5

Forest Structure[1]

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5.1 Introduction

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. The most noted feature of mangrove forest structure is the often conspicuous zonation of tree species into monospecific bands parallel to the shoreline (Snedaker, 1982). Zonation has been a dominant theme in the voluminous literature on mangroves (Frith, 1977; Rollet, 1981), as well as in that on other vegetation types (Whittaker, 1967). Zonation, however, is not the only manifestation of "structure" in mangroves. Lugo and 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. Janzen (1985) recently commented on the apparent lack of a distinct understory in mangrove forests. Other forest types (e.g., oak- hickory, pine, and tropical rainforest) have a suite of species that have adapted to life in the lower strata of the forest. These grasses, herbs, and shrubs are absent from most mangroves. The seedling and sapling size-classes are often absent from the understory as well. Several hypotheses have been advanced to account for this missing understory (Janzen, 1985; Corlett, 1986; Lugo, 1985; Snedaker and Lahmann, 1988). These observations all describe aspects of forest structure.

In this review I will concentrate on those factors that influence the species composition within a mangrove estuary; the distribution of the component forest species across the intertidal zone and along the length of tidal rivers; and the measures of physical attributes of the forest such as stem density and height. Particular attention will be given to comparisons between regional and continental differences of mangrove forests and between mangroves

[1] This chapter is dedicated to the memory of the late William E. Odum, Professor of Environmental Sciences at the University of Virginia, USA. Bill conducted pioneering research on the ecological dynamics of coastal wetlands, including mangroves. But he was more than a scientist. He was a teacher, a mentor, a colleague, and most of all, a friend. He will be sorely missed and always remembered.

and other forest types. I believe that "mangrove" ecologists have all too often considered mangroves to be very different from other forest ecosystems, and so they have felt that any ecological concepts derived from other ecostystems do not apply to mangroves.

5.2 Mangrove Species Richness

Smith and Duke (1987) examined the influence of tidal amplitude, average temperature (hottest and coldest months), annual rainfall, rainfall variability, runoff, catchment area, frequency of tropical cyclones, and estuary length on the tree species richness of 92 mangrove-dominated estuaries in northern Australia. Their analysis indicated that the suite of environmental parameters which had the greatest influence on species richness were different for estuaries in eastern versus western Australia. In both regions, temperature and tidal amplitude affected species richness. Increasing temperatures led to greater species richness. Species richness decreased with increasing tidal amplitude. In eastern, but not in western, Australian mangroves, the size of the surrounding catchment, the variation in rainfall, and the frequency of tropical cyclones all influenced species richness in the forest. Estuaries which are long and have large catchments tend to have more species than estuaries which are shorter and have small catchments. High interannual rainfall variability and frequent cyclones tended to decrease species richness in eastern Australian mangrove forests but had no effect in western Australia. Interestingly, the amount of freshwater runoff did not appear to be important in either region. This result did not support the hypothesis of Saenger and Moverly (1985), who felt that runoff was a key factor in controlling mangrove species richness.

A factor not considered by Smith and Duke (1987) was freshwater seepage into the intertidal zone. In many mangrove forests worldwide, the highest intertidal zone terminates rather abruptly at a hill or ridge. At this topographic juncture, fresh water often seeps into the intertidal area and reduces salinity. This results in what Seminiuk (1983, 1985) terms "hinterland fringe" mangrove communities. These areas tend to be species rich in comparison to other portions of the forest. Along the dry western and northwestern Australian coast, freshwater seepage is an important determinant of species richness in mangroves. Estuaries that receive freshwater seepage have more mangrove species than those which do not (Semeniuk, 1983). The process also operates along the northeast Queensland coast but does not appear to be as important because of the generally higher rainfall there (This author, pers. obs.). The importance of freshwater seepage to the maintenance of species richness in mangrove forests elsewhere in the world is unknown. However, Thomson (1945) provides evidence that in Sierra Leone, freshwater seepage may actually decrease species richness. Forests with pronounced freshwater seepage contained only *Rhizophora*; those without freshwater seepage had *Rhizophora* and *Avicennia* (Thomson, 1945).

Species richness within an estuary is probably not a result of the dispersal properties of mangrove propagules. The long-distance dispersal ability and propagule longevity of many mangrove species is a paradigm in the literature (Gunn and Dennis 1973, Rabinowitz 1978c). Viable *Rhizophora mangle* propagules are routinely dispersed to the beaches and estuaries of
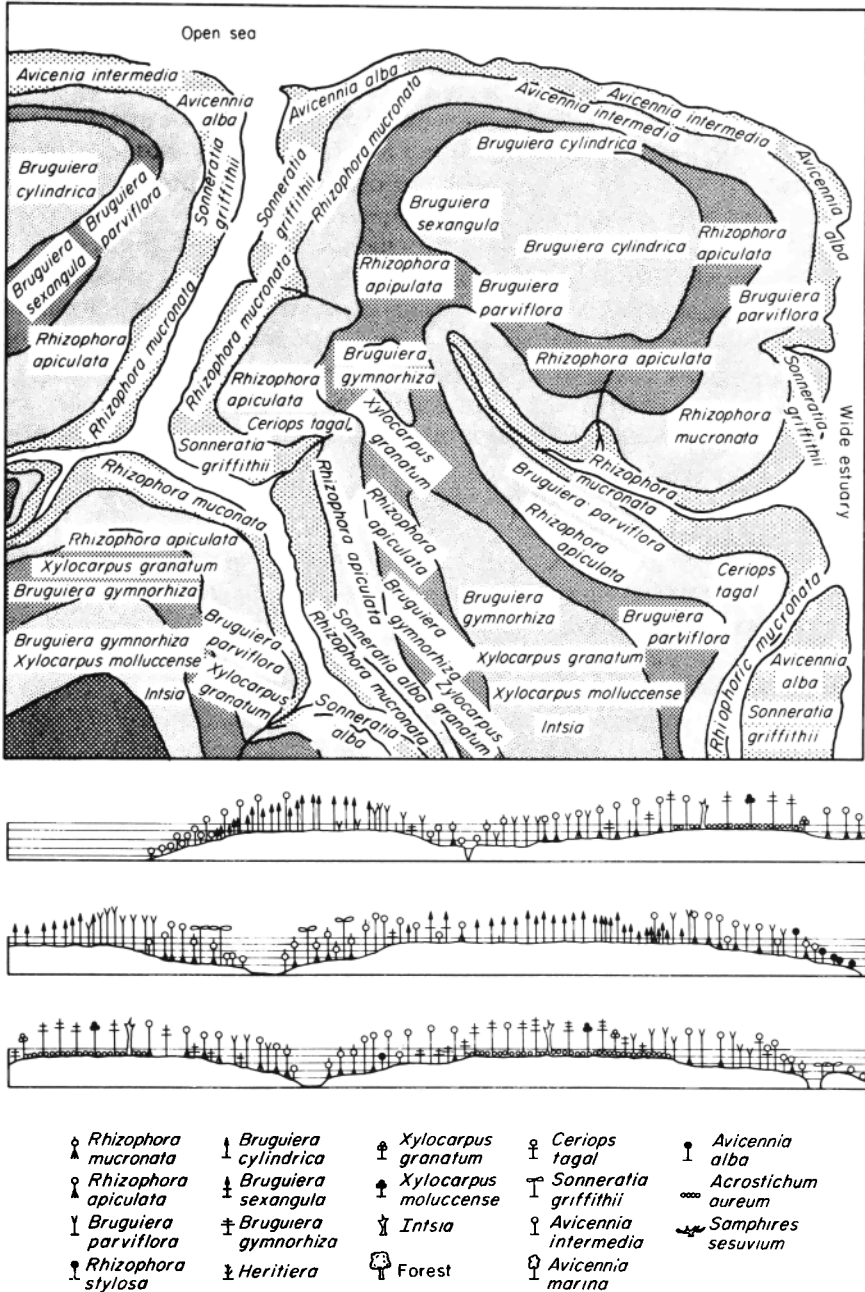
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Figure 1. Stylized representation of mangrove zonation in Malaysia (from Watson, 1928). The figure does not represent actual transects through a forest but rather, Watson's synthesis of zonation based on his extensive surveys in peninsular Malaysia.

south Texas (Sherrod and McMillan, 1985; Sherrod *et al.,* 1986). These propagules are from populations several hundred kilometers to the south in Mexico. Although some may become established, regular, severe winter freezes will eventually kill them all (Sherrod *et al.,* 1986). Thus, the local species richness is limited to mangroves that are freeze tolerant. At a biogeographic scale, however, dispersal properties of mangrove propagules may play a very important role in determining the species richness of a region (Tomlinson, 1986; and see Chapter 4, this volume). In an interesting recent paper, Clarke and Myerscough (1991) reported that very few *Avicennia marina* propagules were dispersed away from the parent tree. Most propagules stranded and established near the parent. This is interesting as *A. marina* has the largest geographic range of all mangroves (Duke, 1990).

5.3 Species Zonation Patterns

Zonation patterns have been described for Malaysia (Watson, 1928), east Africa (Walter and Steiner, 1936; Grewe, 1941, Macnae, 1968), Australia (Macnae, 1969; Semeniuk 1980; Elsol and Saenger, 1983), Papua New Guinea (Johnstone, 1983), Indonesia (Van Steenis, 1957; Prawiroatmodjo *et al.,* 1985), India (Sidhu, 1963), Burma (Stamp, 1925), Florida (Bowman, 1917; Davis, 1940), west Africa (Thomson, 1945), and Panama (Rabinowitz, 1978a-c) to name but a few. Typical zonation patterns from the Indo-Pacific region show *Aegiceras, Avicennia,* and *Sonneratia* occupying the lowest intertidal zones; various species of *Bruguiera* and *Rhizophora* in the mid-intertidal areas; and *Heritiera, Xylocarpus,* and numerous other species in the higher intertidal regions (Figure 1). Walter and Steiner (1936) found *Avicennia* in the highest intertidal (Figure 2). Macnae (1969) and Johnstone (1983) have reported "double distributions." These are situations in which a species may be abundant in two different zones of the forest. For example, *Avicennia marina* is often the dominant species in both the lowest and highest intertidal zones and is rare or absent in the middle intertidal (Figure 3). Observations such as these make interpreting zonation patterns difficult. Bunt and Williams (1981) concluded that "generalizations from relatively local observation may be expected to continue as a source of needless debate."

In addition to describing zonation patterns across the intertidal, early workers also noted patterns of distribution along the length of an estuary (e.g., Grewe, 1941; Figure 4). Some species which are common at the seaward mouth of an estuary are not present nearer the fresher, more riverine, headwater regions of the estuary (Bunt *et al.,* 1982a).
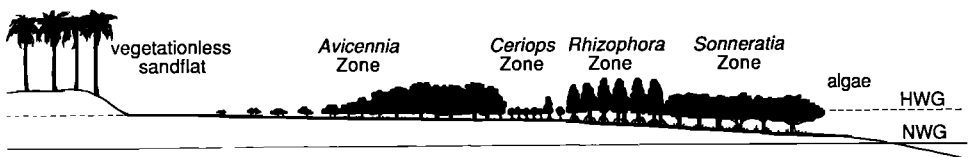

Figure 2. Mangrove zonation in east Africa (after Walter and Steiner, 1936).
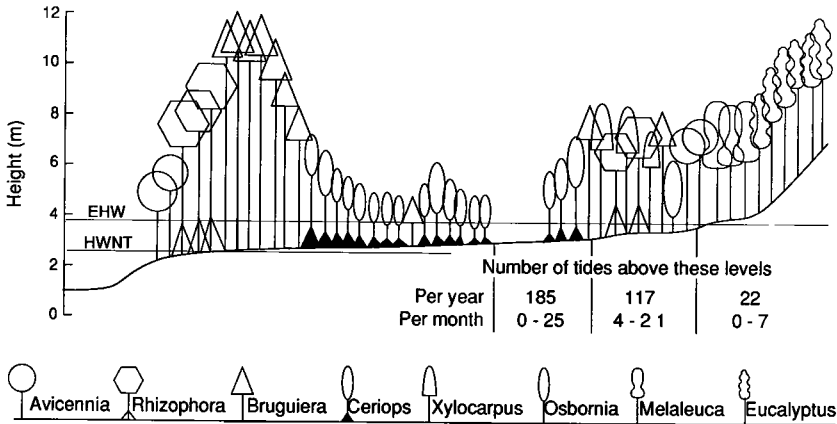
Figure 3. Zonation along a transect through mangroves near Townsville, north Queensland, Australia (from Macnae, 1969). Note "double" distribution of *Rhizophora* and *Avicennia*.
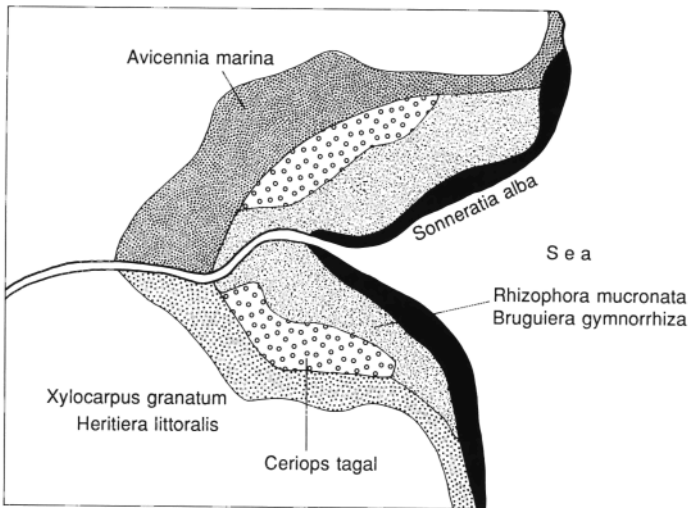

Figure 4. Mangrove zonation in Madagascar showing both across intertidal and upstream - downstream patterns (after Grewe, 1941).

Chapman (1976) provides an extensive synthesis of the early literature describing mangrove forest zonation. These observations led to the paradigm that zonation was the classical feature of mangrove forests and was present in almost all mangroves worldwide (Chapman, 1976).

Not all researchers reported this "classical" view of mangrove zonation, however. Thom (1967) and Thom *et al.,* (1975) describe spatial patterns of occurrence that are not in accordance with the classical view. West (1956) was unable to describe zones in the mangroves of Colombia. In Tanzania, mangroves have been reported as both zoned (Chapman, 1976) and unzoned (Macnae and Kalk, 1962). Bunt and colleagues performed

extensive surveys in Australian mangrove forests and reported some 29 species associations ("communities"), based on a species pool of only 35 (Bunt and Williams, 1980, 1981; Bunt *et al.*, 1982b). Classical zonation patterns in Australian forests tend to be the exception rather than the rule.

Several hypotheses have been advanced to date, including the following: 1) plant succession due to land building (Davis, 1940), 2) response to geomorphological factors (Thom 1967; Woodroffe, Chapter 2, this volume), 3) physiological adaptation to gradients across the intertidal zone (Macnae, 1968), 4) differential dispersal of propagules (Rabinowitz, 1978a), 5) differential predation on propagules across the intertidal zone (Smith, 1987a), and 6) interspecific competition (Clarke and Hannon, 1971). Unfortunately, there appear to be many papers which give specific examples of mangrove zonation and few papers which provide rigorous experimental tests of the hypotheses which attempt to explain why mangrove zonation occurs.

5.3.1 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 invoked mechanism (Snedaker, 1982). The idea is that species which 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.

Curtiss (1888) makes one of the earliest claims regarding the ability of mangroves to build land, specifically for *Rhizophora mangle* in Florida. Davis (1940) expanded the supposed land-building role of *Rhizophora* into a complete successional sequence in which seagrasses colonized bare, subtidal areas and trapped sediments to the point that *R. mangle* would colonize the area and trap more sediment; *Rhizophora* would then be replaced by *Avicennia germinans*, which in turn would give way to a tropical forest climax association. Chapman (1976) provided a synthesis of the "zonation represents succession" theory and provided examples from around the world. Although Chapman (1976) himself noted numerous exceptions and variations to this theme, he attributed them to differing local environmental factors.

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 *Rhizophora, Laguncularia,* and *Avicennia* in Florida mangroves. Egler (1950) also stated that the idea of land building by mangroves was "part of arm-chair musings of air-crammed minds."

The idea of succession in mangroves still appears in the literature. Elsol and Saenger (1983) and Johnstone (1983) discuss zonation patterns as successional sequences. Johnstone (1983) does not make the claim that mangroves will succeed to dry land, rather he finds a "climax" in forests dominated by *Bruguiera gymnorrhiza*. 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. *B. gymnorrhiza,* one of the most shade-tolerant mangrove species, increased most in abundance (Putz and Chan, 1986). 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 (Shugart, 1984). This succession, however, is not the result of mangroves building land.

5.3.2 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 topography. Mangroves do not override abiotic land-building processes (Thom, 1967; Thom *et al.,* 1975; Woodroffe 1981, 1982, see Woodroffe, Chapter 3, this volume). Stoddart (1980) has expanded these results to include mangroves associated with coral reef environments. 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 (Woodroffe *et al.,* 1985; Ellison and Stoddart, 1991). 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.

5.3.3 Physico-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 (Watt, 1947; Whittaker, 1967). Two flavors of the "gradient" hypothesis exist: the distinct-preference hypothesis and the same-preference hypothesis (Pimm, 1978). The distinct-preference hypothesis (Pimm, 1978) states that each species has its own optimum along the gradient which controls where that species occurs. Because different species have different optima, zonation results. An alternate view is that many species share the same optimum and that other factors (e.g., competition, seed dispersal, predation) cause zonation (Vince and Snow, 1984; Ball, 1988a; Figure 5). The idea of physiological adaptation has been used to explain the zonation patterns observed in a variety of plant communities, including mangroves (Watson, 1928; Macnae, 1968; Clarke and Hannon, 1970). In this section I briefly review the types of data which have been used to make inferences concerning mangrove physiology and forest structure. The data are of three general varieties: field observations, field experiments, and laboratory experiments. First, however, we need to look at the types of physico-chemical gradients which occur in the intertidal zone.
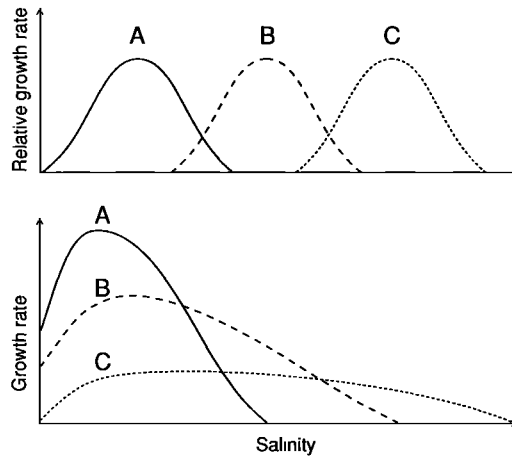
Figure 5. Hypothetical ecological distribution of three mangrove species along a salinity gradient as a result of their physiological response to salinity (from Ball, 1988).

Which gradients occur in the intertidal zone?

Frequency of tidal inundation is the most obvious parameter which varies across the intertidal zone, and is most often cited as a cause of zonation. Low intertidal areas are inundated much more frequently than high intertidal regions. Tidal action, however, introduces two other gradients: soil pore water salinity and soil waterlogging (Giglioli and Thornton, 1965; Clarke and Hannon, 1967). These two gradients may not vary in the same way as frequency of inundation. The pattern of soil pore water salinity across the intertidal zone is influenced by the salinity of the flooding tidal water, rainfall, and freshwater runoff and seepage. Pore water salinity in the lowest intertidal area approximates the salinity of the flooding water: 35‰ near the ocean and <1‰ at the upstream end of riverine mangrove systems (Bunt *et al.*, 1982b). The pattern of salinity variation in the high intertidal zone is complex and usually site specific. In arid regions, pore and surface water salinities in the high intertidal zone may exceed 90‰ (Wells, 1982). High intertidal zone salinities are often lower than that of the flooding water in regions with abundant rainfall, freshwater runoff and / or seepage (Semeniuk, 1983).

Other factors that vary across the intertidal zone include nutrients such as nitrogen and phosphorus (Boto and Wellington 1983, 1984), oxidation-reduction potential (Nickerson and Thibodeau, 1985; McKee *et al.*, 1988), pH (Thornton and Giglioli, 1965), pore water sulfide concentrations (Carlson *et al.*, 1983) and soil texture (Watson, 1928). These gradients are often intercorrelated. For example, fine- grained, clay sediments are often the most highly reduced, whereas, coarser sands are more oxidized (Giglioli and Thornton, 1965). An almost unstudied aspect of mangrove forest ecology is the influence of the fauna on physico-chemical gradients. In particular, organisms which burrow have the potential for modifying chemical and physical factors (see Chapter 3, this volume). For example, burrowing by crabs has been shown to alter the topography and textural properties of mangrove soils (Warren

and Underwood, 1986).   Recently burrowing has been shown to influence soil nutrient and redox characteristics and hence forest productivity.   In the absence of crab burrowing redox potentials increased and forest productivity decreased (Smith *et al.*, 1991).

Field observations of zonation and physico-chemical gradients

Numerous authors have used field surveys to make inferences concerning the tolerances of mangroves to various environmental parameters.   Extensive reviews can be found in Chapman (1976) and Hutchings and Saenger (1987).   Based on this voluminous literature the conclusion could be drawn that most mangroves have extremely wide tolerances to many factors including: salinity, pH, nutrients, redox potential and soil texture.   Data for two factors, salinity and pore water sulfide concentration, illustrate this point.

Wells (1982) conducted extensive field work in the mangroves of northern Australia.   He found seedlings of a many species were found growing in soils with salinities over 65‰ (eg. *Avicennia marina, A. officianalis, B. exaristata, Rhizophora stylosa*, see Table 1). There were a few species, however, which appeared to be restricted to soils with salinities less than 40‰ (e.g. *B. sexangula, R. mucronata, Lumnitzera racemosa, Sonneratia caseolaris*, see Table 1). Wells (1982) also examined the texture of the soils and found that virtually every species could be found in sand, silt or clay soils. Jimenez and Soto (1985) reported similar observations for mangroves in the eastern Pacific and Caribbean.   Most species where found over an extremely broad range of soil salinities, some at salinities in excess of 90‰ (Table 1).   Only three species appeared to be restricted to soil salinities less than 40‰ (*Pelliciera rhizophorae, A. tonduzii, R. racemosa*, see Table 1).   These data may indicate two groups of mangroves: one group having extremely broad salinity tolerances and another with slightly narrower tolerances.

Field measurements of soil redox potential and pore water sulfide concentration have been used to speculate about mangrove zonation in the Caribbean.   Nickerson and Thibodeau (1985) and Thibodeau and Nickerson (1986) correlated the distribution of *A. germinans* and *R. mangle* to pore water sulfide concentrations.   They hypothesized that these species oxidized anaerobic substrates differently, which explained their differing distribution patterns in the field.   They found that the substrate around *A. germinans* roots had much less pore water H_2S and was less reduced than substrates away from *Avicennia* roots.   They found no differences in these parameters around *Rhizophora* roots.   From these results Nickerson and Thibodeau (1985) and Thibodeau and Nickerson (1986) concluded that *Avicennia* is able to exploit lower intertidal, more highly reduced substrates than is *Rhizophora*.   McKee *et al.*, (1988) reexamined the issue because many species of mangrove are known to have well developed aerenchyma, which reportedly allow effective gas transport from the air to the rhizosphere (Scholander *et al.*, 1955; Saenger, 1982). McKee *et al.*, (1988) found that redox potential and pore water sulfide concentrations were significantly correlated with the presence of roots of both species. Their results suggested that *Rhizophora* and *Avicennia* were equally capable of exploiting highly reduced sediments as long as their respective pathways for root aeration remained functional.   This suggests that soil redox potential might not be a determinant of zonation between these species.

Table 1. Ecological characteristics of various mangrove species. Under "Shade": T = Tolerent, I = Intolerent; "Salinity" (in ‰): MS = Maximum Porewater Salinity measured in the field at sites where the species was growing, OG = salinity for Optimum Growth based on culture studies. ?? = unknown at present time. Data have been extracted from Clarke and Hannon (1970), Clough (1984), Downton (1982), Jimenez (1984, 1990), Jimenez and Soto (1985), Macnae (1968), MacMillan (1971), Putz and Chan (1984), Rabinowitz (1978a), Saenger (1982), Sidhu (1975), Smith (1987a, 1988b), Steinke (1975), Watson (1928), Wells (1982).

Species	Shade		Salinity	
	T	I	MS	OG
Acanthus ilicifolius	X		65	8
Aegialitis annulata		X	85	??
Aegiceras corniculatum		X	67	8-15
Avicennia marina		X	85	0-30
A. officianalis		X	63	??
A. germinans		X	100	<40
A. bicolor		X	90	??
Bruguiera exaristata		X	72	8
B. gymnorrhiza	X		50	8-34
B. sexangula	X		33	??
B. parviflora		X	66	8-34
B. cylindrica	X		??	??
Ceriops decandra	X		67	15
C. australis		X	80	15-30
C. tagal		X	45	0-15
Rhizophora mangle		X	70	??
R. racemosa		X	40	??
R. apiculata		X	65	8-15
R. stylosa		X	74	8
R. mucronata		X	40	8-33
R. harrisonii		X	65	??
Camptostemon schultzii	X		75	??
Excoecaria agallocha	X		85	??
Lumnitzera littorea		X	35	??
L. racemosa		X	78	??
Laguncularia racemosa		X	90	??
Pelliciera rhizophorae	X		37	??
Sonneratia alba		X	44	??
S. caseolaris		X	35	??
Xylocarpus granatum	X		34	8
X. mekongensis	X		76	8
Heritiera littoralis	X		??	??
Osbornia octodonta		??	56	??
Scyphiphora hydrophyllacea		??	63	??

Inferences concerning mangrove physiological adaptation based on field observations and measurements must be made with care. Firstly, many published observations are based on the distribution of adult individuals. The physiological tolerances of seedlings may be much narrower than those of adults (Ball, 1988a; McKee *et al.*, 1988). Secondly, the environmental conditions at a site may change over time such that adults persist, but seedlings can no longer become established. Reports of long-term observations from mangrove forests are rare in the literature (but see Putz and Chan, 1986). Thirdly, the entire suite of physico-chemical parameters is rarely measured. Therefore it is virtually impossible to separate the influence of a single factor (e.g. salinity) from other variables (e.g. redox potential). Finally, and most importantly, the data are correlative, and correlation does not prove causation. Correlative data are useful, even necessary, for developing hypotheses. These hypotheses must then be tested with controlled experiments in order to make strong inferences regarding underlying causal mechanisms (Platt, 1947).

Field experiments

Transplant experiments have also been used to examine the question of mangrove zonation. Rabinowitz (1978a), working in Panama, planted seedlings of four species (*R. mangle, A. germinans, P. rhizophorae, and Laguncularia racemosa*) in forests dominated by conspecific adults and forests dominated by each of the other three species. In general, she found that all of the species could grow in any of the "zones" in the forest. In fact, most species grew best away from the "parent" zone of the forest. Recently, Jimenez and Sauter (1991), working in Costa Rica, found that *A. bicolor* grew best in a lower intertidal zone which was dominated by *R. racemosa*. *R. racemosa* grew best in its home zone, but it did survive and grow in higher intertidal forests dominated by *A. bicolor*. In both of these studies the authors concluded that physiological adaptation could not explain the observed distributional patterns of the species across the intertidal zone and that some other mechanism must be operating.

In Australia, Smith (1987b) planted propagules of four species (*A. marina, B. gymnorrhiza, C. australis* and *R. stylosa*) into both high and low intertidal forests that differed in both frequency of inundation and salinity. The high intertidal forest was characterized by low frequency of inundation and high soil salinity, whereas soil salinity was low and inundation frequency high in the low intertidal forest. All four species had their greatest survival in the high intertidal compared to low intertidal zones. Relative growth rates of *R. stylosa, C. australis* and *A. marina* were also greater in the high intertidal zone. Relative growth rates for *B. gymnorrhiza* did not vary between sites. Although *R. stylosa, B. gymnorrhiza,* and *A. marina* survived best in the high intertidal sites, they reached their greatest natural densities in lower intertidal forests. *C. australis* was the only species that survived and grew best in the zone in which it naturally occurs, but even there it was outperformed by the other three species. The results of this experiment also appear to not support the physiological adaptation hypothesis.

Osborne (1988) examined the influences of salinity (upstream versus downstream river location) and intertidal position (high versus low) on the survival and growth of *Aegiceras*

corniculatum seedlings in the Murray River estuary of northeast Queensland. Her results indicated that survival and growth were generally higher in the low intertidal zone in both the upstream, low-salinity (<5‰) portions of the estuary and in the higher salinity estuary mouth (>35‰). Her results are partially supportive of the physiological adaptation hypothesis for *A. corniculatum*. While salinity did not appear to influence where this species grew best, frequency of tidal inundation did.

Criticisms of the field experimental approach include the lack of an adequate control and that most of the experiments are not complete (or even partial) factorial designs. For example, Rabinowitz (1978a) had no controls and in my own study (Smith 1987b) two factors (salinity and frequency of inundation) covaried so it was not possible to separate them. Osborne (1988) selected her field plots such that the factors of interest (salinity and inundation frequency) were not confounded. Additionally, most published field experiments have not reported the cause of death of the seedlings. It is assumed to be the physico-chemical environment in which the seedling has been planted. An examination of Rabinowitz's field notes (on file in the library of the Smithsonian Tropical Research Institute) indicates that many propagules were actually consumed by crabs. Smith (1987b) did record cause of death. In the low intertidal zone 100% of the *Rhizophora* propagules were killed by larvae of a scolytid beetle, a biological vector having nothing to do with a seedling's physiological tolerance.

Laboratory experiments

Laboratory culture studies provide the best data with which to examine the tolerance of mangroves to various physico-chemical parameters. Salinity has been well studied. Clarke and Hannon (1970) found that *Avicennia marina* and *Aegiceras corniculatum* seedlings survived and grew at salinities from 0-35‰, but that maximum growth occurred between 7-14‰. Downton (1982) reported a larger optimal growth range for *A. marina* of 3-20‰. Clough (1984) tested the hypothesis that *A. marina* had a broader salinity tolerance than *R. stylosa*. Both species had growth optima at 9‰. Biomass accumulation in *R. stylosa* fell sharply at salinities over 18‰, whereas *A. marina* showed extended growth responses up to 26‰. Both of these species had the least growth at 0 and 35‰ (Clough, 1984). Clough (1984) attributed the broader growth response of *A. marina* to its ability to excrete salt via salt glands in its leaves. This may account for Bunt *et al.'s* (1982a) observation that *R. stylosa* was restricted to river mouth situations, but *A. marina* was likely to be encountered almost anywhere along an estuary.

Smith (1988b) made detailed comparisons between the observed seedling distributions of *Ceriops tagal* and *C. australis* (see Ballment *et al.*, 1988) in the field and their survival and growth performance along a laboratory salinity gradient. 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 were measured. Both species grew best at 15‰ 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‰.

Ball and colleagues have conducted a series of elegant laboratory studies on carbon gain and water use efficiency of several mangrove species in Australia (Ball and Cowan, 1984; Ball, 1988b; Ball *et al.*, 1988). Ball (1988b) reported that *Aegiceras corniculatum* had a less conservative water use strategy than did *A. marina*. The growth rate of *Aegiceras* was high at low salinities and dropped rapidly as salinity increased. *Avicennia* however, had a lower growth rate, but one that did not drop sharply as salinity increased (Ball, 1988b). She interpreted this to account for the dominance of *Aegiceras* in low salinity areas where it purportedly would be able to outcompete the slower growing *Avicennia*. *Avicennia* in turn would dominate higher salinity areas because *Aegiceras* simple can't tolerate high salinities. In a second study, Ball *et al.*, (1988) showed that water use efficiency was related to salinity tolerance and leaf size in several mangroves. *Ceriops tagal* var. *australis* had the most conservative water use, the smallest leaves and was most salinity tolerant. *Bruguiera gymnorrhiza* had larger leaves, was least efficient at water use and was least salinity tolerant (Ball *et al.*, 1988). These results also support Ball's view that zonation along salinity gradients is a result of differing water use efficiencies between species.

A problem with the above studies is that they examined a single potential causal agent individually. As noted earlier, there are a number of factors which vary across the intertidal zone. Controlled experiments describing the growth responses of mangroves to two or more factors simultaneously are virtually non-existent in the mangrove literature. The possibility of interactive effects between variables cannot be discounted.

In fact, McMillan (1975) has clearly demonstrated this phenomena for two mangroves. He found that the salinity tolerances of *A. germinans* and *L. racemosa* were highly modified by soil texture. Seedlings grown in hypersaline conditions in sand failed to survive. Seedlings grown in soil composed of 90% sand and 10% clay had 100% survival in hypersaline conditions, but showed some leaf discoloration. At 75% sand and 25% clay there was 100% survival with no observable effect on the leaves (McMillan, 1975).

Reconciling experimental results with field observations

The multi-factored, intercorrelated nature of the environmental gradients found in mangrove forests makes the deduction of causal agents from field observations impossible. Furthermore, the extrapolation of single factor laboratory experiments (e.g. Ball, 1988b), no matter how well controlled or elegantly performed, to the multiple factor field situation is tenuous at best. This is because the plant's physiological response to one factor often varies depending on the level of other factors present in the environment (e.g. McMillan, 1975). Multi-factor, controlled experiments are necessary to fully elucidate the physiological mechanisms involved in zonation. In particular the interaction of salinity, soil texture, and sediment redox potential on seedling establishment and growth deserves study (McKee and Mendelssohn, 1987; McKee *et al.*, 1988).

The studies to date clearly demonstrate that many mangroves can grow over the broad range of conditions found across the intertidal zone (Table 1). Data relating species

distributions to soil salinities suggest that two groups of mangroves exist (Table 1). 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 predominately upstream distributions in river dominated estuaries (e.g., *R. mucronata*) or those restricted to geographic areas of abundant rainfall (e.g., *P. rhizophorae*). In this regard it seems that some adaptation to salinity gradients may have occurred which influences distributions within and between estuaries. This view is supported by very limited experimental results for less than 10 mangrove species (Ball, 1988b; Ball *et al.,* 1988). Much more data for other physico-chemical factors (e.g., soils, nutrients, redox potential) are required before the physiological adaptation hypothesis can be fully tested as an underlying cause of mangrove zonation patterns.

5.3.4 Propagule Dispersal and Zonation

Rabinowitz (1978b) hypothesized that zonation in Panamanian mangrove forests was controlled by the influence of tidal action on mangrove propagules. She observed that the species were distributed from the low to high intertidal zone in a manner inversely related to the size of their propagules (Rabinowitz, 1978b). *Avicennia* and *Laguncularia* 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 *Rhizophora* and *Pelliciera*, 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.

Rabinowitz (1978c) also attempted to relate zonation to the dispersal properties of mangrove propagules, such as floating and rooting time. Her experiments indicated that *Avicennia* and *Laguncularia* required 5-7 days to take root in mangrove soils, whereas *Rhizophora* and *Pelliciera* needed 11-15 days to become rooted. Based on these results, one would expect the species with smaller propagules to be more abundant in the lower intertidal zone because that zone experiences periods of inundation at shorter intervals. The high intertidal, with long periods between inundations, should be favorable to all species. The pattern of zonation reported by Rabinowitz (1978a-c) is exactly the opposite of what would be expected based on her own results.

The "tidal sorting" hypothesis has recently been resurrected by Jimenez and Sauter (1991) to explain the zonation of *R. racemosa* and *A. bicolor* in Costa Rica. They interpreted the results of their reciprocal transplant studies as being supportive of tidal sorting. They observed that the high intertidal *A. bicolor* dominated forest they studied was being invaded by *R. racemosa*. They attributed this to a rise in sea level which would permit more high tides to penetrate the forest.

Observations of species distributions in Australia and elsewhere, however, indicate clearly that tidal sorting is not a mechanism which influences zonation patterns. Species in the genus *Sonneratia* routinely colonize the lowest intertidal zone (Watson, 1928; Duke 1984). The seeds of *Sonneratia* are only some 10-15mm in length, which is small in

comparison to most other mangroves (Tomlinson, 1986). In discussing *Sonneratia*, Rabinowitz (1978b) mistakenly referred to the entire seed capsule (which may contain >500 seeds) as the unit of dispersal. The capsule sinks very quickly and then releases individual seeds, which are then dispersed. The genera *Aegiceras* and *Avicennia* also have small propagules and are typically abundant in low intertidal areas (Watson, 1928; Bunt and Williams, 1981; Wells, 1982). They are also common in the highest intertidal areas (Wells, 1982; Johnstone, 1983; Smith, 1987c; Osborne and Smith, 1990). Saenger (1982) provides data on seedling recruitment in mangrove forests at Port Curtis, on the central Queensland coast of Australia. He found that seedlings of all species were found in all plots. *Rhizophora stylosa*, which had the largest propagules, was found across the entire intertidal gradient. It is obvious that tidal action delivers propagules of all species to all portions of the intertidal zone. The question is not so much does dispersal take place?, as much as it is, which factors regulate post-dispersal establishment, survival, and growth?

5.3.5 Seed Predation and Forest Structure

Predation on seeds has been recognized as an important process in a variety of ecosystems (Janzen, 1971; Whelan *et al.*, 1990). Watson (1928) and Noakes (1955) commented on the role of crabs as consumers of mangrove propagules, particularly in the managed forests of west Malaysia. (Because most mangroves are viviparous the unit of dispersal is a propagule, not a true seed.) Watson (1928) stated, "The most serious enemies to mangroves are crabs" and "It is doubtful whether these pests do much damage under natural conditions, but they can, and do, cause great trouble in plantations." Noakes (1955) claimed that "...crabs are a major pest and may entirely prevent regeneration or planting by their attacks on seedlings." He went on to say, "... nothing is known of their effect on natural regeneration, the presence of crabs being no proof that it is likely to fail." The crabs to which Watson and Noakes 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 (Jones, 1984) and biomass (Golley *et al.*, 1962).

Recent experimental evidence has revealed that consumption of mangrove propagules by grapsid crabs greatly effects natural regeneration and influences the distribution of certain species across the intertidal zone. Smith and colleagues (Smith, 1987a,c, 1988a; Smith *et al.*, 1989; Osborne and Smith, 1990; Smith and Duke, In review) conducted a series of experiments in which mangrove propagules were tethered in the forest and then the amount of consumption was determined over time. 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 (Figure 6, Smith 1987a). 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 (Smith 1987b). *A. marina* is usually absent from this region of the intertidal zone (Macnae, 1969; Johnstone, 1983; see Figure 3). The results indicated that when protected from crabs, *A. marina* propagules survived and grew. The conclusion was that virtually 100% of the *A. marina* propagules that were
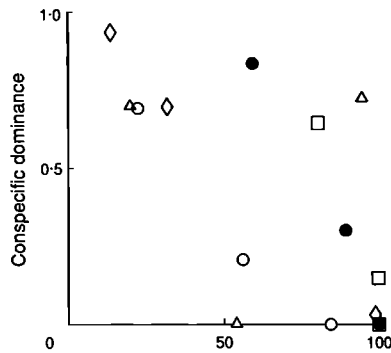
Figure 6. Relationship between conspecific dominance and cumulative amount of predation on five mangrove species from north Queensland, Australia (from Smith, 1987a, reproduced with permission from *Ecology*). Square = *Avicennia marina*, Solid circle = *Bruguiera exaristata*, Open circle = *B. gymnorrhiza*, Triangle = *Ceriops australis*, Diamond = *Rhizophora stylosa*.

dispersed into middle intertidal forests were consumed by crabs; hence, seed predation was an important determinant of the forest's species composition and structure (Smith, 1987b).

Subsequent studies indicated that seed predation was important over a much larger geographic region than northeast Queensland. Data from Malaysia and Florida revealed high levels of predation on the propagules of *A. officianalis* and *A. alba* in Malaysia and on *A. germinans* in Florida (Smith *et al.,* 1989). 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* and *Brugiuera,* 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* were consumed in a forest where the species was present in the canopy than were consumed in a forest where it was absent (Smith *et al.,* 1989).

More extensive propagule predation experiments have now been conducted in Panama. These studies utilized some of the same forests that Rabinowitz used some 15 years ago and were carried out along both the Pacific and Caribbean coasts (Smith and Duke, In Review). These new results indicate that predation on propagules may effectively preclude the establishment of *A. germinans* and *Laguncularia racemosa* in forests dominated by *R. mangle* and *Pelliciera rhizophorae.* However, the reverse is not true. The amount of predation on *R. mangle* and *P. rhizophorae* propagules in forests dominated by *Avicennia* and *Laguncularia* was not high. Therefore, it seems that predation is not sufficient to account for all of the species distribution patterns observed in Panamanian forests, however, it does account for some (Smith and Duke, In Review).

Predation on propagules has also been proposed as an influence on succession in north Queensland mangrove forests (Smith, 1988a). For example, no *A. marina* saplings were observed in a forest in which the canopy size-class was dominated by this species. The sapling size-class was composed of *B. gymnorrhiza, B. exaristata,* and *C. australis.*

Predation studies showed that >95% of the *A. marina* propagules were consumed in this forest, but <25% of the propagules of the other species were eaten (Smith 1988a). The question arises, how did this forest become dominated by *Avicennia?* Did the predators move into the forest after *Avicennia* became dominant? Long-term studies of the crab populations and their food sources are needed (Whelan *et al.*, 1990).

Crabs are not the only consumers of mangrove propagules. Robertson *et al.*, (1990) have recently shown that insects attack and kill a substantial number of the seeds and propagules of some mangroves. *Heritiera littoralis, Xylocarpus granatum,* and *X. australasicus* all have seeds with hard pericarps that are highly resistant to attack by crabs. More than 55% of the seeds of these species were attacked by insect predators (Robertson *et al.*, 1990). Growth and survival of insect damaged and non-damaged control seeds from seven mangrove species were compared by these authors. Insect attack reduced survival and growth in *X. granatum* and *X. australasicus. B. parviflora* had decreased survival but no differences in growth. *A. marina* and *B. exaristata* had no differences in survival, but insect damage resulted in decreased growth. *R. stylosa* and *B. gymnorrhiza* showed no differences in survival or growth between control and insect damaged propagules. Robertson *et al.*, (1990) concluded that insects are a major determinant of seed survival and possibly of seedling distribution for these north Queensland mangrove species.

The role of insects as seed predators in mangrove forests elsewhere in the world is equivocal. In Florida and the Caribbean, conflicting observations have been published. Onuf *et al.*, (1977) found that infestations of a scolytid beetle in *R. mangle* propagules significantly reduced their growth and survival. In Panama, Rabinowitz (1977) found no effect from insect borers on the propagules of *R. harisonii.* Detailed experimental analyses appear to be lacking.

Seed predation studies have also revealed both local- and biogeographic-scale patterns in the process. Consumption of propagules appears to be least in the lowest intertidal zone and increases to maximum amounts in the high intertidal zone (Smith, 1988a; Smith *et al.*, 1989; Osborne and Smith, 1990; Smith and Duke, In review). Grapsid crab populations tend to be greatest in high intertidal areas (Frusher *et al.*, unpub. data). Additionally, there is often a marked zonation in the crab fauna both across the intertidal zone and upstream - downstream along the length of the estuary (Verwey, 1930; Tweedie, 1950; Snelling, 1959; Berry, 1964; 1972; Hartnoll, 1965, 1973, 1975; Barnes, 1967; Warner, 1969; Sasekumar, 1974; Icely and Jones, 1978; Jones, 1984). An understanding of what determines crab zonation is almost totally lacking at this time. Preliminary observations from northeastern Queensland suggest that salinity is not as important as soil textural properties such as organic matter content and percentages of sand, silt, and clay (Frusher *et al.*, unpub. data; Smith *et al.*, unpub data).

Biogeographic patterns have also been noted in the consumption of mangrove propagules (Smith and Duke, In review). Rates of predation are highest in the Indo-Pacific region, decrease towards the east across the Pacific Ocean to Panama, and are least in the western Atlantic. A latitudinal gradient also exists from Panama northward to Florida (unfortunately, the potential of latitudinal gradients in predation has not been addressed in Australia). Similar patterns have been observed in a number of other tropical marine communities. In

coral reef ecosystems, higher rates of predation by fish on invertebrates were observed in the Pacific than in the Atlantic (Bakus, 1966, 1969). Palmer (1978) observed higher predation on molluscs in the eastern Pacific than in the western Atlantic. The scarcity and lower profile of algae on eastern Pacific reefs relative to that on Caribbean reef systems was attributed by both Earle (1972) and Glynn (1972) to higher levels of predation. Vermeij (1976, 1978) provides extensive data, both experimental and observational, that indicates higher levels of predation in the Indo-Pacific than in the Caribbean. He showed that gastropods of the Indo-Pacific were much more highly evolved in their predator defenses than were gastropods in the western Atlantic.

It is interesting that the predator guilds change across this same broad region. The grapsid crabs are most diverse in the Indo-Pacific, with diversity steadily decreasing eastward across the Pacific to the western Atlantic (Jones, 1984). The grapsid fauna changes latitudinally as well (Jones, 1984). Only five species are found in the mangroves of southwest Florida (Smith, pers. obs.). Unfortunately, accurate measures of abundance and/or biomass of the crab fauna in mangroves have not been made. This author's personal experience indicates that both biomass and abundance follow the same pattern as diversity. In both Australia and Malaysia the grapsid crabs composed >95% of the predators on propagules. In south Florida, however, they accounted for <6% of propagule consumption. The snails *Melampus coeffeus* and *Cerithidea scalariformis* consumed >70% of the propagules in Florida (Smith *et al.*, 1989). These predators are only capable of consuming *Avicennia* and possibly *Laguncularia*, which was not tested (Smith *et al.*, 1989).

5.3.6 Competition and Forest Structure

Competition has been studied in a variety of wetland plant communities (e.g., Grace and Wetzel, 1981; Silander and Antonivics, 1982), but few studies have examined the role of competitive interactions in mangrove forests. Ball (1980) examined the colonization of high intertidal habitats in south Florida by *R. mangle* and *L. racemosa*. Based on historical aerial photographs and measurements of living and dead tree densities and the densities of saplings and seedlings, she inferred that *Laguncularia* was being replaced by *Rhizophora*. Competition was the mechanism invoked by Ball (1980) to account for the replacement. Unfortunately, Ball's study was observational, not experimental, so other possible alternatives (e.g., seed predation or changing environmental conditions) for the species replacement were not examined.

Smith (1988b) tested for possible competitive interactions between *C. tagal* and *C. australis* along an experimental salinity gradient. Seedlings were grown in mono- and poly-cultures at salinities from 0-60‰. *C. tagal* grew better than *C. australis* did at lower salinities, whereas the reverse was true at high 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 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's* effect on *C. tagal* (Smith 1988b). For salinities >45‰, however,

Table 2. Ecological characteristics of pioneer- and mature-phase terrestrial forest communities with mangrove forest species and communities. Modified from Tomlinson (1986).

Specific Characters	Pioneer Phase	Mature Phase	Mangroves
Propagule size	Small	Large	Variable
Propagule number	Numerous	Few	Numerous
Propagule production	Continuous	Discontinuous	Continuous
Propagule dormancy and viability	Long	Short	Long
Dispersal agent	Often abiotic (e.g. wind)	Usually biotic (e.g. birds)	Always abiotic (water)
Dispersibility	Wide	Limited	Wide
Seedlings dependent on	Light-demanding, dependent on seed seed reserves	Not light demanding, and many dependent reserves	Light demanding on seed reserves
Reproductive age	Early	Late	Most early
Geographic range	Broad	Narrow	Variable
Life span	Short	Long	Vivparous - long Nonvivparous - short
Leaf palatability	High	Low	Most low
Wood	Soft, light	Heavy, dense,	Most heavy, dense
Crown shape	Uniform	Varied	Uniform
Competitiveness	For light	For many resources	Mainly for light
Pollinators	Not specific	Highly specific	Rarely specific
Flowering period	Prolonged	Short	Prolonged
Breeding mechanism	Usually inbreeding	Usually outbreeding	Inbreeding favored
Community Characters			
Species richness	Poor	Rich	Poor
Stratification	Few or no strata	Many strata	Few or no strata
Size distribution	Even-sized	Uneven-sized	Mainly even-sized
Large stems	Absent	Present	Present only in old, undisturbed stands
Undergrowth	Dense	Sparse	Usually absent
Climbers	Few	Many	Few
Epiphytes	Few	Many	Few

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. Smith (1988b) hypothesized that both may be outcompeted at lower salinities by species such as *Heritiera littoralis, Xylocarpus granatum,* or *Bruguiera gymnorrhiza*. Additional experimental analyses and long-term studies of permanent forest plots would be very helpful at unravelling the role of competition in mangrove forests.

5.4 Stand Structure in Mangroves

Stand structure in mangrove forests is relatively simple when compared to that of other forest types (Table 2). 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. Janzen (1985) commented on this "missing" understory. Subsequent hypotheses have postulated that the combination of salinity-stress and the need for light is enough to prohibit the development of understory vegetation and therefor poses an evolutionary hurdle which has not been crossed (Lugo, 1985; Snedaker and Lahmann, 1988). There are mangrove forests with understories, however. These tend to be in areas with abundant year-round rainfall and freshwater runoff (Corlett, 1986). 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 (Tomlinson, 1986).

The age- (or size-) class structure of mangrove forests is also characteristic of pioneer formations (Table 2). Most mangrove forests have an even-aged size-class structure. The question of how this arises in mangroves has not been addressed. The possibility exists that 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 (Odum *et al.,* 1982).

Stand height, density, and biomass accumulation appear to be related to climatic factors, particularly rainfall. Pool *et al.,* (1977) combined measures of species richness, stem density, canopy height and basal area into a complexity index to make geographic scale comparisons across the Caribbean region. They found that the least complex stands were in arid regions. These stands were marked by high stem density, but low species richness, height, and basal areas. Complex stands, characterized by tall canopies, high basal areas, and lower stem densities, were common in wet, high rainfall areas (Pool *et al.,* 1977). Complementary results that are based on different methods are available from the Indo-Pacific region (e.g., Boto *et al.,* 1984; Putz and Chan, 1986). Rainfall and freshwater runoff appear to be major determinants of stand structure.

5.5   Mangroves and Recent Theories of Forest Ecology

Over the past 40 years ecologists have developed the view that pattern in vegetation is the result of dynamic processes operating over a continuum of spatial and temporal scales: from days and weeks to centuries and from square meters to hundreds of square kilometers. In particular, the influence of natural disturbances on vegetation structure has been the subject of intense interest (Watt, 1947; White, 1979; Pickett and White, 1985; Whitmore, 1989). Forests and other ecosystems are now seen in the context of "gap dynamics" and "patch phase mosaics" (Shugart, 1984; Pickett and White, 1985). In this context the landscape is viewed as a patchwork quilt in which the individual patches are different ages or stages of

development. This view of forest ecosystems has proven especially amenable to the development of ecosystem level models to explore successional patterns, nutrient cycling, and other system dynamics (Shugart, 1984). Almost all types of forest systems have been examined in light of this "gap-dynamic" or "patch phase mosaic" paradigm, with the exception of mangrove forests (e.g., Barden, 1989; Brokaw, 1985; Christensen, 1985; Lorimer, 1989; Spies and Franklin, 1989; Runkle, 1985; Veblen, 1985). But are mangrove forests really different from other forest types? Processes such as primary production, decomposition, herbivory, and competition, which operate in other forest systems, certainly operate in mangrove forests. So must the processes of natural disturbance that generate canopy gaps and forest mosaics.

This modern view of forest ecology began with the realization that forest trees can be grouped into two classes based on their reproductive strategies (e.g., Swaine and Whitmore, 1988; Whitmore, 1989). The climax class contains those species which have seeds that can germinate under the forest canopy and which have seedlings that can become established in shade. The pioneer group consists of those species that become established in the full sunlight of canopy gaps.

Mangrove species and the mangrove community have characteristics of both pioneer- and mature-phase forest communities (Table 3). For example, they produce a copious seed rain, a pioneer-phase trait. Jimenez (1990) estimated that >2,000,000 propagules/ha were produced in an *A. bicolor* forest in Costa Rica. Other species may be as productive (Duke *et al.*, 1981). Mangrove propagules, however, are often rather large and have a very long period of dispersal and longevity. These are mature-phase traits. On balance, it seems that mangroves have more pioneer-phase characteristics and therefor they should be viewed as pioneer communities (Tomlinson, 1986). Pioneer species have adapted to natural disturbance.

A number of authors have alluded to the importance of disturbance and gap dynamics in mangrove forests (e.g., Watson, 1928; Macnae, 1968; Rabinowitz, 1978a; Wells, 1982; Putz and Chan, 1986; Smith, 1987b,c; Jimenez, 1988, 1990), but no detailed analysis has been made to date. Watson (1928) commented on the shade intolerance of the seedlings of many mangrove species in Malaysia. He also remarked on the regular occurrence of gaps in the canopy, which provided the habitat needed for these species to regenerate. Macnae (1968) provided a partial classification of species into shade tolerant and shade intolerant based on his observations in the Indo-Pacific region. Wells (1982) classed Australian mangrove species as shade intolerant and shade tolerant based on his extensive observations (Table 1). Only a few experimental studies have been published that relate to gap dynamics in mangroves.

In Panama, Rabinowitz (1978a) related rates of seedling mortality to initial propagule size. She noted that mortality was inversely related to propagule size. Species with smaller propagules (*Avicennia* and *Laguncularia*) established cohorts on the forest floor every year, and these cohorts died relatively rapidly. *Rhizophora* and *Pelliciera,* however, which have larger propagules, had cohorts which overlapped; that is, seedlings were always present, but there was a constant turnover of the seedling pool (Rabinowitz 1978a). She also reported that *Pelliciera* grew better under a closed canopy than did *Rhizophora*. Rabinowitz (1978a)

Table 3. Current status of several hypotheses proposed to explain mangrove zonation.

Hypothesis	Status
1. Zonation represents land building and plant succession	Not supported by the data.
2. Geomorphological control	Geomorphological factors that regulate sediment supply, soil type, texture, accretion and erosion all play an important role in setting the framework within which mangrove forests develop. Climatic factors, particularly rainfall and freshwater runoff, are also important.
3. Physiological adaptation to gradients	Application of the results of single factor experiments to the field situation is tenuous at best. Extensive controlled, multi-factor, experiments are needed to fully test this hypothesis. Based on salinity tolerances, two groups of mangroves can tentatively be identified: one with an extremely broad range and the other with a narrower range of tolerance.
4. Tidal sorting of propagules	Not supported by the data.
5. Differential predation on propagules	More important for some mangroves (e.g, *Avicennia*) and in certain regions (e.g., the Indo-Pacific) than for other groups or regions.
6. Interspecific competition	Very limited data indicate that competitive interactions occur which could influence zonation.

suggested that if light gaps were important, then *Rhizophora* and *Pelliciera* would probably have an advantage in colonizing them.

Putz and Chan (1986) reported a relationship between the abundance of mangrove seedlings and the illumination of the forest floor in Malaysian mangrove forests. The forest canopy was very dense in the 1920s and seedlings were scarce. As the canopy matured and individual trees began to die, seedling abundance increased (Putz and Chan, 1986).

5.5.1 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 wind storms (Putz *et al.*, 1984), lightning strikes (Paijmans and Rollet, 1977), frost damage (Lugo and Patterson-Zucca, 1977) that may be very patchy but may extend over large areas, and whole-scale destruction of the forest by hurricanes (Craighead and Gilbert, 1962). 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; the predominant natural disturbance is lightning strikes. To the north, in Belize, frost is again unimportant, but hurricanes and lightning strikes are common. 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.

Smith and Duke (1987) found a positive relationship between large- scale disturbance (cyclones) and species richness in the mangrove forests of northeastern Queensland, Australia. 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 (Bunt *et al.,* 1982b). In the Sunderbans mangroves of Bangladesh, the Rhizophoraceae are minor components of the forest community (Blasco *et al.,* 1975). The Sunderbans are struck by up to 40 cyclones a year.   The Rhizophoraceae's inability to coppice, in comparison to other groups (e.g., *Avicennia, Laguncularia, Excoecaria* and *Xylocarpus*), may account for their vunerability to cyclones.

5.5.2 Gap Dynamics in Mangroves

Canopy gaps are common in mangrove forests. In addition to what most forest ecologists would recognize as a canopy gap, Smith (1987c) observed that 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. Most gaps (the traditional kind) are probably 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 (Duke *et al.,* 1991). Seedlings that are present under the canopy are often killed as well. Smith (unpub. data) surveyed 391 gaps in northeast Queensland; they ranged from <10m^2 to >500m^2 in size (Figure 7), with the modal size 40- 60m^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 (Smith, 1987a,c).

The physical environment in light gaps is substantially different from that under the surrounding canopy (Figure 8). Measurements made in light gaps in high and low intertidal areas in Australia indicated differences in photosynthetically active radiation (PAR), pore water salinity, and soil temperature (Smith, 1987c). 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 light 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.

The entire Murray River estuarine system in north Queensland was surveyed for gaps using recent and historical aerial photographs. It was determined that between 4-15% of the
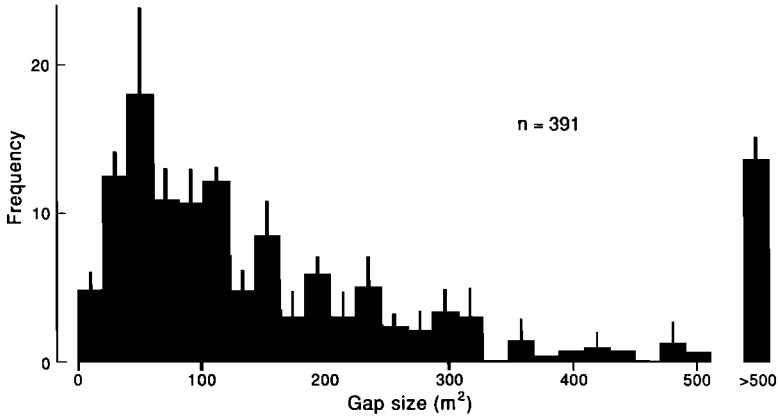
Figure 7. Frequency distribution of canopy gaps by size class from northern Australia and southern Papua New Guinea. Data based on surveys of 391 gaps. Gaps were randomly assigned to three groups and then the mean (± 1SD) was calculated. Data are previously unpublished from the author.
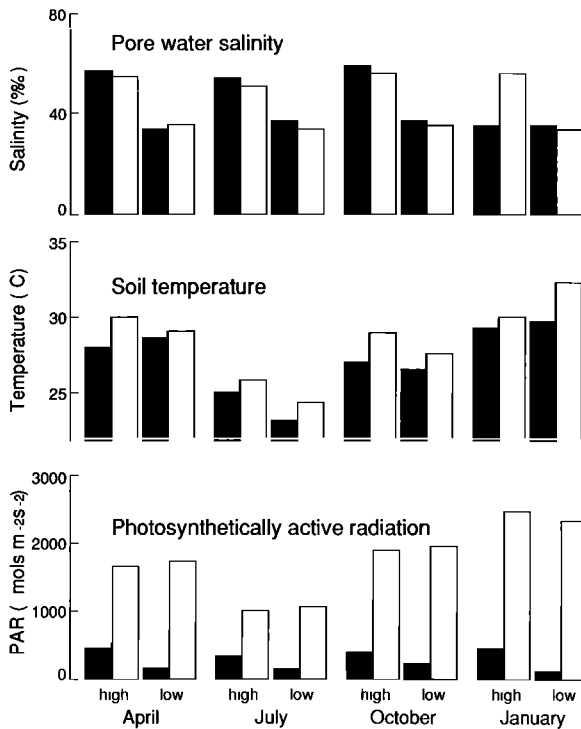

Figure 8. Seasonal variation in some physical characteristics of gap (open bars) and understory (solid bars) environments for both high and low intertidal habitats in north Queensland, Australia (from Smith, 1987b, used with permission). Mean ± 1SD, for n=5.
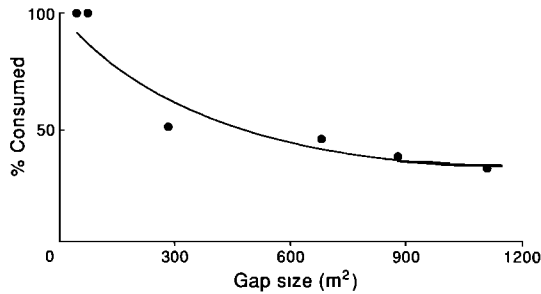
Figure 9. Amount of predation (%) on *Avicennia marina* propagules located in canopy gaps as a function of gap size (m^2), from Osborne and Smith (1990). Actual data points and their best fit nonlinear regression equation as shown. The regression equation is given by: %Consumed $=100 \cdot e^{-0.001275 \text{ gap size}}$ and is highly significant ($F_{1,4}=73.1$, $p \leq 0.01$, $r^2=0.96$). Reproduced with permission of *Vegetatio*.

forest was in the gap- phase at any one time and that the forest "turned over" approximately every 150-170 years (Smith, unpub. data). Comparable data are not available for mangroves elsewhere in the world. However, given the very high frequency of thunderstorms, and hence lightning strikes, in south Florida (Michaels *et al.*, 1987) and visual observation of the forests, it appears that a larger percentage of Florida mangroves are in the gap-phase stage than are forests in northern Australia (Smith, pers. obs.).

Seedling survival and growth for several mangrove species have been examined in gap and understory habitats in both high and low intertidal zones. Smith (1987b,c) found that 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. Osborne (1988) found that *A. corniculatum* survived and grew best on open (unshaded) accreting mudbanks. Within high intertidal forests, survival and growth was greatest in canopy gaps, but was still lower than on accreting mudbanks. Duke (unpub. data) tagged a number of seedlings of *C. australis, B. gymnorrhiza, X. granatum*, and *H. littoralis*, all of which were growing under a shaded canopy. Growth of all species was minimal, <1cm/yr, measured over 10 years of observation. Survival, however, was >80% for *B. gymnorrhiza, X. granatum*, and *H. littoralis*. For *C. australis* survival was <20%.

In Australia canopy gaps may provide some mangroves with a refuge from seed predators. Osborne and Smith (1990) observed that predation on propagules of *A. marina* was higher in small gaps and decreased with increasing gap size (Figure 9). Visual observations indicated that the crab fauna in gaps was dominated by ocypodids (Ocypodidae, primarily *Uca*), whereas grapsids dominated under the canopy. Ocypodids are not known to consume mangrove propagules, but grapsids do (Smith, 1987b). The increase in soil temperatures that accompany gap formation may underlie this shift in the crab fauna, as *Uca* appear to prefer warmer sediments (Jones, 1984).

5.6 Conclusions

Despite several thousand publications concerning mangrove forests (Frith, 1977; Rollet, 1981), a clear understanding of the dynamics in mangrove ecosystems is just beginning to emerge. Of the hypotheses advanced to account for species zonation, several warrant further attention, but others should be laid to rest (Table 3). In particular, hypotheses concerning zonation as plant succesion 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 tentatively identified based on salinity tolerance data; one has a very broad range (0-80‰) and the other has a narrower range (<40‰) of tolerance. Extensive controlled experimentation is required to fully understand how mangrove physiological responses to other environmental gradients (e.g., soil texture, redox potential, nutrients) may influence observed zonation patterns. In particular experiments which address potential interactions between variables are needed. Biotic factors such as predation on propagules, are important influences on the distributional patterns of some groups of mangroves and in certain geographic regions (Table 3). 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 mosiacs are applicable to mangrove ecosystems and will provide a fruitful avenue for further research.

5.7 Acknowledgements

5.8 References

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