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

by

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CHAPTER 2. AUTECOLOGY OF MANGROVES

2.1 ADAPTATIONS TO NATURAL STRESS - ANAEROBIC SEDIMENTS

Mangroves have a series of remarkable adaptations which enable them to flourish in an environment characterized by high temperatures, widely fluctuating salinities, and shifting, anaerobic substrates. In this section we review a few of the most important adaptations.

The root system of mangroves provides the key to existence upon unfriendly substrates (see Gill and Tomlinson 1971 for an anatomical review of mangrove roots). Unlike most higher plants, mangroves usually have highly developed aerial roots and modest below-ground root systems. The aerial roots allow atmospheric gases to reach the underground roots which are embedded in anaerobic soils. The red mangrove has a system of stilt or prop roots which extend a meter (3 ft) or more above the surface of the soil and contain many small pores (lenticels) which at low tide allow oxygen to diffuse into the plant and down to the underground roots by means of open passages called aerenchyma (Scholander et al. 1955). The lenticels are highly hydrophobic and prevent water penetration into the aerenchyma system during high tide (Waisel 1972).

The black mangrove does not have prop roots, but does have small air roots or pneumatophores which extend vertically upward from the underground roots to a height of 20 to 30 cm (8 to 12 inches) above the soil. These pneumatophores resemble hundreds of tiny fingers sticking up out of the mud underneath the tree canopy. At low tide, air travels through the pneumatophores into the aerenchyma system and then to all living root tissues. The white mangrove usually does not have either prop roots or pneumatophores, but utilizes lenticels in the lower trunk to obtain oxygen for the aerenchyma system. "Peg roots" and pneumatophores may be present in certain situations (Jenik 1967).

Mangroves achieve structural stability in at least two ways. Species such as the red mangrove use the system of prop

roots to provide a more or less firm foundation for the tree. Even though the prop roots are anchored with only a modest assemblage of underground roots, the horizontal extent of the prop root system insures considerable protection from all but the worst of hurricanes. Other mangrove species, including the black mangrove, obtain stability with an extensive system of shallow, underground "cable" roots that radiate out from the central trunk for a considerable distance in all directions; the pneumatophores extend upward from these cable roots. As in all Florida mangroves, the underground root system is shallow and a tap root is lacking (Walsh 1974). As Zieman (1972) found, individual roots, particularly of red mangroves, may extend a meter or more downward in suitable soils.

From the standpoint of effectiveness in transporting oxygen to the underground roots, both prop roots and cable roots seem equally effective. From the perspective of stability, the prop roots of red mangroves appear to offer a distinct advantage where wave and current energies are high.

Unfortunately, as pointed out by Odum and Johannes (1975), the same structure which allows mangroves to thrive in anaerobic soil is also one of the tree's most vulnerable components. Exposed portions of the aerial root system are susceptible to clogging by fine suspended material, attack by root borers, and prolonged flooding (discussed further in section 12.1). Such extended stress on the aerial roots can kill the entire tree.

2.2 ADAPTATIONS TO NATURAL STRESS - SALINITY

Mangroves accommodate fluctuations and extremes of water and soil salinity through a variety of mechanisms, although not all mechanisms are necessarily present in the same species. Scholander et al. (1962) reported experimental evidence for two major methods of internal ion regulation which they identified in two different groups of mangroves: (1) the salt

exclusion species and (2) the salt excretion species. In addition, some mangroves utilize succulence and the discarding of salt-laden organs or parts (Teas 1979).

The salt-excluding species, which include the red mangrove, separate freshwater from sea water at the root surface by means of a non-metabolic ultra-filtration system (Scholander 1968). This "reverse osmosis" process is powered by a high negative pressure in the xylem which results from transpiration at the leaf surface. Salt concentration in the sap of salt-excluding mangroves is about 1/70 the salt concentration in sea water, although this concentration is almost 10 times higher than found in normal plants (Scholander et al. 1962).

Salt-secreting species, including black and white mangroves (Scholander 1968), use salt glands on the leaf surface to excrete excess salt. This is probably an enzymatic process rather than a physical process since it is markedly temperature sensitive (Atkinson et al. 1967). The process appears to involve active transport with a requirement for biochemical energy input. As a group, the salt secreters tend to have sap salt concentrations approximately 10 times higher (1/7 the concentration of sea water) than that of the salt excluders.

In spite of these two general tendencies, it is probably safe to say that individual species utilize a variety of mechanisms to maintain suitable salt balance (Albert 1975). For example, the red mangrove is an effective, but not perfect, salt excluder. As a result this species must store and ultimately dispose of excess salt in leaves and fruit (Teas 1979). Most salt secreters, including white and black mangroves, are capable of limited salt exclusion at the root surface. The white mangrove, when exposed to hypersaline conditions, not only excludes some salt and secretes excess salt through its salt glands, but also develops thickened succulent leaves and discards salt during leaf fall of senescent leaves (Teas 1979).

There appears to be some variation in the salinity tolerance of Florida mangroves. The red mangrove is probably limited by soil salinities above 60 to 65 ppt. Teas (1979) recalculated Bowman's (1917) data and concluded that transpiration in red mangrove seedlings ceases above 65 ppt. Cintron et al. (1978) found more dead than living red mangrove trees where interstitial soil salinities exceeded 65 ppt.

On the other hand, white and black mangroves, which both possess salt excretion and limited salt exclusion mechanisms, can exist under more hypersaline conditions. Macnae (1968) reported that black mangroves can grow at soil salinities greater than 90 ppt. Teas (1979) reported dwarfed and gnarled black and white mangroves occurring in Florida at soil salinities of 80 ppt.

There may be an additional factor or factors involved in salinity tolerance of mangroves. McMillan (1975) found that seedlings of black and white mangroves survived short-term exposures to 80 ppt and 150 ppt sea water if they were grown in a soil with a moderate clay content. They failed to survive these salinities, however, if they were grown in sand. A soil with 7% to 10% clay appeared to be adequate for increased protection from hypersaline conditions.

Vegetation-free hypersaline lagoons or bare sand flats in the center of mangrove ecosystems have been described by many authors (e.g., Davis 1940; Fosberg 1961; Bacon 1970). These features have been variously called salitraws (Holdridge 1940), salinas, salterns, salt flats, and salt barrens. Evidently, a combination of low seasonal rainfall, occasional inundation by sea water, and high evaporation rates results in soil salinities above 100 ppt, water temperatures as high as 45°C (113°F) in any shallow, standing water, and subsequent mangrove death (Teas 1979). Once established, salinas tend to persist unless regular tidal flushing is enhanced by natural or artificial changes in tidal circulation.

Although salinas occur frequently in Florida, they are rarely extensive in area. For example, between Rookery Bay and Marco Island (south of Naples, Florida) there are a series of salinas in the black mangrove-dominated zone on the upland side of the mangrove swamps. These hypersaline lagoons occur where the normal flow of fresh water from upland sources has been diverted, presumably resulting in elevated soil salinities during the dry winter months.

In summary, salinity is a problem for mangroves only under extreme hypersaline conditions. These conditions occur naturally in Florida in irregularly flooded areas of the "high swamp" above the normal high tide mark and are accompanied by high soil salinities. Florida mangroves, listed in order of increasing salinity tolerance, appear to be red, white, and black.

2.3 REPRODUCTIVE STRATEGIES

As pointed out by Rabinowitz (1978a), virtually all mangroves share two common reproductive strategies: dispersal by means of water (van der Pijl 1972) and vivipary (Macnae 1968; Gill and Tomlinson 1969). Vivipary means that the embryo develops continuously while attached to the parent tree and during dispersal. Since there is uninterrupted development from zygote through the embryo to seedling without any intermediate resting stages, the word "seed" is inappropriate for viviparous species such as mangroves; the term "propagule" is generally used in its place.

While the phenology of black and white mangroves remains sketchy, Gill and Tomlinson (1971) thoroughly described the sequence of flowering in the red mangrove. Flowering in this species may take place at any time of the year, at least in extreme south Florida, but reaches a maximum in the late spring and summer. The flowers open approximately 1 to 2 months after the appearance of buds. The flower remains intact only 1 to 2 days; this

probably accounts for the low fertilization rate, estimated by Gill and Tomlinson at 0% to 7.2%. Propagule development is slow, ranging from 8 to 13 months. Savage (1972) mentions that on the Florida gulf coast, red mangrove propagules mature and fall from the tree from July to September. Within the Everglades National Park, black mangroves flower from May until July and bear fruit from August until November while white mangroves flower from May to August and bear fruit from July to October (Loope 1980).

The propagules of the three species of Florida mangroves are easy to differentiate. The following descriptions all come from Rabinowitz (1978a). White mangrove propagules are small and flattened, weigh less than a gram, are about 2 cm long, are pea-green when they fall from the parent tree, and turn mud-brown in two days or so. The pericarp (wall of the ripened propagule) serves as a float and is not shed until the seedling is established. During dispersal the radicle (embryonic root) emerges from the propagule. This germination during dispersal has led Savage (1972) to refer to the white mangrove as "semi-viviparous".

The propagules of the black mangrove when dropped from the tree are oblong-elliptical (resemble a flattened olive), weigh about 1 g and are about 2 cm long. The pericarp is lost within a few days after dropping from the tree; at this point the cotyledons (primary leaves) unfold and the propagule resembles two butterflies on top of one another.

Propagules of the red mangrove undergo extensive vivipary while on the tree. When propagules fall from the tree they resemble large green beans. They are rod-shaped with pointed ends, about 20 cm long, and weigh an average of 15 g.

Propagules of all three species float and remain viable for extended periods of time. Apparently, there is an obligate dispersal time for all Florida mangroves, i.e., a certain period of time must elapse during dispersal for germination to be

complete and after which seedling establishment can take place. Rabinowitz (1978a) estimates the obligate dispersal period at approximately 8 days for white mangroves, 14 days for black, and 40 days for red. She further estimates the additional time for root establishment at 5, 7, and 15 days for white, black, and red mangroves, respectively. Her estimate for viable longevity of the propagules is 35 days for white mangroves and 110 days for black. Davis (1940) reports viable propagules of red mangroves that had been kept floating for 12 months.

Rabinowitz (1978a) also concluded that black and white mangroves require a stranding period of 5 days or more above the influence of tides to take hold in the soil. As a result, these two species are usually restricted to the higher portions of the mangrove ecosystem where tidal effects are infrequent.

The elongated red mangrove propagule, however, has the potential to become established in shallow water with tidal influence. This happens in at least two ways: (1) stranding in a vertical position (they float vertically) or (2) stranding in a horizontal position, rooting and then vertical erection by the plant itself. Lawrence (1949) and Rabinowitz (1978a) felt that the latter was the more common method. M. Walterding (Calif. Acad. Sci., San Francisco; personal communication 1980) favors vertical establishment; based upon his observations, surface water turbulence works the propagule into the substrate during falling tides.

Mortality of established seedlings seems to be related to propagule size. Working in Panama, Rabinowitz (1978b) found that the mortality rate of mangrove seedlings was inversely correlated with initial propagule size. The white mangrove, which has the smallest propagule, has the highest rate of seedling mortality. The black mangrove has an intermediate mortality rate while the red mangrove, with the largest propagule, has the lowest seedling mortality rate. She

concluded that species with small propagules establish new cohorts annually but die rapidly, while species such as the red mangroves may have long-lived and often overlapping cohorts.

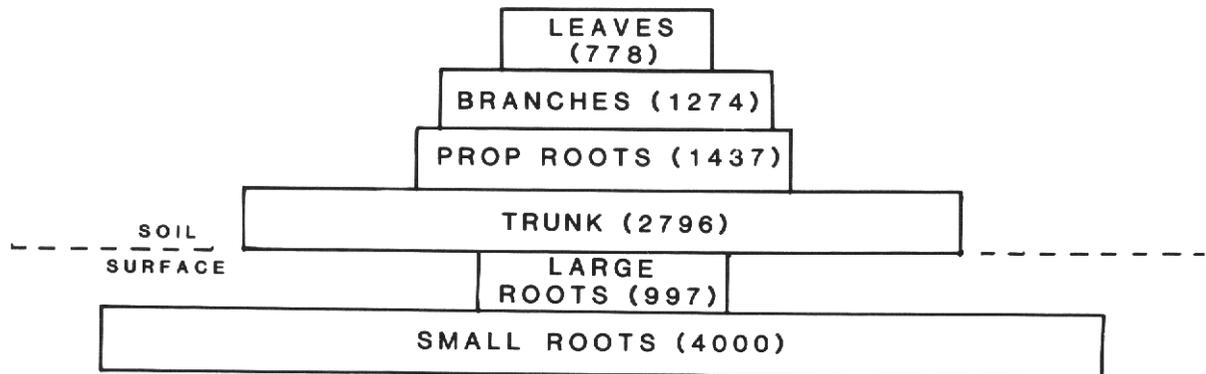
Propagule size and seedling mortality rates are particularly important in considerations of succession and replacement in established mangrove forests. Light is usually the most serious limiting factor underneath existing mangrove canopies. Rabinowitz (1978b) suggested that species with short-lived propagules must become established in an area which already has adequate light levels either due to tree fall or some other factor. In contrast, red mangrove seedlings can become established under an existing, dense canopy and then, due to their superior embryonic reserves, are able to wait for months for tree fall to open up the canopy and present an opportunity for growth.

2.4 BIOMASS PARTITIONING

Few investigators have partitioned the total biomass, aboveground and belowground, contained in a mangrove tree. An analysis of red mangroves in a Puerto Rican forest by Golley et al. (1962) gives some insight into what might be expected in south Florida. Aboveground and belowground biomass existed in a ratio of 1:1 if fine roots and peat are ignored (Figure 5). In this case, peat and very fine roots (smaller than 0.5 cm diameter) exceeded remaining biomass by 5:1. Lugo et al. (1976) reported the following values for a south Florida red mangrove overwash forest. All values were reported in dry grams per square meter, plus and minus one standard error, and ignoring belowground biomass. They found 710 ± 22 g/m² of leaves, 12.8 ± 15.3 g/m² of propagules, 7043 ± 7 g/m² of wood, 4695 ± 711 g/m² of prop roots and 1565 ± 234.5 g/m² of detritus on the forest floor.

Biomass partitioning between different species and locations must be highly variable. The age of the forest will influence the amount of wood biomass;

(A)



(B)

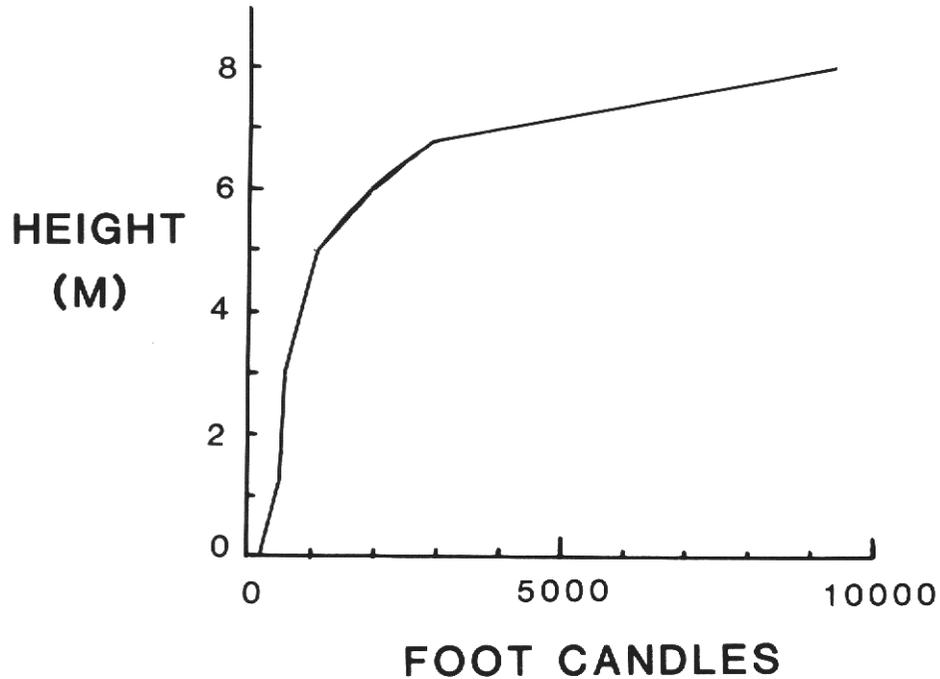


Figure 5. (a) Aboveground and belowground biomass of a Puerto Rican red mangrove forest. Values in parentheses are dry g/m²; large roots = 2 cm+ in diameter, small roots = 0.5 - 1.0 cm. (b) Vertical distribution of light intensity in the same forest; canopy height is 8 m (26 ft) (both figures adapted from Golley et al. 1962).

detritus varies enormously from one site to the next depending upon the amount of fluvial transport. The biomass characteristics of a scrub forest probably bear little resemblance to those of a fringing forest. At the present time, there is not enough of this type of data available to draw many conclusions. One intriguing point is that red mangrove leaf biomass averages between 700 and 800 g/m² at various sites with very different forest morphologies (Odum and Heald 1975a). This may be related to the tendency of mangrove canopies, once they have become established, to inhibit leaf production at lower levels through self-shading.

Golley et al. (1962) showed that the red mangrove canopy is an extremely efficient light interceptor. Ninety-five percent of the available light had been intercepted 4 m (13 ft) below the top of the canopy (Figure 5). As a result, 90% of the leaf biomass existed in the upper 4 m of the canopy. Chlorophyll followed the same pattern of distribution.

The leaf area index (LAI) of mangrove forests tends to be relatively low. Golley et al. (1962) found a LAI of 4.4 for a Puerto Rican red mangrove forest. Lugo et al. (1975) reported a LAI of 5.1 for a Florida black mangrove forest and 3.5 for a Florida fringe red mangrove forest. A different black mangrove forest, in Florida, was found to have values ranging from 1 to 4 and an average of 2 to 2.5 (Lugo and Zucca 1977). These values compare with LAI's of 10 to 20 recorded for most tropical forests (Golley et al. 1974). The low leaf area values of mangrove forests can be attributed to at least three factors: (1) effective light interception by the mangrove canopy, (2) the inability of the lower mangrove leaves to flourish at low light intensities, and (3) the absence of a low-light-adapted plant layer on the forest floor.

2.5 PRIMARY PRODUCTION

Prior to 1970 virtually no information existed concerning the productivity

of mangroves in Florida. Since that time knowledge has accumulated rapidly, but it is still unrealistic to expect more than preliminary statements about Florida mangrove productivity. This deficiency can be traced to (1) the difficulties associated with measurements of mangrove productivity and (2) the variety of factors that affect productivity and the resulting variations that exist from site to site.

Productivity estimates come from three methods: (1) harvest, (2) gas exchange, and (3) litter fall. Harvest methods require extensive manpower and knowledge of the age of the forest. They are best employed in combination with silviculture practices. Since silviculture of south Florida mangroves is practically non-existent, this method has rarely been used in Florida. Noakes (1955), Macnae (1968), and Walsh (1974) should be consulted for productivity estimates based on this technique in other parts of the world.

Gas exchange methods, based on measurements of CO₂ changes, have the advantage of precision and response to short-term changes in light, temperature, and flooding. They include both above-ground and belowground production. On the negative side, the necessary equipment is expensive and tricky to operate properly. Moreover, extrapolations from short-term measurements to long-term estimates offer considerable opportunity for error. Nevertheless, the best estimates of productivity come from this method.

The litter fall technique (annual litter fall x 3 = annual net primary production) was proposed by Teas (1979) and is based on earlier papers by Bray and Gorham (1964) and Golley (1972) for other types of forests. This is a quick and dirty method although the lack of precision remains to be demonstrated for mangroves. An even quicker and dirtier method proposed by Teas (1979) is to (1) estimate leaf standing crop (using various techniques including harvesting or light transmission relationships) and (2) multiply by three. This assumes an annual leaf

turnover of one, which is supported by the data of Heald (1969) and Pool et al. (1977).

Mangrove productivity is affected by many factors; some of these have been recognized and some remain totally obscure. Carter et al. (1973) propose lumping these factors into two broad categories: tidal and water chemistry. We believe that a number of additional categories should be considered.

A minimal, though incomplete, list of factors controlling mangrove productivity must include the following:

- species composition of the stand
- age of the stand
- presence or absence of competing species
- degree of herbivory
- presence or absence of disease and parasites
- depth of substrate
- substrate type
- nutrient content of substrate
- nutrient content of overlying water
- salinity of soil and overlying water
- transport efficiency of oxygen to root system
- amount of tidal flushing
- relative wave energy
- presence or absence of nesting birds
- periodicity of severe stress (hurricanes, fire, etc.)
- time since last severe stress
- characteristics of ground water

- inputs of toxic compounds or nutrients from human activities
- human influences such as diking, ditching, and altering patterns of runoff.

In spite of the difficulties with various methods and the interaction of controlling factors, it is possible to make general statements about certain aspects of mangrove productivity. For example, Waisel's (1972) statement that mangroves have low transpiration rates seems to be generally true in Florida. Lugo et al. (1975) reported transpiration rates of 2,500 g H₂O/m²/day for mangrove leaves in a fringing red mangrove forest and 1,482 g H₂O/m²/day for black mangrove leaves. This is approximately one-third to one-half the value found in temperate broad leaf forests on hot dry days, but comparable to tropical rainforests (H.T. Odum and Jordan 1970). The low transpiration rates of mangroves are probably related to the energetic costs of maintaining sap pressures of -35 to -60 atmospheres (Scholander et al. 1965).

Litter fall (leaves, twigs, bark, fruit, and flowers) of Florida mangrove forests appears to average 2 to 3 dry g/m²/day in most well-developed mangrove stands (see discussion in section 3.4). This can be an order of magnitude lower in scrub forests.

Wood production of mangroves appears to be high compared to other temperate and tropical trees, although no measurements from Florida are available. Noakes (1955) estimated that the wood production of an intensively managed Malayan forest was 39.7 metric tons/ha/year. Teas (1979) suggested a wood production estimate of 21 metric tons/ha/year for a mature unmanaged red mangrove forest in south Florida. His figure was calculated from a litter/total biomass relationship and is certainly subject to error.

Representative estimates of gross primary production (GPP) net primary

production (NPP), and respiration (R) of Florida mangroves are given in Table 1a. Compared to net primary production (NPP) estimates from other ecosystems, including agricultural systems (E.P. Odum 1971), it appears that mangroves are among the world's most productive ecosystems. Healthy mangrove ecosystems appear to be more productive than sea grass, marsh grass and most other coastal systems.

Further examination of Table 1a reveals several possible tendencies. The first hypothetical tendency, as discussed by Lugo et al. (1975), is for red mangroves to have the highest total net production, black to have intermediate values and white the lowest. This conclusion assumes that the plants occur within the zone for which they are best adapted (see section 3.2 for discussion of zonation) and are not existing in an area with strong limiting factors. A scrub red mangrove forest, for example, growing under stressed conditions (high soil salinity or low nutrient supply), has relatively low net productivity (Teas 1979). The pre-eminent position of red mangroves is shown by the comparative measurements of photosynthesis in Table 1b; measurements were made within canopy leaves of trees growing within their zones of optimal growth.

A second noteworthy tendency is that red mangrove GPP decreases with increasing salinity while GPP of black and white mangroves increases with increasing salinity up to a point. Estimates of Hicks and Burns (1975) demonstrate that this may be a real tendency (Table 1c).

Data presented by Miller (1972), Carter et al. (1973), Lugo and Snedaker (1974), and Hicks and Burns (1975) suggest a third hypothetical tendency, assuming occurrence of the species within its adapted zone. It appears that the black mangrove typically has a much higher respiration rate, lower net productivity, and lower GPP/R ratio than the red mangrove. This can be attributed at least partially, to the greater salinity stress under which the black mangrove usually grows; this leads to more osmotic work.

These three apparent tendencies have led Carter et al. (1973) and Lugo et al. (1976) to propose a fourth tendency, an inverted U-shaped relationship between waterway position and net mangrove community productivity (Figure 6). This tendency is best understood by visualizing a typical gradient on the southwest coast of Florida. At the landward end of the gradient, salinities are very low, nutrient runoff from terrestrial ecosystems may be high and tidal amplitude is minor. At the seaward end, salinities are relatively high, tidal amplitude is relatively great and nutrient concentrations tend to be lower. At either end of the gradient, the energetic costs are high and a large percentage of GPP is used for self-maintenance; at the landward end, competition from freshwater plant species is high and at the seaward end, salinity stress may be limiting. In this scenario, the highest NPP occurs in the middle region of the gradient; salinity and tidal amplitude are high enough to limit competition while tidal flushing and moderate nutrient levels enhance productivity. Hicks and Burns (1975) present data to support this hypothesis.

In addition to these hypotheses generated from field data, there have been two significant, published attempts to derive hypotheses from mathematical simulation models of mangroves. The first (Miller 1972) is a model of primary production and transpiration of red mangrove canopies and is based upon equations which utilize field measurements of the energy budgets of individual leaves. This model predicts a variety of interesting trends which need to be further field tested. One interesting hypothesis generated by the model is that maximum photosynthesis of red mangrove stands should occur with a leaf area index (LAI) of 2.5 if no acclimation to shade within the canopy occurs; higher LAI's may lead to decreased production. Another prediction is that red mangrove production is most affected by air temperature and humidity and, to a lesser degree, by the amount of solar

Table 1a. Estimates of mangrove production in Florida. All values are $gC/m^2/day$ except annual NPP = metric tons/ha/yr. GPP = gross primary production, NPP = net primary production, L.F. = annual litter fall X 3, R = red mangrove, W = white mangrove, B = black mangrove. Observations 6 and 7 were on sunny days, 8 and 9 on cloudy days.

Species	GPP	Respiration	NPP	Annual NPP	Method	Reference
Mixed R, W,B	24.0	11.4	12.6	46.0	Gas exchange	Hicks & Burns (1975)
B	18.0	12.4	5.6	20.5	Gas exchange	Lugo & Snedaker (1974)
Mature R	--- ^a	--- ^a	8.8	20.5	L.F.	Teas (1979)
Scrub R	--- ^a	--- ^a	1.0	3.8	L.F.	Teas (1979)
Basin B	--- ^a	--- ^a	2.4	8.6	L.F.	Teas (1979)
R (June)	12.8	7.3	5.5	20.3	Gas exchange	Miller (1972)
R (Jan.)	9.4	5.1	4.3	15.7	Gas exchange	Miller (1972)
R (June)	10.3	6.8	3.5	12.8	Gas exchange	Miller (1972)
R (Jan.)	10.2	5.0	5.2	18.8	Gas exchange	Miller (1972)
Mixed R,W, B(riverine)	13.9	9.1	4.8	17.5	Gas exchange	Carter et al. (1973)
Mixed R,W, B(basin)	11.8	4.3	7.5	27.4	Gas exchange	Carter et al. (1973)
B	9.0	6.2	2.8	9.4	Gas exchange	Lugo et al. (1976)
R	6.3	1.9	4.4	16.1	Gas exchange	Lugo et al. (1976)

^aMethod does not produce this data.

Table 1b. Comparative measurements of photosynthesis in $\text{gC/m}^2/\text{day}$ (Lugo et al. 1975).

Mangrove type	Daytime net photosynthesis	Nighttime respiration	P_n/R
Red	1.38	0.23	6.0
Black	1.24	0.53	2.3
White	0.58	0.17	3.4
Red (seedling)	0.31	1.89	negative

Table 1c. Gross primary production (GPP) at different salinities (Hicks and Burns 1975).

Mangrove type	Average surface salinity (ppt)	GPP ($\text{gC/m}^2/\text{day}$)
Red	7.8	8.0
Red	21.1	3.9
Red	26.6	1.6
Black	7.8	2.3
Black	21.1	5.7
Black	26.6	7.5
White	21.1	2.2
White	26.6	4.8

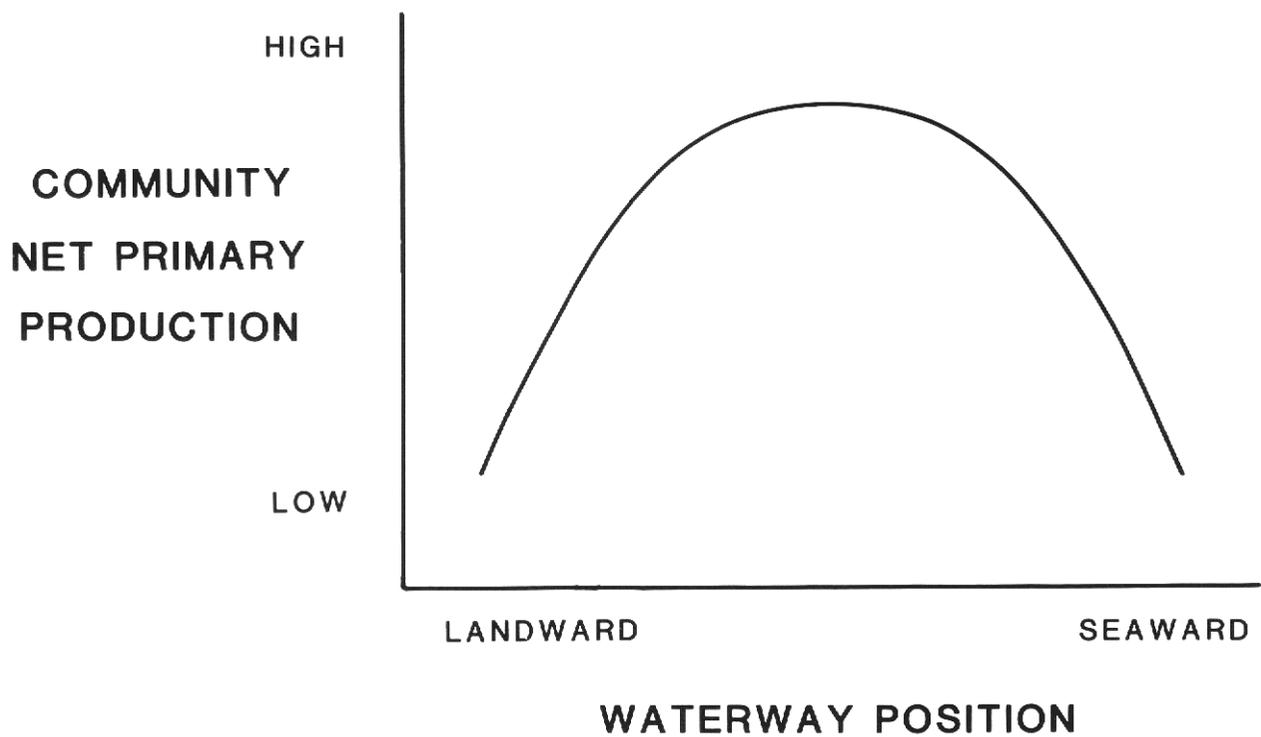


Figure 6. The hypothetical relationship between waterway position and community net primary production of Florida mangrove forests (based on Carter et al. 1973).

radiation within the ambient range. Gross photosynthesis per unit leaf area was greater at the top of the tree canopy than at the bottom, although the middle levels had the greatest production.

Miller (1972) concluded by suggesting that the canopy distribution of red mangrove leaves is nearly optimal for efficient water utilization rather than production. This indicates that the canopy is adapted to maximizing production under conditions of saturated water supply.

The mangrove ecosystem model reported by Lugo et al. (1976) provides hypotheses on succession, time to arrive at steady state conditions (see section 3.2), and several aspects of productivity. The model output suggests that the relative amount of tidal amplitude does not affect GPP significantly; instead, GPP appears to be extremely sensitive to inputs of terrestrial nutrients. It follows that locations with large amounts of nutrient input from terrestrial sources (riverine mangrove communities) have high rates of mangrove production (see section 3.3). All simulation model-generated hypotheses need to be field tested with a particularly critical eye, since the simplifying assumptions that are made in constructing the model can lead to overly simplistic answers.

Mangrove productivity research remains in an embryonic stage. Certain preliminary tendencies or hypotheses have been identified, but much work must be done before we can conclude that these hypotheses cannot be falsified.

2.6 HERBIVORY

Direct herbivory of mangrove leaves, leaf buds, and propagules is moderately low, but highly variable from one site to the next. Identified grazers of living plant parts (other than wood) include the white-tailed deer, Odocoileus virginianus, the mangrove tree crab, Aratus pisonii, and insects including beetles, larvae of

lepidopterans (moths and butterflies), and orthopterans (grasshoppers and crickets).

Heald (1969) estimated a mean grazing effect on North River red mangrove leaves of 5.1% of the total leaf area; values from leaf to leaf were highly variable ranging from 0 to 18%. Beever et al. (1979) presented a detailed study of grazing by the mangrove tree crab. This arboreal grapsid crab feeds on numerous items including beetles, crickets, caterpillars, littoral algae, and dead animal matter. In Florida, red mangrove leaves form an important component of the diet. Beever et al. (1979) measured tree crab grazing ranging from 0.4% of the total leaf area for a Florida Keys overwash forest to 7.1% for a fringing forest at Pine Island, Lee County, Florida. The researchers also found that tree crab grazing rates are related to crab density. Low densities (one crab/m³) resulted in low leaf area damage (less than 1% of total leaf area). High densities (four crabs/m³) were accompanied by leaf area damage ranging from 4% to 6% (see section 6.2).

Onuf et al. (1977) investigated insect herbivory in fringing and overwash red mangrove forests in the Indian River estuary near Ft. Pierce, Florida. They found six major herbivorous insect species, five lepidopteran larvae and a beetle. Comparisons were made at a high nutrient site (input from a bird rookery) and a low nutrient site. Both red mangrove production and leaf nitrogen were significantly higher at the high nutrient site. This resulted in a four-fold greater loss to herbivores (26% of total leaf area lost to grazing); this increased grazing rate more than offset the increased leaf production due to nutrient input.

Calculations of leaf area damage may underestimate the impact of herbivores on mangroves. For example, the larvae of the olethreutid moth, Ecdytolopha sp., develops within red mangrove leaf buds and causes the loss of entire leaves. All stages of the beetle, Poecilips

rhizophorae, attack mangrove propagules while still attached to the parent tree (Onuf et al. 1977).

2.7 WOOD BORERS

Many people have the mistaken idea that mangrove wood is highly resistant to marine borers. While this may be true to a limited extent for certain mangrove species in other parts of the world, none of the Florida mangroves have borer-resistant wood. Southwell and Boltman (1971) found that the wood of red, black, and white mangroves has no resistance to Teredo, Pholad and Simnoriid borers; pieces of red mangrove wood were completely destroyed after immersion in ocean water for 14 months.

An interesting controversy surrounds the ability of the wood boring isopod, Sphaeroma terebrans, to burrow into the living prop roots of the red mangrove. Rehm and Humm (1973) were the first to attribute apparently extensive damage of red mangroves stands within the Ten Thousand Islands area of southwestern Florida to an isopod, Sphaeroma. They found extensive damage throughout southwest Florida, some infestation north to Tarpon Springs, and a total lack of infestation in the Florida Keys from Key Largo south to Key West. The destruction process was described as follows: the adult isopod bored into the prop roots (5-mm diameter hole); this was followed by reproduction within the hole and development of juveniles within the root. This process, combined with secondary decomposition from fungi and bacteria, frequently results in prop root severance near the mean high tide mark. These authors attributed loss of numerous prop roots and, in some cases, loss of entire trees during storms to isopod damage.

The extent of damage in the Ten Thousand Islands region led Rehm and Humm (1973) to term the phenomenon an "ecocatastrophe" of possibly great importance. They further stated that shrinking of mangrove areas appeared to be occurring as

a result of Sphaeroma infestation; this point was not documented.

Enright (1974) produced a tongue-in-cheek rebuttal, on behalf of Sphaeroma and against the "terrestrial invader", red mangroves. Snedaker (1974) contributed a more substantial argument in which he pointed out that the isopod infestation might be an example of a long-term ecosystem control process.

Further arguments against the "ecocatastrophe" theory were advanced by Estevez and Simon (1975) and Estevez (1978). They provided more life history information for Sphaeroma and suggested a possible explanation for the apparently destructive isopod infestations. They found two species of isopods inhabiting red mangrove prop roots, S. terebrans and a sympatric congener, S. quadridentatum. The latter does not appear to be a wood borer but utilizes S. terebrans burrows. Neither species appeared to utilize mangrove wood as a food source. Estevez and Simon (1975) found extensive burrowing into seedlings in addition to prop root damage. In general, infestations appeared to be patchy and limited to the periphery of mangrove ecosystems. In areas with the highest density of burrows, 23% of all prop roots were infested. There appeared to be more colonization by S. terebrans in regions with full strength sea water (30 to 35 ppt).

The most important finding by Estevez and Simon (1975) and Estevez (1978) was that periods of accelerated activity by S. terebrans were related to periods of fluctuating and slightly increased salinity. This suggests that fluctuations in isopod burrowing may be related to the magnitude of freshwater runoff from the Everglades. These authors agree with Snedaker (1974) and suggest that root and tree loss due to Sphaeroma activity may be beneficial to mangrove ecosystems by accelerating production and root germination. Simberloff et al. (1978) amplified this last suggestion by showing that root branching, which is beneficial to individual trees, is stimulated by isopod activity.

This ecocatastrophe versus beneficial stimulus argument is not completely resolved. Probably, Sphaeroma root destruction, in areas of low isopod density, can be a beneficial process to both the individual tree and to the entire mangrove stand. Whether changes in freshwater runoff have accelerated this process to the point where unnatural and widespread damage is occurring is not clear. The data and research perspective to answer this question do not exist. As a result, we are reduced to providing hypotheses which cannot be tested with available knowledge.

2.8 MANGROVE DISEASES

Published research on mangrove diseases is rare. The short paper by Olexa and Freeman (1975) is the principal reference for diseases of Florida mangroves. They reported that black mangroves are affected by the pathogenic

fungi, Phyllosticta hibiscina and Nigrospora sphaerica. These authors found that P. hibiscina caused necrotic lesions and death of black mangrove leaves. They felt that under conditions of high relative humidity coupled with high temperatures, this fungus could pose a serious threat to individual trees, particularly if the tree had been weakened by some other natural agent, such as lightning or wind damage. Nigrospora sphaerica was considered to be of little danger to black mangroves. Another fungus, Cylindrocarpum didymum, appears to form galls on the prop roots and stems of red mangroves. Olexa and Freeman (1975) noted mortality of red mangroves in areas of high gall infestations, although a direct causation link was not proven.

Further research on mangrove diseases is badly needed. Viral disease must be investigated. The role of pathogens in litter production and as indicators of mangrove stress may be very important.