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THE ECOLOGY OF THE MANGROVES OF SOUTH FLORIDA:
A COMMUNITY PROFILE

by

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CHAPTER 3. ECOSYSTEM STRUCTURE AND FUNCTION

3.1 STRUCTURAL PROPERTIES OF MANGROVE FORESTS

Published information about the structural aspects of Florida mangrove forests is limited; most existing data have been published since the mid-1970's. This lack of information is unfortunate since quantitative structural data greatly aid understanding of processes such as succession and primary production. Even more important, the response of mangrove forests to stress, both climatic and man-induced, can be followed quantitatively with this type of data.

Ball (1980) contributed substantially to understanding the role of competition in mangrove succession by measuring structural factors such as basal area, tree height, and tree density. Lugo and Zucca (1977) monitored the response of mangrove forests to freezing temperatures by observing changes in structural properties of the trees.

Baseline studies of forest structure have been published by Lugo and Snedaker (1975), and Pool, Snedaker and Lugo (1977). For example, Lugo and Snedaker (1975) compared a fringing mangrove forest and a basin forest at Rookery Bay, near Naples, Florida. They found the fringing forest, which was dominated by red mangroves, to have a tree diversity of $H = 1.48$, a basal area of $15.9 \text{ m}^2/\text{ha}$, an aboveground biomass of $17,932 \text{ g/m}^2$, and a non-existent litter layer. The nearby basin forest was dominated by black mangroves, had a tree diversity of $H = 0.96$ and a basal area of $23.4 \text{ m}^2/\text{ha}$. The litter layer in the basin forest averaged 550 dry g/m^2 . Tree diversity in a hurricane disturbed section of the Rookery Bay forest was 1.62. Similar data were presented for mangrove forests in the Ten Thousand Islands area (Table 2).

Data of this type are useful for many purposes including impact statements, environmental surveys, and basic scientific questions. Cintron et al. (1978) gave an indication of the direction in which future research might proceed. Working in a mangrove stand in Puerto Rico, they found

tree height to be inversely proportional ($r = 0.72$) to soil salinity in the range 30 to 72 ppt. Above 65 ppt salinity, dead tree basal area was higher than live tree basal area and above 90 ppt there was no live tree basal area.

It should be possible to investigate the relationship between a variety of mangrove structural properties and factors such as flushing frequency, soil depth, nutrient availability, pollution stress, and other measures of human impact. Ultimately, this should lead to an ability to predict the form and structure of mangrove forests resulting from various physical conditions or artificial impacts. One example of this potential tool is Ball's (1980) documentation of structural changes in mangrove forests resulting from alterations in the hydrological conditions of south Florida.

3.2 ZONATION, SUCCESSION AND "LAND-BUILDING"

Much of the world's mangrove literature consists of descriptive accounts of zonation in mangrove forests and the species composition within these zones. Although general agreement has been lacking, various hypotheses have been put forth concerning the possible connection between zonation, ecological succession, competition, and the role of physical factors such as soil salinity and tidal amplitude. In this section we review briefly the dominant ideas about mangrove zonation and succession and present our interpretation of the current status of knowledge.

Davis (1940), working in south Florida, was one of the first investigators to describe distinct, almost monospecific, zones within mangrove ecosystems. In what has become the classical view, he argued that mangrove zonation patterns were equivalent to seral stages in succession. The most seaward zone, dominated by red mangroves, was regarded as the "pioneer stage". More landward zones were dominated by white mangrove, black mangrove, buttonwood and, finally, the climatic climax, a tropical forest. Since

Table 2. Aboveground biomass of mangrove forests in the Ten Thousand Islands region of Florida. Values are based on 25 m² clearcuts and are expressed in dry kg/ha. Data are from Lugo and Snedaker (1975).

Compartment	Scrub mangroves	Overwash mangroves		Fringe mangroves			Riverine mangroves	
		A	B	A	B	C	A	B
Leaves	712	7,263	6,946	5,932	5,843	7,037	3,810	9,510
Fruit & flowers	no data	20	236	28	210	131	148	1
Wood	3,959	70,380	70,480	57,960	84,270	128,510	79,620	161,330
Prop roots	3,197	51,980	41,920	22,270	27,200	17,190	14,640	3,060
Litter	1,140	17,310	13,990	22,730	60,250	98,410	42,950	33,930

Total above-ground biomass	9,008	146,953	133,572	108,920	177,773	251,278	141,168	207,831

these zones were regarded as progressively later stages in succession, the entire mangrove ecosystem was believed to be moving seaward through a process of sediment accumulation and colonization. Davis based his argument primarily upon the sequence of observed zones and cores which showed red mangrove peat underlying black mangrove peat which, in turn, occurred under terrestrial plant communities.

Unfortunately, this Clementsian interpretation of mangrove zonation was widely accepted, but rarely tested. For example, Chapman (1970) expanded Davis' original successional concept from south Florida to explain zonation in mangrove forests in other parts of the world. Walsh (1974) thoroughly reviewed the mangrove succession/zonation literature.

Fortunately, not everyone accepted Davis' point of view. Egler (1952) and later Thom (1967, 1975) argued that mangrove zonation was a response to external physical forces rather than temporal sequence induced by the plants themselves. Egler (1952) showed that patterns of sediment deposition predicted by Davis' (1940) theory did not always occur. He also showed that in some cases mangrove zones appeared to be moving landward rather than seaward. Sea level has been rising in south Florida at the rate of 1 ft (30 cm) per 100 to 150 years (Provost 1974). Spackman et al. (1966) emphasized the role of sea level change in determining changes in mangrove zonation, both through sea level rise and land subsidence. Both Egler (1952) and Spackman et al. (1966) along with Wanless (1974) and Thom (1967, 1975) suggested that mangroves were reacting passively rather than actively to strong geomorphological processes. This implies that mangroves should be regarded as "land-stabilizers" rather than "land-builders".

Furthermore, field researchers frequently noted that red mangroves were not always the only "pioneer species" on recently deposited sediment. It is not unusual to find seedlings of black, white, and red mangroves growing together on a new colonization site. Lewis and Dunstan

(1975) found that black mangroves and white mangroves along with the saltmeadow cordgrass, Spartina patens, are often the pioneers on new dredge spoil islands in central Florida. On the northern coast of the Gulf of Mexico, where black mangrove is the only mangrove species present, it may be preceded by marsh grasses such as saltmarsh cordgrass, S. patens, smooth cordgrass, S. alterniflora, or the black needle rush, Juncus roemerianus. In Puerto Rico, we observed that white mangrove often pioneers and dominates sites where oceanic overwash of beach sand has occurred. All of these observations detract from Davis' (1940) original contention that red mangroves should be regarded as the initial colonizer of recently deposited sediments. It appears that under certain conditions, e.g., shallow water depths, substrate type, and latitude, white and black mangroves or marsh grasses can be effective pioneer species.

The work of Rabinowitz (1975) added a new perspective to the mangrove zonation debate. Through carefully designed reciprocal planting experiments in Panamanian mangrove forests using species of Rhizophora, Laguncularia, Pelliciera and Avicennia, she demonstrated that each species could grow well within any of the mangrove zones. In other words, physical and chemical factors such as soil salinity or frequency of tidal inundation, within each zone, were not solely responsible for excluding species from that zone. To explain zonation, Rabinowitz proposed tidal sorting of propagules based upon propagule size, rather than habitat adaptation, as the most important mechanism for zonation control.

The most recent piece to be added to the zonation/succession puzzle comes from the work of Ball (1980). Based upon research of mangrove secondary succession patterns adjacent to Biscayne Bay, Florida, she made a strong case for the importance of interspecific competition in controlling zonation. She found that white mangroves, which grow best in intertidal areas, do not occur consistently in the intertidal zone of mature mangrove stands. Instead, white mangroves

dominate higher, drier locations above mean high water where the red mangrove does not appear to have a competitive advantage. She suggested that competition is not so important during the early stages of succession but becomes critical as individual trees reach maturity and require more space and other resources.

Inherent in Ball's concept of zonation is the differential influence of physical factors (e.g., soil salinity, depth to water table) on the competitive abilities of the different mangrove species. She concluded that succession proceeds independently within each zone, although breaks in the forest canopy from lightning strikes or high winds may produce a mosaic of different successional stages within a zone. These openings allow species whose seedlings do not compete well in shade, such as the white mangrove, to become established, at least temporarily, within solid zones of red mangroves.

Zonation of mangrove species does not appear to be controlled by physical and chemical factors directly, but by the interplay of these factors with interspecific competition and, possibly, through tidal sorting of propagules. Once succession in a mangrove zone reaches an equilibrium state, change is unlikely unless an external perturbation occurs. These perturbations range from small-scale disturbance (lightning strikes) to large-scale perturbations (sea level change, hurricane damage) and may cause succession within zones to regress to an earlier stage. There is some evidence in south Florida that hurricane perturbations occur on a fairly regular basis, creating a pattern of cyclical succession.

Except for Ball (1980) and Taylor (1980), the importance of fires as an influence on mangrove succession has been generally ignored. Most fires in the Florida mangrove zone are initiated by lightning and consist of small circular openings in the mangrove canopy (Taylor 1980). These openings present an opportunity for secondary succession within an established zone. For example, we have

frequently observed white mangroves flourishing in small lightning-created openings in the center of red mangrove forests. Fire may also play a role in limiting the inland spread of mangroves. Taylor (1981) pointed out that Everglades fires appear to prevent the encroachment of red and white mangroves into adjacent herbaceous communities.

Finally, Lugo and Snedaker (1974), Cintron et al. (1978) and Lugo (1980) suggested that mangrove ecosystems function as classical successional systems in areas of rapid sediment deposition or upon recently colonized sites such as offshore islands. They concluded that in most areas mangrove forests are an example of steady-state cyclical systems. Conceptually, this is synonymous to E. P. Odum's (1971) cyclic or catastrophic climax. Chapman (1976a, b) suggested the idea of cyclic succession for a variety of coastal ecosystems.

If Florida mangrove ecosystems are cyclic systems, then there should be an identifiable perturbation capable of setting succession back to an early stage. Lugo and Snedaker (1974) suggested that hurricanes may play this role. They pointed out (without substantiating data) that major hurricanes occur about every 20-25 years in south Florida. Coincidentally, mangrove ecosystems appear to reach their maximum levels of productivity in about the same period of time (Lugo and Snedaker 1974). This hypothesis suggests that succession within many mangrove ecosystems may proceed on a cyclical basis rather than in the classical fashion. Possibly other physical perturbations may influence mangrove succession including incursions of freezing temperatures into central Florida, periodic droughts causing unusually high soil salinities (Cintron et al. 1978), and fire spreading into the upper zones of mangrove forests from terrestrial sources.

Although understanding of zonation and succession in mangrove ecosystems remains incomplete, a clearer picture is emerging, at least for south Florida. Contrary to early suggestions, mangrove

species zonation does not appear to represent seral stages of succession except, perhaps, for locations of recent colonization or where sediment is accumulating rapidly. The role of mangroves in land-building seems more passive than active. Geomorphological and hydrological processes appear to be the dominant forces in determining whether mangrove shorelines recede or grow. The role of mangroves is to stabilize sediments which have been deposited by physical processes.

3.3 NUTRIENT CYCLING

Current understanding of nutrient cycles in mangrove ecosystems is far from satisfactory. Sporadic field measurements have been made, but a complete nutrient budget has not been published for any mangrove ecosystem in the world.

Several pioneering field studies were conducted in Florida (Carter et al. 1973; Snedaker and Lugo 1973; Onuf et al. 1977) and one simulation model of mangrove nutrient cycling has been published (Lugo et al. 1976). Preliminary measurements of nitrogen fixation were made (Zuberer and Silver 1975; Gotto and Taylor 1976; Zuberer and Silver 1978; Gotto et al. 1981). Based on these studies, we present the following preliminary conclusions.

Mangrove ecosystems tend to act as a sink (net accumulator) for various elements including macro nutrients such as nitrogen and phosphorus, trace elements, and heavy metals. As we have discussed in section 1.7, these elements are removed from waters flowing through mangrove swamps by the concerted action of the mangrove prop roots, prop root algae, the associated sediments, the fine root system of the mangrove trees, and the host of small invertebrates and microorganisms attached to all of these surfaces. Although the turnover times for these elements in mangrove swamps are not known, it appears that at least a portion may be stored or tied up in wood, sediments, and peat for many years.

Although mangrove ecosystems may tend to accumulate nutrients, there is a continual loss through export of particulate and dissolved substances. If significant nutrient storage and resultant high primary production are to occur, there must be a continual input of nutrients to the mangrove forest from outside the system (Figure 7). Where nutrient influx to the mangrove ecosystem is approximately balanced by nutrient loss in exported organic matter, then nutrient storage will be minimal and mangrove net primary production will be low. This appears to occur in the scrub mangrove community type and to a lesser extent in the basin and hammock community types.

Carter et al. (1973) and Snedaker and Lugo (1973) have hypothesized that the greatest natural nutrient inputs for mangrove swamps come from upland and terrestrial sources. Apparently for this reason, the most luxuriant and productive mangrove forests in south Florida occur in riverine locations or adjacent to significant upland drainage.

Localized sources of nutrients, such as bird rookeries, can result in greater nutrient storage and higher mangrove productivity (Onuf et al. 1977). If however, large bird rookeries (or artificial nutrient inputs) occur in poorly flushed sections of mangrove ecosystems, resultant high nutrient levels may inhibit mangrove growth (R. R. Lewis, III, Hillsborough Community College, Tampa, Fla.; personal communication 1981).

The output from the simulation model of Lugo et al. (1976) suggests that if nutrient input to a mangrove ecosystem is reduced, then nutrient storage levels within the mangrove ecosystem will be reduced and mangrove biomass and productivity will decline. To our knowledge this hypothesis has not been tested in the field.

Nitrogen fixation occurs in mangrove swamps at rates comparable to those measured in other shallow, tropical marine areas (Gotto et al. 1981). Nitrogen

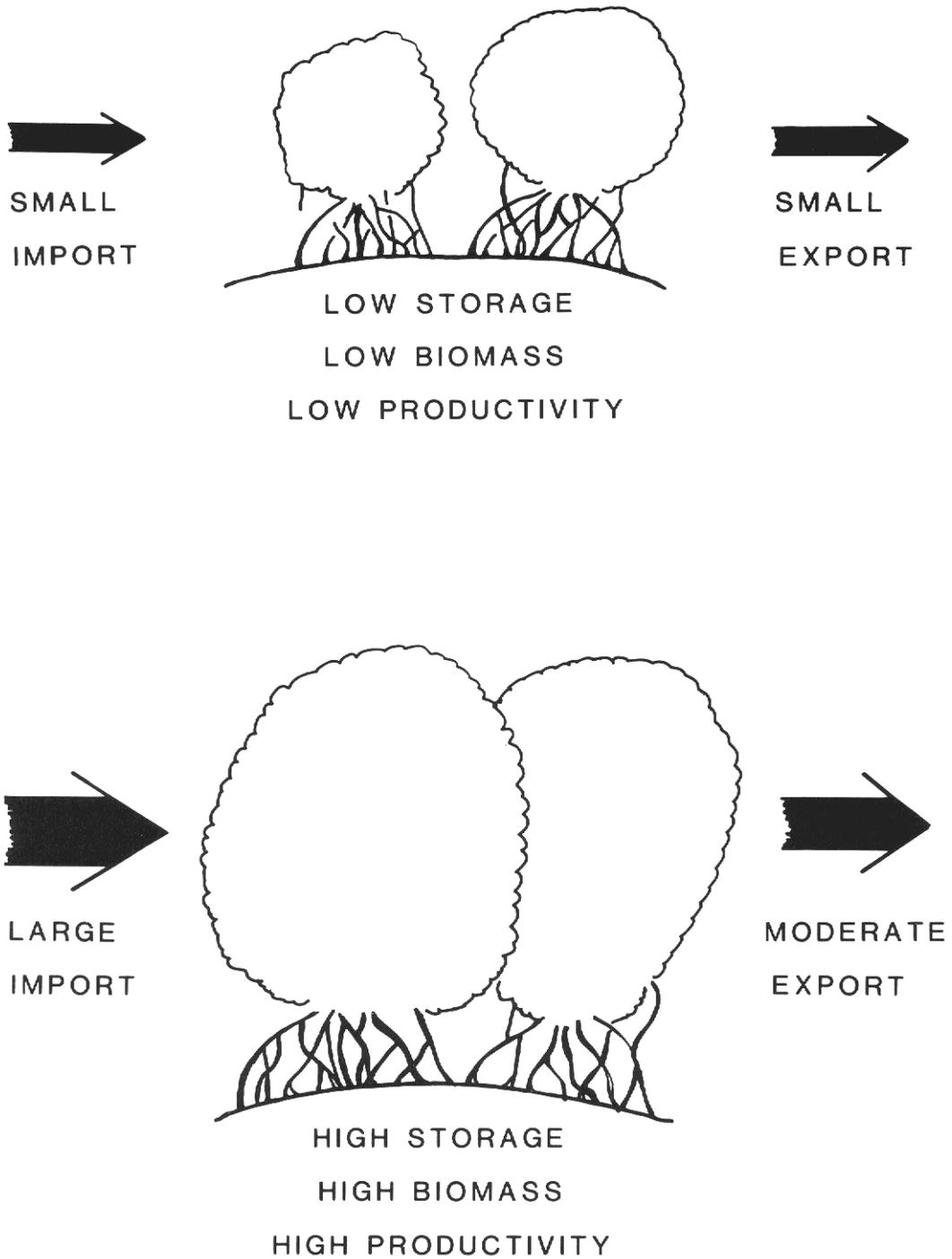


Figure 7. The hypothetical relationship between nutrient input (excluding carbon), biomass, primary productivity, and nutrient export (including carbon) from mangrove ecosystems. Top: small nutrient import. Bottom: large nutrient import.

fixation has been found in association with mangrove leaves, both living and dead, mangrove sediment surfaces, the litter layer in mangrove swamps, and mangrove root systems (Gotto and Taylor 1976; Zuberer and Silver 1978; Gotto et al. 1981). In virtually all cases, nitrogen fixation appears to be limited by the availability of labile carbon compounds. Perhaps for this reason, the highest rates of mangrove nitrogen fixation have been measured in association with decaying mangrove leaves; presumably, the decaying leaves act as a carbon source and thus accelerate nitrogen fixation. Macko (1981), using stable nitrogen ratio techniques, has indicated that as much as 25% of the nitrogen associated with black mangrove peat in Texas is derived from nitrogen fixation.

Zuberer and Silver (1978) speculated that the nitrogen fixation rates observed in Florida mangrove swamps may be sufficient to supply a significant portion of the mangrove's growth requirements. Although this hypothesis is impossible to test with present information, it might explain why moderately productive mangrove stands occur in waters which are severely nitrogen depleted.

In summary, knowledge of nutrient cycling in mangrove swamps is highly speculative. These ecosystems appear to act as a sink for many elements, including nitrogen and phosphorus, as long as a modest input occurs. Nitrogen fixation within the swamp may provide much of the nitrogen needed for mangrove growth.

3.4 LITTER FALL AND DECOMPOSITION

Unless otherwise stated, litter fall refers to leaves, wood (twigs), leaf scales, propagules, bracts, flowers, and insect frass (excrement) which fall from the tree. Mangrove leaves are shed continuously throughout the year although a minor peak occurs during the early part of the summer wet season in Florida (Heald 1969; Pool et al. 1975). Sporadic litter fall peaks may follow periods of stress from cold air temperatures, high soil

salinities, and pollution events. Litter fall typically can be partitioned as 68% to 86% leaves, 3% to 15% twigs and 8% to 21% miscellaneous; the latter includes flowers and propagules.

Litter fall is an important ecosystem process because it forms the energy basis for detritus-based foodwebs in mangrove swamps (see sections 3.5 and 3.6). The first measurements of litter fall in mangrove swamps were made by E.J. Heald and W.E. Odum, working in the North River estuary in south Florida in 1966-69. This was subsequently published as Heald (1969), Odum (1970), and Odum and Heald (1975a). They estimated that litter production from riverine red mangrove forests averaged 2.4 dry g of organic matter/m²/day (or 876 g/m²/year or 8.8 metric tons/ha/year).

Subsequent studies agreed with this early estimate (Table 3), although variation clearly exists between different types of communities. Scrub forests with scattered, very small trees have the smallest amount of leaf fall. Basin and hammock forests, which appear to be nutrient limited, have intermediate leaf fall values. Not surprisingly, the highest values occur in the highly productive fringing, overwash, and riverine forests. Odum and Heald (1975a) suggested that the relatively uniform litter fall values from productive mangrove forests around the world result from the shade intolerance of the canopy leaves and the tendency for the canopy size to remain the same in spite of increasing height. If detailed information is lacking, red mangrove forests of south Florida, which are not severely limited by lack of nutrients, can be assumed to produce litter fall of 2.0 to 3.0 g/m²/day of dry organic matter. Pure stands of black mangroves usually have a lower rate of 1.0 to 1.5 g/m²/day (Lugo et al. 1980).

Decomposition of fallen Florida mangrove leaves has been investigated by a number of researchers including Heald (1969), Odum (1970), Odum and Heald (1975a), Pool et al. (1975), Lugo and Snedaker (1975), Twilley (1980) and Lugo et

Table 3. Estimates of litter fall in mangrove forests. Total litter fall includes leaves, fruits, twigs, flowers, and bark. R = red mangrove, W = white mangrove, B = black mangrove.

Species	Leaf fall (g/m ² /day)	Total litter fall (g/m ² /day)	Annual litter fall (metric tons/ha/yr)	Reference
R (riverine)	1.3	2.4	8.8	Heald 1969
R (riverine)	---	3.6	12.8	Pool et al. 1975
R (overwash)	---	2.7	9.9	Pool et al. 1975
R (fringe)	---	2.7	9.9	Pool et al. 1975
R,B (basin)	---	2.0	7.3	Pool et al. 1975
R (mature)	2.2	2.9	10.6	Teas 1979
R (scrub)	0.2	0.4	1.3	Teas 1979
B (basin)	0.7	0.8	2.9	Teas 1979
B (basin)	---	2.2	8.0	Courtney 1980
B	---	1.3	4.9	Twilley 1980
B	---	1.3	4.8	Lugo et al. 1980
Mixed R,B,W	---	2.5	9.0	Lugo et al. 1980
B	---	0.8	2.9	Pool et al. 1975
Variety of community types	---	0.8 - 2.1	2.9 - 7.7	Heald et al. 1979
26 species (Australia)	---	2.4	8.8	Boto & Bunt (MS. in prep.)

al. (1980). Heald and Odum showed that decomposition of red mangrove leaves proceeds most rapidly under marine conditions, somewhat more slowly in freshwater, and very slowly on dry substrates. For example, using the litter bag method, they found that only 9% of the original dry weight remained after 4 months in sea water. By comparison, 39% and 54% remained at the end of comparable periods in brackish water and freshwater. Under dry conditions, 65% remained. Higher decomposition rates in sea water were related to increased activity of shredder organisms, such as crabs and amphipods.

Heald (1969) and Odum (1970) also found increases in nitrogen, protein, and caloric content as mangrove leaves progressively decayed. The nitrogen content of leaves decaying under brackish conditions (on an AFDW basis) increased from 1.5% (5.6% protein) to 3.3% (20.6% protein) over a 6-month period. Subsequent information (Odum et al. 1979b) suggested that the protein increase may not have been this great since some of the nitrogen increase probably included non-protein nitrogen compounds such as amino sugars. Fell and Master (1973), Fell et al. (1980), Fell and Newell (1980), and Fell et al. (1980) have provided more detailed information on red mangrove leaf decomposition, the role of fungi in decomposition (see section 4), and nitrogen changes and nitrogen immobilization during decomposition. Fell et al. (1980) have shown that as much as 50% of weight loss of the leaf during decomposition is in the form of dissolved organic matter (DOM).

Heald et al. (1979), Lugo et al. (1980) and Twilley (1980) discovered that black mangrove leaves decompose more rapidly than red mangrove leaves and apparently produce a higher percentage of DOM. Pool et al. (1975) have shown that mangrove litter decomposes and is exported most rapidly from frequently flooded riverine and overwash forests. These communities have little accumulation of litter on the forest floor. Communities which are not as well-flushed by the tides, such as the basin and hammock

forests, have slower rates of decomposition and lower export rates.

3.5 CARBON EXPORT

Research from Florida mangrove swamps forms a small portion of the larger controversy concerned with the extent to which coastal wetlands export particulate organic carbon (reviewed by Odum et al. 1979a). Available evidence from Florida, Puerto Rico and Australia (Table 4) suggests that mangrove swamps tend to be net exporters. The values in Table 4 should be regarded as preliminary, however, since all five studies are based upon simplistic assumptions and methodology.

Golley et al. (1962) based their annual estimate of particulate carbon export from a Puerto Rican forest upon a few weeks of measurements. Odum and Heald's estimates were derived from two or three measurements a month. All investigators have ignored the importance of bed load transport and the impact of extreme events. All investigators except Lugo et al. (1980) have failed to measure DOC flux.

It seems relatively clear that mangrove forests do export organic carbon to nearby bodies of water. The magnitude of this export has probably been underestimated due to ignoring bedload, extreme events, and DOC.

The value of this carbon input to secondary consumers in receiving waters is not clear. As shown in section 3.6, food webs based primarily upon mangrove carbon do exist. The relative importance of mangrove carbon to Florida coastal ecosystems remains speculative. We suspect that mangrove-based food webs are dominant in small bays, creeks and rivers within large mangrove ecosystems such as the North River system studied by Heald (1969) and Odum (1970). In intermediate-sized bodies of water, such as Rookery Bay near Naples, Florida, mangroves are probably important but not dominant sources of organic carbon. Lugo et al. (1980) estimate that mangroves supply 32% of the organic carbon

Table 4. Estimates of particulate carbon export from mangrove forests. Lugo et al. (1976) estimated export from a theoretical, steady state forest using a simulation model. Lugo et al. (1980) measured export from an inland black mangrove forest.

Investigators	Location	Export	
		g/m ² /day	tonnes/ha/yr
Golley et al. (1962)	Puerto Rico	1.1	4.0
Heald (1969), Odum (1970) ^a	Florida	0.7	2.5
Lugo and Snedaker (1975)	Florida	0.5	2.0
Lugo et al. (1976)	Florida	1.5 - 1.8	5.5 - 6.6
Boto and Bunt (1981)	Australia	1.1	4.0
Lugo et al. (1980) ^b	Florida	0.2	0.7

^aEstimate only includes carbon of mangrove origin.

^bEstimate includes dissolved and particulate carbon.

input to Rookery Bay. In very large systems, such as Biscayne Bay near Miami, Florida, mangroves are clearly less important than any other sources such as algae and sea grasses, although mangrove carbon may be important in localized situations such as the immediate vicinity of fringing and overwash forests. The magnitude of mangrove carbon export to unenclosed coastal waters and offshore remains a mystery.

3.6 ENERGY FLOW

At least seven sources of organic carbon may serve as energy inputs for consumers in mangrove ecosystems (Figure 8). The pathways by which this energy containing material is processed and made available to each consumer species is indeed complex. Not surprisingly, current understanding of energy flow in Florida mangrove ecosystems exists largely in a qualitative sense; quantitative data are scarce and piecemeal. A variety of investigators have contributed information over the past decade including, but not limited to, Heald (1969), Odum (1970), Odum and Heald (1972), Carter et al. (1973), Snedaker and Lugo (1973), Heald et al. (1974), Lugo and Snedaker (1974, 1975), Odum and Heald (1975a, b), and Pool et al. (1977). Probably, the most complete study to date is the investigation of energy flow in the black mangrove zone of Rookery Bay by Lugo et al. (1980).

It is possible at this time to present a series of hypotheses concerning the relative importance of these energy sources. First, the relative importance of each source can vary from one location to the next. As will be shown in the following discussion, the consumers in certain mangrove forests appear to depend primarily upon mangrove-derived carbon while in other locations inputs from phytoplankton and attached algae are probably more important.

Our second hypothesis is that energy flow based upon phytoplankton is most important in overwash mangrove forests and other locations associated with large

bodies of clear, relatively deep water. Conversely, phytoplankton are hypothesized to be relatively unimportant to the energy budgets of the large riverine forest communities along the southwest coast of Florida. It should be remembered, however, that even where phytoplankton are quantitatively unimportant, they potentially perform an important function as the basis of phytoplankton-zooplankton-larval fish food webs (Odum 1970).

As a third hypothesis, Iver Brook (Rosensteil School of Marine and Atmospheric Sciences, Rickenbacker Causeway, Miami, Fla.; personal communication 1979) has suggested that both sea grasses and benthic algae serve as an important energy source for fringing mangrove communities adjacent to large bodies of water such as Biscayne Bay and Whitewater Bay. Although little evidence exists to test this hypothesis, observations of extensive deposits of sea grass and macroalgal detritus within mangrove forests suggest intuitively that Brook's hypothesis may be correct.

In regions where mangrove shading of the prop roots is not severe, our fourth hypothesis suggests that carbon originating from prop root epiphytes may be significant to community energy budgets. Lugo et al. (1975) have measured net production of periphyton in mangroves fringing Rookery Bay and found average values of 1.1 gC/m²/day. Hoffman and Dawes (1980) found a lower value of 0.14 gC/m²/day. Because these values are roughly comparable to average exports of mangrove leaf carbon (section 3.5), its potential importance is obvious.

The fifth hypothesis states that mangrove organic matter, particularly leaf material, is an important energy source for aquatic consumers. This hypothesis was first espoused by Heald (1969) and Odum (1970), who worked together in the riverine mangrove communities between the Everglades and Whitewater Bay. Clearly, mangrove carbon is of great importance within the riverine and basin communities all along the southwest coast of Florida (Odum and Heald 1975b); Carter et al. (1973) and Snedaker and Lugo (1973)

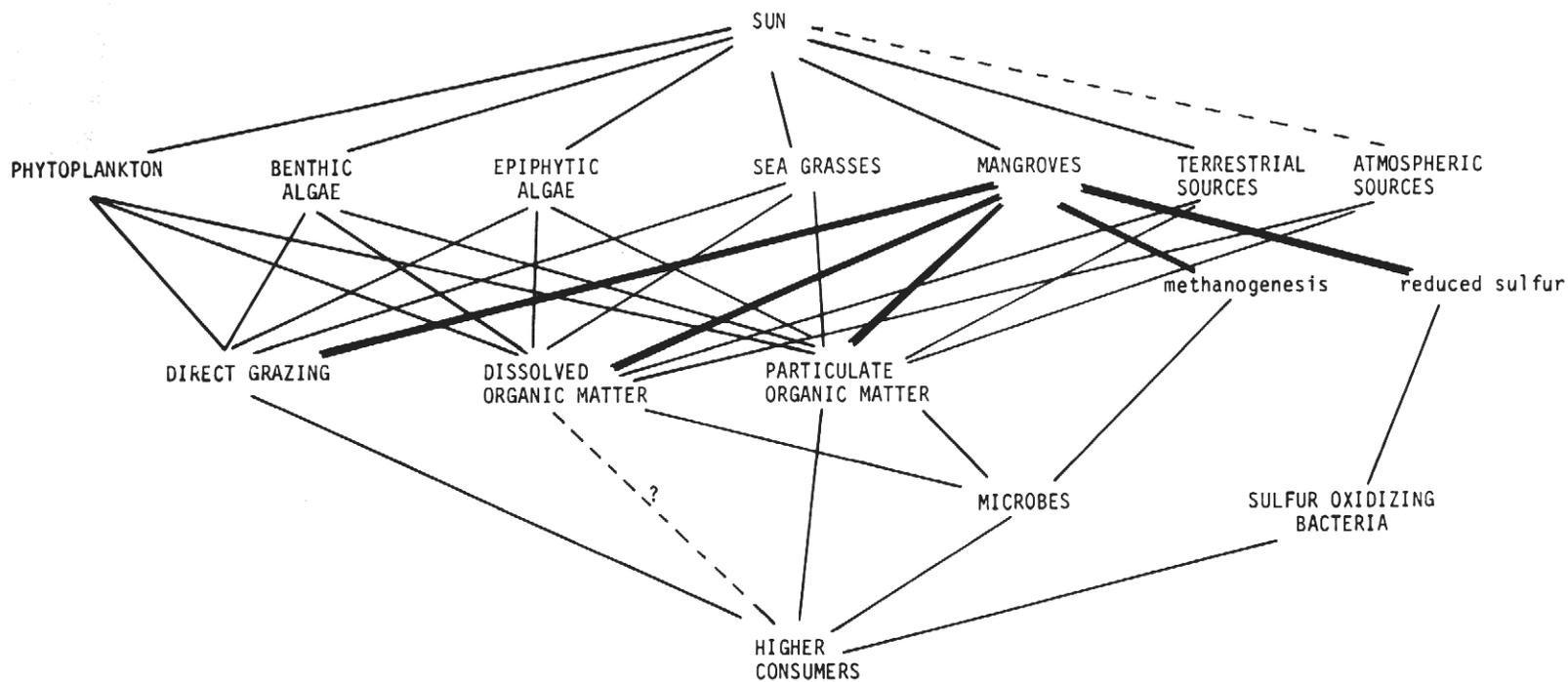


Figure 8. Potential pathways of energy flow in mangrove ecosystems. Not all possible pathways have been drawn; for example, methanogenesis and sulfur reduction could originate from any of the sources of organic matter. Mangrove-based pathways are enhanced for emphasis and in no way imply relative importance.

provided subsequent supportive data. What is not clear, is the relative importance of mangrove carbon to consumers within fringing, overwash, and more isolated mangrove communities.

Our sixth hypothesis involves the assemblage of organisms that graze mangrove leaves directly. A variety of insects (see section 6) and the mangrove tree crab, Aratus pisonii, (Beever et al. 1979) obtain much of their energy directly from living mangrove leaves, even though grazing rarely exceeds 10% of net primary production (Odum and Heald 1975b).

As a seventh hypothesis we suggest that anaerobic decomposition of mangrove tissue, particularly root material, may support an extensive food web based on bacteria associated with methanogenesis or the processing of reduced sulfur compounds. Our suggestion of the importance of reduced sulfur comes directly from Howarth and Teal's (1980) discovery of this potentially important energy pathway in temperate Spartina (cordgrass) marshes. They found that anaerobic decomposition is such an incomplete process that if sulfates are available (from sea water) as much as 75% of the original energy in plant tissues may be converted by sulfur reducing bacteria to reduced sulfur compounds such as hydrogen sulfide and pyrite. Subsequently, if these reduced sulfur compounds are moved hydrologically to an oxidized environment (sediment surface or creek bank) sulfur-oxidizing bacteria (e.g., Thiobacillus spp.) may convert the chemically stored energy to bacterially stored energy with an efficiency as great as 50% (Payne 1970). Presumably, deposit-feeding organisms such as grass shrimp (Palaemonetes) and mullet (Mugil) are capable of grazing these sulfur-oxidizing bacteria from the sediment surface. If this hypothetical trophic exchange does exist, it may be of considerable magnitude and may cause us to reexamine current concepts of energy processing and export from mangrove ecosystems. Since freshwater contains remarkably little sulfate in comparison to seawater, this energy pathway is probably of little importance in mangrove forests

of very low salinity.

Carbon inputs from terrestrial sources may be important to certain mangrove communities. Carter et al. (1973) have shown that terrestrial carbon can reach coastal ecosystems particularly where man has cut deep channels inland for navigation or drainage purposes. The magnitude of this influx has not been adequately measured although Carter et al. did find that mainland forests (including mangroves) contributed approximately 2,100 metric tons of carbon per year to Fakahatchee Bay.

Atmospheric inputs from rainfall appear to be minimal in all cases. Lugo et al. (1980) measured throughfall (precipitation passing through the tree canopy) in Rookery Bay mangrove forests of 15 to 17 gC/m²/year. This would be an overestimate of atmospheric input since it contains carbon leached from mangrove leaves. The best guess of atmospheric input is between 3 to 5 gC/m²/year for south Florida mangrove ecosystems.

Subsequent stages of energy transfer in mangrove community food webs remain largely hypothetical. Odum (1970) and Odum and Heald (1975b) have outlined several pathways whereby mangrove carbon and energy are processed by a variety of organisms (see Figure 8). Apparently, the most important pathway follows the sequence: mangrove-leaf detritus substrate-microbe-detritus consumer-higher consumers. The critical links are provided by the microbes such as bacteria and fungi (see Fell et al. 1975) and by the detritus consumers. The latter group was studied by Odum (1970) and Odum and Heald (1975b) and found to consist of a variety of invertebrates (e.g., caridean shrimp, crabs, mollusks, insect larvae, amphipods) and a few fishes.

Stable carbon studies such as those done by Haines (1976) in Spartina (cordgrass) marshes have not been performed in mangrove ecosystems. Mangroves are C₃ plants and have δ^{13} values in the range of minus 25 to minus 26 (Macko 1981). According to the same author,

mangrove peat has a δ^{13} value of minus 22. Because these values are dramatically different from the values for sea grasses and many algae, the possibilities for using this tool in mangrove ecosystems is excellent. Macko (1981) also suggested the utility of using stable nitrogen ratios for future mangrove food web investigations; he reported δ^{15} values of plus 6.0 to plus 6.5 for mangrove tissue and plus 5 for mangrove peat.

In reviewing contemporary knowledge of energy flow in mangrove ecosystems, three conclusions emerge.

(1) We have a hypothetical framework of mangrove energy flow of a qualitative

nature. This framework appears to be reasonably accurate although subsequent developments, such as elucidation of the reduced sulfur hypothesis, may require some modification.

(2) Measurements of the relative importance of various carbon sources are generally lacking.

(3) Detailed measurements of energy flow including the relative inputs of different carbon sources are critically needed. Technological difficulties, high costs, and difficulties inherent in transferring findings from one estuary to the next present a major challenge to estuarine ecologists of the future.