made further measurements in the estuaries of Fahkahatchee and Fahka Union Bays. They estimated that at least 57%, and in all probability as much as 80%, of the total energy budget of these bays was supported by exports from mangrove forests. They also described a "short-circuiting" effect of man-made canals that effectively decouples natural estuarine ecological processes from their normal input pathways by shunting overland freshwater drainage directly from the uplands to the estuary. In contrast, the natural drainages were found to intercept runoff and redistribute its load of materials throughout the mangrove forest.

[6]Unless otherwise noted, the unit of measure refers to oven-dry organic matter.

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In the black-mangrove dominated forest of Rookery Bay, Snedaker & Lugo (79) found that the amount of litter on the forest floor remained stable during the year of study (550 g/m^2). They measured a total leaf fall of 485 $g/m^2 \cdot yr$, giving an annual turnover rate of 88%. The decomposition rate of litter materials at this site was 287 $g/m^2 \cdot yr$, and thus at the very least this excess of leaf fall over potential decomposition must have been exported to adjacent bays or terrestrial food chains.

The rate of decomposition in mangroves depends on the amount of available oxygen (which increases when the muds are exposed to the atmosphere), the kinds of muds, and the role of animals and microorganisms in accelerating the process. Hesse (36) found that *Avicennia* muds decompose at slower rates than *Rhizophora* muds. The rate of oxygen uptake of these soils varied with moisture content, increasing with increased moisture; optimal decomposition occurred at 50% moisture (35). Rates were accelerated when drying of the soil was followed by rewetting. In their studies in the Fahkahatchee Strand, Carter et al (10) concluded that moisture accelerated litter decomposition by 30%, and under these favorable conditions macroconsumers further accelerated the process by 60%. Snails and other forest floor invertebrates aid in the mechanical breakdown of leaf litter, which is then decomposed at a faster rate by the microflora (10). Mangrove soil respiration rates of 0.20 and 0.37 $gC/m^2 \cdot day$ have been measured by Lugo et al (48) and Golley et al (29), respectively.

In Heald's (34) study, he determined that in one year 60% of red mangrove leaf production was decomposed by the estuarine flora and fauna, and that the rate of decomposition was higher in brackish water than when the leaves were exposed to either the atmosphere or seawater. The export of masses of organic debris into estuaries at the beginning of the wet season is accompanied by a lowering of estuarine photosynthetic rates and an increasing rate of respiration (10). The increased respiration due to the influx of the organic debris reduces the oxygen concentration in the receiving water (81). The resulting oxygen depletion can result in fish kills, observed elsewhere (9) but not documented for mangrove estuaries.

Different mangrove forest types show differing patterns of litter accumulation, decomposition, and export. The balance among these processes is primarily responsive to differences in tidal flushing (79). We observed that in red mangrove zones exposed to daily tides, leaves floated into the bays where they would be consumed and decomposed by metabolic processes of that ecosystem. In more protected inland areas, characteristic of the black mangrove zones, leaves were decomposed in situ and less particulate debris was exported to adjacent bays. Instead, dissolved organic matter was exported in the water flowing through the system. Leaves were consumed in the forest floor by crabs, many of which were observed dragging leaves into their burrows at low tide. Similar observations have been described by Macnae (54). In a computer simulation (48) of south Florida mangroves it was shown that as the tides increase in magnitude the amount of litter accumulated on the forest floor was decreased.

Changes in the quality of waters entering and leaving mangrove forests are particularly important to their cycling processes because these waters are the main transport mechanism in mangrove regions. Walsh (91) found that the tidal waters

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entering a marsh near a mangrove forest were largely depleted of nitrogen, phosphorus, and oxygen by the time they arrived in the forest. However, inside the forest, sedimentation removed anywhere from 10 to 100% of the remaining nitrogen and phosphorus. Hesse (37) reported a high affinity of mangrove muds toward phosphorus and measured rapid rates of phosphorus fixation by these muds. Similar results were reported in our studies of mangrove forests in Florida (48, 79), emphasizing that the mangrove forest substratum is very active in removing essential elements from the circulating surface waters. This activity is attributable to the redox processes of the soil, the activities of periphyton on prop roots and other surfaces, uptake by extensive nets of fine roots at the surface of the soil, and the metabolism of microflora and microfauna.

It is clear from the foregoing discussion and from the diagram in Figure 1 that the cycles of matter in mangrove forests are dependent upon the magnitude of external sources of minerals, on energies that power their flux into, through, and out of the mangrove ecosystems, and on biological mechanisms that entrain those elements essential for the functioning of the forest. Rivers, overland sheet flow, tides, and rainfall transport nutrients with sufficient kinetic energy to distribute them throughout the mangrove forest, where certain physical and physiological processes remove these elements from the water solution, sequestering them in plants or the underlying sediments. Rainwaters dilute salts and leach certain elements from the leaves of the trees, returning them to the forest floor where the same mechanisms act to recycle the elements. Plants fix these elements into organic compounds that are returned to the forest circulation via litter fall and grazing. Animals represent another source responsible for the redistribution of mineral elements and organic products within and outside the system. The net result of the cycling process of mangroves is the import of inorganic compounds from the land and an export of organic products to the sea.

Productivity

The photosynthetic process and associated metabolic activities result in a continual recombination of mineral elements into organic matter. The degradation of organic matter is accompanied by the release of those elements for possible recombination at a later time. These two processes (recombination and degradation) in the cycling of matter can be evaluated by monitoring the rates of fixation and release of carbon, the basic building block, in terms of production and respiration. Measures of community metabolism are proving to be extremely valuable for the functional comparisons of ecosystems.

The productivity data available to us are summarized in Table 2. Each of these studies was conducted using the same methodology (carbon dioxide exchange), and together they offer an opportunity to compare mangrove forests representing different environmental conditions. The reader is referred to the original papers (10, 29, 48, 58, 79) for descriptions of the research techniques and the study locations. In his work, Burns (unpublished) used the same equipment and techniques as Carter et al (10). His research was performed on the southeast coast of Dade County, Florida (see Figure 2). That site is characterized by very oligotrophic inputs of

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seawater and shallow or nonexistent organic deposits. The productivity values for these mangrove sites are arranged in Table 2 in order of decreasing gross primary productivity.

Several agents can be identified as important regulators of mangrove productivity. However, these can be lumped into two factors (tidal and water chemistry), which Carter et al have subdivided into seven categories as follows (10):

1. Tidal factors.
   a. Transport of oxygen to the root system.
   b. Physical exchange of the soil water solution with the overlying water mass, removing toxic sulfides and reducing the total salt content of the soil water.
   c. Tidal flushing interacts with the surface water particulate load to determine the rate of sediment deposition or erosion within a given stand.
   d. Vertical motion of the ground water table may transport nutrients regenerated by detrital food chains into the root zone of the mangroves.
2. Water chemistry factors.
   a. Total salt content governs the osmotic pressure gradient between the soil solution and the plant vascular system, thus affecting the transpiration rate of the leaves.
   b. A high macro-nutrient content of the soil solution has been suggested (Kuenzler, 1969 [sic]) as enabling the maintenance of high productivity in mangrove ecosystems despite the low transpiration rates caused by high salt concentrations in sea water.
   c. Lugo et al (1973)[7] indicate that allochthonous macro-nutrients contained in wet season surface runoff may dominate the macro-nutrient budgets of mangrove ecosystems.

Carter et al (10) also suggested that the gradient of chloride concentration across the soil interface (expressed as the ratio of the chloride gradient between the soil and the overlying water mass to the chloride concentration in the soil water solution) could be considered an index that integrates the effects of both tidal and soil-water chemistry factors.

Applying this reasoning they found that, with an increase in the chloride ratio, the ratio of 24 hr respiration to gross primary productivity (a measure of energy used for maintenance) had a slow exponential decrease. Within the range of salinities studied (8–30‰), the gross primary productivity of mangroves increased as fresh water became available. Respiration rates along the same gradient, however, also increased. The increase in respiration is a reflection of the amount of physiological work associated with the problems of higher salinity environments. The work of Scholander et al (76, 77; see also 45, 90) shows that the rates of water loss are related to salinity adaptations in the plants. Those plants that grow in high salinity environments tend to transpire less than those growing in less saline conditions. Scholander et al (77) discussed some of the physiological costs of these adaptations and indicated that metabolic energy was involved in the process of transpiration. Since the supply of metabolic energy available to drive the translocation process is finite, a

[7]Lugo, Sell & Snedaker (49), available to Carter et al (10) as an unpublished manuscript in 1973. Kuenzler, 1968 (misdated by Carter et al as 1969) appears in this paper as (43).

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Table 2 Summary of primary productivity and respiration data for mangrove ecosystems in several locations in Florida and Puerto Rico

Location	Date	Number Diurnals	gC/m^2 day Gross Primary Productivity	Net Primary Productivity	Total 24 hr Respiration	Reference
Fahkahatchee Bay, Fla.						
Small tidal stream Red, Black & White Mangroves	Dec 72	10	13.9	4.8	9.1	(10)
Lower Fahka Union River Basin, Fla.						
Red, Black & White Mangroves	Dec 72	7	11.8	7.5	4.3	(10)
Upper Fahka Union River, Fla.						
Red, Black & Buttonwood Mangroves	Dec 72	10	10.3	6.6	3.7	(10)
Rookery Bay, Fla.	Aug 71					
Black Mangrove Forest	Jan/Feb 72	17	9.0	2.8	6.2	(48)
La Parguera, Puerto Rico.	Jan 58					
Red Mangrove	May 59, 60	sporadic hourly measures	8.2	0	9.1	(29)
Rookery Bay, Fla.	Aug 71					
Red Mangrove	May 59, 60	15	6.3	4.4	1.9	(48)
Kay Largo, Fla.	Jun 68					
Red Mangrove	Jan 70	6	5.3	0	6.0	(58)
Hammock Forest, Dade Co., Fla.						
Red Mangrove	Oct 73	3	1.9	1.3	0.6	Burns[a]
Scrub Forest, Dade Co., Fla.						
Red Mangrove	Oct 73	4	1.4	0	2.0	Burns[a]

[a] L. A. Burns, unpublished.

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limit is set on the amount of water that a plant can effectively take up and transport against the osmotic gradient with its environment; this limit is also reflected in lower transpiration and higher respiration rates. For this reason, at very high salinities one would expect a decrease in the net productivity of mangroves. At lower salinities, competition with plant species adapted to less saline conditions would become increasingly pronounced. The trend toward high gross productivities (for mangroves) with increasing salinity, discounting nutrient availability, should not be expected to be a linear function at salinities beyond those measured by Carter et al (10). For example, respiration may overtake gross production and the species would consequently be eliminated from the community. Taking these factors into consideration, as well as their findings of greater nutrient availability in areas with lower salinities away from the sea, Carter et al (10) proposed a U-shaped relationship of mangrove metabolic dynamics along tidal and water chemistry gradients. Preliminary data shown as Figure 3 tend to support their contention. At the two extremes of the U the energetic costs of survival are high and most of the production is utilized in self-maintenance processes (respiration). The two extremes represent areas of either high nutrients and low amplitude tides, or low nutrients and high amplitude tides. Between the two extremes, or in the middle of the curve, nutrients and tidal amplitude are in some proper combination and net productivity is maximized.

It appears that environments flushed adequately and frequently by seawater and exposed to high nutrient concentrations are more favorable for mangrove ecosystem

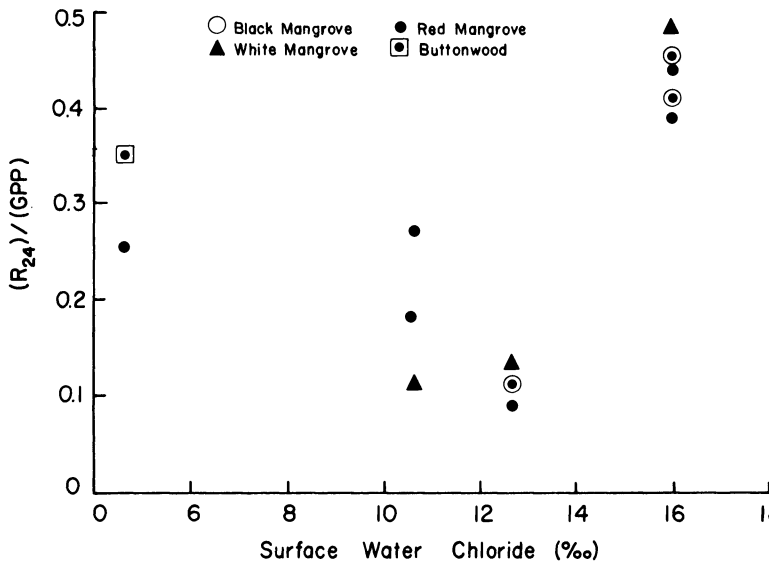

Figure 3 Maintenance metabolism ratio (24 hr respiration/gross primary productivity) of canopy leaves of four species of mangroves as a function of surface water chloride concentration [from Carter et al (10, p. III–28)].

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development; forests in these areas exhibit higher rates of net primary productivity. From Table 2 one could classify the lower Fahka Union mangrove forests and the red mangrove forest at Rookery Bay as representing the most favorable mangrove environments, and the scrub forests on the east coast of Florida as representing the least favorable. The scrub mangrove systems apparently use a larger portion of their energy storages for respiration and low-loss recycling mechanisms, and thus a smaller proportion of their budget is available for growth.

The findings described above have implications with respect to the position of mangrove species along environmental gradients. In our own studies we have found that the rates of photosynthesis and respiration of mangrove species vary with their position in the classic zonation (48, 79).[8] A unit leaf surface area of red mangrove leaves exhibited a higher net primary productivity than those of black mangrove in the next zone or white mangroves interspersed with the black mangroves. The white mangrove exhibited comparable rates with the other species only when growing in conditions conducive to its dominance (10). When a species was out of its normal zone its primary productivity was low in comparison with that of the species characteristic of the zone. Among a wider range of mangrove environments studied by Carter et al (10) 1. the gross primary productivity of red mangrove decreased with increasing salinity; 2. the gross primary productivity of black and white mangroves increased with increasing salinity; 3. in areas of lower salinities and under equal light conditions the gross primary productivity of red mangrove was four times that of the black mangrove; 4. in areas of intermediate salinity the white mangrove had rates of gross primary productivity twice that of red mangrove; and 5. in areas of higher salinities, the white mangrove exhibited a gross primary productivity higher than that of black mangrove, which in turn was higher than the red mangrove. However, when respiration of the species was taken into account, the net productivity of these mangroves accorded well with their dominance in the zones where they were found. The authors feel that the principles emerging from these types of studies may eventually give new meaning to the classic species behavioral postulates of Lotka (47) and Shelford (78).

Quantitative studies of the secondary productivity of the consumers associated with mangrove ecosystems have not been performed, nor is it precisely known to what extent each animal species has a dependence (obligatory or facultative) on mangroves as a food resource. W. Odum (67), however, in his studies of the food habits of south Florida fishes, found that most of the sport and commercial finfish of the Gulf of Mexico were linked to food chains originating with mangrove detritus. His studies have been verified by our associates in the Fahkahatchee and Fahka Union Bays in south Florida (79) and by Austin & Austin (4) in Puerto Rico. These organisms also congregate in mangrove estuarine areas during the early stages of their life cycles where they derive protection from predators as well as food for

[8]The Rookery Bay mangrove forest where the metabolic interpretation for zonation was explored had aggregate exchange surface indices (m^2 of surface/m^2 of ground) of 4.3 for leaves, 0.67 for prop roots, and 0.066 for stems (79), and a complexity index (39) of 61. Data are not available for comparisons with other sites.

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survival. An example of a species with considerable commercial value is the pink shrimp *Penaeus duorarum,* whose food habits and dependence on estuaries have been reported by Sastrakusumah (73) and Kutkuhn (44). In addition, birds utilize mangrove areas as rookeries and feeding grounds (11). Numerous other organisms spend part or the totality of their life cycles on the surface of red mangrove roots (5, 41, 57, 71). Similar functional characteristics were proposed for temperate marsh ecosystems by E. Odum & de la Cruz (63) and for a temperature estuary by Adams & Angelovic (1). That similar regional ecosystems exhibit similar functional mechanisms strengthens the statement of Macnae (54) that the tropical mangrove system is equivalent in geomorphology to the northern marsh shores.

MANGROVE ECOSYSTEM RESPONSES TO STRESS

The term *stress* is used here in a very broad context to describe any action or influence which retards or restricts the normal functioning or development of living biological units (species, populations, communities, or whole systems). Stress can be construed as a drain of potential energy that would otherwise be available for other ecological purposes (65). Obviously, under severe acute or chronic stresses there are thresholds beyond which the biological unit of interest can no longer maintain a normal life cycle or maintain its competitive position in the community; the result is replacement by organisms better adapted to the altered circumstances.

The stresses resulting from man's activities are in many instances analogous to natural stresses to which the mangrove ecosystem or component species may be naturally adapted. However, man-induced stresses tend to be nonselective, of greater intensity, and, relative to the normal periodicities of natural processes, random events. As illustrated in Figure 1, stress may: (*a*) short-circuit a natural pathway (rapid defoliation vs normal litterfall, channelized by-passes vs slow, extensive overland runoff); (*b*) accelerate natural processes such as respiration, remineralization, or organic export; or (*c*) eliminate a pathway, as when siltation prevents gaseous and mineral exchanges between the rhizosphere and the overlying water column or atmosphere. The illustrative stresses were chosen on the basis of their relevance to man's contemporary interactions with mangrove ecosystems and are discussed in this context. This general topic, of peripheral interest to many scientific investigators, is not well documented in the literature.

Channelization, Drainage, and Siltation

Thom (84) has drawn attention to the close relationship between mangrove ecology and geomorphological processes; his discussion describes a self-balancing ecosystem in a state of perpetual change. Channelization, drainage, and siltation are analogous to certain of these geomorphological processes. Such man-induced alterations of the landscape have led to considerable controversy; Lindall (46), for example, cites the extensive manipulations of the hydrology of south Florida as a major threat to estuarine-dependent fisheries. Channelization and drainage divert or short-circuit terrestrial runoff, change estuarine circulation and tidal flushing patterns, and result in altered hydroperiods and salinity regimes (10). In addition to these effects, plus

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the introduction of exotic chemicals into the south Florida estuaries (46), the threat to the fisheries may include subtle decreases in the production of allochthonous materials by the coastal mangrove forest. Two complementary reasons for probable production decreases have been described (10, 49).

The export of mangrove-produced detritus carries with it proportionate amounts of the incorporated mineral nutrients; each unit exported reduces the nutrient stock of the producing system by that amount. In order for mangroves to remain productive, in the broadest context, they must receive equivalent inputs of mineral nutrients from other sources. The rate of in situ organic matter decomposition and remineralization is insufficient to replenish this stock internally (49). Based on field measurements and analog computer modelling studies of south Florida mangroves, Lugo, Sell & Snedaker (49) determined the probable response of mangrove production to reductions in upland runoff and the associated mineral nutrient burden. Reductions in such inputs to approximately 50% of normal reduced mangrove production proportionately. Nutrient input reductions below 50% induced declines to production levels similar to those observed for the scrub mangroves. The response time was on the order of ten years.

Carter et al (10) were able to demonstrate that upland drainage in south Florida reduced the overall productivity of the uplands, and that drainage canals short-circuited the flow of nutrients directly into the coastal estuary with corresponding reductions in sheet flow through the mangroves. They also provided evidence to suggest that even under conditions of adequate nutrient inputs, the mechanical pumping action of the tides was necessary to provide for the maximum exchange of materials between tidal water and the muds.

In the siltation or sedimentation process the slow accretion of muds fosters seral changes in mangrove ecosystems (84) characterized by slow replacement of the assemblage of species. Extremely rapid, or acute, accretion may cause mass mortality in the recipient community followed by an invasion of species better adapted to the changed conditions. Several examples of acute siltation thus affecting the living components of ecosystems have been reported for dredging and filling operations (46) and cyclonic disturbances. Mangrove communities that survived hurricanes and typhoons have succumbed afterward to the direct and indirect effects of acute sedimentation (13, 74) and related changes in local water levels (8).

Changes, by whatever means, in the hydrology and geology of a mangrove ecosystem and the upland and estuarine systems to which they are coupled thus produce corresponding changes in the structure and functioning of the living components. Man's interaction with mangrove ecosystems, in this context, is largely manifested as an acceleration of analogous natural processes. Perception of these changes as a social problem seems to be dependent on the rapidity with which the induced changes in the mangrove system occur.

Hurricanes and Herbicides

In many respects effects of hurricanes and herbicides on the ecosystem are similar: both cause defoliation at a relatively low level of intensity, selective damage at intermediate levels, and complete structural destruction at maximum levels. The

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general result is the conversion of the living structure into organic debris (Figure 1), which may be decomposed or oxidized in situ, or exported. The ability of mangrove ecosystems to recover after a hurricane is well known, whereas recovery from extensive herbicide damage is a matter of conjecture (cf 87, 96).

The destruction of mangroves by hurricanes is highly variable in terms of spatial patterns and species affected. The spatial variability is due to variations in wind direction and velocity, local topography, type and size of vegetation, and the susceptibility or tolerance of individual species to mechanical damage and the altered physical environment following the storm (2, 14). White mangrove is reported to be less resistant to storm damage than red mangrove (89), which has been found to be less resistant than the black mangrove when both are present in the seaward zone.[9] Tebeau (83), however, in his historic account of man in the Everglades described the red mangrove forest as the safest place to be during a tropical storm.

In the aftermath of Hurricane Donna in 1960 in Florida, Craighead & Gilbert (14) made estimates of the mortality of storm-torn and defoliated mangroves and concluded that mortality ranged between 25 and 75% over some 100,000 acres and around 90% on the lowest ground. They also observed that seeds of *A. germinans* and *R. mangle* were widely distributed over the devastated area and suggested that *R. mangle* would form a high proportion of the new stands. Their observations suggest that hurricanes may have a very large role in determining the ratios of species within vegetation types over large areas.

Hurricanes may also shape the structure of forests as well as limit their overall development. H. Odum (in 64, p. H–11) noted that forests in the hurricane zone do not have emergent trees (i.e. the crown surface is relatively uniform), unlike comparable forests geographically outside the influence of hurricanes. In Panama, for instance, the biomass of the mangrove forest can attain levels about two times that reported for Florida and Puerto Rico (Table 1), which lie in the hurricane zone. The probable mean frequency for hurricanes in Florida and Puerto Rico lies between 20 and 24 yr (49) and mangroves in both areas are reported (13, 17, 88) to reach maturity at around 20–25 yr. Thus the maximum biomass and structure that can develop are probably limited by hurricanes, all other environmental constraints being equal. The significance of the export of decomposing woody debris during the years following a destructive storm may have been generally overlooked in studies of organic export from mangrove ecosystems.

Tschirley (87) reported that about 20% of South Viet Nam's half million hectares of mangroves was destroyed by herbicides during the Viet Nam war and that he expected these forests to recover in 20 years. This would appear to be a reasonable estimate as it is comparable to the recovery time for mangroves destroyed by hurricanes. Westing (96), however, disagreed with both estimates and suggested that recovery would take much longer. He further observed that mangrove trees are killed outright by herbicides and after several years little regeneration was present in the field. Walsh et al (92) experimented with the same chemicals used in Viet Nam

[9]Wilcox, L. V. et al 1968/69. *Scientific progress report: program in Bahamian ecology.* Grant from Arnold Bernhard Foundation to Earlham College. Unpublished manuscript. 3 vols.

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and found that mangrove seedlings were very sensitive to residual herbicides. They also observed mangroves to be more sensitive to defoliation[10] than other temperate and tropical species tested. Thus two questions were posed: are mangroves killed by defoliation, and will mangroves regenerate in the denuded areas?

Defoliation from natural causes has been reported, for example, in hurricanes in Puerto Rico (89) and Florida (14), following cold stress (74), and as a coincidental occurrence in areas of high incidence of gall formation (probably induced by *Cylindrocarpon didymum*) on red mangroves (68). In all instances the areas remained or are remaining dominated by mangroves. A computer model simulating the expected recovery of mangroves in Viet Nam suggested that regeneration (in the Rung Sat area) was limited primarily by seedling availability (Sell, in 66). Also Holdridge (38) reported that in Puerto Rico drainage of mangroves, if accompanied by cutting, resulted in changes in the salinity of the soil, which then precluded natural regeneration. It thus seems likely that a given stress such as losing leaves, although insignificant at low levels, when done on a large scale may trigger secondary changes that become the limiting factors to survival. In the Viet Nam controversy, no one has presented enough information about those localities to indicate whether one or another factor, or predicted rate of recovery, represents the real situation in those mangrove regions. Until this is done it will be difficult to pinpoint the explanation or the management actions that are needed to guide future conservation programs.

Thermal Loading

Although several authors (51, 52, 54, 55, 74, 81) have discussed the tolerance of mangroves to low temperature, as this affects geographical distribution, their tolerance and response to elevated temperatures are largely unknown. Our observations of mangroves growing in the discharge areas of coastal power plants suggest difficulties in distinguishing those effects due solely to thermal loading from related conditions associated, for instance, with circulation (i.e. tidal stage and velocity). From studies made downstream from a power plant at Guayanilla Bay, Puerto Rico, Kolehmainen & Morgan (42) showed the diversity of organisms living on the prop roots of *R. mangle* to be inversely related to water temperature above 34°C. Kolehmainen (41) also reported greater densities of prop roots in areas of thermal loading (5°C above ambient). We too have observed increased prop root densities and also that *R. mangle* leaf sizes become smaller even though the ratio of length to width remains relatively stable (Table 3). Davis (17) reported an influence of salinity changes per se on leaf sizes, which points up the difficulty of separating confounded causal effects in the absence of detailed studies.

Miller (58) suggested, based on modelling studies of *R. mangle* bioclimate, leaf temperatures, and primary production in south Florida, that production is de-

[10]We have twice, five months apart, manually defoliated four *R. mangle* trees in south Florida. In all cases the test trees put out new foliage even when all terminal buds were pinched off. Recovery times were slowest during the winter and on debudded trees that developed new foliage from lateral buds. It remains to be seen if chemical defoliation per se results in equally rapid recovery.

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Table 3 Variations in *Rhizophora mangle* leaf dimensions in four mangrove locations[a]

Location	Mean Leaf Length (±1 SD)	Mean Leaf Width (±1 SD)	Length/Width Ratio
Guayanilla, Puerto Rico (water temperature 35°C)	6.4 (±0.8)	3.0 (±0.3)	2.1
Guayanilla, Puerto Rico (water temperature ambient)	6.9 (±0.8)	3.6 (±0.3)	1.9
Jobos, Puerto Rico	9.2 (±1.9)	4.2 (±0.8)	2.2
Rookery Bay, Florida	10.0 (±1.0)	4.9 (±0.4)	2.0

[a] Lugo, A., Snedaker, S. C., Pool, D. Unpublished manuscript.

creased by increasing air temperature and humidity. Metabolism studies have not been made in mangroves under the influence of elevated water temperatures. However, to the extent that mangrove ecosystems are ecological analogs of salt marshes, similar responses may be expected under similarly altered conditions. Thus the expected response of mangrove ecosystems to thermal enrichment may be inferred from the community metabolism (carbon dioxide exchange method) work of Young (97) in a Florida salt marsh receiving thermal (cooling water) discharges from a power plant. His studies indicated a salt marsh community respiration of 5.71 $gC/m^2 \cdot$ day in a "thermal marsh" and 2.21 $gC/m^2 \cdot$ day in a nearby "control marsh." The overall effect, however, appears to be increased levels of carbon turnover and metabolism; the balance between production and respiration was similar at both study sites.

CONCLUDING REMARKS

Mangrove ecosystems are self-maintaining coastal landscape units that are responsive to long-term geomorphological processes and to continuous interactions with contiguous ecosystems in the regional mosaic. They are open systems with respect to both energy and matter and thus can be considered "interface" ecosystems coupling upland terrestrial and coastal estuarine ecosystems. The fact that mangrove ecosystems are open has presented man with difficult problems in terms of management and conservation, particularly with respect to estuarine-dependent fisheries. There is no precise boundary to distinguish mangroves from the upstream and downstream ecosystems upon which they are dependent. Such dilemmas force us to confront our collective ignorance of ecosystem functioning and the spatial organization of ecosystems in a regional setting.

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