# MANGROVE ECOLOGY:
## A Manual for a Field Course

A Field Manual Focused on the
Biocomplexity on Mangrove Ecosystems

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# A. Mangrove Ecosystems: Definitions, Distribution, Zonation, Forest Structure, Trophic Structure, and Ecological Significance
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## Major Points of Chapter
1.  Mangroves are a taxonomically diverse group of tropical trees and shrubs, yet are all adapted to growth in the intertidal zone.
2.  The major controls on mangrove distribution are climate, salinity, tidal fluctuation, sedimentation, and wave energy.
3.  Mangrove species distributions across the intertidal zone often lead to distinct zonation patterns, which vary depending on floristic composition, geomorphology, and local factors.
4.  Mangrove forests also vary in structural attributes such as species richness, canopy height, basal area, tree density, and understory development.
5.  Although mangrove ecosystems are typically characterized as based on a detrital food web, a grazing food web also exists.
6.  Although once thought of as unproductive, transitional systems, mangrove swamps are now viewed as highly productive, ecologically important ecosystems.

## Definitions
The term "mangrove" refers to an assemblage of tropical trees and shrubs that grows in the intertidal zone. Mangroves include approximately 16 families and 40 to 50 species (depending on classification). According to Tomlinson (1986), the following criteria are required for a species to be designated a "true or strict mangrove":

1.  Complete fidelity to the mangrove environment.
2.  Plays a major role in the structure of the community and has the ability to form pure stands.
3.  Morphological specialization for adaptation to the habitat.
4.  Physiological specialization for adaptation to their habitat.
5.  Taxonomic isolation from terrestrial relatives.

Thus, mangrove is a non-taxonomic term used to describe a diverse group of plants that are all adapted to a wet, saline habitat. Mangrove may typically refer to an individual species. Terms such as mangrove community, mangrove ecosystem, mangrove forest, mangrove swamp, and mangal are used interchangeably to describe the entire mangrove community.

## Distribution
Mangrove distribution is circumglobal with the majority of populations occurring between the latitudes of 30° N and S (Tomlinson 1986). At one time, 75% of the world's tropical coastlines was dominated by mangroves. Unfortunately, mangrove extent has been significantly reduced due to human activities in the coastal zone. There are two centers of mangrove diversity: the Eastern group (Australia, Southeast Asia, India, East Africa, and the Western Pacific) where the total number of species is approximately 40 and the Western group (West Africa, Caribbean, Florida, Atlantic South America, and Pacific North and South America) where the number of species is only 8. Thus, New World forests are relatively depauperate compared to Old World forests.

In Belize, there are three true mangrove species: *Rhizophora mangle* (red), *Avicennia germinans*

(black), and *Laguncularia racemosa* (white). A fourth species, *Conocarpus erectus*, is an important mangrove associate in Belize that is transitional between the true mangroves and non-mangrove species.  At first glance, these species may appear very similar, but closer inspection reveals differences in morphology, physiology, and reproductive biology.  These species can be distinguished using characteristics such as growth form, bark, and structure of leaves, twigs, aerial roots, flowers, and fruits/ propagules.

**Reproductive Strategies**

Mangroves have little capacity for vegetative propagation and are thus dependent on seedlings for forest maintenance and spread  (Tomlinson 1986).  Although some species (*A. germinans* and *L. racemosa*) can resprout from stumps (coppicing), this process is not equivalent to propagation. Mangroves exhibit two relatively unique reproductive strategies: hydrochory and vivipary (Tomlinson 1986; Rabinowitz 1978).  Hydrochory (dispersal by water) is a major means which mangrove spreads seeds, fruit, and/or propagules.  Tidal action can carry mangrove diaspores great distances from their point of origin.  Vivipary refers to the condition in which the mangrove embryo germinates while still attached to the parent tree.  A number of mangrove species, including *R. mangle*, for example, may remain attached to the parent tree for 4 to 6 months and attain lengths of 25 to 35 cm at "maturity," they fall to the ground or into the water where they are dispersed by the tides.  The embryo of *A. germinans* breaks through the seed coat but remains enclosed in the fruit wall until detachment.  Upon falling into the water, the thin pericarp is quickly shed, leaving the seedling, which is composed of two folded cotyledons.  *Laguncularia racemosa* is not considered to be viviparous, but germination often occurs during dispersal. Vivipary increases the chances of successful establishment in an unpredictable environment where germination of seeds would typically be inhibited.

**Limits on Mangrove Distribution**

Extensive development of mangroves has occurred in the estuaries of large rivers flowing over shallow continental shelves, such as the Ganges in Bangladesh, Fly River in Papua New Guinea, and the Mekong Delta in Vietnam.  The Amazon and Congo, the two largest rivers in the world, do not have extensive stands of mangroves primarily because of the huge outflow of freshwater. The following factors are considered to be the major determinants of mangrove distribution:

1. Climate.  Mangroves are tropical species and are not tolerant of freezing temperatures.  Their latitudinal limits worldwide vary depending on air and water temperatures (Tomlinson 1986; Waisel 1972; Sherrod *et al*. 1986; Sherrod & McMillan 1985).  The abundance of mangroves is also affected by aridity, and development is much greater along coasts that have high inputs of rainfall (Macnae 1968; Golley *et al.* 1975).
2. Salinity.  Salt is generally not a requirement for growth, since most mangroves can grow in freshwater (Tomlinson 1986; Ball 1988).  However, they do not develop in strictly freshwater habitats because of competition from freshwater species.  Salinity is thus important in eliminating other vascular plant species that are not adapted for growth in a saline habitat.
3. Tidal fluctuation. Tidal influence is also not a requirement, but plays an important indirect role:
   a. Inundation with saltwater helps exclude most other vascular plants and reduces competition.
      b. Tides bring saltwater up estuaries against the outflow of freshwater and extend mangrove development inland.
      c. Tides transport sediment, nutrients, and clean water into the mangrove environment and

export organic carbon and reduced sulfur compounds.
    d.  Where evaporation is high, tides help flush soils and decrease salinity.
  The effect of this "tidal subsidy" can be seen on two landscape scales:
    1)  A regional or geographic scale—mangroves reach their greatest development around
        the world in low-lying regions with large tidal ranges (Tomlinson 1986; Macnae 1968;
        Golley *et al.* 1975).
    2)  A local scale—trees closest to the edges of land masses, which are subject to the largest
        fluctuations of the tide, are obviously larger and more productive than trees in the interior
        (Mendelssohn & McKee 2000).
  4.  Sediment and wave energy.  Mangroves grow best in a depositional environment with low wave
      energy according to Tomlinson (1986).  High waves prevent propagule establishment, expose the
      shallow root systems, and prevent accumulation of fine sediments.


**Zonation**

Spatial variation in species occurrence and abundance is frequently observed across
environmental gradients in many types of ecosystems (Davis 1940; Smith 1992; Mendelssohn &
McKee 2000).  Zonation of plant communities in intertidal habitats is particularly striking and often
results in monospecific bands of vegetation occurring parallel to the shoreline.  Although zonation
patterns are usually depicted in a manner that suggests a rigid sequence proceeding from the
shoreline to upland regions, many patterns resemble a mosaic with vegetational patterns occurring
repeatedly where the land mass is interrupted by watercourses or other variations in topography.

Mangroves exhibit zonation patterns in a number of different geographic regions (Davis
1940; Smith 1992; Mendelssohn & McKee 2000).  The large variation in floristic composition of
mangrove communities means that patterns of species distribution across the intertidal zone will
vary substantially among geographic regions.  For example, patterns for Florida and the Caribbean
often show *R. mangle* (red mangrove) occupying the seaward zone, followed by *A. germinans* (black
mangrove), and *L. racemosa* (white mangrove) in the most landward position.  That pattern may be
contrasted with a profile for northeastern Australia (Queensland), which is not only more complex
due to a higher number of species, but the relative position of congeneric species is reversed from
that in Florida (*e.g.*, *Avicennia* spp. in the seaward position and *Rhizophora* spp. in the landward
position).

Zonation patterns in mangrove forests may also vary on a local scale.  Occurrence of species
may differ across an estuary, apparently in response to differences in freshwater input.  For example,
species found at the seaward end of the estuary may be absent from the headwaters.  Although
zonation typically refers to patterns created by segregation of different species, differences in stature
and productivity of plants across environmental gradients may also result in readily discernible
patterns.  Zones may be comprised of different architectural forms that represent variations in height
and vigor.

Several hypotheses have been proposed to explain species zonation patterns in mangroves: 1)
zonation reflects land building and plant succession (Davis 1940); 2) geomorphological processes
cause vegetation zonation (Thom 1967); 3) differential dispersal of propagules across a gradient results
from a physical "sorting out" of species by tidal action (Rabinowitz 1978); 4) differential predation of
propagules across the intertidal zone eliminates some species from certain zones (Smith 1987; *Smith et
al.*1989, but see McKee 1995); 5) physiological specialization limits distribution of species to certain
portions of the gradient where physicochemical conditions differ (Ball 1988; McKee 1993, 1995); and

6) interspecific competition (Ball 1980).

Succession due to land building is not considered to be a viable explanation for zonation by many mangrove ecologists, since evidence shows that mangroves respond to, rather than cause, coastal propagation (Thom 1967). However, it's clear that some mangrove systems in sediment-poor environments have built vertically through deposition of organic matter (mangrove peat) (Woodroffe 1983; McKee & Faulkner 2000). Mangroves are probably best viewed as steady-state cyclical systems migrating toward or away from the sea depending on sea-level rise or fall, sedimentation rates, topography and tidal energy (Lugo 1980). Coastal geomorphology is important in determining physical and chemical conditions for mangrove development and may explain regional differences in zonation patterns. Geomorphology as an explanation of intertidal zonation patterns is unsatisfactory, however, because it provides no insight as to how the interaction of geomorphological processes with vegetation causes a segregation of species. The remaining four hypotheses—dispersal dynamics, seed predation, physiological tolerance, and interspecific competition—offer clear explanations for mangrove zonation. The relative importance of these processes is currently uncertain, but probably varies among geographic regions.

In addition to horizontal spatial patterns, mangroves exhibit vertical stratification. There are three major strata that are readily observed along tidal creeks: supratidal, intertidal, and subtidal. A unique assemblage of organisms associated with the mangrove vegetative structures characterizes each of these strata. The supratidal stratum includes the arboreal portions of the forest and is occupied by birds, reptiles, crabs, snails, insects, and spiders. The intertidal stratum extends from the high to low water tidal heights and encompasses the aerial root systems of the mangroves and peat banks. The organisms inhabiting this zone (*e.g.*, barnacles, isopods, crabs, oysters, amphipods, snails, and algae) experience periodic submergence by the tides. The subtidal stratum occurs below the low water mark where the mangrove roots and peat banks provide substrate for organisms adapted to constant submergence (*e.g.*, algae, sponges, tunicates, anemones, octocorals, shrimp, polychaetes, brittlestars, nudibranchs, jellyfish, and seagrasses).

## Forest Structure

In addition to zonation, mangrove forests are also characterized by attributes such as species richness, canopy height, basal area, tree density, age/size class distribution, and understory development. Lugo & Snedaker (1974) described six mangrove forest types based on size, productivity, and composition in Florida: riverine, overwash, fringe, basin, scrub, and hammock. These forest types reflect differences in geomorphology and hydrology and are generally applicable to forests in the Caribbean Region. Species richness appears to be influenced by temperature, tidal amplitude, rainfall, catchment area, freshwater seepage, and frequency of cyclones (Tomlinson 1986; Lugo & Snedaker 1974).

Another structural characteristic of mangrove forests is the frequent absence of understory species, which are usually found in other forest systems (Janzen 1985). Shrubs, grasses, lianas, and other herbaceous plant species do not usually occur under the closed canopy in the mangrove forests. The lack of understory is probably related to the combination of salinity and flooding stresses and low light levels, which exceeds the tolerance limits of plants (Lugo 1986). An understory may develop, for example, where the canopy is open (allowing light penetration to the forest floor) or where rainfall or freshwater runoff lowers salinity levels. There may also be a second layer composed of mangrove seedlings and juveniles, but densities are greatest in light gaps.

Although mangrove forests are usually described as having an even-aged size class structure,

the data supporting this viewpoint are not extensive.  It is thought that large-scale disturbances such as hurricanes kill large areas of forest, which then regenerate at about the same time from seedlings or previously established juveniles.  This view of even-aged structure in mangrove forests does not agree with what is known about the dynamic processes in other forest ecosystems.  Forest systems are now viewed as mosaics of patches that vary in size and contain individuals of different ages or stages of development.  These patches have resulted from natural disturbance events that create openings or gaps in the forest.  Preliminary work indicates that gap dynamics may be an important process structuring mangrove forests.  Natural disturbances such as lightening strikes, wind damage, and frost are often associated with the development of patches or gaps in mangrove forests.  Recent work in Belize, however, demonstrates that wood-boring insects are primarily responsible for the creation of gaps in red-mangrove forests (Feller & McKee 2001).

Forest structural characteristics such as canopy height, tree density, and biomass accumulation may be influenced primarily by climatic factors such as rainfall and by nutrient input (Golley *et al*. 1975; Smith 1992).  Areas characterized by high rainfall typically have tall canopies, high basal areas, and low tree densities.  Similarly, larger, more productive trees typify mangrove forests receiving high inputs of nutrients—for example, those areas used as bird rookeries.

## Trophic Structure

Trophic structure refers to the complex interrelationships among the various organisms in an ecosystem through the transfer of food energy from one trophic level to another.  The first trophic level (the producer level) is comprised of green plants; the second trophic level (primary consumer level) is comprised of herbivores (plant-eaters); the third trophic level (secondary consumer level) is comprised of carnivores, etc.  These trophic levels are linked through food chains; food chains form interlocking patterns called food webs.  There are two basic types of food chains: the grazing food chain (green plants to grazing herbivores to carnivores) and the detrital food chain (dead organic matter to detritus-feeding organisms to predators of detritivores).

The traditional view is that mangrove ecosystems are based on the detrital type of food web (Odum & McIvor 1990).  Work by Heald (1969) and Middleton & McKee (2001) demonstrated that the leaves of the mangroves fall into the water where they are then consumed by various detritivores, which are in turn eaten by fish and other organisms that feed on the detritus consumers.  The grazing pathway is considered to be unimportant in mangroves, since it has been estimated that only 5% of the leaf material is removed by grazing insects before leaf abscission.  This value may be an underestimate, however, since work by Onuf *et al*. (1977) shows substantial variation in leaf herbivory among mangrove species and locations.  In addition, the contribution of wood-feeding insects to the grazing pathway has not been quantified.  Wood-boring beetles may consume living wood and in the process kill branches or whole trees (Feller & McKee 1999; Feller 2002).  These activities produce standing dead wood that is then utilized by secondary wood feeders such as termites, which in turn support secondary consumers such as arthropods, lizards, snakes, and birds (Feller & Mathis 1997).

## Ecological Significance

Although early workers regarded mangrove forests as unimportant, transitional communities with a low productivity, most ecologists today view them as highly productive, ecologically important systems.  Four major roles of mangrove swamps are recognized:

1.    Mangroves contribute to soil formation and help stabilize coastlines.

2. Mangroves act as filters for upland runoff.
3. Mangrove systems serve as habitat for many marine organisms such as fish, crabs, oysters, and other invertebrates and wildlife such as birds and reptiles.
4. Mangroves produce large amounts of detritus that may contribute to productivity in offshore waters.

In addition to these ecologically important roles, mangrove forests possess attributes that are specifically important to humans:

1. Mangrove forests serve as protection for coastal communities against storms such as hurricanes. It has been suggested that the large loss of life (300,000 to 500,000 lives) in Bangladesh during the 1970 typhoon was partly due to the fact that many of the mangrove swamps protecting those populated coastal regions had been removed and replaced by rice paddies.
2. Mangrove forests serve as nurseries and refuge for many marine organisms that are of commercial or sport value. Areas where widespread destruction of mangrove has occurred usually experience a decline in fisheries.
3. Many threatened or endangered species reside in mangrove forests.
4. Mangrove forests are also important in terms of aesthetics and tourism. Many people visit these areas for sports fishing, boating, bird watching, snorkeling, and other recreational pursuits.

## B.  Mangrove Forest Structure
By Thomas J. Smith III

**Major Points of Chapter**
1. A noted feature of mangrove forest structure is the zonation of tree species into monospecific bands parallel to the shoreline.
2. Several hypotheses have been put forth to explain zonation, including a) plant succession due to land building b) geomorphological factors, c) physiological adaptation to gradients, d) differential dispersal of propagules, e) differential predation on propagules, and f) interspecific competition.
3. The structure of mangrove stands is relatively simple, consisting of only the main canopy and, in some forests, a layer of seedlings beneath it. Understories usually only develop in areas with abundant year-round rainfall and freshwater runoff.
4. In Florida, agents of local natural disturbance in mangrove forests include wind storms, lightning strikes, and frost damage. Hurricanes are sources of large-scale disturbance.
5. Conditions in light gaps differ from those under the canopy in both physical parameters (*e.g.,* temperature and salinity) and biotic characteristics (*e.g.,* crab fauna and frequency of propagule predation). Seedling survival and growth has been demonstrated to be greater in gaps.

Description of a forest's structure may include measures of species composition, diversity, stem height, stem diameter, basal area, tree density, and the age-class distributions and spatial distribution patterns of the component species in the forest. A noted feature of mangrove forest structure is the often-conspicuous zonation of tree species into monospecific bands parallel to the shoreline. Zonation has been a dominant theme in the voluminous literature on mangroves as well as in that on other vegetation types. Zonation, however, is not the only manifestation of structure in mangroves. Lugo & Snedaker (1974) described six types of mangrove forests in Florida, a region with only three mangrove species. Their classification of forests into riverine, overwash, fringe, basin, scrub, and hammock was based on differences in size, productivity, and composition of Florida mangroves, which were caused by differing geomorphic and hydrologic factors.

## Mangrove Zonation Patterns
Zonation patterns have been described for Malaysia, East Africa, Australia, Papua New Guinea, Indonesia, India, Burma, Florida, West Africa, and Panama to name but a few. In Belize, the red mangrove *(Rhizophora mangle)* often grows in the low intertidal, while the white *(Laguncularia racemosa)* and black *(Avicennia germinans)* mangroves are more common in the high intertidal zones. Sometimes a species may have a "double distribution." This is a situation in which a species may be abundant in two different zones of the forest.

For example, in the Indo-Pacific region, *Avicennia marina* is often the dominant species in both the lowest and highest intertidal zones and is rare or absent in the middle intertidal. Observations such as this make interpreting zonation patterns difficult.

Several hypotheses have been advanced to explain zonation, including the following:
1) plant succession due to land building
2) response to geomorphological factors
3) physiological adaptation to gradients across the intertidal zone

4) differential dispersal of propagules
*5)* differential predation on propagules across the intertidal
6) interspecific competition.

At the present time, there is a lively debate among scientists as to just what factor or factors cause zonation in mangrove forests.

1.  **Land building and plant succession**. The view that zonation in mangroves represents a successional sequence from pioneer colonizers to mature climax forest is by far the most popular and most often cited mechanism. The idea is that species that grow in the lowest intertidal zone successfully trap sediments. Over time, the sediment builds up and new mangroves are able to invade and outcompete the colonizers. The process continues until the land is no longer intertidal. The key to this explanation is the ability of the colonizer to trap and hold sediment and thus build land.

    Criticism of the "zonation represents succession" hypothesis appeared early in the literature. Watson (1928) claimed that mangroves responded to depositional processes rather than causing them. In Watson's view, frequency of tidal inundation, salinity, and soil type were the important determinants of mangrove zonation. Egler (1950) presented evidence that each mangrove zone behaved differently in terms of its development and control. He emphasized the roles of disturbance from fire and hurricanes as factors influencing the distribution of *R. mangle, L. racemosa,* and *A. germinans* in Florida.

    The idea of succession in mangroves still appears in the literature. Putz and Chan (1986) analyzed over 60 years of forest composition and growth data from permanent plots in the Matang mangroves of Malaysia. They reported increased species diversity of the forest over time, as shade-tolerant species invaded the understory. *Bruguiera gymnorrhiza*, one of the most shade-tolerant mangrove species, increased most in abundance. It is obvious that within a mangrove forest classical ecological succession can and does occur, as it does in every other of the world's forest types. This succession, however, is not the result of mangroves building land.

2.  **Geomorphological influences**. It is now widely recognized that mangroves respond to geomorphological changes rather than cause the changes themselves. Detailed studies by Thom, Woodroffe, and coworkers have established that mangrove vegetation is directly dependent on the dynamics of sediment topography. Mangroves do not override abiotic land-building processes. Detailed analyses of long-term stratigraphic records from peat deposits also show the dependence of mangrove forest development on geomorphic factors, in particular on relatively stable sea level. During periods of rapid sea-level rise, the size and extent of mangrove forests decrease. Results of these studies, however, leave unanswered questions regarding explanations of zonation based in terms of different biological adaptations of individual species to contrasting physiographic factors within the intertidal environment.

3.  **Physio-chemical gradients and zonation**. A dominant theme in vegetation ecology is the idea that a species adapts physiologically to physico-chemical gradients in the environment. Two forms of the "gradient" hypothesis exist: the distinct-preference hypothesis and the same-preference hypothesis. The distinct-preference hypothesis states that each species has its optimum along the gradient which controls where that species occurs. Because different species have different optima, zonation results. An alternate view is that all species share

the same optimum and that other factors (*e.g.,* competition, seed dispersal, predation) cause zonation. The idea of physiological adaptation has been used to explain the zonation patterns observed in a variety of plant communities, including mangroves.

Many environmental parameters vary across the intertidal zone. The most obvious of these, and most often cited, is the frequency of tidal inundation. Low intertidal areas are inundated much more frequently than high intertidal regions. Tidal action introduces two other gradients: soil pore-water salinity and soil waterlogging. These two gradients may not vary in the same way as frequency of inundation. The pattern of soil pore-water salinity across the intertidal is influenced by the salinity of the flooding tidal water, rainfall, and freshwater runoff and seepage. Porewater salinity in the lowest intertidal area tends to approximate the salinity of the flooding water: 35‰ near the ocean and <1‰ at the up stream end of riverine mangrove systems. The pattern of salinity variation in the high intertidal zone is complex. In arid regions, pore- and surface-water salinities in the high intertidal may exceed 90‰. In regions with abundant rainfall and freshwater runoff and seepage, high intertidal salinities are often lower than that of the flooding water. Other factors that vary across the intertidal zone include nutrients such as nitrogen and phosphorus, oxidation-reduction potential, and soil texture. These gradients are often correlated. For example, fine-grained, clay sediments are usually the most highly reduced, whereas coarser sands are more oxidized.

Salinity is one of the most investigated gradients in mangrove distribution ecology. Mangroves, however, are not obligate halophytes. They are fully capable of growing in freshwater. Propagules are capable of survival, but with less than optimal growth, over a broad salinity range (0-100‰ depending on species). Maximum seedling growth for a variety of species occurs between 8-15‰ based on laboratory culture studies.

Seedling establishment by *A. germinans* in Texas was not related to salinity. Survival of experimental seedlings was 100% for salinities 0-57‰, 80% at 65 ‰ and 10% at 75‰. Detailed comparisons between the observed seedling distributions of *Ceriops tagal* and *C. australis* (two Australian mangroves) in the field and their survival and growth performance along a laboratory salinity gradient have been made. The salinity at which seedlings of both species reached their maximum abundance in the field did not correspond to the laboratory salinity at which maximal growth or survival was measured. Both species grew best at l5‰ in the laboratory. In the field, seedlings of *C. tagal* were most abundant between 20-35‰, whereas *C. australis* reached greatest abundance between 50-60‰. Together, these studies indicate that although many mangrove species probably share an optimal salinity range for growth (10-20‰), they are physiologically capable of tolerating an extreme range of soil salinity.

The studies conducted to date clearly demonstrate that many mangroves can grow over the broad range of conditions found across the intertidal zone. Data relating species distributions to soil salinities suggest that two groups of mangroves exist. The first has very broad tolerances and can grow and survive in salinities two to three times that of seawater. The second group appears to be restricted to salinities less than 40‰. This latter group is composed of species that have predominantly upstream distributions in river-dominated estuaries (*e.g.*, *R. mucronata)* or those restricted to geographic areas of abundant rainfall (*e.g.*, *Pelliciera rhizophoreae*). In this regard, it seems that some adaptation to salinity gradients may have occurred which influences distributions within

and between estuaries. Not enough data for other physical gradients (*e.g.*, soils, nutrients, redox potential) have been collected to examine adequately the physiological adaptation hypothesis.

4. **Propagule dispersal and zonation**. It was hypothesized that zonation in Panamanian mangrove forests was controlled by the influence of tidal action on mangrove propagules. (Because most mangroves are viviparous the unit of dispersal is a propagule, not a true seed.) The mangroves were distributed from low to high intertidal in a manner inversely related to the size of their propagules. *Avicennia germinans* and *L. racemosa* were restricted to high intertidal zones because they had small propagules that high tides would carry the farthest inland. Large propagules, such as those of *R. mangle* and *P. rhizophorae,* would become snagged and not get carried into higher intertidal areas. Thus, tidal action "sorted" the propagules across the intertidal inversely according to their size, which resulted in species zonation.

   Observations of species distributions in Australia and elsewhere, however, indicate that tidal sorting was not a mechanism that influences mangrove zonation patterns. *Sonneratia* spp. routinely colonizes the lowest intertidal zone. The seeds of *Sonneratia* spp. are only some 10-15 mm in length, which is small in comparison to most other mangroves. *Aegiceras* spp. and *Avicennia* spp. also have small propagules and are typically abundant in low intertidal areas. They are also common in the highest intertidal areas. It is obvious that tidal action delivers propagules of all species to all portions of the intertidal zone. The question is not so much whether or not dispersal takes place, as much as it is what factors regulate post-dispersal establishment, survival, and growth.

5. **Propagule predation and forest structure**. Predation on seeds has been recognized as an important process in a variety of ecosystems. Watson (1928) commented on the role of crabs as consumers of mangrove propagules, particularly in the managed forests of west Malaysia. He stated, "The most serious enemies to mangroves are crabs." The crabs to which he referred belong to the family Grapsidae. This group is a ubiquitous feature of mangrove forests, especially in the Indo-Pacific region. Crabs are the dominant macrofauna of mangrove forest soils in terms of both numbers and biomass.

   Consumption of mangrove propagules by grapsid crabs greatly affects natural regeneration and influences the distribution of certain species across the intertidal zone. A series of experiments were performed in which mangrove propagules were tethered in the forest and then the amount of consumption was determined over time (Smith & Duke 1987; Smith 1987a, 1987b). The initial experiments were conducted in northeastern Queensland, Australia. For *A. marina, R. stylosa, B. gymnorrhiza,* and *B. exaristata* there appeared to be an inverse relationship between the dominance of the species in the canopy and the amount of predation on its propagules. This relationship was not found for *C. australis,* however. Caging experiments were used to study the establishment and growth of *A. marina* in middle intertidal forests. *Avicennia marina* is usually absent from this region of the intertidal zone. The results indicated that when protected from crabs, *A. marina* propagules survived and grew. The conclusion was that virtually crabs consumed 100% of the A. marina propagules that were dispersed into middle intertidal forests; hence, propagule predation was an important determinant of the forest's species composition and structure (Smith 1992).

   Subsequent studies indicated that propagule predation was important over a

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much larger geographic region than northeast Queensland (Smith *et al.* 1989). Data from Malaysia and Florida revealed high levels of predation on the propagules of A. *officinalis* and *A. alba* in Malaysia and on *A. germinans* in Florida. For all three species, predation was higher where the species was absent from the canopy, and it was lower in forests where conspecific adults were present. For *Rhizophora* spp. and *Bruguiera* spp., however, equivocal results were obtained. In Malaysia, results for *B. cylindrica* supported the predation hypothesis, whereas results from *B. gymnorrhiza* did not. No predation on *R. mangle* in Florida was observed, but in Panama more *R. mangle* propagules were consumed in a forest where the species was present in the canopy than were consumed in a forest where it was absent. Studies at Twin Cays in Belize have shown that both *R. mangle* and *A. germinans* propagules are consumed but not in the manner predicted (McKee 1995). The predation hypothesis thus explains only a portion of the observed patterns of mangrove forest zonation.

6. **Competition and forest structure**. Competition has been studied in a variety of wetland plant communities, but few studies have examined the role of competitive interactions in mangrove forests. Competitive interactions between *C. tagal* and *C. australis* have been studied over a salinity gradient in the laboratory. Seedlings were grown in mono- and polycultures at salinities from 0-60‰. *Ceriops tagal* grew better than *C. australis* did at lower salinities, whereas the reverse was true at higher salinities. Competition was gauged by comparing the reduction in growth of each species in the presence of the other to the growth of that species alone. Growth of *C. tagal* was reduced less at salinities from 0 and 15‰ than was *C. australis* at all densities. The effect of *C. tagal* on *C. australis* was some two to four times greater than *C. australis* effect on *C. tagal.* For salinities >45‰, however, this result was strongly reversed, suggesting that *C. australis* was the superior competitor at higher salinities. In the field, however, it was observed that both species were shifted to salinities higher than their growth optima salinities in the laboratory. Additional experimental analyses and long-term studies of permanent forest plots would be very helpful at unraveling the role of competition in mangrove forests.

## Stand Structure in Mangroves

Stand structure in mangrove forests is relatively simple when compared to that of other forest types, such as tropical rainforests. The number of strata is often reduced to one: the main canopy. In some forests, a carpet of seedlings may form a second layer, but the abundant lianas and subcanopy trees and shrubs common to most tropical forests are largely absent in mangrove forests. Several hypotheses have suggested that the combination of salinity stress and the need for light are enough to prohibit the development of understory vegetation and, therefore, pose an evolutionary hurdle that has not been crossed. There are mangrove forests with understories, however. These tend to be in areas with abundant year-round rainfall and freshwater runoff. In this situation, a number of smaller tree and shrub species can be found in the forest as mangrove associates, but these species are much more common in freshwater swamp or rainforest environments.

The age- (or size-) class structure of mangrove forests is also characteristic of pioneer, or early successional, formations. Many mangrove forests have an even-aged size-class structure. The question of how this arises in mangroves has not been studied. The possibility exists that a large-scale disturbance will destroy large tracts of forest, which then regenerate at approximately the same time. It has been hypothesized that mangroves in Florida have adapted to a 25-year disturbance

cycle, the approximate return time for major hurricanes.

Stand height, density, and biomass accumulation appear to be related to climatic factors, particularly rainfall. A "complexity index," which combines measures of species richness, stem density, canopy height, and basal area, has been used to make geographic scale comparisons across the Caribbean region. The least complex stands were in arid regions. High stem density, but low species richness, height, and basal areas marked these stands. Complex stands, characterized by tall canopies, high basal areas, and lower stem densities, were common in wet, high rainfall areas. Complementary results that are based on different methods are available from the Indo-Pacific region. Rainfall and freshwater runoff appear to be major determinants of stand structure.

## Natural Disturbance in Mangroves

A variety of natural disturbance regimes affect mangrove forests. These may be relatively local-scale events such as breakage of branches during windstorms, lightning strikes, frost damage (in more northern areas), and whole-scale destruction of the forest by hurricanes. Gradients in the types and frequency of disturbance are also present across the geographic range of mangrove forests. For example, the mangroves of Panama are not subjected to frost or hurricanes, but are vulnerable to lightning strikes. In south Florida, disturbances from frost, hurricanes, and lightning are common (Odum *et al.* 1982). The influence of disturbance on the structure and function of mangrove forests is poorly investigated and most reports are anecdotal.

A positive relationship between large-scale disturbance (cyclones) and species richness in the mangrove forests of northeastern Queensland, Australia, has been reported. Forests that were impacted, on average, by one cyclone every *5* years had more species than forests affected by fewer storms. Species in the Rhizophoraceae often dominate these forests. In the Sunderbans mangroves of Bangladesh, the Rhizophoraceae is a minor component of the forest community. The Sunderbans are struck by to 40 cyclones a year. The Rhizophoraceae's inability to coppice, in comparison to other groups may account for their vulnerability to cyclones.

## Gap Dynamics in Mangroves

Canopy gaps are common in mangrove forests. In addition to what most forest ecologists would recognize as a canopy gap, the low intertidal, accreting mudbanks also act as "light gaps." Individuals in these areas are exposed to more light than are individuals under the nearby canopy. In south Florida, many gaps are created by lightning strikes. Lightning strikes create relatively circular patches in the forest from the top of the canopy to the forest floor. An interesting aspect of lightning strikes is that a number of trees are usually killed rather than a single individual, and those dead trees often remain standing for several years. Seedlings that are present under the canopy are often killed as well. Gaps ranged in size from <10 $m^2$ to >500 $m^2$ with the modal size 40-60 $m^2$. Gaps were evenly distributed across the forest from low to high intertidal zones and from upstream to downstream along the length of the estuaries. Saplings of several species, including *A. marina, B. parviflora, B. exaristata,* and *R. apiculata,* were found to be significantly more abundant in these gaps than under the surrounding canopy.

The physical environment in light gaps is substantially different from that under the surrounding canopy. Measurements made in light gaps in high and low intertidal areas in Australia indicated differences in photosynthetically active radiation (PAR), porewater salinity, and soil temperature. The canopy was so dense that it dampened the annual cycle in PAR, which was pronounced in nearby gaps. There were consistent differences in soil temperature. Sediments in gaps

were 3-5°C warmer than were soils under the canopy. Pore-water salinity was also lower in gaps, by 1-2‰ than under nearby canopies.

Seedling survival and growth for several mangrove species have been examined in gap and understory habitats in both high and low intertidal zones. In Australia, survival of A. *marina, R. stylosa, B. gymnorrhiza* and *C. australis* was higher in gaps than under the canopy and greater in high intertidal gaps than in low intertidal gaps. Relative growth rates for all species except *B. gymnorrhiza* were also greater in light gaps.

In Australia, canopy gaps may provide some mangroves with a refuge from seed predators. Predation on propagules of *A. marina* was higher in small gaps and decreased with increasing gap size. Fiddler crabs (primarily *Uca* spp.) dominated the crab fauna in gaps, whereas grapsids dominated under the canopy. Fiddler crabs are not known to consume mangrove propagules, but grapsids do. The increase in soil temperatures that accompanies gap formation may underlie this shift in the crab fauna, as *Uca* spp. appear to prefer warmer sediments.

**Conclusion**

Despite several thousand publications concerning mangrove forests, a clear understanding of the dynamics in mangrove ecosystems is just beginning to emerge. Of the several hypotheses advanced to account for species zonation, several warrant further attention, but others should be laid to rest. In particular, hypotheses concerning zonation as plant succession and the tidal sorting of propagules clearly are not supported by the available data. Geomorphological factors establish much, but not all, of the framework within which mangrove forests develop. Climatic factors, particularly rainfall, are important determinants of species richness, stand structure, and growth dynamics in mangrove forests. Two groups of mangroves can be identified based on salinity tolerance data, one has a very broad range (0-80‰) and the other has a narrower range (<40‰) of tolerance. Physiological responses to other environmental gradients in the intertidal zone (*e.g.*, soil texture, redox potential, nutrients) do not appear to be sufficient to influence observed zonation patterns. However, more data are needed to address this question adequately. Biotic factors such as predation on propagules are important influences on the distributional patterns of some groups of mangroves and in certain geographic regions. Competitive interactions may be important in determining some aspects of forest structure, but much more experimental and long-term observational work is needed.

A more important consideration is that the dynamics of mangrove forest systems fit within current theories and paradigms developed for other vegetation systems. Ideas of gap-phase dynamics, natural disturbance, and forest mosaics are applicable to mangrove ecosystems and will provide a fruitful avenue for further research.

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