

2001

## **Factors Affecting Community Structure of Mangroves Associated With Point Bars and Islands in a Costa Rican Estuary.**

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**FACTORS AFFECTING COMMUNITY STRUCTURE OF MANGROVES ASSOCIATED WITH  
POINT BARS AND ISLANDS IN A COSTA RICAN ESTUARY**

**A Dissertation**

**Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy**

**In**

**The Department of Oceanography and Coastal Sciences**

**by  
Patricia Delgado-Sanchez  
B.S., Universidad Nacional de Costa Rica, 1991  
M.S., Louisiana State University, 1995  
May 2001**

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**To my colleague, best friend and husband, Philippe and my little Nicolas.  
Together we made it possible...**

**To my parents, for their unconditional support and encouragement...**



## **ACKNOWLEDGMENTS**

I would like to thank all those, who by one way or another helped to make this work possible. Special thanks go to my major professor Dr. John W. Day, Jr. for his support, encouragement and valuable inputs throughout the entire process leading to this dissertation. I would also like to thank all my committee members Dr. Karen McKee, Dr. David Longstreth, Dr. Lawrence Rouse, Dr. Robert Gambrell and Dr. Ramsay Smith; their support and comments to the manuscript were of great value for the completion of this work.

During my work in Costa Rica, I would like to give special thanks to Dr. Jorge Jiménez, for his contributions to this study, also for his support and encouragement along the way. Also, I would like to recognize the support and help of Dr. Mario Morales, Norma and Jorge, whose significant contribution for the realization of the soil physical analyses I very much appreciated. This work is indebted to Dr. Philippe Hensel who's invaluable and numerous contributions in the field, statistics and editorial work made this dissertation possible. I am also very grateful to all our friends that assisted us in the field in spite of the mud, mosquitoes and crocodiles. Thanks to Dr. Eugenio González, Ulises, Salomón, Francisco, Daisy, Xinia and park rangers of the Palo Verde Station, whose help, company and good humor made of our stay in Palo Verde a wonderful one.

This research was partially supported by a Fulbright research scholarship, and a grant from the International Union for the Conservation of Nature (IUCN). The Organization for Tropical Studies (OTS), and the Area de Conservación Tempisque (ACT), Palo Verde National Park, gave valuable support in logistics. Dr. Donald Cahoon from the U.S. Geological Survey (USGS) kindly donated the equipment necessary to measure sedimentation.

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## ABSTRACT

A conceptual model of relationships between mangrove community structure and their physico-chemical environment is developed for point bars and islands in the Tempisque-Bebedero estuarine system, Pacific coast, Costa Rica. The model identifies key variables whose relationships to mangrove forest structure are the focus of extended field and mesocosm studies.

Point bars and islands are very dynamic features constantly modified by hydrology and sediment dynamics. In the Tempisque-Bebedero system, they are additionally modified by extensive agricultural activities. High riverine sediment loads, associated with irrigation and seasonal wind-driven re-suspension, result in significantly higher sediment deposition in lower intertidal zones; upper intertidal zones are less affected due to their elevation and less frequent flooding.

This study shows significant relationships between mangrove forest structure and position along the intertidal gradient. Laguncularia racemosa is the pioneer species colonizing emerging mud banks, and dominates lower intertidal zones in terms of basal area and stem density. Rhizophora racemosa, Avicennia germinans, and A. bicolor dominate basal area of upper intertidal zones. The correlation between forest structure, hydrology and sediment deposition implies that mangroves in this region are distributed according to inter-specific differences in tolerances to inundation and sedimentation dynamics.

Soil physico-chemical variables changed significantly across the intertidal gradient, implying that edaphic factors are important affecting the observed mangrove distributional patterns. Laguncularia dominates the lower intertidal zone characterized by lower soil stability and “richer” soils than the upper zone. Riverine source of nutrient-rich, low salinity water and sediments is important and explains the high structural development of these mangrove communities.

The effect of hydrology and biotic factors in species distribution are important during the early phases of mangrove development by determining species-specific ability of establishment. Compared to Avicennia, Laguncularia propagules had higher establishment in mud banks, implying that Laguncularia's specific propagule characteristics are important in determining this species' successful colonization of lower intertidal zones. Intensive crab predation in upper intertidal zones, however, restricts its distribution in upper intertidal zones.

**Mangrove structure in the Tempisque-Bebedero system is therefore sensitive to a combination of physical and biological factors, which deserve attention considering the impact of further alterations to this estuarine system.**

## **CHAPTER 1.**

### **MANGROVE STRUCTURE DYNAMICS AND ITS RELATIONSHIPS TO BIOTIC AND PHYSICO-CHEMICAL VARIABLES**

## **1.1. INTRODUCTION**

Mangroves are very important ecosystems that colonize sheltered intertidal habitats, including estuaries, deltas and lagoons, along tropical and subtropical coasts (Twilley 1998). Ecologically, mangrove forests are an important habitat and food source for many species of animals, some of them of economic importance such as fish, crabs, shrimps and molluscs. They act as buffer zones controlling water quality (Twilley 1998). Mangrove ecosystems have also been recognized because of their role in soil formation and stabilization of coastal environments (Carlton 1974, Augustinus 1995). Socio-economically, mangroves are an important source of timber, poles and charcoal; and some species have medicinal value (Bandaranayake 1998). They also protect coastal zones from erosion and hurricanes (Tomlinson 1986, Mazda et al. 1997), and in some regions are being exploited for tourism.

Because of the recognized importance of mangroves within coastal areas, the growing anthropogenic alterations to these systems (Twilley 1998), and the increasing threat of climate change to the sustainability of these environments (Ellison and Stoddart 1991, Field 1995, Snedaker 1995), the understanding of mangrove ecosystem functioning is the focus of many studies. Mangroves in general are structurally simple ecosystems; in the New World especially, they are composed of a low number of species and normally do not show a pronounced understory (Tomlinson 1986, Smith 1992). Under favorable conditions, however, such as those dominated by riverine environments, mangroves show great structural development and are among the most productive ecosystems in the world (Day et al. 1987). An aspect of mangrove structure that has received considerable scientific attention is species distribution, and it has been studied on different geographic scales: global, regional, estuarine and intertidal (Duke et al. 1998). Many studies, conducted at the intertidal scale, have shown a considerable variation of mangrove zonation patterns (Bunt 1996), which makes generalizations explaining species distribution very difficult.

Mangrove zonation is controlled by different biotic and physico-chemical variables, which depending on geomorphic processes define specific environmental settings with specific mangrove species distributions and mangrove characteristics (Tomlinson 1986, Semeniuk 1985, Thom 1967). Selective predation (Smith 1987, McKee 1995a, Dahdouh-Guebas et al. 1998), interspecific competition (Ball 1980, Kangas and Lugo 1990, Clarke and Myerscough 1993, Patterson et al. 1993), dispersal

dynamics (Rabinowitz 1978a and 1978b, Steinke 1986, McGuinness 1997), physiological tolerance to stressors (waterlogging and salinity; Clarke and Hannon 1970, Ball 1988), and soil physico-chemical characteristics (i.e. salinity, sulfides, nutrients, sedimentation; Soto and Jiménez 1982, Nickerson and Thibodeau 1985, Ukpong 1991, Sherman et al. 1998, Patterson and Mendelssohn 1991, McKee 1993, Chen and Twilley 1999a) are some of the factors which have been reported to affect species distribution, and other mangrove structural attributes under particular geomorphic settings.

In the estuarine system of the Tempisque and Bebedero rivers in the Pacific coast of Costa Rica, Laguncularia racemosa (L.) Gaertn. f. is the dominant species colonizing newly formed mud banks and lower intertidal zones of point bars and islands (Jiménez 1994). In these dynamic environments, Laguncularia forms some of the most extensive monospecific fringe stands in the country. Rhizophora racemosa G.F.W. Meyer, Avicennia germinans (L.) Stearn, A. bicolor Standley and Pelliciera rhizophorae Triana and Planchon colonize mainly intermediate and upper intertidal zones. Rhizophora mangle L. is absent from the system. This specific pattern of species distribution does not follow the traditional distribution described for other mangrove communities in the New World (Thom 1967, Ball 1980, Lugo 1990). However, it is common in this environmental setting, and it has been described in similar environments elsewhere (Pool et al. 1977, Conde and Alarcón 1993, Cantera and Arnaud 1997, Fromard et al. 1998).

Islands and point bars in the Tempisque-Bebedero system are low-energy sedimentary environments, characterized by low salinity, unconsolidated soils in lower intertidal zones and more consolidated soils in upper intertidal zones. In these dynamic, high sedimentation environments, sedimentation is likely to play an important role influencing mangrove structural characteristics. Deposited sediments are not only important for soil vertical accretion but also an important source of nutrients, which can directly affect plant dynamics by stimulating plant growth (DeLaune et al. 1979, Lynch 1989, DeLaune et al. 1990a, Cahoon et al. 1996). Lynch (1989) measured sedimentation and nutrient accumulation in mangroves of the Gulf of Mexico, and showed the importance of nutrient delivery and accumulation through sediment deposition to mangrove productivity.

Sedimentation, through changes in soil elevation and nutrient dynamics, can also influence plant community structure by affecting species composition and zonation (Fujimoto and Miyagi 1993,



Callaway et al. 1997, Day et al. 1999, Duke and Khan 1999, Fujimoto et al. 1999), plant colonization and development (Fujimoto et al. 1996, Alleng 1998, Panapitukkul et al. 1998), and plant physiognomy (Young and Harvey 1996). For example, in the southwestern coast of Thailand, a forest dominated by Rhizophora apiculata changed to a mixed forest dominated by Bruguiera, Ceriops or Xylocarpus spp as a result of an increase in surface elevation (Fujimoto et al. 1999). Extreme sediment deposition, however, can be detrimental to mangroves and other coastal communities (Jurik et al. 1994, Wang et al. 1994, Terrados et al. 1997, Ellison 1998).

The importance of soil physico-chemical variables determining mangrove forest structural characteristics in point bars and islands has not been studied for the Tempisque-Bebedero system. Studies conducted in other regions and under different environmental settings have shown, however, that soil properties are important in influencing species distribution and other community structure characteristics (Pool et al. 1977, Nickerson and Thibodeau 1985, McKee et al. 1988, Ukpong 1992, McKee 1993, Ukpong 1997, Cardona and Botero 1998, Sherman et al. 1998, Chen and Twilley 1999a). Salinity, for example, is a controlling factor for species distribution and productivity for many coastal communities around the world (Soto and Jiménez 1982, Boto and Wellington 1984, Ukpong 1992, Cardona and Botero 1998). Soil pore water sulfide has been correlated to the spatial distribution of Rhizophora mangle and Avicennia germinans in a Bahamas mangrove forest (Nickerson and Thibodeau 1985). In the Shark river estuary of the Everglades National Park, Florida, a nutrient gradient from the estuary mouth to the upper estuary was the controlling factor of mangrove forest species composition, basal area and productivity (Chen and Twilley 1999a).

Biotic factors are also important in affecting mangrove structural characteristics. Intrinsic characteristics are important in determining a species' ability to cope with adverse environmental conditions, and to compete with other species (Ball 1980 and 1988). A number of factors have been determined to influence mangrove zonation and structure, and most of them imply a close biotic-environment relationship. For example, distribution explained by tidal sorting depends on propagule size-weight-floating characteristics and hydrological conditions (Rabinowitz 1978b). Distribution by selective predation depends on crab populations and propagule nutritious properties (Smith 1987, Smith et al. 1989, McKee 1995a). Distribution by competition for space and resources is determined by

interspecific differences in physiological abilities to cope with stressors (e.g., waterlogging, salinity and sulfides), and is highly conditioned by the characteristics of the environment (Clarke and Hannon 1970, Ball 1980 and 1988).

Point bars and islands in the Tempisque-Bebedero system as constructive environments seem to reflect two stages of mangrove development: a young and expanding forest in lower intertidal zones and a more mature forest occupying the more consolidated upper intertidal zones. Differential forest structural characteristics observed across this gradient, including species distribution, likely reflects spatial and temporal variability in physico-chemical factors and biotic effects. Considering mangroves as age-class structured communities, the effect of these factors should be separately analyzed throughout the different stages of development (propagules to seedlings to saplings to trees), for a better understanding of ecosystem dynamics.

During the early phases of mangrove colonization and distribution, propagule dispersal dynamics and establishment is very important (Duke et al. 1998). Both processes are important first steps for colonization and are influenced by such factors as propagule availability, buoyancy, period of obligate dispersal, anchoring time, and hydroperiod (Rabinowitz 1978a, Foote and Kadlec 1988, Schneider and Sharitz 1988, Clarke and Myerscough 1991, Clarke 1993, McGuinness 1997, Panapitukkul et al. 1998). For example, in Biscayne Bay, Florida the absence of *A. germinans* in mangrove forests was attributed to a limited source of propagules and to physical factors affecting propagule dispersal such as direction of winds and currents (Ball 1980). In northern Sweden, the frequency and distribution of vascular plants along river banks was related to seed floating capacity (Johansson et al. 1996, Danvind and Nilsson 1997). In mangroves, those propagules able to remain buoyant and viable for longer periods of time increase the effective range of dispersal (Steinke 1975, Rabinowitz 1978a, Steinke 1986, Johansson et al. 1996, Duke et al. 1998).

Furthermore, when propagules reach a colonizing habitat, other factors become important in determining establishment success and survival, including predation (Louda 1982, Smith 1987, White 1993, McKee 1995a, Dahdouh-Guebas et al. 1998); interspecific competition (Ball 1980, Kangas and Lugo 1990, Clarke and Myerscough 1993, Patterson et al. 1993); flooding (Jiménez and Sauter 1991, Clarke and Myerscough 1993); and soil physical-chemical characteristics (Nickerson and Thibodeau

1985, Patterson and Mendelsohn 1991, Ukpong 1991, McKee 1993, White 1993, Sherman et al. 1998). For example, in Australia, Smith (1987) showed the importance of selective crab predation in determining the intertidal distribution of different mangrove species. In Twin Cays, Belize differential establishment abilities and differential seedling tolerances of physico-chemical conditions were important factors determining spatial recruitment patterns across intertidal zones (McKee 1995b).

Overall, mangroves are a specialized plant community adapted to particular hydrological regimes and physico-chemical characteristics. In many cases, mangroves live under ecological conditions that approach their limit of tolerance, making them sensitive to changes in their habitat. As a result, mangroves are being used, in different regions, as biological indicators of coastal change or sea level rise (Field 1995, Blasco et al. 1996). The stability of mangrove communities under different geomorphic settings, therefore, depends also on the stability of the environment (especially with regards to hydrological patterns) and the ability of mangroves to respond to natural or human induced changes. Currently, coastal environments around the world are being heavily impacted by human activities such as agriculture, aquaculture, and the construction of dikes, dams, channels and impoundments, among others (Day et al. 1995, Twilley 1998, Day et al. 1999). As a result of most of these activities, as well as predicted sea level rise, coastal wetlands are experiencing significant changes in hydroperiod, which modifies their structural characteristics, eventually causing habitat loss (Field 1995). In Ciénaga Grande de Santa Marta, Colombia, for example, a road constructed in the area interrupted the hydrology of the system (water exchange, nutrients and sediment supply), causing the mortality of approximately 21,778 hectares of mangrove forests (Cardona and Botero 1998). Important deltaic systems in United States and Europe such as the Mississippi Delta, the Rhône Delta and Venice Lagoon are currently experiencing severe wetland loss. This is the result of habitat destruction, construction of river dikes, channelization, dams and impoundments, which have altered the natural supply of water, nutrients and sediments within these systems (Day et al. 1995, Day et al. 1999). The Tempisque-Bebedero system in Costa Rica is not an exception to this pattern. Currently, the waters of the Tempisque River are being used to supply an irrigation project of extensive agricultural fields, especially during the dry season. As a result, reduced riverine discharge and increased sediment load seem to be gradually changing the hydrology and natural sedimentation dynamics within the system.

Within the context of ecosystem impact, the system will gradually experience structural changes (reduced establishment, growth and productivity, and variations in species composition and distribution) before habitat is lost, which can be considered as indicators of community impact (Bacon 1994). These changes as a response to natural or human alterations are, however, not always detrimental to the system. Anthropogenic changes may increase sediment or freshwater discharge to the system, and mangrove colonization and growth is enhanced (Augustinus 1995).

In general, mangroves are structurally diverse communities reflecting the great diversity of geomorphic settings within the coastal environment (Thom 1967). Mangrove communities are also characterized by the complexity of their responses to different biotic and physico-chemical variables and human impacts. From this perspective, ecosystem modeling, as a comprehensive approach, is a useful tool in studying mangrove ecosystem dynamics, not only for identifying and establishing important relationships between the plant community and its environment, but also to predict community changes as a response to human induced alterations. The use of modeling to study coastal ecosystem functioning is especially important considering that long-term studies are necessary for a better understanding of the system, but are difficult to conduct. In spite of this, few models have been developed for mangrove communities (Lugo et al. 1976, Burns and Ogden 1985, Clarke 1995, Chen and Twilley 1998 and 1999b, Delgado et al. 1999).

#### **1.1.1. Objectives and Hypotheses**

This dissertation addresses three hypotheses: 1) In active sedimentary environments such as point bars and islands in the Tempisque-Bebadero system, I hypothesize that sedimentation dynamics and hydroperiod act together to create conditions favoring the establishment of Laguncularia racemosa within the lower intertidal zone. 2) I hypothesize that changes in soil physico-chemical characteristics across the intertidal gradient are related to the observed species distributional pattern at point bars and islands. 3) I hypothesize that in this environmental setting, biotic and physical factors affect the intertidal species distribution at point bars and islands by acting upon the early stages of mangrove establishment.

Each hypothesis will be tested within the framework of a designed experiment and headed as a separate chapter. Therefore, the main objectives for each of the three following chapters are: 1) Characterize sedimentation dynamics in point bars and islands and test its relationship to mangrove

community structure. 2) Characterize soil physico-chemical characteristics across the intertidal zones of point bars and islands and relate them to mangrove structural characteristics, especially species distribution. 3) Determine the importance of various biological and physical properties of mangrove propagules and the mangrove environment, which make Laguncularia a successful colonizer of lower intertidal zones in point bars and islands.

The main objective of this present chapter is to develop a conceptual model within which the three specific hypotheses given above can be understood within a larger ecosystem framework. The model therefore explores the main relationships between biotic and physico-chemical factors and the mangrove community, setting the stage for field studies to address their relative importance in explaining the mangrove structural characteristics at point bars and islands in the Tempisque-Bebedero system.

It is my concern that the present and projected increase in the usage of Tempisque river water for irrigation might cause significant alterations to the plant communities in the Tempisque-Bebedero system, especially mangroves. Considering the ecological and socio-economic importance of these mangrove communities, the use of modeling to predict their responses to altered hydrological conditions becomes of great value for both management and legal purposes. The development of a conceptual model, however, is only the first step to this goal and should be followed by comprehensive field and literature data collection.

## **1.2. THE TEMPISQUE-BEBEDERO ESTUARINE SYSTEM**

The Tempisque-Bebedero estuarine system is located in the northern region of the Gulf of Nicoya, a tropical estuary on the Pacific Coast of Costa Rica (Figure 1.1). This estuary is the second most important region colonized by mangroves in the country, covering an area of approximately 15 176 ha (Jiménez and Soto 1985, Jiménez 1994). Climatically this area is a low-land dry tropical forest life zone (Holdridge 1967). Rainfall varies from less than 50 mm month<sup>-1</sup> during the dry season (December through April) to over 600 mm month<sup>-1</sup> during the rainy season (May through November). The annual precipitation for the region is between 1500 and 2000 mm (Peterson 1960).

During the dry season, especially in December, January and February, strong northeasterly winds (up to 55-65 km hr<sup>-1</sup>) blow for periods of one half to four or five days (Peterson 1960). These winds are responsible for water column mixing and re-suspension of shallow deposits (Peterson 1960),

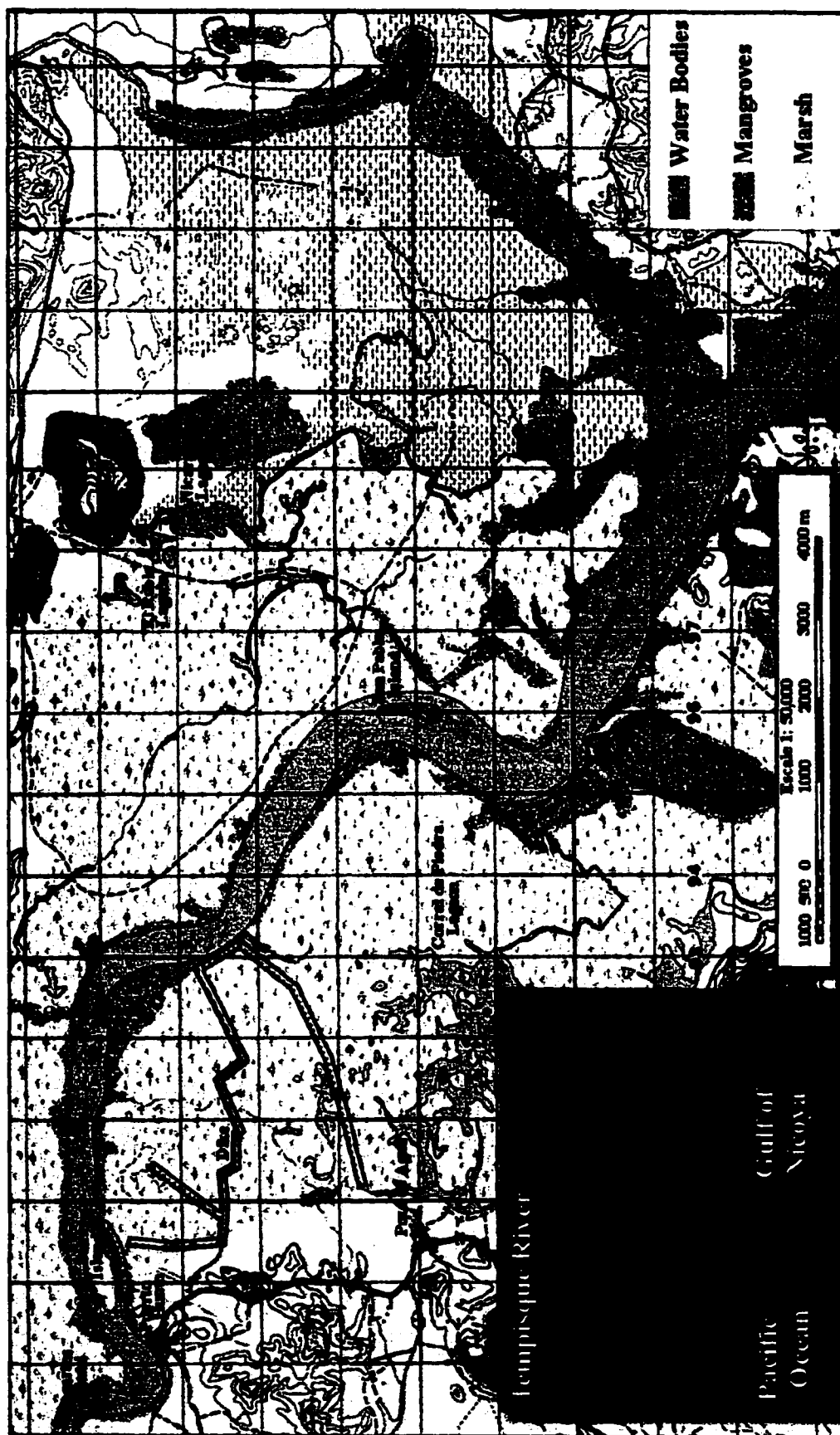


Figure 1.1. Map of the Tempisque-Bebedero estuarine system, Gulf of Nicoya, Pacific coast of Costa Rica.

and the Tempisque River is the most turbid at this time (pers. obs.). During the rainy season, Costa Rica lies within the tropical low-pressure zone, or doldrums, and the prevalent northerly winds of the dry season are replaced by predominantly southwesterly winds (Peterson 1960). During this time of the year episodic storm events with high precipitation will occasionally cause flooding in the lowlands along the alluvial plain.

The Tempisque river watershed is the largest of the country with an extension of 4 952 km<sup>2</sup> (Bravo et al. 1991), and an average annual discharge of 27.4 m<sup>3</sup> s<sup>-1</sup> (Source: Instituto Costarricense de Electricidad, ICE, Costa Rica). This river is the most important source of fresh water, sediment and nutrients to the upper Gulf of Nicoya (Epifanio et al. 1983, Voorhis et al. 1983), and follows very closely the seasonal regime of precipitation in the region (Figure 1.2). Typical discharges of the Tempisque River at the height of the rainy season are between 40-60 m<sup>3</sup> s<sup>-1</sup> (Figure 1.2).

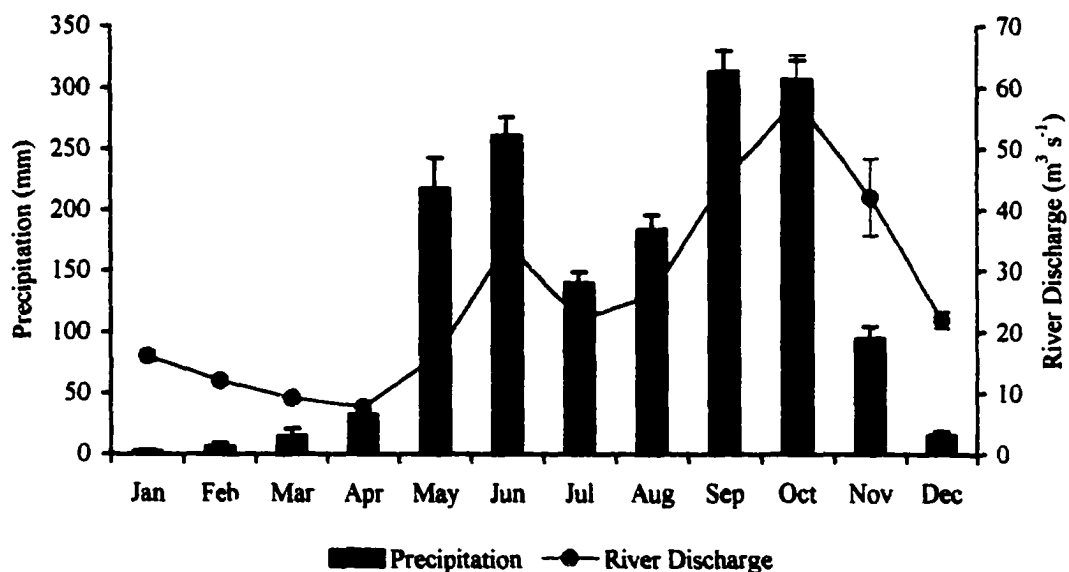


Figure 1.2. Precipitation vs. Tempisque River discharge. Precipitation is given as an average for the period: 1927-1999 and river discharge for the period: 1951-1993. Dry season: December through April, rainy season: May through November.

Tides in the Gulf of Nicoya are dominated by the semi-diurnal lunar tide, but are complicated by semi-diurnal harmonics and a small diurnal component (Voorhis et al. 1983). Tide amplitude is determined by the gulf's bathymetry and shape (Voorhis et al. 1983). Within the Tempisque-Bebedero

system the tide effect can be observed as far as 30 km upstream. The tidal range varies from two to three meters, and its significant influence within the system is evident since the river current direction always follows that of the tide.

In summary, the hydrology within the Tempisque-Bebedero estuarine system is controlled by three main forcing functions: precipitation, river discharge and tides. In addition to the expected fluctuations of these factors as a function of seasonality, episodic natural events are also important determining overall changes of the hydroperiod within the system. Precipitation and river discharge, for example, are modified by the occurrence of sporadic tropical storms, which are associated with very high precipitation, and occasionally flooding within the river basin. River discharge is lower during the dry season not only because of reduced rainfall but also because of the intensive use of river water for agricultural irrigation.

Similar to many other important riverine and estuarine systems around the world (Day et al. 1995, Hensel et al. 1998, Day et al. 1999) the Tempisque and Bebedero have been impacted by human activities. Recently, an extensive network of channels was constructed within the Tempisque basin, which is used especially during the dry season for irrigation of extensive rice fields, melon, sugarcane, and other crops. During this time of the year, a large amount of water from the river is pumped out, and eventually drains back into the Tempisque, loaded with sediments (Ministerio de Ambiente y Energía officials, MINAE, pers. comm). As a result, a reduced riverine discharge and increased sediment load seems to be changing the hydrology and natural sedimentation dynamics within the system, especially as regards the development of islands and point bars. It is likely that this reduction in discharge has caused increases in the tidal prism, tidal currents, and the maximum extent of salinity intrusion upstream. In contrast, the Bebedero, which joins the Tempisque several kilometers downstream, has an increased riverine discharge due to the drainage of water from an adjacent watershed, which is used for both hydroelectric power generation and agricultural irrigation.

The Tempisque-Bebedero is a very dynamic system, and geomorphological changes are evident within short time periods. Lagartos Island (Figure 1.1), for example, an approximately two hectare island now dominated by Laguncularia, emerged from a sand bar in the Tempisque River only 20 years ago, according to MINAE officials. During the past two years this island became attached to the mainland, as



a result of sediment accumulation. The presence of active accreting and erosive environments are characteristic. At river meanders, sediments are mostly deposited in the low energy environments or point bars, while erosion takes place in the opposite cut banks. As sediments are deposited surface elevation increases, and eventually newly formed land is plant colonized.

Mangroves are the dominant plant communities colonizing point bars and islands and seem to show a characteristic zonation, possibly controlled by both environment physical characteristics and specific plant tolerances and growth strategies. Laguncularia racemosa, a shade-intolerant species, with small and abundant propagules and tolerant of a wide range of salinities, successfully colonizes the emergent mud banks and lower intertidal zones in the Tempisque-Bebedero estuary. Other mangrove species such as Rhizophora racemosa, Pelliciera rhizophorae, Avicennia germinans and A. bicolor are also found, but are distributed differently along the intertidal gradient. The presence of Laguncularia covering the fringe zone does not follow the typical distribution generally described for mangrove communities in the New World (Lugo 1990, Thom 1967, Ball 1980), but seems to be characteristic of this environmental setting. This particular distribution has been described in similar environments elsewhere (Pool et al. 1977, Conde and Alarcón 1993, Cantera and Arnaud 1997, Fromard et al. 1998). Along the cut banks, R. racemosa is the main species fringing the channels. Laguncularia is always absent, and Avicennia and Pelliciera are sometimes present. These observations suggest that mangroves found on the edges of cut banks represent upper intertidal zones of a previous point bar that has been eroded away. Within this estuarine system, point bar and islands, which represent the most active depositional (constructive) geomorphic settings are probably the most sensitive areas to human-induced changes in hydrology, because they are the youngest, most un-consolidated environments, and the most susceptible to erosion and compaction.

### **1.3. A CONCEPTUAL MODEL OF MANGROVE STRUCTURE DYNAMICS**

The conceptual model integrates different biotic and physico-chemical factors, which were considered to be the most important in determining mangrove structural characteristics at point bars and islands in the Tempisque-Bebedero system (Figures 1.3 and 1.4). This model is a simplified version of the factors and interrelationships that describe the system under natural conditions. In view of

## Module 1

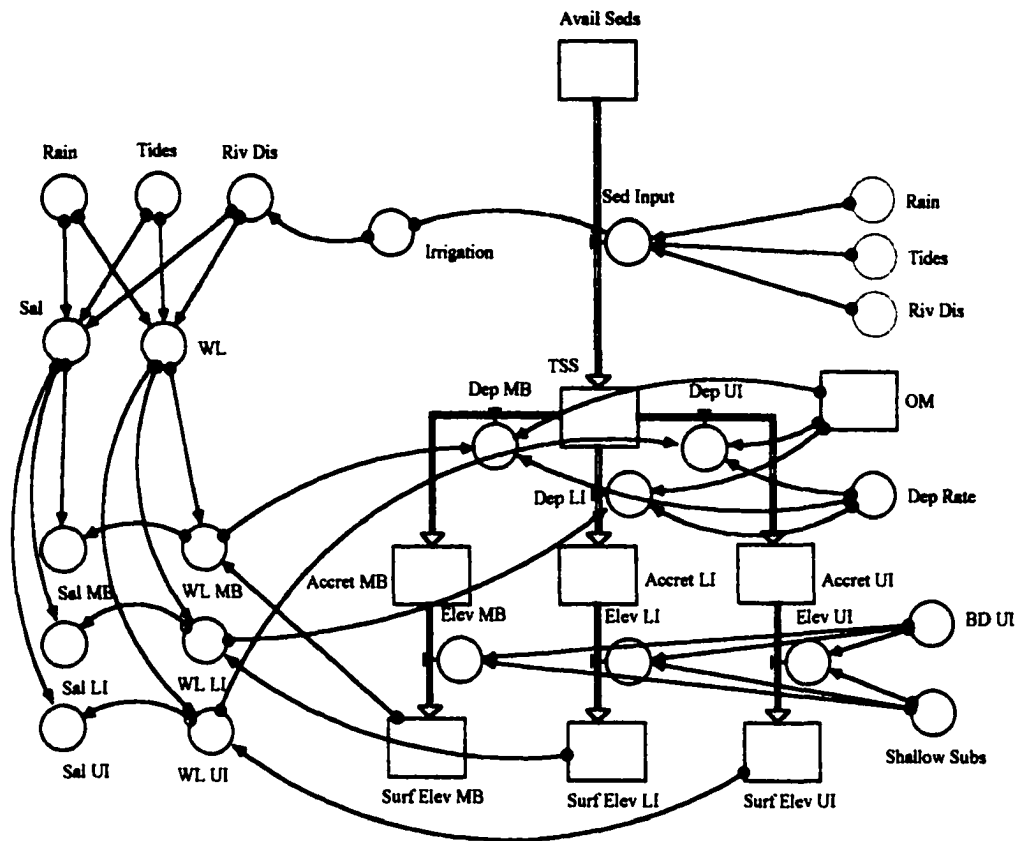


Figure 1.3. Conceptual model of mangrove structure dynamics (Stella® diagram) showing Module 1: sedimentation dynamics. State variables are rectangles, circles are forcing functions, pipes with circles attached are fluxes between state variables, and arrows are interactions. Other abbreviations are as follows: Avail Seds=available sediments, Riv Dis=river discharge, Sal=salinity, WL=water level, TSS=total suspended sediments, Accret=accretion, Surf Elev=surface elevation, OM=organic matter, Dep Rate=deposition rate, BD=bulk density, Shallow Subs=shallow subsidence, MB=mud bank, LI=lower intertidal, and UI=upper intertidal.

management practices, a simplified model incorporating the main relationships has more practical value because it can be transformed to a working model with sufficient field and literature data collection.

For practical reasons the model was divided into four interrelated modules: 1) sedimentation dynamics, 2) propagule dispersal and establishment, 3) soil physico-chemical variables, and 4) forest structure. Each module will be presented separately and its connections to other modules addressed. Because mangrove structure at point bars and islands shows a distinctive zonation across the intertidal gradient, each module will include three separate intertidal zones, based on differences in elevation and frequency and duration of flooding. The first zone is the mud bank region (MB), characterized by a

## Module 2

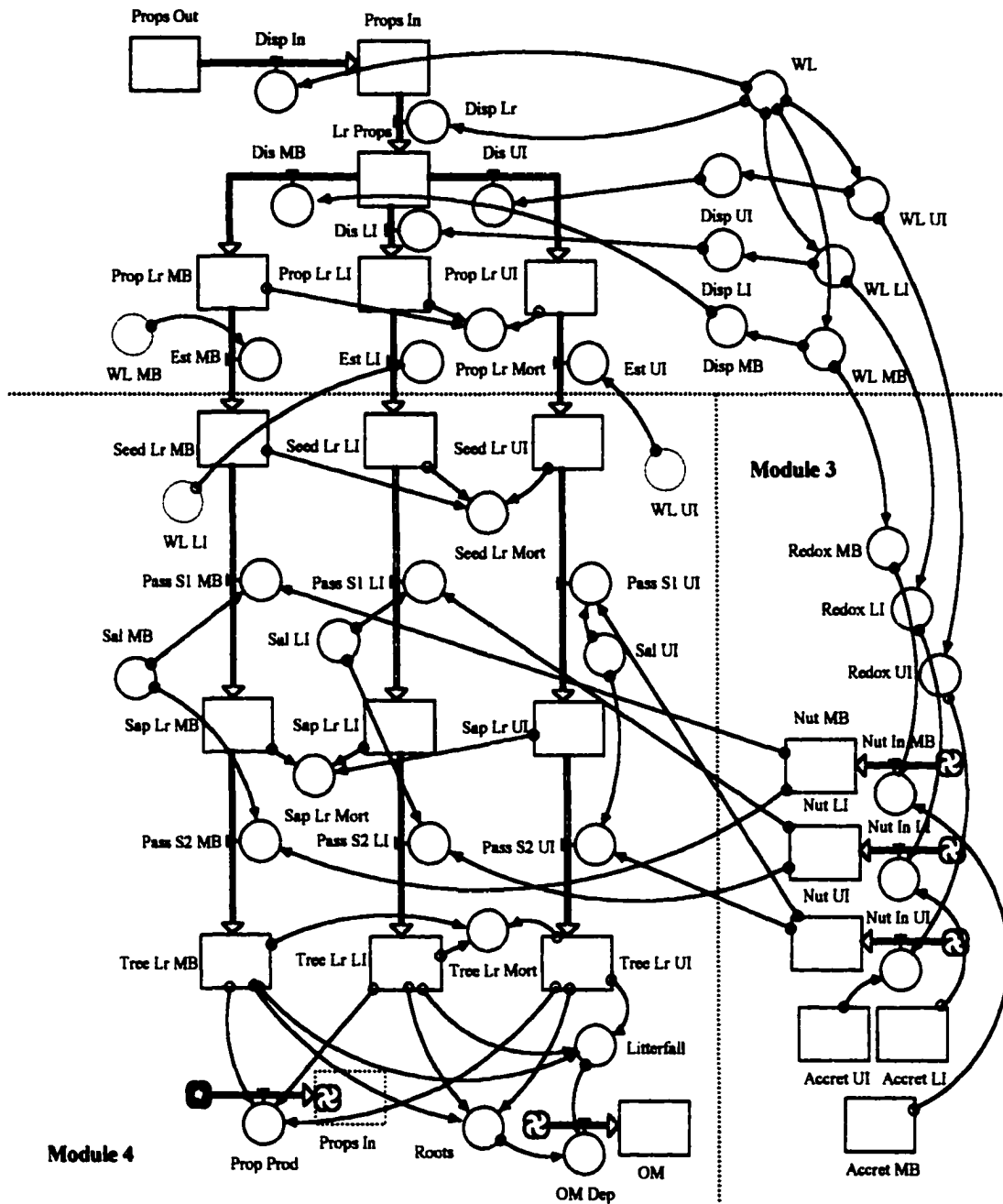


Figure 1.4. Conceptual model of mangrove structure dynamics (Stella® diagram) showing modules 2, 3 and 4: propagule dispersal and establishment, soil physico-chemical variables, and forest structure, respectively. State variables are rectangles, circles are forcing functions, pipes with circles attached are fluxes between state variables, and arrows are interactions. Other abbreviations are as follows: Lr=*Laguncularia racemosa*, WL=water level, Props=propagules, Disp=dispersal, Mort=mortality, Seed=seedling, Sap=sapling, Sal=salinity, Nut=nutrients, OM=organic matter, Accret=accretion, MB=mud bank, LI=lower intertidal, and UI=upper intertidal.

relatively lower elevation and higher frequency and duration of flooding. The second zone is the lower intertidal zone (LI) characterized by values of elevation and flooding intermediate between the MB zone and the third zone or upper intertidal zone (UI). Even though several species of mangroves colonize point bars and islands, the model only includes Laguncularia. Other species (Rhizophora and Avicennia), however, can be easily added.

#### **1.3.1. Module 1: Sedimentation Dynamics**

Sedimentation dynamics in the Tempisque-Bebedero system is regulated by the hydroperiod of the region. Rainfall, tides and river discharge are the main sources of water and sediments within the system (Figure 1.3). Rainfall is especially important during the rainy season by increasing water runoff and sediment transport from upland deforested areas into the rivers. During the rainy season the average discharge of the Tempisque River increases from approximately  $13 \text{ m}^3 \text{ s}^{-1}$  to  $35 \text{ m}^3 \text{ s}^{-1}$  (Figure 1.2). Semidiurnal tides in combination with river discharge are the most important factors controlling material fluxes (water, sediments and nutrients) between the mangroves and the adjacent water body. Ground water was not considered within the model, but its importance should be further investigated.

Irrigation is an important external factor modifying river discharge and sediment input to the system (Figure 1.3). During the dry season, when the Tempisque river discharge is the lowest, a large proportion of its discharge is extracted and pumped through an extensive network of channels for irrigation of agricultural fields. Eventually, some of this water flows back into the river with high sediment concentrations.

As total suspended sediments (TSS) are transported through the system, sediment deposition takes place, especially in low energy environments formed by point bars and islands. Mangroves and other coastal environments generally show an intertidal sedimentation gradient, with decreasing sediment deposition towards interior wetland areas (French and Spencer 1993, Furukawa and Wolanski 1996). This gradient is mainly controlled by the hydroperiod, where zones with higher frequency and duration of flooding will normally experience higher sedimentation (Conner and Day 1991, Cahoon et al. 1996, Kemp et al. 1999). Therefore, in the model, the distribution of sediments across the intertidal gradient is controlled by the water level, which is specified by intertidal zone (MB, LI and UI, Figure 1.3). Sediment deposition results in vertical accretion but a number of factors influence surface elevation

change (Cahoon et al. 1999). These include erosion and shallow subsidence, which is caused by compaction, de-watering and decomposition. Surface elevation then feeds back on water level such that as soil elevation changes, the flooding regime will also change.

Interstitial soil salinity, a component of module 3, is controlled by tides, rain and river discharge (Figure 1.3). Tides are the main source of salts to the system by bringing saltier waters from the Gulf of Nicoya. Salinity is decreased as saltier water from the Gulf is mixed with fresh water from the rivers and rainfall. Water level is also modified by rain, tides and river discharge and is a very important forcing function within the system (Figure 1.3). Its influence can be observed throughout the different components of the model. There is a strong seasonality in sedimentation dynamics indicating that a temporal component should be added for purposes of running the model.

### **1.3.2. Module 2: Propagule Dispersal and Establishment**

An important mechanism influencing spatial mangrove distribution is propagule dispersal (Rabinowitz 1978b, Duke et al. 1998). The propagule population pool in a particular area is formed by those propagules produced within the area and those brought in from outside the area. The dispersal of these propagules throughout the intertidal gradient is mainly controlled by the water level (Figure 1.4). Less frequently flooded environments (UI) will experience more limited propagule dispersal than more frequently flooded environments (MB and LI). In addition to water level, other factors such as the presence of herbaceous vegetation and debris on the forest floor and interspecific differences in propagule characteristics (buoyancy, propagule size, etc.) also affect propagule dispersal (Rabinowitz 1978b). For simplification of the model, water level was the only factor considered influencing dispersal.

Propagule mortality, as a result of loss of viability, desiccation and/or predation, represents an indirect control of establishment by modifying propagule availability. Water level, however, can act directly on establishment by limiting propagule contact with the forest floor necessary for stranding. Some mangrove species such as Avicennia germinans seem to require low water levels to be able to establish (McMillan (1971). Strong water movement sometimes associated with tidal flooding can also have a negative impact on propagule establishment success by limiting stranding (Clark and Myerscough 1993, McKee 1995b).

### **1.3.3. Module 3: Soil physico-Chemical Variables**

Hydroperiod is an important forcing function acting upon soil physico-chemical characteristics in coastal environments (Mitsch and Gosselink 1986). Flooding conditions, expressed as water level in the model (Figure 1.4), have confounding effects on the soil nutrient pool. Through flooding, soils are exposed to dissolved and particulate nutrients in the water column. Also, by modifying the redox potential of the soil, flooding affects chemical transformations occurring within the soil, thus influencing nutrient availability for plant uptake (Mitsch and Gosselink 1986, Clough 1992).

Soil nutrient concentration in mangrove ecosystems is an important factor affecting plant growth and productivity (Boto and Wellington 1983, Feller 1995, Feller et al. 1999). Represented as a “black box” within the model, soil nutrients include a wide variety of elements (Ca, K, Mg, TN, NO<sub>3</sub>, NH<sub>4</sub>, P, etc.). Their individual concentration within the soil, and availability for plant uptake, is differentially affected by the soil conditions and in some cases conditioned by the presence or absence of another element.

Three important sources of nutrients are identified in the model: dissolved elements in the water column, from suspended sediments deposited on the soil (accretion), and as a result of organic matter deposition (Figure 1.4). The relative importance of each source contributing to the nutrient pool is still unknown for this environment and requires further research. The dynamics of organic matter in mangrove systems are affected by both biological and physical factors (Twilley 1998, Chen and Twilley 1999a). The main sources of organic matter in the model are litterfall and root growth (autochthonous source, Figure 1.4). Import of organic matter to the system (allochthonous source) was not included in the model, mainly because in this system it is minor compared to *in situ* organic matter deposition. In addition of being a source of nutrients, organic matter also contributes to soil vertical accretion (Nyman et al. 1990). Organic matter deposition, especially under environments of restricted hydrology, can represent the most important source of accretion, as compared to mineral matter deposition in other environments (DeLaune et al. 1990b, Nyman et al. 1990).

### **1.3.4. Module 4: Forest Structure**

This module represents the distribution of Laguncularia, as stem density, during different life stages (propagules, seedlings, saplings and trees) and across the intertidal gradient (Figure 1.4). By

considering rates of growth, mortality and transition to the next age class, it is possible to model changes in the population structure through time (Delgado et al. 1999). It is also possible to predict changes in the forest structure caused by alterations to the system, for example, a drastic change in the system hydroperiod. By modifying factors such as water level within the model, and supplying the model with basic information about the effect this change will have on the different life stages (in terms of mortality, growth or productivity), it is possible to predict the population response within a particular time frame.

#### **1.4. HYPOTHESES TESTING WITHIN THE FRAME OF THE CONCEPTUAL MODEL**

Ecosystem Models are simplified versions of the complex natural environment they represent. Therefore, hypothesis testing derived from the model generally considers the most important relationships among the myriad of forcing functions and state variables. Hypotheses proposed in this study are addressed within the model based on several important relationships. The first hypothesis, which considers the effects of sedimentation and hydrology on mangrove forest structure, is based on the relationship between surface elevation and water level (Figure 1.3). As flooding regimes are modified through sedimentation and elevation change, species' responses to the changing environment are reflected through their establishment ability (Figure 1.4), which is a very important step determining initial community development, later reflected in species distributional patterns.

The second hypothesis, which addresses soil physico-chemical characteristics and mangrove forest structure, was simplified in the model by considering two main relationships. Nutrient concentrations within the soil, as the end result of a chain of prior interactions between physical and chemical factors (Figure 1.4), affects mangrove structure by enhancing or diminishing growth potential and ultimately transition from one life stage to the next (Figure 1.4). Salinity, often considered a stressor in coastal environments, also affects forest structure by modifying transition rates (Figure 1.4). Interspecific differences in salt tolerance can also define specific patterns of species' dominance across the intertidal gradient.

The third hypothesis focuses on species' establishment ability in relation to species distribution, propagule availability, dispersal, and water level. It is clear that establishment is limited by propagule availability (in situ and also a function of species distribution and propagule dispersal). The importance of water level is understood as it affects not only dispersal, but also subsequent establishment. It is also

clear that this third hypothesis is directly related to the first as it involves the relationship between sediment elevation and water level. The link with the second hypothesis is given at post-establishment stages, leading up to the observed mangrove forest distribution patterns.

In order for a model to be useful, it must be understandable and must generate useful predictions. The ease of understanding is often a compromise with complexity and accuracy. In this given conceptual model of mangrove distribution in the Tempisque-Bebedero estuary, complexity is sacrificed for the ability to test and understand general relationships, which are considered important in system function. Regarding the usefulness of predictions, it is important to note that although other mangrove succession models have been generated, they address succession at different stages or are developed for environments quite different from the given estuary. These differences necessarily affect the utility of model predictions. The current work is therefore not intended to generate a broad model that may be applicable to mangrove settings elsewhere, although the insights gained can certainly help in the understanding of other systems. It is hoped that the ensuing elaboration of model relationships might provide useful predictions concerning mangrove forest responses to such conditions as are projected with current and planned hydrological modifications to the Tempisque-Bebedero estuary.

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## **CHAPTER 2.**

### **SEDIMENTATION DYNAMICS AND MANGROVE COMMUNITY STRUCTURE AT POINT BARS AND ISLANDS IN THE TEMPISQUE-BEBEDERO ESTUARINE SYSTEM, GULF OF NICOYA, COSTA RICA**

## 2.1. INTRODUCTION

Sedimentation represents a very important forcing function in coastal ecosystems. Either directly or indirectly, sedimentation often controls soil formation, hydroperiod and plant community development in the intertidal zone (DeLaune et al. 1979, Lynch 1989, DeLaune et al. 1990a, Cahoon et al. 1996). As sediments are deposited, vertical accretion results in an increase in surface elevation, which reduces the frequency and duration of flooding, thereby affecting the hydrological regime. Plant species are distributed according to often narrow tolerances to hydroperiod (Jiménez et al. 1985, Blasco et al. 1996); any sustained changes in hydroperiod can therefore affect species composition. In this way, sedimentation can ultimately affect plant colonization and development in coastal environments. In Segara Anakan, Indonesia, for example, an increase in sediment transport by local rivers caused a rapid extension and exposure of tidal flats, which was then followed by mangrove colonization (Erftemeijer et al. 1988, in Augustinus 1995).

The relationship between sedimentation, hydroperiod and vegetation, however, is not a simple one. Hydroperiod feeds back into the sedimentation process by controlling sediment delivery throughout the intertidal gradient and by changing pore water storage in the substrate, which ultimately influences elevation (Cahoon et al. 1999). Vegetation, on the other hand, affects sediment deposition by reducing water current velocities and inducing suspended sediment settling (Augustinus 1995). Many studies have demonstrated that high vegetation density and the presence of mangrove prop-roots, pneumatophores and pneumathodes decrease water velocities and increase sediment deposition (Pestrong 1972, Spenceley 1977, Furukawa and Wolanski 1996, Young and Harvey 1996). Sediment binding by rootlets was also shown to be important to prevent erosion in mangroves (Spenceley 1977). Vegetation can also affect soil formation through biomass accumulation in the root zone and through organic matter deposition on the soil surface (e.g. litterfall; DeLaune et al. 1990b, Nyman et al. 1990). This contribution of organic matter to soil formation is very important especially in areas of little inorganic sedimentation, for example, low energy environments with restricted hydrology.

Deposited sediments represent not only a source for soil vertical accretion but also an important source of nutrients. Research, mainly conducted in marsh ecosystems, has shown that through this nutrient supply, sediment deposition can indirectly affect plant dynamics by stimulating plant growth

(DeLaune et al. 1979, Lynch 1989, DeLaune et al. 1990a, Cahoon et al. 1996). Sediment and nutrient accumulation have also been shown to affect mangrove growth rates and productivity (Lynch 1989, Ellison and Farnsworth 1996).

Through changes in sediment elevation and nutrient dynamics, sedimentation can affect plant community structure in the coastal zone, such as species composition and zonation (Fujimoto and Miyagi 1993, Callaway et al. 1997, Day et al. 1999, Duke and Khan 1999, Fujimoto et al. 1999), plant colonization and development (Fujimoto et al. 1996, Alleng 1998, Panapitukkul et al. 1998), and plant physiognomy (Young and Harvey 1996). For example, in the southwestern coast of Thailand, as a result of an increase in surface elevation, a mangrove forest dominated by Rhizophora apiculata changed to a mixed forest dominated by Bruguiera, Ceriops or Xylocarpus spp (Fujimoto et al. 1999).

Sedimentation is a very dynamic process, and there are different factors which determine the spatial-temporal patterns of sediment deposition in coastal wetlands, including geomorphological setting, sediment availability, hydrology (river discharge, tides, freshwater runoff), climatic conditions (wind, storms), and human impacts such as impoundment (Thom 1967, Conner and Day 1991, Augustinus 1995, Cahoon et al. 1995b, Allison et al. 1996, Hensel et al. 1998, Day et al. 1999, Hensel et al. 1999). Differential sediment deposition can occur within a same site as a result of elevation differences, which determine frequency and duration of flooding and therefore sediment availability. Episodic climatic conditions, especially wind and storm events affect the temporal variability of sedimentation (Day et al. 1997).

In the northern region of the Gulf of Nicoya, on the Pacific Coast of Costa Rica, the Tempisque and Bebedero rivers form a very dynamic estuarine system, where the transport of high sediment loads has resulted in the development of islands and point bars. Mangroves are the dominant plant communities colonizing these environments and seem to show a particular zonation, possibly controlled by both environment physical characteristics and specific plant tolerances and growth strategies. The objective of this study is therefore to characterize sedimentation dynamics and test its relationship to mangrove community structure. The study will focus on point bar and island environments, which represent the most active depositional (constructive) geomorphological settings. They are the youngest, most un-consolidated environments, and the most susceptible to erosion and compaction. The main

hypothesis, therefore, that will be addressed is the following: in point bars and islands, unstable sedimentary environments, sedimentation patterns and flooding regimes across the intertidal gradient are important factors conditioning forest structure characteristics of the associated mangrove communities, especially species distribution.

## **2.2. STUDY AREA**

The study was conducted in the mangrove forests of the Tempisque-Bebedero estuarine system in the northern Gulf of Nicoya, a tropical estuary in the Pacific Coast of Costa Rica (Figure 2.1). This estuary is the second most important mangrove region in the country, covering an area of approximately 15 176 ha (Jiménez and Soto 1985, Jiménez 1994). Climatically this area is a low-land dry tropical forest life zone (Holdridge 1967). Rainfall varies from less than 50 mm month<sup>-1</sup> during the dry season (December through April) to over 600 mm month<sup>-1</sup> during the rainy season (May through November). The Tempisque River forms the biggest watershed of the country with an extension of 4 952 km<sup>2</sup> (Bravo et al. 1991). It is the most important source of fresh water, sediment and nutrients entering the upper Gulf of Nicoya (Epifanio et al. 1983, Voorhis et al. 1983).

### **2.2.1. Hydrology**

The hydrology of the mangrove communities in the Tempisque-Bebedero estuarine system is dominated by three main forcing functions: precipitation, freshwater input from the rivers, and tides. The annual precipitation for this region falls between 1 500 and 2 000 mm (Peterson 1960). During the rainy season, episodic storm events with high precipitation will occasionally cause flooding within the lowlands along the alluvial plain (pers. obs.). During the dry season, river discharge and tidal flooding become the dominant forcing functions controlling the hydrology in the mangrove community. To a lesser degree, strong waves caused by strong northeasterly winds also affect transport of water and re-suspended sediments in and out of the lower intertidal zone (pers. obs.).

The mean annual discharge of the Tempisque River is 27.4 m<sup>3</sup> s<sup>-1</sup> (Source: Instituto Costarricense de Electricidad, ICE, Costa Rica), with typical discharge values that vary between 40-60 m<sup>3</sup> s<sup>-1</sup> during the peak of the rainy season (Figure 1.2). River discharge is low during the dry season due to the decrease in rainfall and the intensive use of river water for agricultural irrigation. The Bebedero, in

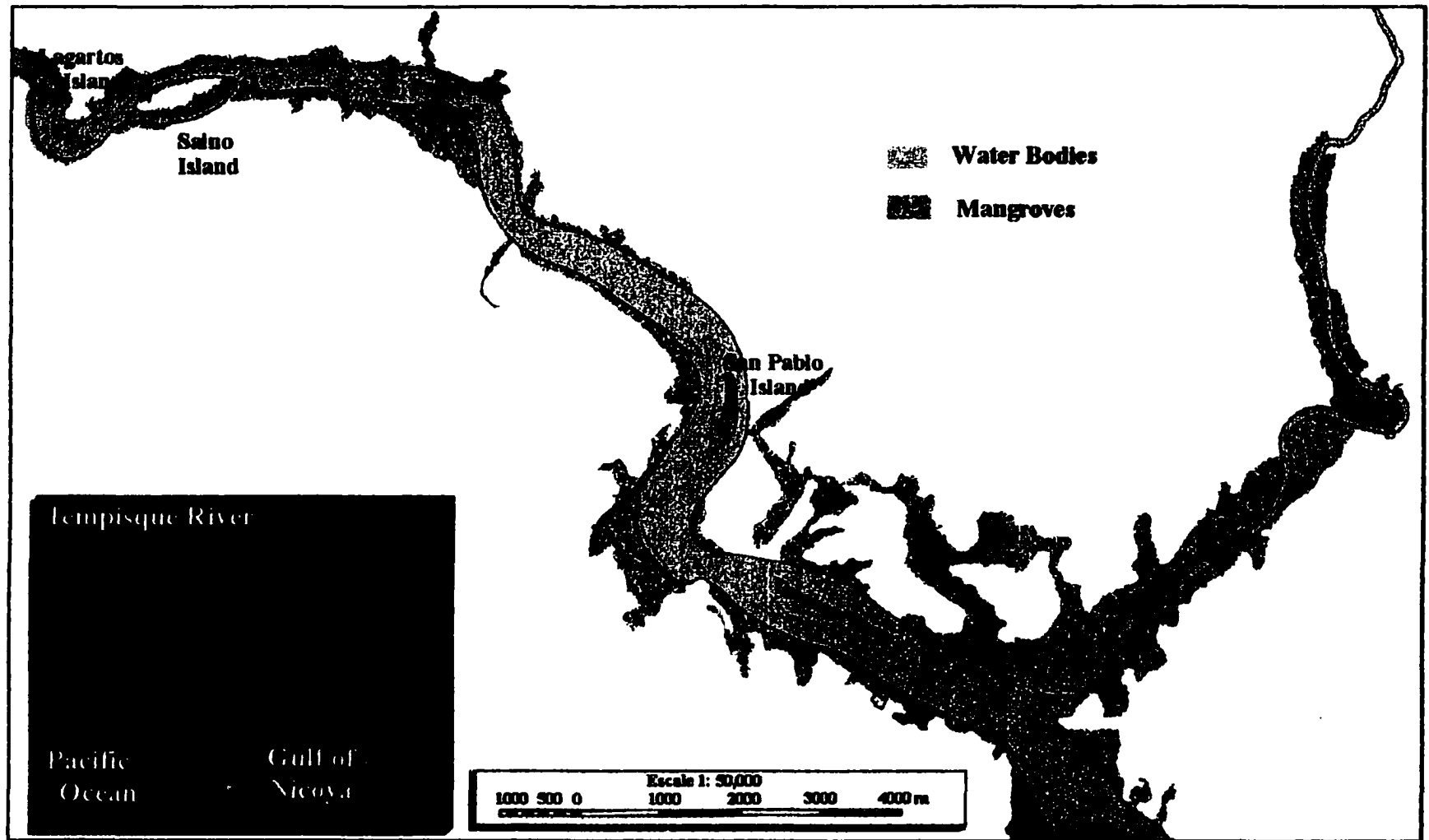


Figure 2.1. Map of the Tempisque-Bebedero estuarine system showing the study areas, numbered from one to six.

contrast, has experienced an increased discharge due to the drainage of water from an adjacent watershed. Under natural conditions, however, inter-annual variation of discharge for both rivers is typically 200%-300% (Voorhis et al. 1983). Tide is semi-diurnal with a range of 2-3 meters, and propagates as far as 30 km upstream.

### **2.2.2. Human Impacts**

Recently, an extensive net of channels was constructed within the Tempisque basin, which is used especially during the dry season for irrigation of extensive agricultural fields. During this time of the year a large amount of water from the river is pumped out, and eventually drains back into the Tempisque, loaded with sediments (MINAE, Ministerio de Ambiente y Energia officials, pers. comm) As a result, a reduced riverine discharge and increased sediment load seems to be changing the hydrology and natural sedimentation dynamics within the system. In contrast, the Bebedero, which joins the Tempisque several kilometers downstream, has an increased riverine discharge due to the drainage of water from an adjacent watershed, which is used for both hydroelectric power generation and agricultural irrigation.

## **2.3. METHODS**

### **2.3.1. Experimental Design**

The experimental design considered three study areas in each of the Tempisque and Bebedero rivers (Figure 2.1). Within each study area three plots of approximately 20 x 15 m were randomly established along the intertidal gradient: lower (LI), middle (MI), and upper intertidal (UI), for a total of three plots per area, or 18 plots in all. The only exceptions to this design were during the measure of surface elevation, which included only LI and UI zones. All data was grouped according to season (dry and rainy seasons), river (Tempisque and Bebedero rivers) and intertidal zone (LI, MI and UI).

The general experimental design used for data analyses consisted of a split plot design. Analyses of variance were conducted to test for the effect of season, river and intertidal zone, and the effect of river, species and intertidal zone for the sedimentation and forest structure data, respectively. Because of frequent unbalanced data and missing values, data analyses were conducted using Proc Mixed (SAS Inst. 1992). Residuals were always checked for normality and the data were transformed as needed. The study was carried out from April 1998 to June 2000.

### **2.3.2. Hydrology**

Maximum water levels were recorded at the LI and UI plots at each study area at approximately two week intervals during the first year of study (August 98 – June 99). Maximum water level was recorded as the filling of small plastic bottles attached at 5cm intervals to a marked pole, up to a height of about 1.5m. Estimates of flood duration at mud bank (MB), LI, MI and UI zones were made for study areas 1 and 2 in December 1998 and for study areas 1,2, 4 and 6 in February 2000. The initial and final time of flooding per zone was registered for a tidal cycle (12-h period: including flood and ebb tides), the difference between the two gave an estimate of total flooding time per zone. Because these observations were conducted during the dry season and around the time of highest tides (full and new moon), these measurements represent a maximum estimate. In addition, relative elevation profiles for four of the study areas (areas # 1, 2, 4 and 6, Figure 2.1) were made by taking water level measurements at 1-5 m intervals along a transect across the intertidal zones. An analysis of variance following a split plot design was conducted to test for differences in maximum water levels by season, river and zone. For study areas 1, 2, 4 and 6, separate ANOVAS were conducted to test for significant differences in relative elevation among intertidal zones within each area.

### **2.3.3. Total Suspended Sediments**

Total suspended sediments (TSS) was measured from water samples collected along the main river channels, and within the forest following the intertidal gradient. A total of eight samples per river (Tempisque and Bebedero) were collected along the main stream during the dry season. An additional seventeen water samples were collected during the rainy season, but only for the Tempisque River. During the dry season, a total of 14 water samples for study area 1, and 22 samples for study area 3 were collected within the forest during flood and ebb tides and across the intertidal gradient. For all TSS analyses an aliquot of 10 ml per water sample was drawn with a 60 cc plastic syringe rinsed with sample water and filtered through pre-weighed Whatman® 2.5 cm GFF glass-fiber filters. In the laboratory, the filters were dried at 60 °C for 48 hrs and weighed for total suspended sediments (TSS).

Differences in dry-season riverine TSS between the Tempisque and Bebedero rivers were evaluated with a t-test, since data for both rivers were only available in this season. The effect of seasonal differences in TSS was evaluated in the Tempisque using another t-test. For study areas 1 and 3, an

ANOVA was conducted to test for significant differences in TSS among intertidal zones for each ebb and flood tides.

Short-term sedimentation, vertical accretion and soil elevation change were measured for all study areas across the intertidal gradient, by using three different methods: filter traps, marker horizons, and the surface elevation table (SET, Boumans and Day 1993). Filter traps were used to measure sediment deposition on a weekly basis (Reed 1992). Marker horizons were used to measure vertical accretion, which reflects superficial sedimentation through deposition of mineral matter and organic debris, and surface root growth (Cahoon and Turner 1989). The SET technique was used to measure surface elevation change, which reflects both vertical accretion and subsurface processes such as compaction, decomposition, de-watering, swelling, shrinkage and root growth (Boumans and Day 1993, Cahoon and Lynch 1997).

#### **2.3.4. Short-term Sedimentation**

Triplicate ash-less 9cm diameter filter traps were placed in each plot (LI, MI and UI) for each of the six study areas, for a total of 54 filters per sampling period. Due to disturbance by crabs and other animals, a modification to the original method included the use of small chicken-wire enclosures and the soaking of the filters in gasoline (Hensel et al. 1998). Filters were replaced approximately every two weeks for a year (July 1998 – June 1999), and included sampling during both the dry and rainy seasons. Samplings were considered independent, since they were made with replacement. Filters collected from the field (including sediments plus any type of organic material deposited on top of the filter area) were dried at 60 °C for 3-4 days and weighed to obtain total dry weight of sediment deposition per filter per sampling period. Short-term sedimentation was then expressed as  $\text{g m}^{-2} \text{d}^{-1}$ , and an averaged value per area, zone and sampling period was calculated ( $n=3$ ). Correction factors for filters partially damaged by crabs or other organisms were applied when necessary.

To obtain an estimation of combustible organic matter (COM) filters plus sediments were combusted at 550-650 °C for two hours and then re-weighed. COM was calculated by weight differences and was also expressed as  $\text{g m}^{-2} \text{d}^{-1}$ . When high sediments were deposited on the filters, only part of the filter and sample was combusted, then a correction factor was applied. Due to the high deposition of leaves, sticks, small branches, flowers and propagules in some of the filters, an additional correction



factor for COM was calculated. To do this, ash residuals of samples after combustion were classified in six different categories: low, medium and high sediments, with or without organic materials. Ten pre-weighed sub-samples of ash residuals from each category were digested using 10 cc of hydrochloric acid at 10%, the solution was filtered using Whatman® #41 filters, then dried at 60 °C and re-weighed (Morales, pers. comm.). The difference between ash weight before and after digestion was used to calculate a percentage of recovery of organic materials from the ash residuals, a value that was then applied as a correction factor when calculating total COM.

An analysis of variance following a split plot design was conducted to test for differences in short-term sedimentation and COM by season, river and intertidal zone. For multiple comparisons, a Bonferroni-adjusted family-wise Type I error rate of  $\alpha = 0.05$  was used.

#### **2.3.5. Vertical Accretion and Soil Elevation Change**

Triplicate kaolin marker horizons of 0.25 m<sup>2</sup> were randomly placed in each plot (LI, MI and UI) per study area, for a total of 54 marker horizons. At each sampling date, a small sediment plug or core was taken from each marker horizon and the depth (mm) to the marker horizon was measured at several locations around the plug or core. Measurements were averaged per marker horizon, and the three horizons were averaged to obtain a single value per area and zone. Vertical accretion rates were expressed as cm yr<sup>-1</sup>.

A total of 12 SET stations were established: at each location in the two rivers (n=6), one SET station was established in the LI plot and one was established in the UI plot. The SET used had nine pins and was measured in eight positions, given a total of 72 elevation measurements per SET station at each sampling interval. Occasionally, several pins or even entire positions could not be evaluated due to trees, branches, prop roots, or other physical obstacles. Elevation measurements were averaged over pins and positions to obtain a single value of elevation per SET station. Surface elevation change was expressed in units of centimeters per year (cm yr<sup>-1</sup>).

Both marker horizons and SET measurements were taken approximately every six months from July 1998 to June 2000. Vertical accretion and surface elevation were expressed as incremental change between successive sampling intervals in all statistical analyses to minimize serial correlation. The annual rate of vertical accretion and soil elevation change was estimated by using linear regressions.

Analyses of variance following a split plot design were conducted to test for differences between vertical accretion and elevation change by season, river and intertidal zone. For multiple comparisons, a Bonferroni-adjusted family-wise Type I error rate of  $\alpha = 0.05$  was used. Shallow subsidence, defined as vertical accretion minus elevation change (Cahoon et al. 1995a), was also calculated, and the data was analyzed using the same statistical model as described above.

#### **2.3.6. Forest Structure**

Species composition, density (propagules, seedlings, saplings and trees), and tree diameter at breast height (DBH) were measured in each plot (LI, MI and UT). Measurements were made once during the period of study. DBH of all trees greater than two centimeters DBH was tallied, and basal areas calculated (Cintrón and Schaeffer-Novelli 1984). Stem density of dead and live trees was distinguished, when applicable.

Total numbers of dispersed propagules, established seedlings and saplings were estimated for each mangrove species. Seedlings were defined as plants smaller than 1.5m height with no branch ramification; saplings were defined as plants taller than 1.5m height, smaller than 2.0 cm in DBH, with branch ramification. In the case of propagules and seedlings, density was calculated using five replicate plots of 1 m<sup>2</sup> per intertidal zone. Counts of propagules and seedlings were made twice: September 98 and January-February 99. Species composition of non-mangrove species was recorded as presence/absence. Species importance values (IV) were calculated by integrating a species influence in the community through its contribution to stand density, basal area, and frequency (Curtis and McIntosh 1951).

Statistical analyses were conducted on sapling and tree densities, and basal areas. A split plot analyses of variance was used to test for the effects of river, species and intertidal zone. To meet the normality requirement on the model residuals, density of trees and saplings was log-transformed after adding the constant 1 to correct for zero values. After several transformations, normality of basal area residuals was not met, so the model was run on the raw data. Essentially, the residuals failed the Shapiro-Wilks test of normality due to kurtosis, which does not represent a very serious problem for maximum likelihood techniques based on the normal distribution (Montgomery 1991). For multiple comparisons a Bonferroni-adjusted family-wise Type I error rate of  $\alpha = 0.05$  was used.

## **2.4. RESULTS**

### **2.4.1. Hydrology**

The semi-diurnal tide has a range between 2-3 meters. However, not all tides are strong enough to flood the MI and HI zones of the mangrove forest on a daily basis (pers. obs.). These differences in flooding frequency are determined by the differences in soil elevation along the intertidal gradient. Soil elevation profiles of study areas 1, 2, 4 and 6 showed a significant elevation change between MB and LI zones ( $P < 0.05$ ), and between LI and MI ( $P < 0.05$ ), but no significant differences were found between MI and UI zones (Figure 2.2). The elevation difference between MB and MI zones for study areas 4 and 6 was almost three meters, resulting in a decrease of the duration and frequency of flooding. During the twelve-hour tidal cycle measured during the dry season and at highest tides of the month, the following flooding durations were recorded: MB, 4-5 hrs; LI, 2-3 hrs; MI, 0-1.5 hrs; UI, 0-1 hr. Even though duration of flooding might show variability in time and space, inter zone differences should change proportionally. Frequency of flooding was higher in the lower than the upper intertidal zones. During the dry season, MI and UI zones are generally flooded only during the highest tides of the month (usually around new and full moon). MB and LI zones, however, are generally flooded daily, although during very low water levels, the LI zone may not be completely covered. During the wet season, rain sometimes caused an accumulation of up to three centimeters of water on the soil surface in some UI study areas (pers. obs.). Statistical analyses on maximum water level data did not show a significant season effect, but showed a significant river by zone interaction ( $P=0.086$ ). Maximum water depths were higher at LI than UI for both rivers, but in LI the Bebedero River showed higher values than the Tempisque (Figure 2.3).

### **2.4.2. Total Suspended Sediments**

The Tempisque and Bebedero are very dynamic rivers and one can observe visible changes in island and channel geomorphology on the time scale of months. During the period of study we observed, for example, that Lagartos Island (study area 1) joined the main land as a result of gradual and episodic events of high sediment deposition. Point bars and islands are active sedimentary environments where riverine suspended sediments are both deposited and re-suspended along the intertidal gradient. During the dry season the Tempisque River had significantly higher total suspended sediments (TSS) than the

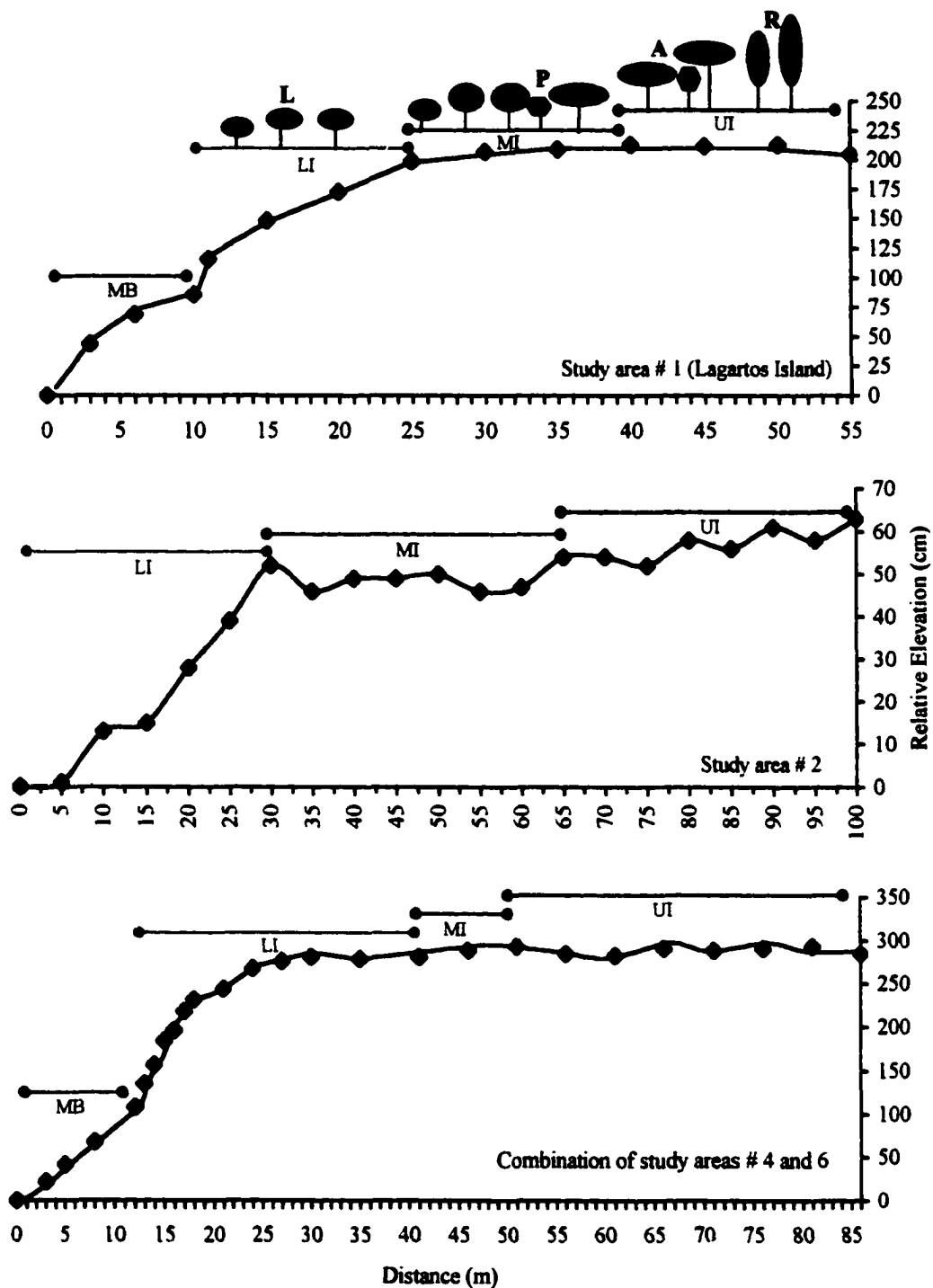


Figure 2.2. Surface elevation profiles for four study areas following the intertidal gradient: mud bank (MB), lower (LI), middle (MI) and upper intertidal (UI). A common distribution of mangrove species among study areas is also shown, where L= *Laguncularia racemosa*, A= *Avicennia germinans* and *A. bicolor*, R= *Rhizophora racemosa*, and P= *Pelliciera rhizophorae*.

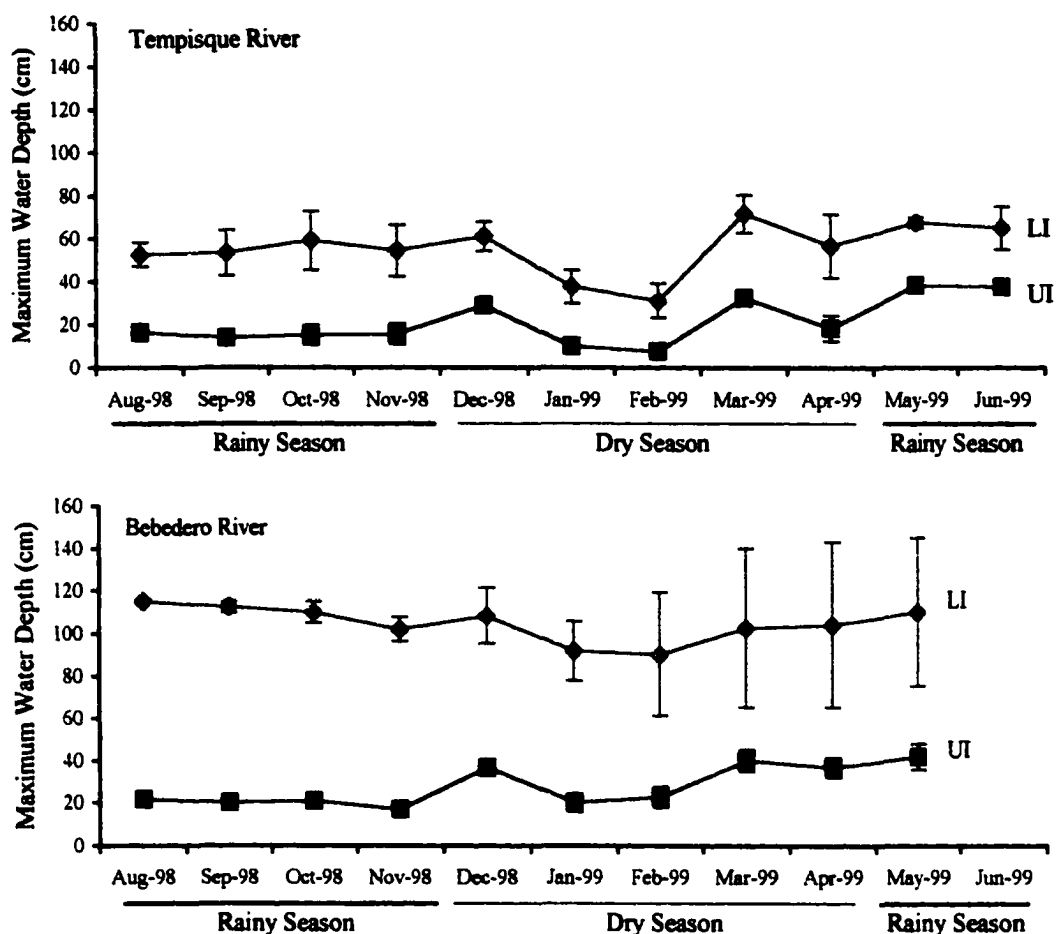


Figure 2.3. Average maximum water levels observed on the study areas for lower (LI) and upper intertidal (UI) zones in the Tempisque and Bebedero rivers.

Bebedero River ( $P < 0.05$ ), with values of  $12\,880 \pm 2\,280$  and  $810 \pm 110 \text{ mg l}^{-1}$ , respectively. During the rainy season, TSS values in the Tempisque River were significantly lower ( $320 \pm 70 \text{ mg l}^{-1}$ ,  $P < 0.05$ ) than during the dry season ( $12\,880 \pm 2\,280 \text{ mg l}^{-1}$ ).

At study area 1 (Lagartos Island) no significant differences among zones for either flood and ebb tides were found, and no overall trends between flood and ebb tides were apparent (Figure 2.4).

However, at study area 3 (Pájaros Island), there was a significant decrease in TSS concentrations from LI to UI ( $P < 0.05$ ) during the flood tide, but no significant differences were found during the ebb tide (Figure 2.4). Overall, TSS concentrations at Pájaros Island were higher during the flood tide than during

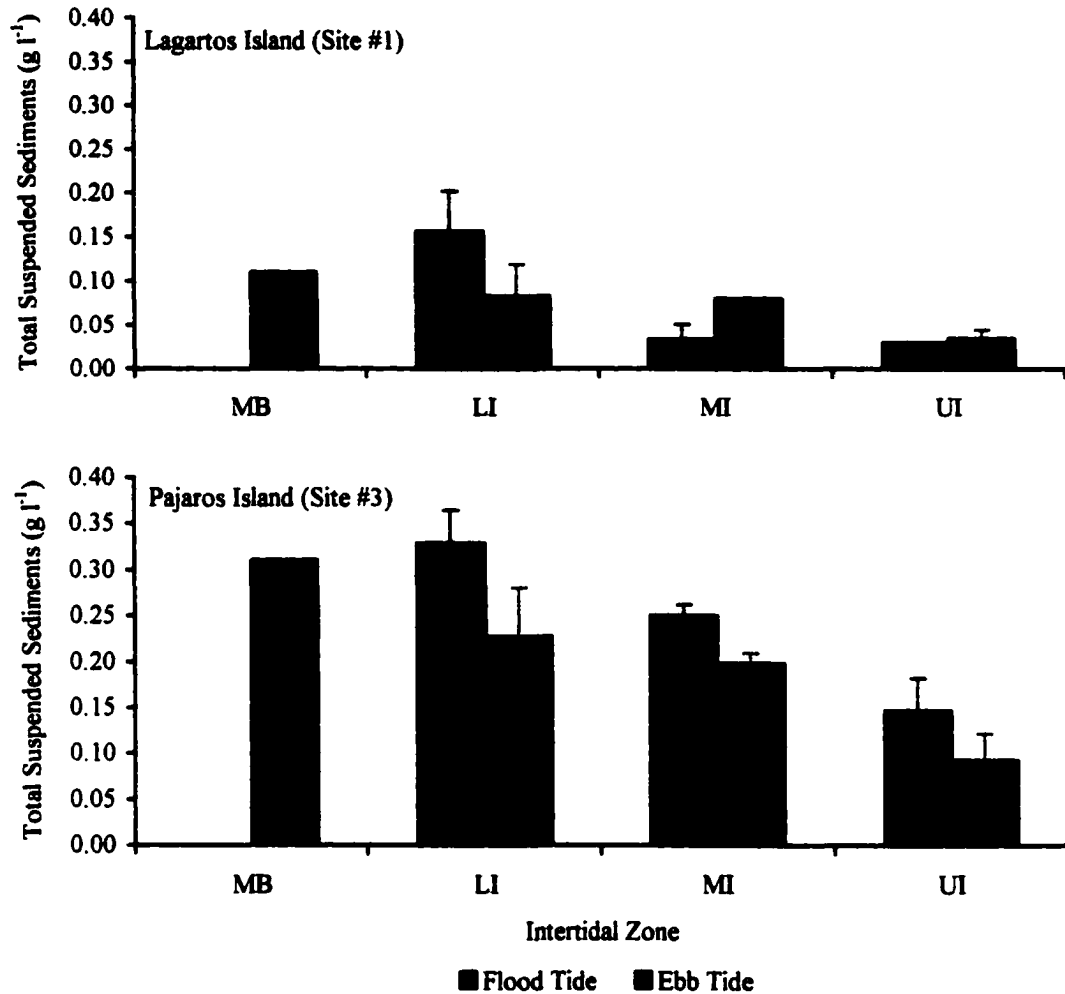


Figure 2.4. Total suspended sediments (TSS) measured during flood and ebb tides in two study areas of the Tempisque river. Mud bank (MB), lower (LI), middle (MI) and upper intertidal (UI).

the ebb tide (Figure 2.4). These observations at Pájaros Island corroborate the idea of net sediment deposition.

#### 2.4.3. Short-term Sedimentation

Short-term sedimentation showed significant differences between rivers and among intertidal zones based on seasonality ( $P < 0.05$ ). In the Bebedero, total short-term sedimentation did not change significantly by season (dry season:  $76.37 \pm 40.48 \text{ g m}^{-2} \text{ d}^{-1}$ , rainy season:  $81.73 \pm 22.01 \text{ g m}^{-2} \text{ d}^{-1}$ ). In the Tempisque, however, deposition was significantly higher during the dry season ( $92.96 \pm 31.94 \text{ g m}^{-2} \text{ d}^{-1}$ ) than during the rainy season ( $52.93 \pm 16.86 \text{ g m}^{-2} \text{ d}^{-1}$ ,  $P < 0.05$ ). During the dry season, LI ( $156.77 \pm 0.01$

g m<sup>-2</sup> d<sup>-1</sup>) had significantly higher sedimentation than both MI (45.59 ± 17.61 g m<sup>-2</sup> d<sup>-1</sup>) and UI (51.63 ± 7.27 g m<sup>-2</sup> d<sup>-1</sup>) (P< 0.05, Figure 2.5). During the rainy season, LI (103.33 ± 22.42 g m<sup>-2</sup> d<sup>-1</sup>) was also higher than both MI (57.25 ± 2.00 g m<sup>-2</sup> d<sup>-1</sup>) and UI (41.43 ± 18.78 g m<sup>-2</sup> d<sup>-1</sup>), but differences were only significant between LI and UI (P< 0.05, Figure 2.5). LI was higher during the dry season than in the rainy season (P< 0.05). No significant inter-season differences were found in the other two zones.

Short-term COM deposition showed significant differences among intertidal zones. LI (20.43 g m<sup>-2</sup> d<sup>-1</sup> ± 2.54) was higher than both MI (10.91 g m<sup>-2</sup> d<sup>-1</sup> ± 1.09) and UI (8.64 g m<sup>-2</sup> d<sup>-1</sup> ± 1.93), which corresponded to 31.5%, 34.2% and 35.1% of the total sediments deposited for LI, MI and UI, respectively. COM was significantly higher in the rainy season (15.18 g m<sup>-2</sup> d<sup>-1</sup> ± 3.92) than in the dry season (11.48 g m<sup>-2</sup> d<sup>-1</sup> ± 3.33, P< 0.05).

#### **2.4.4. Vertical Accretion and Soil Elevation Change**

Vertical accretion showed significant differences between intertidal zones throughout the study. Accretion was significantly higher at LI than at both MI and UI (P< 0.05, Figure 2.6). The annual rate estimated for LI, MI and UI was 8.37, 2.55 and 1.85 cm yr<sup>-1</sup>, respectively. Accretion patterns differed between rivers based on seasonality, with the Bebedero (5.07 cm yr<sup>-1</sup> ± 2.97) showing significantly higher rates than the Tempisque (2.52 cm yr<sup>-1</sup> ± 1.23) in the rainy season (P<0.05). In the dry season there were no significant differences between rivers (Bebedero = 4.31 cm yr<sup>-1</sup> ± 2.53, Tempisque = 4.53 cm yr<sup>-1</sup> ± 1.58). In the Bebedero, overall accretion was greater in the rainy season, but no significant differences were found. In the Tempisque, however, accretion was significantly greater in the dry season (P = 0.07).

Soil elevation change, similar to vertical accretion, was significantly higher at LI than UI (P<0.05, Figure 2.6). Soil elevation change for LI and UI was 3.76 and -0.44 cm yr<sup>-1</sup>, respectively. Results also suggest significant differences among a combination of seasons, rivers and zones (P = 0.08). Multiple comparisons showed two main results: 1) during the dry season, elevation change was higher in LI than UI for the Bebedero River (P<0.05); 2) there was also greater dry season elevation change in the Bebedero compared to the Tempisque in LI (P<0.05). Therefore, higher vertical elevation was associated with LI in the Bebedero during the dry season (Table 2.1).

Throughout all sampling periods vertical accretion was always higher than elevation change (Figure 2.6), and erosion was not evident. Shallow subsidence (vertical accretion – elevation change)

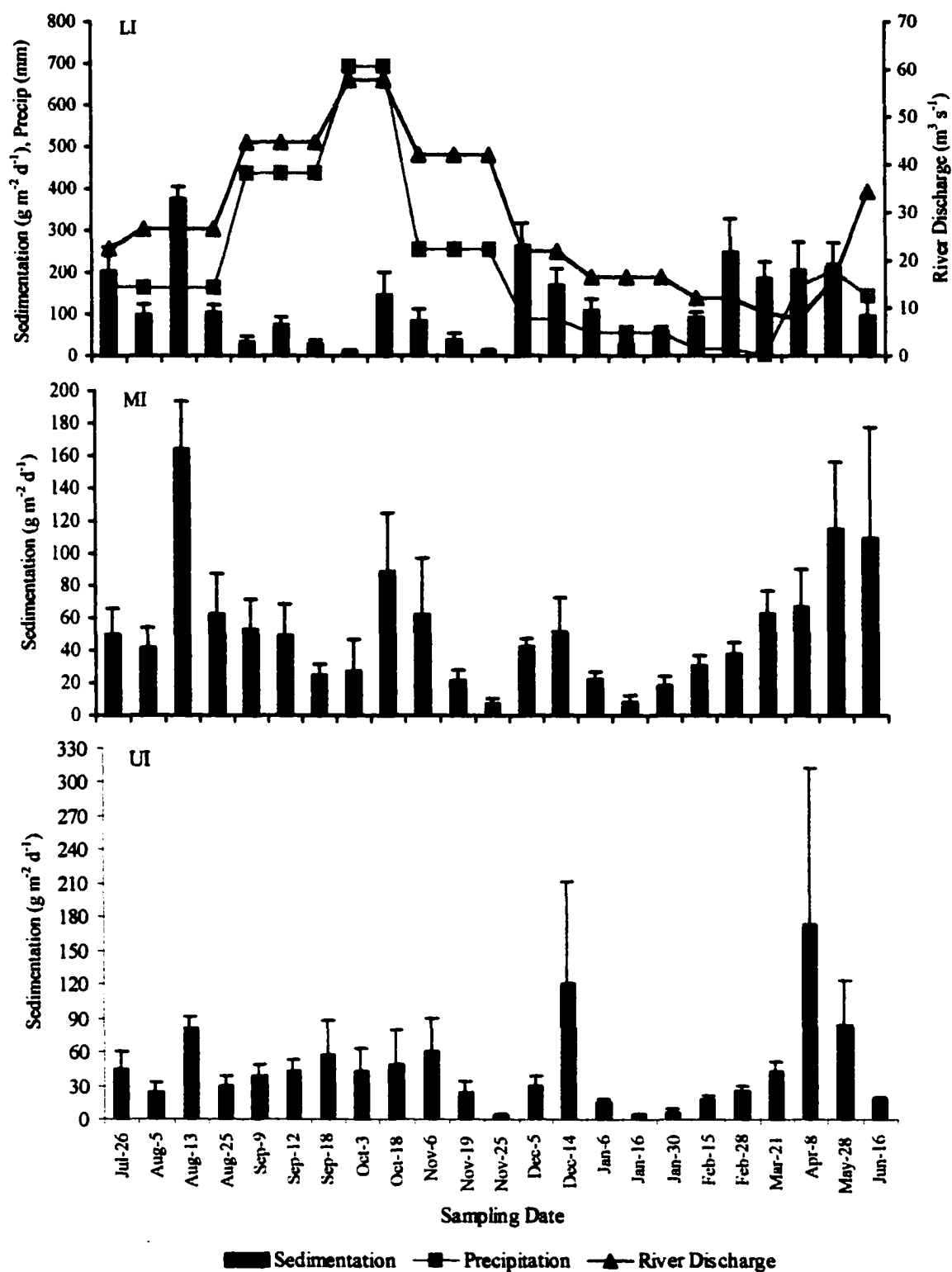


Figure 2.5. Total (inorganic + organic) short term sedimentation along the intertidal gradient: lower (LI), middle (MI) and upper intertidal (UI). Sedimentation was averaged across rivers. Average River discharge corresponds to the Tempisque River, and precipitation is given for the sampling period: July 1998-June 1999. Dry season: December to April, rainy season: May to November. Note the differences in scale.



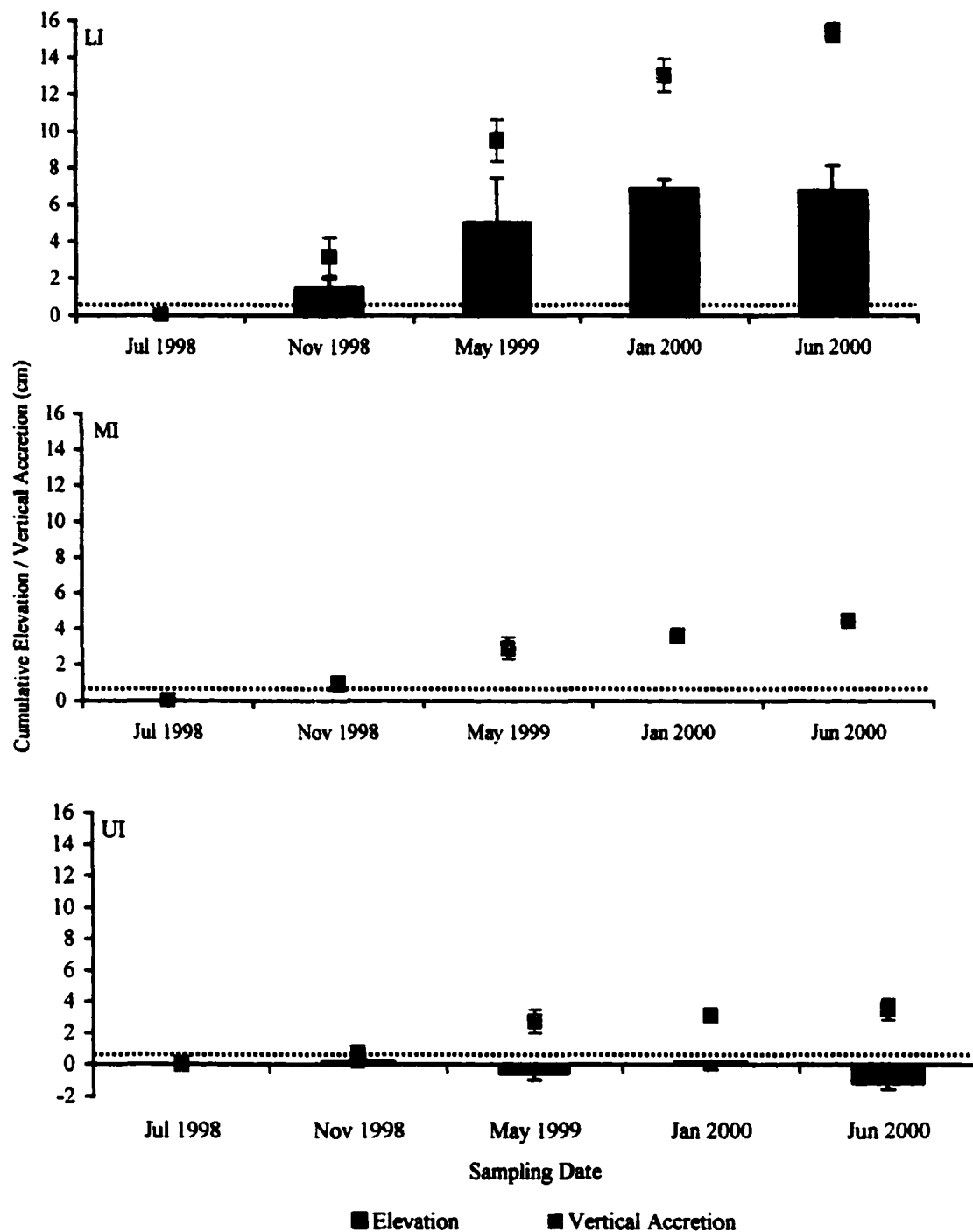


Figure 2.6. Vertical accretion and soil elevation change of the mangrove study areas following the gradient: lower (LI), middle (MI) and upper intertidal (UI). Dotted line indicates a predicted sea level rise value of 0.46 cm yr<sup>-1</sup> (Gornitz 1995).

Table 2.1. Surface elevation change ( $\text{cm yr}^{-1} \pm \text{se}$ ), and shallow subsidence ( $\text{cm yr}^{-1} \pm \text{se}$ ) of point bars and islands given by season (dry and rainy season), river (Tempisque and Bebedero) and intertidal zone (lower and upper intertidal). The three way interaction: season by river by zone was significant at  $P = 0.08$  for surface elevation change, and at  $P < 0.05$  for shallow subsidence.

Surface Elevation Change				
	Dry Season		Rainy Season	
	Tempisque	Bebedero	Tempisque	Bebedero
LI	$-2.08 \pm 1.59$	$8.49 \pm 5.77$	$2.27 \pm 1.89$	$5.60 \pm 0.80$
UI	$-1.65 \pm 0.67$	$-2.49 \pm 0.82$	$0.91 \pm 1.22$	$1.40 \pm 0.67$

Shallow Subsidence				
	Dry Season		Rainy Season	
	Tempisque	Bebedero	Tempisque	Bebedero
LI	$9.72 \pm 0.47$	$-1.68 \pm 5.82$	$2.49 \pm 2.38$	$5.85 \pm 2.76$
UI	$4.17 \pm 1.43$	$3.85 \pm 2.84$	$-0.68 \pm 1.61$	$0.12 \pm 1.94$

was  $4.61 \text{ cm yr}^{-1}$  and  $2.29 \text{ cm yr}^{-1}$  for LI and UI, respectively, corresponding to 55% and 124% of the measured accretion. Shallow subsidence showed significant differences among combinations of zones, rivers and seasons ( $P=0.05$ ). Multiple comparisons indicated two main results: 1) Tempisque River shallow subsidence was significantly higher in LI than in UI ( $P < 0.05$ ) during the dry season; 2) also, the Tempisque River experienced significantly higher dry season shallow subsidence in LI when compared to the Bebedero ( $P < 0.05$ ). Therefore, during the dry season, LI zones of the Tempisque River are generally experiencing the largest shallow subsidence within the system (Table 2.1).

## 2.4.5. Forest Structure

### 2.4.5.1. Species Composition and Spatial Distribution

The mangrove forests of the Tempisque-Bebedero system are mainly colonized by five mangrove species: Rhizophora racemosa, Laguncularia racemosa, Avicennia germinans, Avicennia bicolor and Pelliciera rhizophorae. However, other species (classified as marginal vegetation and facultative marginal vegetation by Jiménez and Soto 1985) were also observed: Tabebuia palustris, Anona glabra, Cocoloba caracasana, Phytocelobium lanceolatum, Machaderium lunatum, Lonchocarpus, Bactaris minor, Crinum erubescens, Echinochloa polystachya, Panicum maximum, and some unidentified vines. Many of these associated species showed strong distributional patterns among the different intertidal zones. Crinum had an average of 26%, 24% and 13% cover for LI, MI and UI, respectively (Figure 2.7). The grasses Echinochloa and Panicum were also relatively abundant in some study zones,

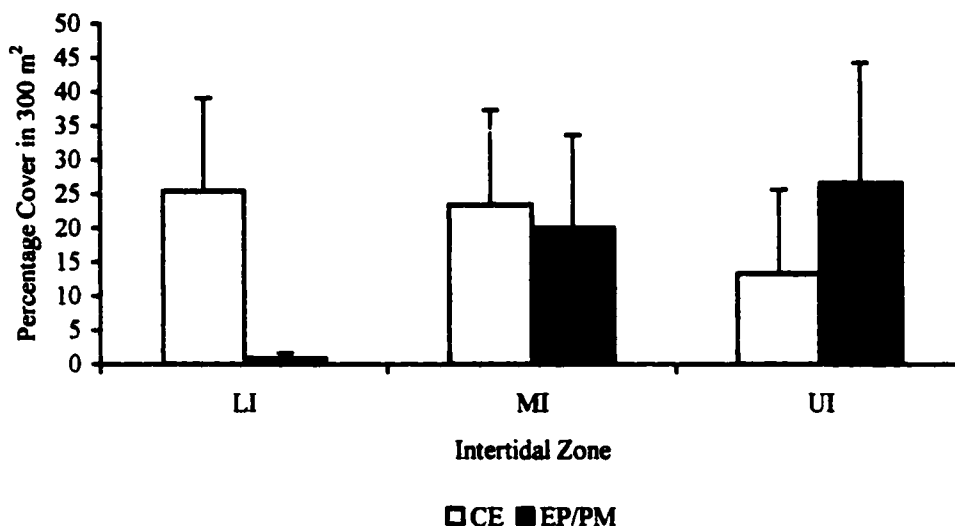


Figure 2.7. Percent cover of the lily *Crinum erubescens* (CE) and the grasses *Echinochloa polystachya* and *Panicum maximum* in the Tempisque-Bebadero system along the intertidal gradient: lower (LI), middle (MI) and upper intertidal (UI).

reaching combined average cover values of 1%, 20% and 27% for LI, MI and UI, respectively (Figure 2.7). In some study areas such as Pájaros and Lagartos islands (study areas 1 and 3), *Echinochloa* dominated most of the surface in the UI, representing a problem for mangrove regeneration. In other areas along the Tempisque River these grasses were also growing in sections of accreting mud banks.

*Laguncularia* was found predominantly in LI zones forming mono-specific patches 17 to 40m wide. In MI it was also very abundant, but formed a more mixed forest with other species such as *Avicennia*, *Pelliciera* and/or *Rhizophora* (Figure 2.2 and 2.8, Table 2.2). The width of MI zones varied between 13 and 43m. For most of the study areas *Rhizophora* and *Avicennia* were the main species colonizing the UI zones, but with scattered occurrence of *Laguncularia*, *Pelliciera* and/or more upland vegetation (Figure 2.2 and 2.8, Table 2.2). The width of this zone varied from 18 to 100m or more.

#### 2.4.5.2. Basal Area and Species Distribution by Diameter Class

Total mangrove basal area in LI, MI and UI were 29.4, 21.4 and 57.3 m<sup>2</sup> ha<sup>-1</sup>, respectively, with respective densities of 9 855, 3 934 and 1 270 stems ha<sup>-1</sup> (Table 2.2). Although tree density decreased from LI to UI, mean DBH was higher in UI. Tree density showed significant differences among rivers and among intertidal zones, but the patterns were contingent on the individual tree species ( $P < 0.05$ ).

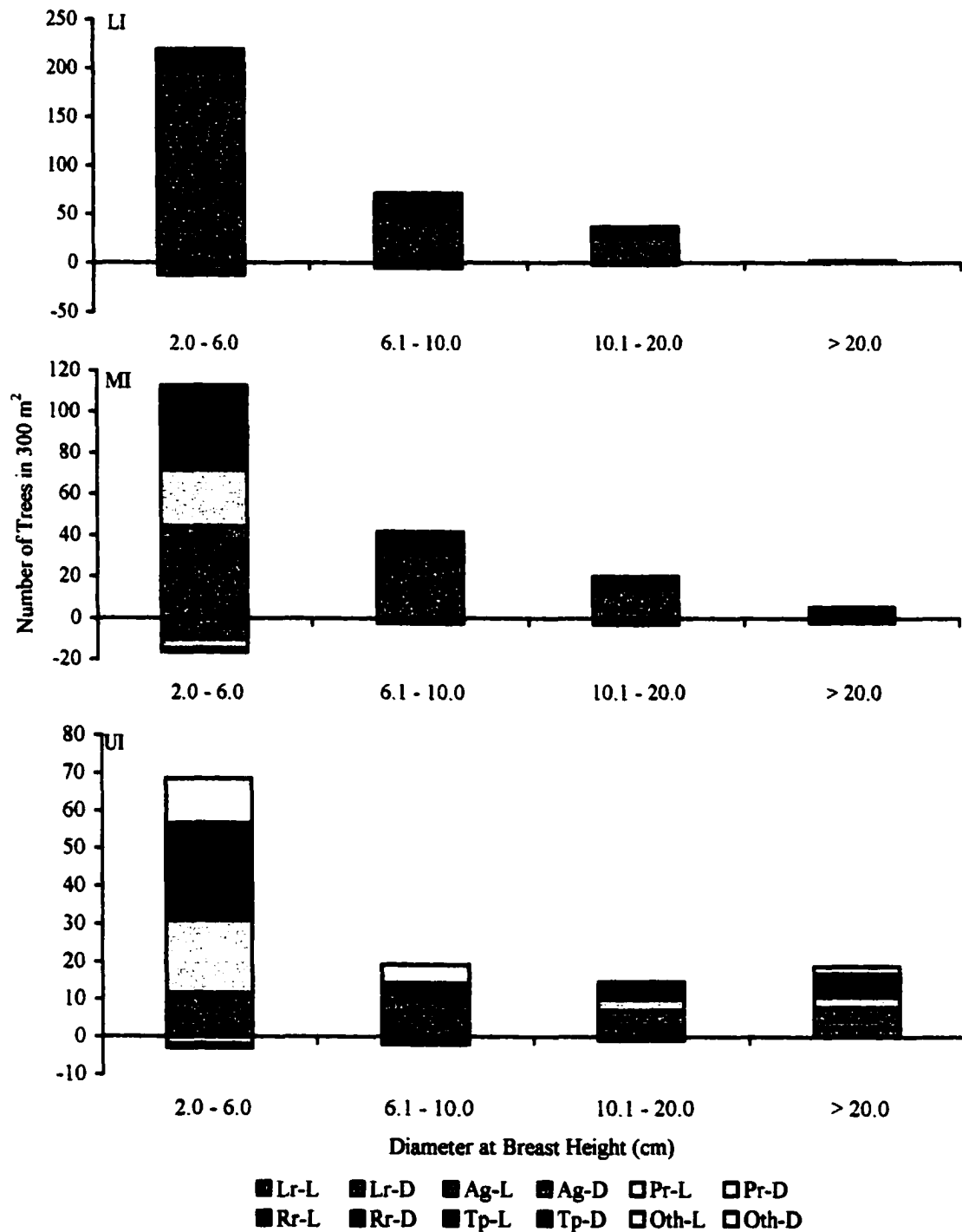


Figure 2.8. Mangrove species distribution by diameter class for the lower (LI), middle (MI) and higher intertidal (HI) zones. Abbreviations for species are as follows: Lr = Laguncularia racemosa, Ag = Avicennia germinans, Pr = Pelliciera rhizophorae, Rr = Rhizophora racemosa, Tp = Tabebuia palustris and Oth = other species, where L and D stands for life and dead trees, respectively. Negative values correspond to dead trees.

Table 2.2. Structural characteristics of the mangrove community at point bars and islands following a flooding and sedimentation gradient: lower (LI), middle (MI) and upper intertidal (UI). Only trees equal or higher than 2.0 cm DBH were considered in this analysis.

	Species	Density (Stems ha <sup>-1</sup> )	DBH (cm)	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Relative Abundance	Relative Dominance	Frequency	IV
LI	<i>L. racemosa</i>	9 556 ± 3 034	6.0 ± 0.6	25.0 ± 2.1	97.2	85.0	100	282
	<i>A. germinans</i>	100 ± 33	8.5 ± 5.5	2.1 ± 1.9	0.9	7.2	50	58
	<i>P. rhizophorae</i>	100 ± 67	4.3 ± 1.0	0.7 ± 0.6	1.0	2.3	50	53
	<i>R. racemosa</i>	33 ± 33	9.2 ± 0.0	1.1 ± 0.0	0.2	3.9	17	21
	<i>T. palustris</i>	33 ± 33	4.8 ± 0.0	0.4 ± 0.0	0.3	1.5	17	19
	Other species	33 ± 33	3.0 ± 0.1	0.1 ± 0.02	0.5	0.2	67	68
	TOTAL	9 855		29.4				
MI	<i>L. racemosa</i>	2 800 ± 1 106	7.7 ± 0.4	13.0 ± 3.6	71.1	60.7	100	232
	<i>A. germinans</i>	167 ± 67	13.3 ± 7.1	4.0 ± 2.0	4.5	18.9	83	106
	<i>P. rhizophorae</i>	367 ± 300	5.4 ± 0.9	1.8 ± 1.7	9.0	8.5	67	85
	<i>R. racemosa</i>	233 ± 167	6.3 ± 1.8	1.2 ± 0.6	6.1	5.7	67	79
	<i>T. palustris</i>	367 ± 367	3.5 ± 0.1	1.2 ± 1.2	9.2	5.7	33	48
	Otras especies	0 ± 0	6.4 ± 0.0	0.1 ± 0.0	0.1	0.5	17	18
	TOTAL	3 934		21.4				
UI	<i>L. racemosa</i>	304 ± 194	9.0 ± 1.1	5.1 ± 2.8	23.8	8.8	50	83
	<i>A. germinans</i>	133 ± 67	31.8 ± 9.9	25.2 ± 11.7	11.0	44.0	67	122
	<i>P. rhizophorae</i>	233 ± 167	9.8 ± 4.9	3.9 ± 2.8	17.4	6.8	33	57
	<i>R. racemosa</i>	200 ± 67	23.7 ± 10.7	17.0 ± 9.0	15.7	29.6	67	112
	<i>T. palustris</i>	200 ± 133	2.6 ± 0.1	0.4 ± 0.03	16.4	0.7	33	50
	Other species	200 ± 167	11.2 ± 6.4	5.8 ± 3.4	15.7	10.2	33	59
	TOTAL	1 270		57.3				

*Pelliciera* was the only species that had a significantly higher tree density in the Bebedero than in the Tempisque River ( $P < 0.05$ ). In LI and MI *Laguncularia* had the highest importance value ( $IV=282$ ). In both intertidal zones, it showed a significantly higher tree density ( $P < 0.05$ ), compared to any of the other species in any of the three zones (Table 2.2). Although *Laguncularia* density did not change significantly between LI and MI zones, there was a significant difference between LI and UI ( $P < 0.05$ ), indicating a greater abundance of this species in the lower intertidal zones.

Even though most of the *Laguncularia* trees were in the smallest diameter classes, there was a relatively high basal area (Table 2.2, Figure 2.8). The basal area of *Laguncularia* in LI was significantly greater than that of the other species in any of the zones ( $P < 0.05$ ), with the exception of *Avicennia* and

Rhizophora in UI zones. Basal area of Laguncularia was not significantly different between LI and MI, but it was between LI and UI ( $P < 0.05$ ).

In MI, even though Laguncularia was still the dominant species in terms of tree density, there was a higher representation of other mangrove species, forming a transitional zone towards a more mature mixed or monospecific forest in UI (Table 2.2, Figure 2.8). In UI, Laguncularia represented only a 24% of the total number of trees and its IV was lower than that of Avicennia and Rhizophora. Although these two species showed similar densities to Laguncularia in UI most trees were bigger and of greater basal area (Table 2.2, Figure 2.8). Exceptions to this general pattern were study areas 1 (Lagartos island) and 3 (Pájaros island). In Lagartos Laguncularia was still the dominant species in UI, while in Pájaros this zone was almost completely covered by the grass Echinochloa.

Density of dead trees was low, and most had low DBH (Figure 2.8). In LI the highest percentage of dead trees, estimated in relation to the total tree density per species, were Rhizophora with a value of 22%. In MI and UI the highest values were for Pelliciera with values of 14% and 7%, respectively.

#### **2.4.5.3. Propagule, Seedling and Sapling Distribution**

Laguncularia had higher propagule and seedling density throughout the intertidal gradient compared to the other mangrove species (Figure 2.9). Seedling densities were as follows: LI =  $46 \pm 21$ , MI =  $51 \pm 29$  and UI =  $22 \pm 15$  seedling  $m^{-2}$ . Mean densities for the other mangrove species varied between 0 and 10 seedlings  $m^{-2}$ , with the highest values reported for Avicennia (LI and UI), and Rhizophora (UI), (Figure 2.9). There were 0.2 seedlings  $m^{-2}$  of Laguncularia in the MB. Even though results indicate a higher average seedling density of Laguncularia than the other species in UI, observations showed a lack of regeneration of this species in four of the six UI areas sampled. In addition, approximately four months after the first seedling survey, (September 98) the density of Laguncularia seedlings decreased significantly in MI and UI zones (Jan-Feb 99, Figure 2.9).

Sapling densities varied depending on combinations of species and river ( $P < 0.05$ ). Rhizophora was the only species that showed a significant difference between rivers with higher sapling density in the Bebedero than the Tempisque ( $P < 0.05$ ). Even though a species by zone interaction was not significant, results suggest a dominance of Laguncularia in LI ( $110 \pm 41$  saplings  $m^{-2}$ , Figure 2.10), with a decrease

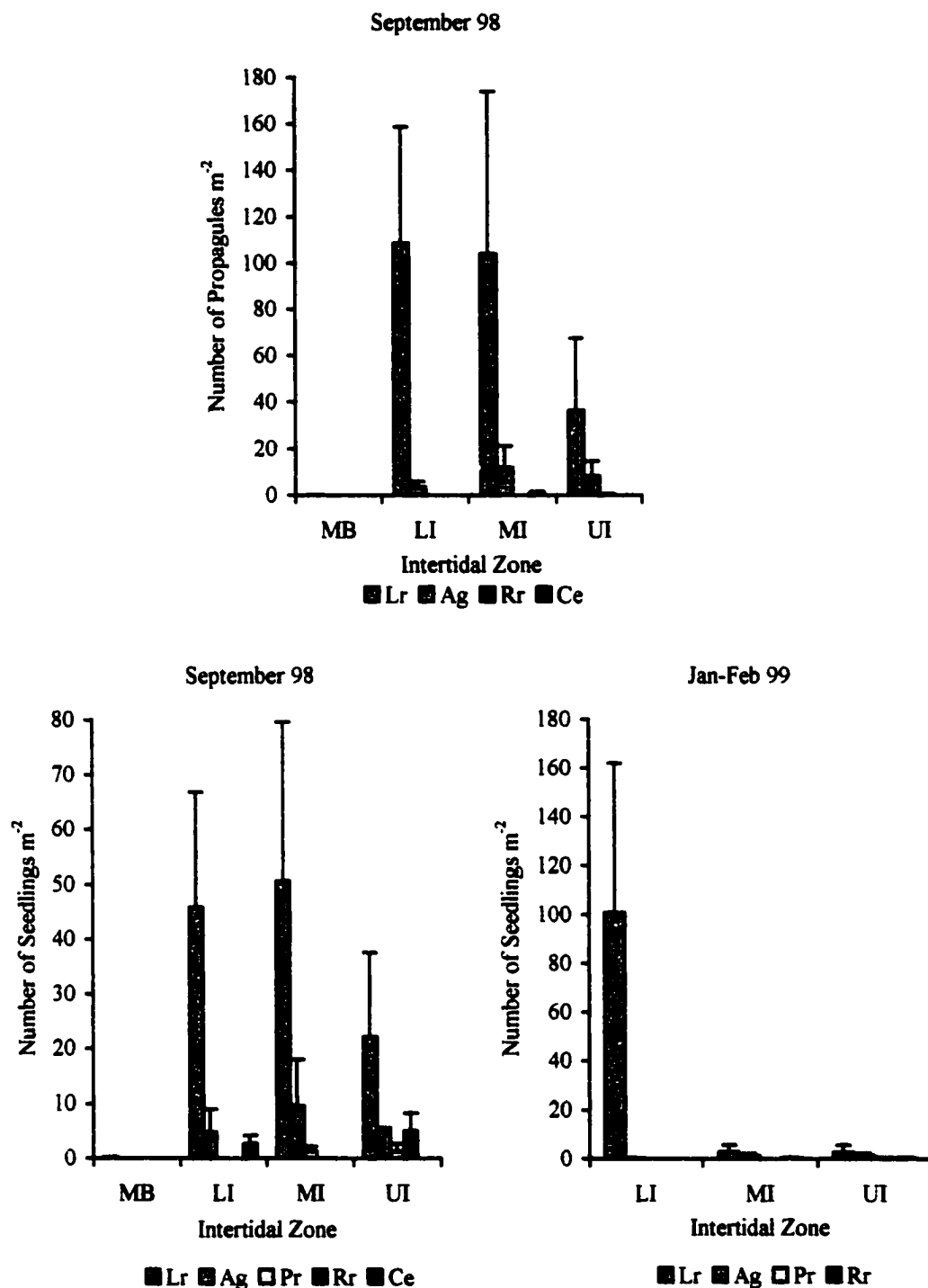


Figure 2.9. Distribution of propagules and seedlings following the gradient: lower (LI), middle (MI) and upper intertidal (UI). Abbreviations for species are as follows: Lr = Laguncularia racemosa, Ag = Avicennia germinans, Pr = Pelliciera rhizophorae, Rr = Rhizophora racemosa, Ce = Crinum erubescens.

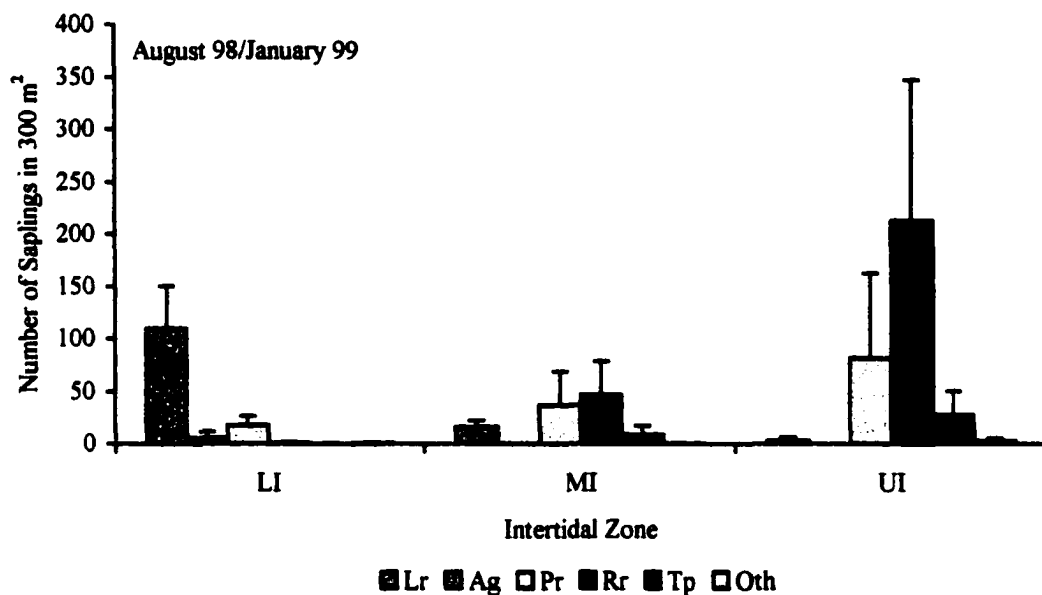


Figure 2.10. Distribution of saplings following the gradient: lower (LI), middle (MI) and upper intertidal (UI). Abbreviations for species are as follows: Lr = *Laguncularia racemosa*, Ag = *Avicennia germinans*, Pr = *Pelliciera rhizophorae*, Rr = *Rhizophora racemosa*, Tp = *Tabebuia palustris*, and Oth = other species.

towards MI ( $16 \pm 7$  saplings  $m^{-2}$ ) and UI zones ( $3 \pm 3$  saplings  $m^{-2}$ , Figure 2.10). In these upper intertidal areas other species such as *Rhizophora* (MI=  $47 \pm 31$ , UI=  $213 \pm 135$  saplings  $m^{-2}$ ), *Pelliciera* (MI=  $37 \pm 32$ , UI=  $81 \pm 81$  saplings  $m^{-2}$ ), and *Tabebuia* (MI=  $9 \pm 9$ , UI=  $28 \pm 23$  saplings  $m^{-2}$ ) showed greater sapling density (Figure 2.10).

## 2.5. DISCUSSION

### 2.5.1. Sedimentation Dynamics

The spatial and temporal patterns of sedimentation observed at mangrove-colonized point bars and islands in the Tempisque-Bebedero riverine system reflected specific hydrological and geomorphological characteristics of the environment, and the effect of human activities within the river basin. Contrarily to common trends, Tempisque river areas showed higher sedimentation during the dry season in spite of the higher river discharge observed during the rainy season. This is not a true season effect, however, but instead is the result of the very high TSS concentrations during the dry season, associated with agricultural activities in the area and wind induced sediment re-suspension. During the dry season a large amount of water from the Tempisque is pumped out for agricultural irrigation and eventually some drains back but with high sediments. Also during the dry season, the influence of strong



northeasterly winds causes re-suspension of shallow deposits increasing the sediment concentration of the Tempisque River (pers. obs.). As a result of the high TSS concentration in the Tempisque, in the dry season, there is increased sediment deposition. Bebedero sites did not show a seasonal difference in sedimentation, which indicates similar TSS values between seasons, suggesting that sediments transported by the Tempisque during the dry season might be also reaching depositional areas in the Bebedero

In summary, the high concentration of sediments into the Tempisque River during the dry season as a result of intensive agricultural activities and wind induced sediment re-suspension leads to higher accretion in the dry season. Under the current conditions, short-term sedimentation in point bars and islands of the Tempisque-Bebedero system does not show a significant true season effect. In contrast, under more natural conditions or lack of sediment supply, areas under riverine influence generally show higher sedimentation during times of higher river discharge, which is generally associated to higher suspended sediments (Childers et al. 1993, Allison et al. 1996, Hensel et al. 1998, Day et al. 1999, Kemp et al. 1999, Saad et al. 1999). Sediment accretion measured at a mangrove forest in Malaysia was significantly higher during the monsoon season, associated with higher discharge and sediment load of the Kemaman River (Saad et al. 1999). Similarly, riverine wetlands connected to the Rhône River in France showed higher short-term sedimentation during periods of higher river discharge (Hensel et al. 1998).

Short-term sedimentation in our study sites was highly variable, ranging from 0 to 1 526 g m<sup>-2</sup> d<sup>-1</sup>, where the lowest rate occurred at UI and the highest at LI. Average short-term sedimentation values given by river and season and by season and intertidal zone were generally much higher than values reported for other coastal wetlands around the world. In riverine, impounded and marine wetland habitats of the Rhône Delta, France short term sedimentation ranged from < 1.0 to 38.0 g m<sup>-2</sup> d<sup>-1</sup>. The highest rate occurred at the riverine habitat, which showed an average sedimentation of 5.4 g m<sup>-2</sup> d<sup>-1</sup> (Hensel et al. 1998). Short-term sedimentation rates in salt marshes in Venice Lagoon, Italy, ranged from 0.1 to 73 g m<sup>-2</sup> d<sup>-1</sup>, with an average of 3-7 g m<sup>-2</sup> d<sup>-1</sup> (Day et al. 1999). At Oyster Bayou in the Mississippi river deltaic plain, a *Spartina alterniflora* dominated marsh, had an average short-term sedimentation rate of 0.93 g m<sup>-2</sup> d<sup>-1</sup>, despite its proximity to the mouth of the Atchafalaya River (Kemp et al. 1999). Across the intertidal

gradient, LI zones showed higher sediment deposition than UI zones during both dry (156.77 vs. 51.63 g m<sup>-2</sup> d<sup>-1</sup>, respectively) and rainy seasons (103.33 vs. 41.43 g m<sup>-2</sup> d<sup>-1</sup>, respectively) indicating a spatial sedimentation gradient. A gradient in sedimentation across the intertidal zone (for both dry and rainy seasons) is a common pattern that has been reported for other coastal wetlands worldwide (Lynch et al. 1989, French and Spencer 1993, Furukawa and Wolanski 1996, Childers et al. 1993, Hensel et al. 1998). For example, Furukawa and Wolanski (1996) showed that net sedimentation rates in Cairns mangrove forest in Australia decreased exponentially with distance from the tidal creek. Similarly, in an estuarine mangrove forest in Malaysia, accretion rates decreased towards the back of the mangrove (Saad et al. 1999).

LI zones, because of their position at the fringe and their lower elevation relative to MI and UI zones, are flooded more frequently and for longer periods of time, which accounts for higher sediment availability and deposition. Higher elevations are flooded less frequently, and the water that does reach these upper limits has already lost some of sediments, limiting their availability for settling (Furukawa and Wolanski 1996). At study area 3, for example, TSS concentrations measured during the flood tide were significantly higher at LI than at UI. Several studies have shown the influence of frequency and duration of flooding in sediment deposition (Richard 1978, Conner and Day 1991, Cahoon and Reed 1995, Cahoon et al. 1996, Kemp et al. 1999). High accretion rates in a fringe mangrove forest in the East Coast of Malaysia were attributed to higher flooding frequency and the fringe's close location with respect to fluvial and tidal sediment sources (Saad et al. 1999). Vertical accretion measured in fresh water swamp forests bordering Lake Verret, Louisiana, showed a positive relationship with duration of flooding; vertical accretion was the greatest at the edge of the Lake (0.37cm month<sup>-1</sup>) and was the least 100 m inland (0.11cm month<sup>-1</sup>, Conner and Day 1991). At the same site, sedimentation in a bottomland hardwood forest was 0.01, 0.04 and 0.07cm month<sup>-1</sup> for dry, intermediate and wet sites, respectively (Conner and Day 1991).

Wind was also an important factor influencing short-term sedimentation, at the LI zone. In our study areas, the northeasterly trade winds blow strongly during the dry season, and are associated with wave formation in both the Tempisque and Bebedero rivers. Although wind and waves can cause erosion (Anderson et al. 1981), they also re-suspend recently deposited shallow sediments (Anderson et al. 1981,

Augustinus 1995). Both processes result in suspended sediments that can be deposited in sheltered environments, such as vegetated fringes (Anderson 1973, Reed 1989, Conde and Alarcón 1993, Hensel et al. 1998). Mangroves enhance sedimentation by decreasing water velocities leading to sediment settling (Augustinus 1995, Furukawa and Wolanski 1996, Massel et al. 1998). In Magnetic Island, Queensland, Spenceley (1977) showed, two different hydraulic functions of Avicennia pneumatophores (similar structures to pneumathodes for Laguncularia): under low energy conditions, water velocities are reduced and deposition occurs; under medium-high energy conditions, eddy currents are formed leading to localized scour and erosion. Young and Harvey (1996) also demonstrated a relationship between accretion and pneumatophore density of Avicennia marina in mangrove forests in the Hauraki Plains, New Zealand. The high sedimentation during the dry season and in the mangrove fringe of both the Tempisque and Bebedero rivers conforms to this idea of wind-induced sediment suspension, transport, and deposition within the vegetated mangrove fringe. The low water levels associated with the dry season, however, would preclude most MI and UI zones from frequent inundation by these sediment-laden waters. In summary, water TSS concentrations (independent of river discharge), frequency and duration of flooding, presence of vegetation, and wind effect are important factors determining short-term sedimentation at point bars and islands in the Tempisque-Bebedero system, especially in lower intertidal zones, and during the dry season.

Organic matter deposition is important for sediment accretion in microtidal environments and/or in areas of restricted hydrology (DeLaune et al. 1990b, Nyman et al. 1990). In microtidal environments, this is due to insufficient sediment delivery due to the reduced capacity of the tidal fluxes to carry inorganic sediments. Likewise, in areas of restricted hydrology, the problem is both sediment source and sediment delivery. On the other hand, in macrotidal and riverine environments, inorganic sediments are both more available and more easily transported, so inorganic deposition plays a larger role (Nyman et al. 1990, Thom 1992, Fujimoto and Ohnuki 1995, Callaway et al. 1997, Hensel et al. 1999).

Short-term organic matter sedimentation in the zones LI, MI and UI showed average combustible organic matter values of 31.5%, 34.2% and 35.1%, respectively. Even though inorganic material was still the dominant portion of deposited sediments (as expected for a river-influenced environment), organic matter deposition is also an important source for soil elevation in these

environments. Although the contribution of organic matter may be low on a weight basis, its contribution to soil volume is proportionally much greater (Nyman et al. 1990). Organic matter not only is important for sediment elevation, but can represent an important carbon sink or temporary storage prior to export to the estuary.

The contribution of organic matter to short term sedimentation in this estuarine mangrove system was significantly higher at MI and UI compared to the more frequently flooded LI zone. This agrees with findings from other areas where percent organic matter is low with higher riverine influence, while organic matter is more important in areas of restricted hydrology. For example, in the Rhône Delta, France the contribution of organic matter was 7%, 14% and 15% for riverine, impounded and marine wetland habitats respectively, but because of high decomposition rates, these values were not considered important for soil formation (Hensel et al. 1999). A fringe and a basin mangrove forest at Rookery Bay, Florida had 12% and 60% of soil organic matter, respectively. High values in the basin forest were attributed to high plant litter and root accumulation due to restricted tidal flushing (Cahoon and Lynch 1997). Organic matter content in the upper 10cm of the soil in low tidal-range sites dominated by Rhizophora and Avicennia mangrove forests at the Florida Keys had values of 56% and 61%, respectively (Callaway et al. 1997). At Cooley Landing, on the southwestern edge of San Francisco Bay, also a micro-tidal environment, the organic content of sediments under a Spartina and Salicornia marsh was of 14.6% and 18.3%, respectively. Spartina stands were located at the lower elevations adjacent to the meandering channels, while Salicornia was restricted to the upper levels of the marsh under more reduced hydrological conditions (Pestrong 1972).

Short-term organic matter sedimentation is also affected by forest structure. The LI zone received significantly less percent COM than the other two zones. When expressed as grams deposited per area per day ( $\text{g m}^{-2} \text{d}^{-1}$ ), however, the trend is reversed, with significantly higher COM in LI compared to both MI and LI. LI was dominated by a young Laguncularia forest with high tree density, where there was often a layer of small branches, twigs and leaves covering the soil surface, a pattern that decreased towards the upper zones, where tree density was significantly lower and trees were of greater diameter (pers. obs.). These patterns, however, suggest that in the long run organic matter deposition in

LI zones might not be as important for soil accretion as it might be in upper zones, where inorganic sediment input is more limited than in LI due to more restricted flooding.

Both spatial and temporal patterns of vertical accretion estimated using marker horizons technique were similar to those of short-term sedimentation. Vertical accretion decreased in an inland direction (LI= 8.04, MI= 2.26 and UI= 1.85cm yr<sup>-1</sup>). Annual vertical accretion rates estimated for LI, MI and UI zones were generally higher than those calculated for other ecosystems due to the very high values of TSS. In Magnetic Island, Australia, sedimentation across a mangrove intertidal gradient varied between -0.38 and 0.4cm yr<sup>-1</sup> in the fringe zone (Avicennia/Sonneratia forest), between -0.65 and 0.46cm yr<sup>-1</sup> in an intermediate zone (dominated by Rhizophora), and between -0.82 and 1.10cm yr<sup>-1</sup> for the farthest inland zone (dominated by Ceriops, Spenceley 1982). In the Rhizophora and Ceriops zones, there was a net deposition behind prop and buttress roots and erosion in the open. In the Avicennia/Sonneratia fringe, however, erosion occurred close to the prop roots and pneumatophores, and deposition in the open within the front of the Rhizophora zone due to differences in tidal energy (Spenceley 1982). In contrast to our work which showed no sign of erosion, this study showed significant erosion episodes, whose frequency and intensity decreased as surface elevation increased inland (Spenceley 1982). Other studies have also shown decreases in vertical accretion in lower-energy environments with more restricted hydrology, such as carbonate peat-based systems in Florida. In Rhizophora mangle fringe and mixed basin forests in Rookery Bay, vertical accretion was 0.72 and 0.60 cm yr<sup>-1</sup>, respectively. Similarly, R. mangle forests colonizing overwash exposed islands, and overwash sheltered islands had vertical accretion values of 0.63 and 0.44 cm yr<sup>-1</sup>, respectively (Cahoon and Lynch 1997). Accretion determined from <sup>137</sup>Cs analyses in Rhizophora fringe and interior Avicennia forests at the Florida Keys was 0.40cm yr<sup>-1</sup> and 0.27cm yr<sup>-1</sup>, respectively (Callaway et al. 1997). A Brazilian mangrove forest on the Rio Cunani sandflat, had a sediment accumulation rate of 2.4cm yr<sup>-1</sup>, which is comparable to this study (Allison et al. 1996). In the highly human impacted Rhône Delta, France riverine, marine and impounded wetland habitats had average accretion rates of 1.34, 0.11 and 0.12 cm yr<sup>-1</sup>, respectively (Hensel et al. 1999).

Vertical accretion at our sites was always positive indicating active soil accretion and very little or no erosion. Other studies have shown thus, by contrast, the importance of erosion in determining

wetland elevation change (Diemont and van Wijngaarden 1975, Richard 1978, Spenceley 1982, Cahoon and Lynch 1997, Day et al. 1999). A fringe forest at Rookery Bay, Florida, dominated by R. mangle showed significant erosion over a 2.5-year study period (Cahoon and Lynch 1997). Anderson et al. (1981) showed that sedimentation and erosion were occurring simultaneously in different areas of the same tidal flat. At Magnetic island, Australia, both depositional and erosional episodes occurred within a same zone, with erosion along the gradient (Spenceley 1982).

There was also higher elevation gain in LI than in UI. The annual rate of elevation change estimated for LI ( $3.76\text{ cm yr}^{-1}$ ), was higher than values reported in the literature for other ecosystems. The UI rate of elevation change ( $-0.44\text{ cm yr}^{-1}$ ), however, was in many cases lower than reported values and comparable to environments with limited hydrology and reduced sediment input. Riverine, impounded and marine wetland habitats in the Rhône Delta, France, showed elevation change values of 1.13, 0.04 and  $0.06\text{ cm yr}^{-1}$ , respectively. The Rhône Delta, in contrast to the Tempisque-Bebedero system, is characterized as a wave dominated environment with a microtidal receiving basin, and an extensive hydrological control (Hensel et al. 1999). In spite of these differences, results from both systems highlight the importance of riverine-borne sediments in relation to vertical accretion and elevation gain. In this Rhône Delta, impounded and marine habitats showed small positive surface elevation changes, in contrast to more hydrologically restricted UI sites, which showed a slight loss in elevation. This difference is due to differences in shallow subsidence. Shallow subsidence in the UI zone, that was 112% of accretion, is much higher than the 64% and 50% measured for the impounded and marine habitats in the Rhône Delta (Hensel et al. 1999). In Rookery Bay, Florida, an A. germinans/R. mangle dominated basin forest had an elevation change of  $0.37\text{ cm yr}^{-1}$  (Cahoon and Lynch 1997). This value is also higher than our estimate for UI, which is related to higher shallow subsidence.

The proximity of a wetland site to riverine sediments has been shown to be very important to vertical elevation change. In Rookery Bay, Florida, a microtidal environment with no riverine influence, R. mangle-dominated forests in fringe, overwash exposed and overwash sheltered islands showed elevation change values of 0.35, 0.25 and  $0.06\text{ cm yr}^{-1}$ , respectively (Cahoon and Lynch 1997). These values are significantly lower than we observed at the Laguncularia fringe riverine-influenced site. The highest rate of elevation change reported for the Mid Inlet estuary, South Carolina was in locations close

to freshwater input. Annual average elevation changes were 1.19, 0.30 and 0.64cm yr<sup>-1</sup> for a marsh influenced by freshwater input, and a mid and low marsh at South Town Creek near Winyah Bay, respectively (Childers et al. 1993). Marshes in Venice Lagoon, Italy had soil elevation change rates that ranged from -3.20 to 1.38cm yr<sup>-1</sup>, with the highest values at river mouth sites (Day et al. 1999).

Shallow subsidence (vertical accretion minus elevation change), was an important factor determining surface elevation in point bars and islands of the Tempisque-Bebedero system. In LI shallow subsidence was 6.53cm yr<sup>-1</sup>, and in UI it was 4.2cm yr<sup>-1</sup>, which represented 78% and 112% of the measured accretion, respectively. Within the system, the highest shallow subsidence was observed during the dry season in LI zones of the Tempisque River, where the largest sediment deposition occurred. Shallow subsidence has been reported for different coastal habitats including salt and brackish marshes and mangrove forests, from three geomorphic settings: coastal/estuarine fringe, delta and back barrier. Values ranged between -0.97 and 2.29cm yr<sup>-1</sup>, with no significant trends within or among habitat types and geomorphic settings (Cahoon et al. 1999).

Several processes can cause shallow subsidence including sediment compaction, belowground production and decomposition, swelling and shrinkage associated with vertical water movement and seasonal changes of water storage (Cahoon et al. 1999). In our study areas, soil shrinkage and swelling, compaction of recently deposited sediments, and organic matter decomposition are likely important factors contributing to shallow subsidence. After examining values of vertical accretion and elevation based on an analysis of 43 different wetland sites, Cahoon et al. (1999) concluded that shallow subsidence was more likely to occur in recently formed low salt marshes with unconsolidated mineral sediments, and marshes with highly organic soils or unstable substrates. Our lower intertidal sites are recently formed environments with unconsolidated sediments and unstable substrates. As reported for other studies, our results showed that vertical accretion by itself is not always a good estimate of elevation change, and that sediment deposition does not always translate into a positive change in elevation (Cahoon et al. 1995a, Cahoon et al. 1999, Day et al. 1999). Thus, surface elevation change at point bars and islands in the Tempisque-Bebedero system is controlled by both accretion and shallow subsidence.

Considering the rapid rate of elevation change measured at LI, these zones would be able to withstand the present global mean sea level rise of  $0.1\text{--}0.2\text{ cm yr}^{-1}$  (Gornitz 1995). This estimate is certainly in excess of current predictions regarding sea level rise within the next century (I.P.C.C. 1996) and it is higher than rates reported for other estuarine/riverine mangrove and wetland ecosystems (Cahoon et al. 1999). It is possible, however, that local hydrological changes as a response to high sedimentation could lead to forest community alterations as suggested elsewhere (Callaway et al. 1997, Day et al. 1999). For example, along the Southwestern coast of Thailand, depositional areas showed a change from the dominant mangrove species Rhizophora apiculata to Bruguiera, Ceriops or Xylocarpus spp., while zones of low sedimentation remained R. apiculata habitat (Fujimoto et al. 1999). In the Netherlands the salt marsh grass Atriplex portulacaoides increased in dominance over 10 yrs with a sedimentation rate of about  $5\text{ mm yr}^{-1}$  (Leendertse et al. 1997). Similar observations have also been described for other mangrove and marsh ecosystems (White 1993, Meeder et al. 1996, Duke and Khan 1999, Fujimoto et al. 1999).

#### 2.5.2. Forest Structure

In point bars and islands of our study area, Laguncularia is the pioneer species colonizing the rapidly emerging mud banks and lower intertidal zones, where it becomes the dominant species. In the New World, however, R. mangle is generally reported as colonizing lower intertidal zones (Lugo 1990, Thom 1967, Detweiller et al. 1975, Pool et al. 1977, Ball 1980, Soto and Jiménez 1982, Jiménez and Soto 1985, Day et al. 1987, Jiménez 1994, Augustinus 1995, Cantera and Arnaud 1997). Even though it is not “typical” to find dominant Laguncularia forests in the fringe zone, this has been reported in similar environments elsewhere (Pool et al. 1977, Conde and Alarcón 1993, Cantera and Arnaud 1997, Fromard et al. 1998). For example, in Buenaventura Bay, Colombia (a riverine dominated system), Laguncularia colonized the margins of point bars in the upstream region of estuaries (Cantera and Arnaud 1997). Similarly, along the Guianese coast, Laguncularia was found colonizing emergent mud deposits (Fromard et al. 1998). These results show that under conditions of lower salinity, soil instability, dynamic sedimentation, and lower energy conditions, such the ones found in point bars and islands of upstream river-influenced environments, Laguncularia seems to occupy a parallel habitat to that occupied by R. mangle in the downstream region of the estuary.



Even though Laguncularia can occur throughout the entire estuary (Duke et al. 1998), it is not dominant in downstream regions presumably because it is out-competed by R. mangle as indicated by successional patterns in a mangrove forest in Biscayne Bay, Florida (Ball 1980) and a restored mangrove stand in southwestern Florida (Proffitt and Devlin in Review). Similar to R. mangle, Laguncularia can develop a special growth form that enables it to better colonize lower intertidal environments, which are characterized by high frequency and duration of flooding, high water levels, and low sediment stability. In these environments R. mangle generally shows a prostrated growth form and high aerial root density (Jiménez and Soto 1985). In our study sites, Laguncularia showed a type of horizontal branching in areas that showed greatest sediment instability. Trees growing almost horizontally on the soil surface formed abundant secondary root growth on the lower part of the stem and lower branches, simulating extensive root systems that extended over the area, enabling them to cover the substrate efficiently. In many occasions branches grew perpendicularly from the main trunk as individual trees. A similar Laguncularia growth form was observed under high flooding conditions in the mangroves of Ciénaga Grande of Santa Marta, Colombia (Elster and Perdomo 1998), and in high accreting environments in the Guianese coast (Fromard et al. 1998). This particular growth form seems to be a response to unstable environments since Laguncularia trees 25m tall with straight stems have been reported on the southern Pacific coast of Costa Rica and many other places, under more stable sediment conditions (Jiménez and Soto 1985). Another adaptation to this highly dynamic environment is the production of specialized root systems, which play a role in binding and stabilizing sediments. In this way, the pneumathodes of Laguncularia behave similarly to the aerial roots of Rhizophora and the pneumatophores of Avicennia (Spenceley 1977).

Numerous studies have illustrated the role of mangroves and marsh plants in land building and soil stabilization in coastal environments (Pestrong 1972, Carlton 1974, Furukawa and Wolanski 1996). High vegetation density and morphological characteristics such as prop-roots, pneumatophores and pneumathodes decrease water velocities and increase sediment deposition (Pestrong 1972, Spenceley 1977, Augustinus 1995, Ellison and Farnsworth 1996, Furukawa and Wolanski 1996). Similar processes have also been described for salt marshes, grassed channels and seagrass beds (Augustinus 1995).

Laguncularia dominated the lower intertidal zones at point bars and islands in the Tempisque-Bebedero estuary, forming monospecific fringe forests that varied between 17 and 40m wide. These

forests were characterized by high tree density (9 556 trees ha<sup>-1</sup>). Although these trees were of very small diameter, they contributed to a relatively high basal area (25.0 m<sup>2</sup> ha<sup>-1</sup>) compared with other mangrove forests of the same species. In Laguna Verde, México, for example, a Laguncularia fringe forest had a low structural development (density: 1,800 trees ha<sup>-1</sup>, basal area = 9.9 m<sup>2</sup> ha<sup>-1</sup>), which was attributed to the lack of water movement and the frequent occurrence of storms (Flores-Verdugo et al. 1987). In Laguna de Términos, México, a low-salinity riverine site dominated by A. germinans and L. racemosa, Laguncularia had a density and basal area of 960 stems ha<sup>-1</sup> and 11.5 m<sup>2</sup> ha<sup>-1</sup>, respectively. And in a high-salinity fringing site dominated by R. mangle and L. racemosa, Laguncularia had a density and basal area of 2 574 stems ha<sup>-1</sup> and 9.5 m<sup>2</sup> ha<sup>-1</sup>, respectively (Day et al. 1987). In a natural mangrove forest on Naples Bay, Florida, Laguncularia dominated sites had densities ranging from 960 to 2 520 trees ha<sup>-1</sup> (Proffitt and Devlin, in review).

A high density of small diameter trees in an accreting environment, is often an indication of young forests (Lugo 1990, Fujimoto et al. 1995, Fromard et al. 1998), as in our fringing sites. As the point bar or island develops, the fringe remains in a young phase, while the interior matures. Similar to our study, pioneer mangroves establishing in rapidly accreting mud banks along the Guianese coast were characterized by small diameters, high stem density and limited tree height (Fromard et al. 1998). In these environments Laguncularia was the dominant species with densities (at two different sites) of 41 111 stems ha<sup>-1</sup> and 11 778 stems ha<sup>-1</sup> (dbh<10cm), with basal areas of 13.7 m<sup>2</sup> ha<sup>-1</sup> and 20.6 m<sup>2</sup> ha<sup>-1</sup>, respectively. Similarly, a pioneer A. germinans stand showed a high density of 31 111 stems ha<sup>-1</sup> (dbh<10cm) and a basal area of 12.5 m<sup>2</sup> ha<sup>-1</sup> (Fromard et al. 1998).

Even though Laguncularia remained the most abundant species in MI, other mangrove species were also present. As a result, a more transitional zone was apparent with species from both LI and UI zones. In terms of basal area, Rhizophora and Avicennia were the dominant species in the UI zone, characterized by less flooding, lower sedimentation and higher soil stability. This distribution, in which R. racemosa and Avicennia species dominate the interior forest under more consolidated environments has been reported before in other areas (Pool et al. 1977, Jiménez and Soto 1985, Conde and Alarcón 1993, Cantera and Arnaud 1997, Fromard et al. 1998). In the upper intertidal zone, tree density was generally low but trees were larger in diameter, an indication of a more mature forest. Similarly, mature

mangrove forests along the Guianese coast had lower tree density and higher diameters than pioneer stages (Fromard et al. 1998). In the present study, some UI areas with low salinity and reduced flooding, were characterized by the presence of other species, classified by Jiménez and Soto (1985) as marginal vegetation and facultative marginal vegetation. The result was an increase in the species richness of the UI zone. In French Guiana, the mangrove community became more diversified moving inland from the river mouth (Fromard et al. 1998). Along the erosive cut banks of the Tempisque and Bebedero, R. racemosa was the main species fringing the channels. Laguncularia was always absent, and Avicennia and Pelliciera were sometimes present. These observations suggest that mangroves found on the edges of cut banks represent the MI and UI zones of a previous point bar that has been eroded away. Similarly, in coastal lagoons in Tabasco, Mexico, when coastal erosion became dominant the front zone dominated by Rhizophora was removed by undercutting, and Avicennia became exposed (Thom 1967). Along erosive coastline sections in French Guiana, mangroves disappear as the coast retreats (Fromard et al. 1998).

Average basal area values estimated for the mangrove community at LI, MI and UI were 29.4, 21.4 and 57.3 m<sup>2</sup> ha<sup>-1</sup>, respectively, with respective densities of 9 855, 3 934 and 1 270 trees ha<sup>-1</sup>. These values are comparable or even higher than other mangrove forests of high structural development (Pool et al. 1977, Jiménez and Soto 1985, Jiménez 1988, Cantera and Arnaud 1997, Imbert and Ménard 1997, Fromard et al. 1998). For example, Pool et al. (1977) measured densities that varied between 1 100 and 4 000 trees ha<sup>-1</sup> with basal areas between 20.9 and 96.4 m<sup>2</sup> ha<sup>-1</sup>. A freshwater influenced A. germinans forest in la Baie de Fort-de-France, Martinique, had a tree density of 1 321 trees ha<sup>-1</sup> (Imbert and Ménard 1997). In the Pacific coast of Costa Rica, a R. racemosa mangrove forest influenced by river discharge, surface runoff and seepage had a basal area of 17.43 m<sup>2</sup> ha<sup>-1</sup> and a density of 2 024 trees ha<sup>-1</sup> (Jiménez 1988). In the same study area, plant density and basal area were 4 350 ha<sup>-1</sup> and 41 m<sup>2</sup> ha<sup>-1</sup>, respectively, for an A. bicolor forest (Jiménez 1990). Basal area and tree density for fringe forests ranges from 11.3 and 41.6 m<sup>2</sup> ha<sup>-1</sup>, and from 3 420 and 7 970 stems ha<sup>-1</sup>, respectively under different hydrological characteristics (Lugo 1990). Values for basal area in our sites were also higher than other mangroves located in the same region of the north pacific of Costa Rica. These other forests were associated with smaller rivers, therefore were characterized by higher salinities, which affected their development. For example, the mangroves of Puerto Soley had a density of 1 708 trees ha<sup>-1</sup>, with a total basal area of 19.7

$\text{m}^2 \text{ha}^{-1}$  (Soto and Jiménez 1982). And the mangroves of Jicaral had a density of  $1\,773 \text{ trees ha}^{-1}$  and a basal area of  $7 \text{ m}^2 \text{ha}^{-1}$ , (Jiménez and Soto 1985).

In addition to the occurrence of dominant mangrove species, other species such as A. glabra, C. caracasana, P. lanceolatum, Lonchocarpus, T. palustris, M. lunatum (trees and shrubs), B. minor (palm), C. erubescens (lily), E. polystachya and P. maximum (grasses) were also present. The occurrence of these species in such mangrove-dominated environments is an indication of the low salinity conditions of the Tempisque-Bebedero system. Most of these species were distributed in the interior areas of the forest at higher elevations, with the exception of C. erubescens, T. palustris and the grasses, which could also be found in lower intertidal zones.

The presence of seedlings, saplings and trees from a wide diameter range across the intertidal gradient indicates that active regeneration and recruitment into different diameter classes is taking place, and the forest is growing. Laguncularia was dominant in both LI and MI zones and, as a result, there was a large distribution of propagules and seedlings along the intertidal gradient during the time of forest crop production. After establishment, however, a period of high seedling mortality followed (pers. obs.), a phenomenon also reported for other mangrove species elsewhere (Lugo 1990, Jiménez 1988, Jiménez 1990). Mortality was especially high in MI and UI zones, due mainly to crab herbivory (see Chapter 4). In the mud bank zone, Laguncularia had an average density of  $0.2 \text{ seedling m}^{-2}$ , a very low value when compared to both LI, which ranged from  $45.9$  to  $100.2 \text{ seedlings m}^{-2}$ , and MI ( $50.7 - 2.9 \text{ seedlings m}^{-2}$ ) and UI, which ranged from  $22.1 - 2.8 \text{ seedlings m}^{-2}$ ). This difference seems to be an indication of the slow colonization process that is taking place in the lower and non-vegetated zones. The MB is characterized by low soil surface consolidation, higher frequency and duration of flooding, and a higher mechanical effect of tides, waves, and currents, factors that affect seedling establishment success (Clarke and Allaway 1993, Clarke and Myerscough 1993, Osunkoya and Creese 1997). In Thailand, rapid colonization of Avicennia alba over an accreting mud flat was supported by a large influx of propagules to the area ( $2000 - 4000 \text{ fruits day}^{-1}$ , Panapitukkul et al. 1998). In successional mangrove sites along Biscayne Bay, Florida, Laguncularia and R. mangle seedlings were found along the intertidal gradient with densities ranging from  $0$  to  $3.6 \text{ m}^{-2}$  and  $0$  to  $2.4 \text{ m}^{-2}$ , respectively (Ball 1980). An average value of  $17 \text{ seedlings m}^{-2}$  was reported for a mangrove forest dominated by Rhizophora mangle in Puerto Rico

(Golley et al. 1962). Densities from 89 to 220 seedlings  $\text{m}^{-2}$ , and from 3.9 to 14.1 seedlings  $\text{m}^{-2}$  were reported for a monospecific and a mixed forest of A. bicolor on the Pacific of Costa Rica, respectively (Jiménez 1990, Jiménez and Sauter 1991). In the same study site, seedling densities ranged from 3-10 seedlings  $\text{m}^{-2}$  of R. racemosa for monospecific and mixed mangrove stands, respectively (Jiménez 1988, Jiménez and Sauter 1991). Even though there was no significant species by zone interaction for saplings, sapling distribution across the intertidal gradient suggested a dominance of Laguncularia in LI environments, and a dominance of Rhizophora and Pelliciera in MI and UI zones. The lack or reduced presence of Avicennia saplings in MI and UI, however, suggests that this species might lose some importance value in these areas in the future, and other species such as Pelliciera might become more dominant.

## 2.6. CONCLUSIONS

Sedimentation patterns at point bars and islands along the Tempisque-Bebedero estuarine system showed the significant effect that these rivers have on sediment delivery and deposition within the mangroves of the area, especially at mud banks and within the lower intertidal zones. Inorganic sediments constituted the greatest contribution to sediment deposition (by g dry weight). Organic matter of deposited sediments varied between 30% to 35%, but importance of organic soil formation should be addressed along with studies of soil volume constituents, decomposition and tidal export.

Currently, agricultural activities within the Tempisque basin are affecting the natural sedimentation dynamics of the system. During the dry season, the use of Tempisque water for irrigation of extensive agricultural fields has resulted in a decrease of the river discharge and a significant increase of its sediment load. In addition to these changes, sediment re-suspension by wind induced waves is leading to higher levels of sediment deposition in the lower intertidal zones during the dry season.

Sediment deposition in the lower intertidal zone was always higher than the upper intertidal zone for both the Tempisque and Bebedero rivers, creating a gradient from the channel towards the interior of the forest. Frequency and duration of flooding, total suspended sediment concentration (independent of river discharge), wind (especially during the dry season), and tides are the most important factors determining sedimentation in point bars and islands in this system. In spite of the different types and degrees of human

impacts affecting the Tempisque and Bebedero, both rivers showed similar sedimentation patterns along the intertidal gradient, and similar mangrove forest structure.

At these actively accreting environments, shallow subsidence of recently deposited sediments was significant and even though positive accretion was measured at all times, this was not always translated into positive elevation gain. This indicates that both accretion and shallow subsidence controlled soil elevation change, and that measurements of vertical accretion in and of themselves are not a good representation of soil elevation in these environments. Therefore, it is recommended that under environments of high sediment deposition such as these, a combination of marker horizons and SET should be used to account for sub-surface processes of compaction, de-watering and decomposition. In spite of high shallow subsidence, the estimated rate of soil elevation change of lower intertidal zones was about one order or magnitude higher than predicted sea level rise.

Along the intertidal flooding and sedimentation gradient, a specific mangrove distribution was observed. Laguncularia was the pioneer species colonizing the rapidly emergent mud banks and dominated the lower intertidal zones, characterized by young un-consolidated sediment deposits, high accretion, high frequency and duration of flooding and low salinities. In these environments, Laguncularia formed monospecific stands characterized by high density, low diameter trees, which is to be expected for young immature forests. At middle intertidal, Laguncularia was also dominant but the presence of other species became more evident. Upper intertidal zones, characterized by lower frequency and duration of flooding, lower sedimentation and more consolidated soil conditions, were mainly dominated by Rhizophora and Avicennia, which formed more mature forests. The presence of seedlings, saplings, and trees from a wide diameter range of the different nuclear mangrove species, suggested potential forest recruitment across the intertidal gradient, and an active mangrove community development.

The correlation between forest structure and patterns of inundation, sedimentation and surface elevation change implies that mangroves in this region are distributed according to inter-specific differences in tolerances to inundation and sedimentation dynamics. The importance of such physical factors in affecting mangrove distribution is critical for both effective mangrove conservation and restoration. It is clear from this study that the mangrove forest communities along the Tempisque-Bebedero estuary are sensitive to the highly dynamic pattern of sedimentation, which is largely a result of

human impacts and alterations to the natural system. These results therefore suggest that any proposed alterations to the natural environment take into account potential impacts on the estuarine mangrove communities, which represent a very important natural and economic resource.

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### **CHAPTER 3.**

#### **SOIL PHYSICO-CHEMICAL CHARACTERISTICS AND FOREST STRUCTURE ACROSS THE INTERTIDAL GRADIENT OF POINT BARS AND ISLANDS IN A COSTA RICAN ESTUARY**

### 3.1. INTRODUCTION

Under many different environmental settings, soil physico-chemical properties are important in determining plant population structural characteristics in wetland ecosystems. For example, salinity affects species distribution and productivity in mangroves and coastal marshes in different regions around the world (Pool et al. 1977, Soto and Jiménez 1982, Boto and Wellington 1984, Ukpung 1992, Cardona and Botero 1998). Soil texture, nutrients, redox potential and soil pore water sulfide have also been correlated to mangrove community structure (Nickerson and Thibodeau 1985, McKee et al. 1988, Ukpung 1992, McKee 1993, Ukpung 1997, Cardona and Botero 1998, Sherman et al. 1998).

There are many examples in the literature on coastal ecosystems, which document the great variability and complexity of the soil-plant relationships. They offer contrasting results about which particular group of soil properties are important in determining species associations. For example, a comparison between a Rhizophora-dominated fringe and an Avicennia-dominated upper intertidal zone in Sierra Leone showed that the more fibrous soils of Rhizophora had higher pH, higher oxidisable sulphur, nitrogen, phosphorus and carbon than the non-fibrous soils of Avicennia (Hesse 1961). In contrast, in a study conducted in southeastern Brazil, soils under Avicennia had higher organic carbon and nitrogen than soils under Rhizophora (Lacerda et al. 1995). In the Shark river estuary on the west coastal plain of the Everglades National Park in Florida, a nutrient gradient from the estuary mouth (lower estuary) to the upper estuary was the controlling factor of mangrove forest species composition, basal area and productivity (Chen and Twilley 1999). In this environmental setting, a more developed and productive Laguncularia racemosa-dominated forest colonized the most fertile soils of the lower estuary. A less productive and less developed Rhizophora mangle dominated-forest colonized the less fertile soils of the intermediate and upper estuary (Chen and Twilley 1999). In contrast to this system which showed no salinity or sulfide stress, a study conducted in a mangrove forest on the Caribbean coast of Colombia showed salinity as the most influential parameter in the development and distribution of mangrove vegetation in the area (Cardona and Botero 1998). In general, wetland soils can be very heterogeneous, depending on the environmental setting being considered and the prevalent hydrological and sedimentological characteristics (Thom 1967).

On the Pacific coast of Costa Rica, point bars and islands in the Tempisque-Bebedero estuarine system are very active environments characterized by low salinities and high sediment dynamics. Under this environmental setting, mangroves show a particular species distribution across the intertidal gradient. Laguncularia racemosa (L.) Gaertn. f. always grows as a pioneer species in the lower intertidal zone. In some areas, however, scattered trees of this species are also found farther back in the forest, in the middle and upper intertidal zones. Mixed or monospecific forests of Rhizophora racemosa G.F.W. Meyer, Avicennia germinans (L.) L., A. bicolor Standley and/or Pelliciera rhizophorae Triana and Planchon, are generally found in the middle and upper intertidal zones behind the Laguncularia fringe. It is in these particular fringes that Laguncularia forms the largest monospecific stands found in the country. Very little is known about the actual physical or biological factors responsible for the distribution of these mangrove species along the intertidal gradient from the emergent mud bank back into the interior forest of this tropical estuarine system. Therefore, the main objective of this study was to characterize soil physico-chemical characteristics across the intertidal zones and relate them to the existing species distribution, as they might relate to the successful recruitment and development of the mangrove community. We hypothesize that changes in soil physico-chemical characteristics across the intertidal gradient are related to the observed species distributional pattern at point bars and islands. Considering that the hydrology of the Tempisque-Bebedero system is currently being altered as a result of intensive agricultural irrigation, an understanding of how soil characteristics relate to mangrove forest structure is of great importance in order to evaluate how modifications to the system may impact mangrove forest structure in the future.

### 3.2. STUDY AREA

The study was conducted in mangrove forests of the Tempisque-Bebedero estuarine system in the northern Gulf of Nicoya, a tropical estuary on the Pacific Coast of Costa Rica (Figure 3.1). This estuary is the second most important region of mangroves in the country, with an area of approximately 15176 ha (Jiménez and Soto 1985, Jiménez 1994). Climatically this area is a low-land dry tropical forest life zone (Holdridge 1967). Rainfall varies from less than 50 mm month<sup>-1</sup> during the dry season (December through April) to over 600 mm month<sup>-1</sup> during the rainy season (May through November). The annual precipitation for the region falls between 1 500 and 2 000 mm (Peterson 1960). The tidal



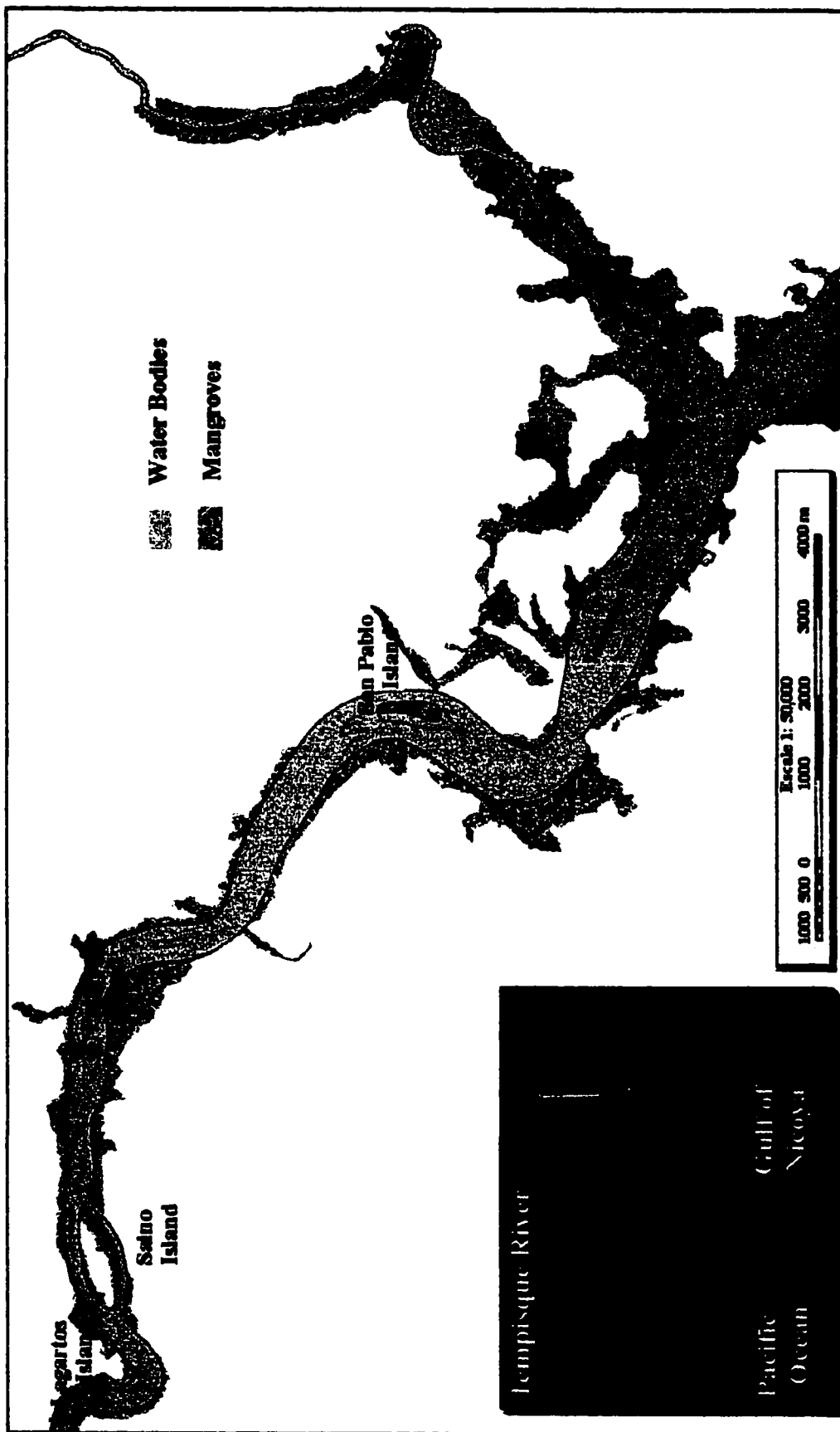


Figure 3.1. Map of the Tempisque-Bebedero estuarine system showing the study areas, numbered from one to six.

regime is semi-diurnal, with an amplitude ranging 2-3 m (Peterson 1960). Recently, an extensive net of irrigation channels and pumping stations was constructed within the Tempisque basin, which is used primarily during the dry season for irrigation of extensive agricultural fields. During this time of the year a large amount of water from the river is pumped out, and eventually drains back into the Tempisque, heavily laden with sediments (MINAE, Ministerio de Ambiente y Energía officials, pers. comm). As a result of the reduced river discharge and increased sediment load, the hydrology and sediment dynamics within the system is changing. The discharge of the Bebedero River, which joins the Tempisque River several kilometers downstream (Figure 3.1) has increased due to the drainage of water from an adjacent watershed, which is used for both hydroelectric power generation and agricultural irrigation. The two rivers, therefore, have different hydrological patterns based on the addition or removal of water, which has implications for materials fluxes and the response of the estuarine environment.

Point bars and islands in this setting are “low” energy sedimentary environments, characterized by a gradient of unconsolidated soils in the lower intertidal zone to more consolidated soils in the upper intertidal. Mangroves are the dominant plant communities colonizing these soils and exhibit characteristic zonation patterns, likely controlled by both environmental physical characteristics and specific plant tolerances and growth strategies. This study focused on point bar and island environments, because they represent constructive environments, which are associated with the initiation of mangrove forest development. Point bars and islands are likely the most sensitive areas in this estuarine system to human-induced changes in hydrology, because they are the youngest, most un-consolidated environments, and the most susceptible to erosion and compaction.

### **3.3. METHODS**

#### **3.3.1. Experimental Design**

The experimental design consisted of six study areas (four established in point bars and two in islands) located within the Tempisque-Bebedero estuarine system (Figure 3.1). Study areas were selected based on two common characteristics: the presence of a mud bank always exposed during low tides and the presence of a *Laguncularia*-dominated fringing forest. Within each study area, three main zones were defined along the intertidal gradient based on elevation and frequency and duration of flooding: mud bank (MB), lower intertidal (LI), and upper intertidal (UI). Relatively lower elevation, higher flooding

frequency and duration and high sediment deposition characterized the un-vegetated MB zone. The UI zone, located landward at the highest elevations within the mangrove forest, was characterized by lower frequency and duration of flooding and lower sedimentation. The LI zone, where the fringe forest is located, had intermediate characteristics of elevation, flooding and sedimentation (see Chapter 2). The width of the three zones varied among the study areas: MB zones varied between 3 to 16m; the LI zone between 17 to 40 m and the UI zone between 18 to greater than 100 m. At each area and within each zone, up to three replicate samples or measurements of soil physical/chemical variables were taken.

The general experimental design used to analyze the soil physico-chemical variables consisted in a completely randomized block design (CRBD), and a CRBD with a factorial arrangement (2 intertidal zones x 6 species) for the forest structural data. Data analyses were conducted using Proc GLM (SAS Inst. 1992). Residuals were always checked for normality and the data were transformed as needed. Forest structural measurements were collected during the dry season of 1999. Soil sampling and analyses were conducted during the dry season of 2000.

### **3.3.2. Forest Structural Characteristics**

Forest structure was measured once in plots of approximately 20 x 15 m established at random in each of LI and UI zones, for a total of two plots per study area, or 12 plots in all. No plots were established at MB due to the lack of mangrove vegetation in those zones. Species composition, tree density, and tree diameter at breast height (DBH) were measured in each plot (LI and UI). DBH of all trees greater than two centimeters DBH was tallied, and basal areas calculated (Cintrón and Schaeffer-Novelli 1984). Species importance values (IV) were calculated by integrating a species influence in the community through its contribution to stand density, basal area, and frequency (Curtis and McIntosh 1951).

An analysis of variance of a 2 x 6 factorial design was used to test for the effects of intertidal zone (LI and UI) and species (Laguncularia, Avicennia, Pelliciera, Rhizophora, Tabebuia and the category: Other-species). The residuals of the model were not normally distributed according to the Shapiro-Wilks test of normality, despite several attempts at data transformation. The distribution showed kurtosis, which does not represent a very serious problem for maximum likelihood techniques based on

the normal distribution (Montgomery 1991). Therefore the model was run on the raw data. For multiple comparisons a Bonferroni-adjusted family-wise Type I error rate of  $\alpha = 0.05$  was used.

### **3.3.3. Soil Physical Characteristics**

Soil shear strength, permeability to air, bulk density, soil texture, organic matter and conductivity were measured at MB, LI and UI zones during the dry season. Soil shear strength was the only variable measured directly in the field by using a pocket vane tester (Forsythe 1985). Fifteen random readings were taken within each intertidal zone. However, for statistical analyses, data was averaged per zone for a total of 18 readings. Soil shear strength measurements were taken during the dry season, when soils are drier and firmer as a result of reduced precipitation and tidal flooding (especially in UI zones). Therefore, these values of soil shear strength represent an upper limit.

To measure the other physical characteristics, superficial soil samples were collected using steel rings (6.7 cm diameter, 3.1 cm high). Three soil cores were randomly collected in MB, LI and UI zones in each of six areas, for a total of 54 samples. Samples were kept cool and immediately taken to the soils laboratory of the University of Costa Rica, Guanacaste, for further analyses. Non-destructive measurements of permeability to air and bulk density were first conducted. Subsequently, soil texture, organic matter and conductivity were measured on the same sample. Before measuring permeability, undisturbed soil samples were placed under a constant pressure (-0.33 bars) for approximately five days until all samples reached a water content equilibrium. Permeability to air,  $k$  ( $\cdot 10^{-7} \text{ cm}^2$ ) was then calculated for each soil sample by using readings from an air permeameter (Hartge and Horn 1989, modified by Morales). Duplicate readings were taken per sample. Due to the high water content of MB and other samples, a gap formed between the soil and the ring wall due to soil compaction after water equilibrium was reached. As a result, measurement of permeability to air in these samples was not possible.

To estimate bulk density ( $\text{g cm}^{-3}$ ), all 54 soil samples were oven dried at 65 °C for fifteen days. A sub-sample (0.5 g) from two of the three replicate soil cores taken (zone x site) were used to determine organic matter content (total 36 samples), following the titration method of Walkley and Black (1938, cited in González 1976). Percent organic carbon in the soil was derived from the data of organic matter by using a multiplication factor of 0.7792 (Morales, pers. comm.). Soil texture (% sand, silt, clay) was

determined by the hydrometer method (Bouyoucos 1962) on two of the three replicate samples (total 36 samples). Soil conductivity ( $\text{mS cm}^{-1}$ ) was measured from 1:5 soil to water suspensions using a conductivity meter HI 8033. One sample from each zone was used, for a total of 18 readings.

The relationship between intertidal zones and soil physical variables was evaluated with an analysis of variance using a completely randomized block design (CRBD). The experimental units were the individual replicate soil samples taken per zone x site. Permeability to air was log-transformed to meet the normality requirement of the model residuals. Orthogonal contrasts were conducted to determine significant differences between means.

#### **3.3.4. Soil Chemical Characteristics**

Interstitial soil salinity (ppt) was measured in the field using a manual refractometer. Soil interstitial water was collected from 50cm long piezometers. The piezometers were placed in the sediment prior to measurements and covered to avoid tidal water penetration. Multiple readings were taken for each LI and UI zone, but for statistical analysis, data was averaged per zone x site for a total of 12 readings. Because the salinity measurements were taken during the dry season, we expect these values to fall within the upper limits.

Soil analyses of pH, exchange acidity, cation exchange capacity (CEC), and macro-nutrients (Ca, Mg, K, P, TN,  $\text{NO}_3$ ,  $\text{NH}_4$ ) were conducted in the Laboratory of the Centro de Investigaciones Agronómicas (CIA) of the University of Costa Rica (following procedures described in Díaz and Hunter, 1978 and Henriquez and Cabalceta, 1999). Approximately one kilogram of soil was collected at random from the top 10-15 cm of the soil surface from each intertidal zone. Samples were kept on plastic bags and ice and immediately transported to the laboratory for analyses. In the lab, each sample was split in half, and analyses were performed on each pseudo-replicate. Acidity (pH) was measured from a 1: 2.5 soil to water suspension using a potentiometer. Exchange acidity was determined by extraction with KCl and titration with NaOH (Henriquez and Cabalceta, 1999). CEC was obtained as the summation of exchangeable cations (Ca, Mg, K, Al/H). Cations (Ca, Mg) were obtained by extraction with 1M KCl and determined by flame photometry (Henriquez and Cabalceta, 1999). K and P were obtained by extraction with the modified Olsen solution ( $\text{NaHCO}_3$ , EDTA) and determined by flame photometry and colorimetry at 660 nm, respectively; a solution of stannic chloride and sulfomolibdic acid was used for

the determination of P (Diaz and Hunter 1978, Henriquez and Cabalceta 1999). Total nitrogen (TN) was determined by the Kjeldahl method.  $\text{NO}_3$  and  $\text{NH}_4$  were obtained by extraction with 1M KCl and determined by colorimetry at 520 nm, using a cadmium-copper reduction column for  $\text{NO}_3$  (Diaz and Hunter 1978, Henriquez and Cabalceta 1999).

The relationship between intertidal zones and soil chemical characteristics was evaluated with an analysis of variance using a completely randomized block design (CRBD). The experimental unit was the average of the two pseudoreplicates taken per zone x site, for a total of 18 observations (6 replicates per zone). Nitrate data was log-transformed to meet the normality requirement of model residuals. Conductivity and exchangeable acidity residuals reached normality after removing two outliers. After several transformations, normality of P and salinity residuals was not met, due to the presence of kurtosis. Kurtosis does not represent a very serious problem for maximum likelihood techniques based on the normal distribution, so the model was run on the raw data. Orthogonal contrasts were conducted to determine significant differences between means.

Sediment deposition might represent an important source of nutrients to the system, given that previous results showed significantly higher sediment accumulation in LI compared to UI (Chapter 2). Nutrient deposition rates for these two intertidal zones were therefore calculated. The equation of Hatton et. al. (1983) was used to calculate rates for the following variables: Ca, Mg, K, P, TN,  $\text{NO}_3$ ,  $\text{NH}_4$ , exchange acidity and CEC. Concentrations based on a per gram dry soil basis ( $\text{g nutrient gdw}^{-1}$  soil) were expressed on a soil -volume basis by using soil bulk density ( $\text{gdw cm}^{-3}$ ). These values were then multiplied by the rate of vertical accretion ( $\text{cm yr}^{-1}$ , based on marker horizon data) to calculate the rate of nutrient deposition (Hatton et al. 1983).

Analyses of variance using a completely randomized design (CRD) were conducted for each of the nutrient deposition variables to test for differences between intertidal zones. Despite several transformations, exchange acidity, P,  $\text{NO}_3$  and  $\text{NH}_4$  did not meet the normality requirement of the model residuals. Therefore, the non-parametric Wilcoxon Kruskal-Wallis test was used to test for zone differences. These nutrient deposition variables, in addition to other soil variables (bulk density, percent sand, silt and clay, organic matter, soil shear strength and conductivity), was also used in a factorial analysis, which is described below.

### 3.3.5. Factor Analysis of Soil Physico-Chemical Variables

Because the different soil physico-chemical properties are correlated, a multivariate approach to study soils and their relationship with the environment has been increasingly applied in the literature (Patterson and Mendelssohn 1991, Ukpong 1992 and 1994, McKee 1995, El-Demerdash 1996). Factor analysis is an example of a useful technique for data reduction, where common factors composed of multiple correlated variables are selected and used for further analyses.

A factor analysis was conducted on the correlation matrix of measured soil physico-chemical variables and linear combinations or factors of multiple edaphic variables were extracted. Since the data had a singular matrix, a principal component solution of the factor method was conducted, and a varimax rotation of the original loadings was used to clarify factor interpretation (Johnson and Wichern 1992). Computed factor scores for each observation were then used as dependent variables in an analysis of variance using a completely randomized design (CRD) to determine differences across intertidal zones.

Due to the high number of soil variables measured (twenty in all) a pre-selection was done before running the factor analysis. Variables such as permeability to air and salinity were not included because of missing values for the MB zone. Other variables such as organic carbon, pH, and calcium, magnesium, potassium were not included because of their correlation with organic matter, exchange acidity and cation exchange capacity (CEC), respectively.

## 3.4. RESULTS

### 3.4.1. Forest Structural Characteristics

The mangrove forests of point bars and islands are mainly colonized by five mangrove species: Rhizophora racemosa, Laguncularia racemosa, Avicennia germinans, Avicennia bicolor and Pelliciera rhizophorae. However, other species (classified as marginal vegetation and facultative marginal vegetation by Jiménez and Soto 1985) also occur: Anona glabra, Cocoloba caracasana, Phytocelobium lanceolatum, Lonchocarpus sp., Tabebuia palustris, Machaderium lunatum (trees and shrubs), Bactaris minor (palm), Crinum erubescens (lily), Echinochloa polystachya, Panicum maximum (grasses), and some unidentified vines. Most of these species occurred in the UI zone, with the exception of Tabebuia, Crinum and Echinochloa, which also colonized the lower intertidal zone in some study areas.

MB zones were generally un-vegetated, with the exception of a few seedlings of Laguncularia, which established in the upper limit of MB in some study areas (see Chapter 2). The LI zone was dominated by Laguncularia, which formed mono-specific patches 17 to 40m wide. Rhizophora and Avicennia were the main species colonizing the UI zones in most of the study areas, but there was scattered occurrence of Laguncularia, Pelliciera and more upland vegetation (Table 3.1). The width of this zone varied from 18 to more than 100 m.

Table 3.1. Structural characteristics of the mangrove community for the lower (LI) and upper intertidal zones (UI). Only trees equal or higher than 2.0 cm DBH were considered in this analysis.

	Species	Density (Stems ha <sup>-1</sup> )	DBH (cm)	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Relative Abundance	Relative Dominance	Frequency	IV
LI	<u>L. racemosa</u>	9 556 ± 3 034	6.0 ± 0.6	25.0 ± 2.1	97.2	85.0	100	282
	<u>A. germinans</u>	100 ± 33	8.5 ± 5.5	2.1 ± 1.9	0.9	7.2	50	58
	<u>P. rhizophorae</u>	100 ± 67	4.3 ± 1.0	0.7 ± 0.6	1.0	2.3	50	53
	<u>R. racemosa</u>	33 ± 33	9.2 ± 0.0	1.1 ± 0.0	0.2	3.9	17	21
	<u>T. palustris</u>	33 ± 33	4.8 ± 0.0	0.4 ± 0.0	0.3	1.5	17	19
	Other species	33 ± 33	3.0 ± 0.1	0.1 ± 0.02	0.5	0.2	67	68
	TOTAL	9 855		29.4				
UI	<u>L. racemosa</u>	304 ± 194	9.0 ± 1.1	5.1 ± 2.8	23.8	8.8	50	83
	<u>A. germinans</u>	133 ± 67	31.8 ± 9.9	25.2 ± 11.7	11.0	44.0	67	122
	<u>P. rhizophorae</u>	233 ± 167	9.8 ± 4.9	3.9 ± 2.8	17.4	6.8	33	57
	<u>R. racemosa</u>	200 ± 67	23.7 ± 10.7	17.0 ± 9.0	15.7	29.6	67	112
	<u>T. palustris</u>	200 ± 133	2.6 ± 0.1	0.4 ± 0.03	16.4	0.7	33	50
	Other species	200 ± 167	11.2 ± 6.4	5.8 ± 3.4	15.7	10.2	33	59
	TOTAL	1 270		57.3				

Tree density and basal area showed significant differences among intertidal zones and among species ( $P < 0.05$ ). Tree density and basal area of Laguncularia were significantly higher in LI than at UI. Laguncularia also had higher density and basal area than any of the other species in any of LI and UI zones ( $P < 0.05$ , Table 3.1), with the exception of Avicennia and Rhizophora in UI zones.

A more mature mixed forest characterized the UI zone, where Avicennia and Rhizophora had the highest importance values (IV= 122 and 112, respectively). Even though these species had a similar tree density to Laguncularia in UI, most of the trees had larger diameters and basal areas, which accounted for their dominance (Table 3.1). In UI, Rhizophora and Avicennia had significantly higher basal areas than in LI ( $P < 0.05$ ). The values of basal and density were also higher than those of the other



species in any of the two zones, except for Laguncularia in LI. Laguncularia was the third most important species in UI, representing 24% of the total number of trees (Table 3.1). Pelliciera, Tabebuia and the “other species” had similar importance values (Table 3.1). Exceptions to this pattern of species dominance were study areas 1 (Lagartos island) and 3 (Pájaros island). In Lagartos, Laguncularia was also the dominant species in UI. In Pájaros, with the exception of a few scattered trees of Avicennia and Rhizophora, this UI was almost completely covered by the grass Echinochloa.

### 3.4.2. Soil Physical Characteristics

Based on the distribution of particles, soils of MB zones are characterized as clay loam, and soils of LI and UI soils as clay silt (Henriquez and Cabalceta 1999). This difference is due to the higher content of sands in MB soils, and of clays in LI and UI soils (Table 3.2). Overall, the percent of sand in the soils across the intertidal gradient was always significantly lower than that of silt and clay ( $P < 0.05$ ).

Table 3.2. Soil physical characteristics of mangrove colonized point bars and islands across the intertidal gradient: mud bank (MB), lower (LI) and upper intertidal (UI). Different letters indicate a significant difference at  $P < 0.05$ .

Soil Properties	MB	LI	UI
Bulk density ( $\text{g cm}^{-3}$ )	$0.52 \pm 0.03^a$	$0.58 \pm 0.02^{ab}$	$0.64 \pm 0.03^b$
Sand (%)	$21.12 \pm 5.02^a$	$11.48 \pm 2.84^a$	$11.89 \pm 5.10^a$
Silt (%)	$44.87 \pm 3.05^a$	$41.54 \pm 3.87^a$	$40.40 \pm 3.56^a$
Clay (%)	$34.01 \pm 4.13^a$	$46.97 \pm 2.98^b$	$47.71 \pm 3.57^b$
Organic matter (%)	$7.27 \pm 0.48^a$	$8.95 \pm 0.55^a$	$8.76 \pm 0.68^a$
Organic carbon (%)	$4.35 \pm 0.28^a$	$5.35 \pm 0.32^a$	$5.23 \pm 0.41^a$
Permeability to air ( $10^{-7} \text{ cm}^2$ )		$1.94 \pm 0.92^a$	$5.26 \pm 0.80^b$
Soil shear strength (Mpa)	$0.00 \pm 0.00^a$	$0.04 \pm 0.01^b$	$0.06 \pm 0.02^b$

The bulk density of MB soils was significantly lower than that of UI soils ( $P < 0.05$ , Table 3.2). Organic matter did not show significant differences among intertidal zones. Soil permeability to air was significantly higher at UI than at LI ( $P < 0.05$ ). Soil shear strength, considered an indicator of soil compaction, was significantly lower in MB soils than in LI and UI soils (Table 3.2). Soil shear strength measured in three of the six UI zones studied reached values equal or higher than the maximum reading given by the pocket vane tester (0.10 Mpa), indicating an under-estimation of this value. These higher

readings for the UI zone were associated with dry soil conditions, which are typical during the dry season when measurements were taken.

### 3.4.3. Soil Chemical Characteristics

Exchange acidity and pH were significantly higher at MB than at UI ( $P < 0.05$ ), but no significant differences were found between LI, MB or UI (Table 3.3). CEC was significantly lower at MB than at LI and UI ( $P < 0.05$ , Table 3.3). Of all the macronutrients analyzed Mg and  $\text{NO}_3$  had significantly lower values at MB than at LI and UI.  $\text{NH}_4$ , however, was significantly higher at MB than at LI and UI ( $P < 0.05$ , Table 3.3). Conductivity, salinity, K, P and TN did not change significantly across the intertidal gradient. In contrast to the results presented in Table 3.3, when soil chemical variables were expressed as a deposition rate, all variables except nitrate were significantly higher at LI than at UI (Table 3.4).

Table 3.3. Soil chemical characteristics of mangrove colonized point bars and islands across the intertidal gradient: mud bank (MB), lower (LI) and upper intertidal (UI). Different letters indicate a significant difference at  $P < 0.05$ , except for pH which was significant at  $P = 0.0589$ .

Soil Properties	MB	LI	UI
Conductivity ( $\text{mS cm}^{-1}$ )	$1.24 \pm 0.19^a$	$1.27 \pm 0.28^a$	$1.00 \pm 0.38^a$
Salinity (ppt)		$1.67 \pm 1.31^a$	$2.40 \pm 2.16^a$
pH	$6.98 \pm 0.20^a$	$6.49 \pm 0.03^{ab}$	$6.33 \pm 0.24^b$
Exchange acidity ( $\text{cmol (+) l}^{-1}$ )	$0.21 \pm 0.01^a$	$0.19 \pm 0.01^{ab}$	$0.17 \pm 0.01^b$
CEC ( $\text{cmol (+) l}^{-1}$ )	$27.00 \pm 2.41^a$	$34.37 \pm 1.41^b$	$33.65 \pm 2.41^b$
Calcium ( $\text{cmol (+) l}^{-1}$ )	$15.05 \pm 1.79^a$	$16.62 \pm 1.76^a$	$14.97 \pm 1.52^a$
Magnesium ( $\text{cmol (+) l}^{-1}$ )	$10.85 \pm 2.38^a$	$16.57 \pm 1.04^b$	$17.42 \pm 1.51^b$
Potassium ( $\text{cmol (+) l}^{-1}$ )	$0.88 \pm 0.21^a$	$0.97 \pm 0.16^a$	$1.07 \pm 0.15^a$
Phosphorus ( $\text{mg l}^{-1}$ )	$25.09 \pm 6.15^a$	$34.02 \pm 16.58^a$	$33.48 \pm 13.62^a$
Total nitrogen (%)	$0.18 \pm 0.01^a$	$0.22 \pm 0.01^a$	$0.20 \pm 0.02^a$
Nitrate ( $\text{mg kg}^{-1}$ )	$6.75 \pm 2.90^a$	$46.94 \pm 34.88^b$	$29.51 \pm 14.41^b$
Ammonium ( $\text{mg kg}^{-1}$ )	$114.75 \pm 22.45^a$	$52.16 \pm 13.44^b$	$29.77 \pm 2.81^b$

### 3.4.4. Factor Analysis of Soil Physico-Chemical Variables

From the thirteen soil variables used in the analysis, three factors were extracted based on the criterion that the eigenvalue is larger than unity (Johnson and Wichern 1992, Table 3.5). These three factors accounted for 84.9% of the variation in the data. The first factor was interpreted as a nutrient

**Table 3.4.** Soil chemical variables of mangrove-colonized point bars and islands for lower (LI) and upper intertidal (UI) zones expressed as a rate of deposition ( $\text{g cm}^{-2} \text{ yr}^{-1}$ ). Different letters indicate a significant difference at  $P < 0.05$ . For soil properties differentiated by the symbol \* a non-parametric analysis was conducted because of lack of normality on the data.

Soil Properties	LI	UI
Exchange acidity *	$0.0103 \pm 0.0014^a$	$0.0023 \pm 0.0003^b$
CEC	$27.63 \pm 1.36^a$	$6.51 \pm 0.46^b$
Calcium	$16.13 \pm 1.71^a$	$3.54 \pm 0.36^b$
Magnesium	$9.65 \pm 0.61^a$	$2.48 \pm 0.21^b$
Potassium	$1.84 \pm 0.30^a$	$0.49 \pm 0.07^b$
Phosphorus *	$0.17 \pm 0.08^a$	$0.04 \pm 0.02^b$
Total nitrogen	$0.01045 \pm 0.00058^a$	$0.00229 \pm 0.00022^b$
Nitrate *	$0.00023 \pm 0.00017^a$	$0.00004 \pm 0.00002^a$
Ammonium *	$0.00025 \pm 0.00007^a$	$0.00004 \pm 0.00000^b$

**Table 3.5.** Correlations of soil physico-chemical variables with factors. Factors were interpreted as follows: factor 1 = nutrient factor, factor 2 = bulk density-texture factor, factor 3 = soil consistency factor.

Soil Properties	Factor		
	1	2	3
Bulk density	-0.464	0.822	0.125
Sand	-0.105	-0.644	0.718
Silt	0.090	-0.086	-0.911
Clay	0.027	0.961	0.177
Organic matter	0.292	-0.777	-0.042
Soil shear strength	0.081	0.461	0.826
Conductivity	0.771	-0.183	-0.105
Exchange acidity	0.965	-0.104	-0.081
CEC	0.790	-0.200	-0.201
Phosphorus	0.883	-0.046	0.274
Total nitrogen	0.841	-0.299	-0.217
Nitrate	0.862	0.062	0.281
Ammonium	0.974	-0.106	-0.097
Percent variance explained by each factor	47.6	21.3	16.0

factor. Ammonium, phosphorus, nitrate, total nitrogen, exchange acidity, cation exchange capacity and conductivity showed high positive loadings. The second factor was interpreted as a bulk density-texture factor, with high positive loadings for bulk density and clay, and high negative loadings for organic matter and sand. The third factor was interpreted as a soil consistency factor, with a high positive loading of soil shear strength and a high negative loading of silt. Sand was also positively correlated to this factor.

Analyses of variance of factor scores showed a significant zone effect only for the nutrient factor ( $P < 0.05$ , Figure 3.2). For this factor, factor scores in the LI zone loaded significantly higher than those in the UI zone. High within -intertidal zone variability probably accounted for the lack of significant differences for other factors across the intertidal gradient.

### 3.5. DISCUSSION

#### 3.5.1. Mangrove Forest Structure

A distinct species distribution is found across the intertidal gradient of point bars and islands of the Tempisque-Bebedero estuarine system, with Laguncularia dominating the LI zone and Rhizophora and Avicennia mainly dominating the UI zone. The dominance of Laguncularia within the fringe zone is different from the classic mangrove distribution patterns commonly cited in the literature (Snedaker 1982), but it is a characteristic pattern observed within this environmental setting. And it has been reported for similar environments elsewhere (Conde and Alarcón 1993, Cantera and Arnaud 1997, Fromard et al. 1998).

Laguncularia dominated the LI zone, forming monospecific fringe forests 17 to 40 m wide. These forests had high tree density (9 556 trees  $\text{ha}^{-1}$ ) and relatively high basal area (25.0  $\text{m}^2 \text{ha}^{-1}$ ) compared with other mangrove forests of the same species (Day et al. 1987, Flores-Verdugo et al. 1987, Chen and Twilley 1999). A Laguncularia fringe forest in Laguna Verde, México, had a density and basal area of 1,800 trees  $\text{ha}^{-1}$  and 9.9  $\text{m}^2 \text{ha}^{-1}$ , respectively; low values attributed to restricted water movement and frequent storm occurrence in the area (Flores-Verdugo et al. 1987). In Laguna de Términos, México, a low-salinity riverine site dominated by A. germinans and L. racemosa, Laguncularia had a density and basal area of 960 stems  $\text{ha}^{-1}$  and 11.5  $\text{m}^2 \text{ha}^{-1}$ , respectively (Day et al. 1987).

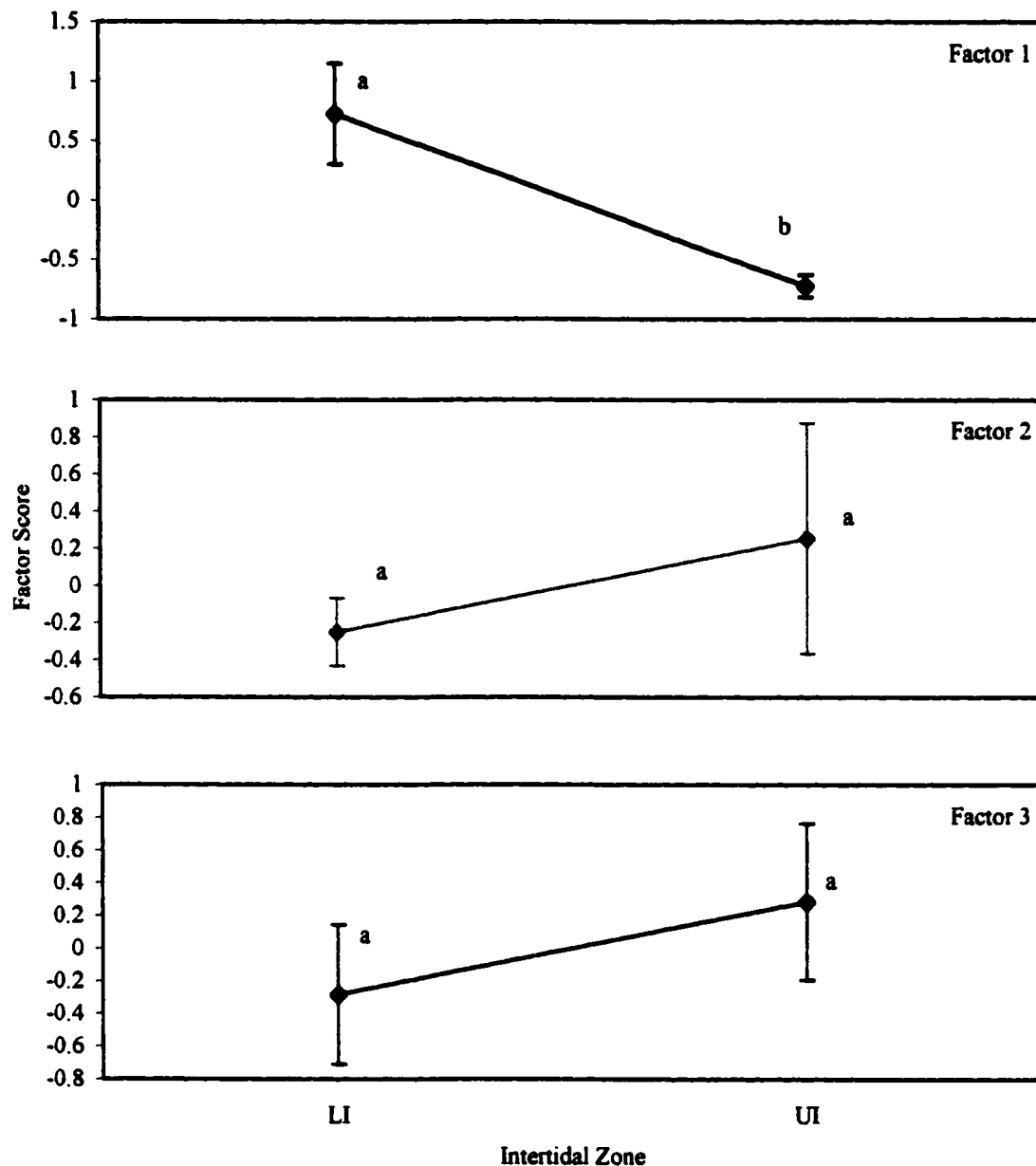


Figure 3.2. Factor score variation across the intertidal zones: lower intertidal (LI) and upper intertidal (UI). Factors were interpreted as follows: factor 1 = nutrient factor, factor 2 = bulk density factor, factor 3 = soil consistency factor. Different letters indicate a significant difference at  $P < 0.05$ .

The occurrence of high density of small diameter trees in an accreting environment such as this, is often an indication of a young forest (Lugo 1990, Fujimoto et al. 1995, Fromard et al. 1998).

Rhizophora and Avicennia dominated basal area in the UI zone, where these species formed monospecific or mixed forests in combination with other species. In this zone, tree density was generally low but trees were larger in diameter, indicating a more mature forest. This structural pattern of higher

density of smaller trees in pioneer stages, and lower density of larger trees in more mature forests is also characteristic in other regions, such as mangrove forests along the Guianese coast (Fromard et al. 1998).

In addition to the occurrence of dominant mangrove species, the presence of less salt tolerant vegetation in such mangrove-dominated environments is the result of the high riverine influence within the system. Most of these species were distributed in the internal areas of the forest in higher elevations, with the exception of Crinum, Tabebuia and some grasses, which could also be found in lower intertidal zones. Both the Tempisque and Bebedero rivers are an important source of freshwater and sediments (see Chapter 2), which is associated to the low salinity ranges and relatively high nutrient concentrations observed in these environments. As a result, mangroves of point bars and islands have a relatively high structural development compared to other mangroves also under riverine influence (Pool et al. 1977, Jiménez 1988, Jiménez 1990, Lugo 1990, Imbert and Ménard 1997).

### **3.5.2. Soil Physico-Chemical Characteristics**

Overall, soils of point bars and islands are characterized by their mineral content and low salinity, a result of the high riverine influence in these environments. Bulk density, which ranged between 0.52 and 0.64 g cm<sup>-3</sup> and low levels of organic matter, between 7% and 9% are characteristics of a more mineral soil (Mitsch and Gosselink 1986), and are comparable with values reported for mangroves under high riverine or marine influence (Ukpong 1992 and 1994). As suggested by the factor analysis (Factor 2, Table 3.5) conducted for LI and UI soils, bulk density is positively correlated to soil clay content and negatively correlated to sand and organic matter content (Mitsch and Gosselink 1986). The low pore water salinity and soil conductivity measured are indicators of low salinity stress. Contrary to reports for other mangrove areas (Soto and Jiménez 1982, Boto and Wellington 1984, Cardona and Botero 1998), salinity in point bars and islands is not a constraint for plant growth and development, as indicated by the high basal area values measured across the intertidal gradient.

The distribution of soil particles across the intertidal gradient showed a reduced percentage of sand and a dominance of silt and clay, which again indicates the riverine influence in these environments. Based on their physical characteristics, soils across the intertidal gradient mainly differed in their degree of consolidation. Increasing soil stability was observed in a landward direction, with MB soils showing lower shear strength than LI and UI soils. These differences are directly related to the gradient in the

frequency and duration of flooding across the intertidal zones. The LI and UI zones experience longer periods of exposure to the atmosphere resulting in a higher consolidation by desiccation (Augustinus and Slager 1971, Morales 1996). Since soil shear strength is highly influenced by the soil water content (Enriquez and Cabalceta 1999), greater spatial and temporal variability of soil shear strength is expected in the LI and UI zones due to less regular flooding. In terms of mangrove dynamics, the lack of soil consolidation probably represents an important factor limiting mangrove establishment in mud banks by affecting propagule anchoring and uplifting (pers. obs., Chapter 4). As a response to unconsolidated soils, in addition to high frequency of flooding, Laguncularia growing in the lower intertidal zone has developed a special type of growth form. By forming extensive horizontal branching and secondary root growth close to the soil surface (simulating extensive root systems), a single Laguncularia tree can cover a more extensive soil area resulting in greater support and stability. A similar Laguncularia growth form was observed under high flooding conditions in the mangroves of Ciénaga Grande of Santa Marta, Colombia (Elster and Perdomo 1998), and in high accreting environments in the Guianese coast (Fromard et al. 1998).

Soil chemical characteristics, as described by the univariate analyses (Table 3.3), showed that MB soils were less acidic, with lower CEC and nitrate, and higher ammonium concentration than LI and UI soils. These differences are mainly associated with the flooding gradient and the presence or absence of vegetation. Tidal inundation is an important factor determining soil redox potential, which in turn controls different chemical transformations occurring within the soil (Mitsch and Gosselink 1986). Since plant presence at the MB zone is absent, a lack of uptake may contribute to the observed ammonium buildup in this zone. While some nitrification might be occurring in an upper, more oxidized layer, nitrate is probably being lost by leaching and/or denitrification. This would explain its lower levels in the MB zone compared to LI and UI zones. In contrast, the lower levels of ammonium and higher levels of nitrate in LI and UI zones seems to be related to plant uptake and probably nitrification in the more oxidized soils, respectively. In the Caribbean coast of Colombia, heavy deteriorated mangrove areas showed higher concentrations of ammonium and nitrate-nitrite than healthier areas, which was attributed to high organic matter decomposition and mineralization of dead material, and to low plant assimilation since most of the vegetation was dead (Cardona and Botero 1998). Similarly, Boto and Wellington

(1984) showed that for a mangrove forest in northern Australia ammonium depletion was correlated to plant uptake during high production periods.

Soil texture, especially clay content and organic matter levels are important factors determining soil fertility. The cation exchange capacity (CEC, Henriquez and Cabalceta 1999) is a measure of the soil capacity to adsorb elements, especially cations. LI and UI soils showed a significantly higher CEC (especially as exchangeable magnesium) than MB soils (Table 3.3), which follows the same pattern of higher content of clay and organic matter in the LI and UI vegetated zones. Similar findings have been reported in other studies (Naidoo 1980, Lee et al. 1996). Higher CEC suggests that these soils could be a better sink for nutrient cations (e.g.  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ).

Hydrology is an important forcing function determining soil physico-chemical characteristics in coastal ecosystems (Boto and Wellington 1984, Tam and Wong 1998). In this study, many of the physical and chemical properties of the soils that changed across the intertidal zones were directly or indirectly associated with the flooding gradient. However, the role of vegetation as an important feedback process modifying soil characteristics and contributing to soil formation should also be considered. Organic matter deposition through litterfall might represent an important source of nutrients to the system (Boto and Wellington 1984, Lacerda et al. 1995, Tam and Wong 1998). Plant nutrient uptake can also affect soil chemical characteristics by modifying the soil nutrient pool (Boto and Wellington 1984, Tam and Wong 1998). Therefore, plant uptake in LI and UI zones probably accounts for some of the differences observed in nutrient concentrations across the intertidal zone. Plants can also modify their immediate soil microhabitat by transporting oxygen through the root system (Boto and Wellington 1984, Thibodeau and Nickerson 1986), which in turn can affect different chemical transformations and nutrient availability (Mitsch and Gosselink 1986). Additionally, mangroves and other coastal wetland vegetation enhance soil stability through binding of sediments (Spenceley 1977, Augustinus 1995).

The average basal area and density estimated for the mangrove communities at LI and UI are comparable to or higher than that of other mangrove forests of high structural development (Pool et al. 1977, Jiménez and Soto 1985, Jiménez 1988, Cantera and Arnaud 1997, Imbert and Ménard 1997, Fromard et al. 1998). This suggests that the nutrient levels in LI and UI zones are not a limiting factor for



mangrove development in point bars and islands of the Tempisque-Bebedero system. Concentrations of Ca, Mg, K, NO<sub>3</sub> and NH<sub>4</sub> measured in this study (Table 3.3) generally showed comparable and sometimes higher values than those reported for other mangrove forests (Naidoo 1980, López-Portillo and Ezcurra 1989, Lacerda et al. 1995, Ukpong 1992 and 1997, Tam and Wong 1998, Vegas-Velarrúbia 2000). Total nitrogen and phosphorus concentrations, however, were generally lower than those reported for mangrove ecosystems in other regions (Boto and Wellington 1984, Cardona and Botero 1998, Chen and Twilley 1999, Coronado-Molina 2000). Similar to other systems under both riverine and marine influence (Boto and Wellington 1984, Lee et al. 1996, Duarte et al. 1998), the input of freshwater and sediments from the Tempisque and Bebedero rivers seems to account for the “richness” of the soils.

When nutrient deposition rates for LI and UI zones were calculated based on sedimentation data, contrasting results were obtained (Tables 3.3 and 3.4). While the first analysis based on nutrient concentrations did not show any significant difference between LI and UI (Table 3.3), both the univariate and factor analyses of nutrient deposition rates showed a significant difference between zones for all nutrient variables, except nitrate (Table 3.4). This indicates the importance of riverine sediment deposition as an immediate source of nutrients to this system, as well as a potential source for a long-term nutrient accumulation. It is important, however, to consider that these estimates of nutrient deposition rates represent only net accumulation, without indicating the extent of nutrient losses.

Phosphorus and total nitrogen deposition rates obtained in our study were in general between one and two orders of magnitude higher than values reported for a wetland system in the Everglades, Florida receiving anthropogenic nutrient inputs (Reddy et al. 1993). In spite of this source of nutrients, the low sedimentation rates reported for this region of Florida probably accounted for the lower nutrient accumulation compared to our sites. Similarly, total nitrogen and total phosphorus accumulation rates calculated for mangrove systems at Rockery Bay, Florida and Términos Lagoon, Mexico (Lynch 1989) were much lower than ours, which again seems to be associated to the very high rates of sedimentation in our study area.

After examination of the analyses of soil physico-chemical variables and mangrove structure, results from this study suggest a relationship between soil properties, especially nutrient concentration, and species distribution. Laguncularia at point bars and islands of the Tempisque-Bebedero system is

colonizing and dominating the “richer” environment of LI zones, while R. racemosa and Avicennia species colonize the “poorer” environments of the UI zone. Results from our study are comparable with results obtained by Chen and Twilley (1999) for the Shark river estuary in Florida. These authors concluded that concentrations of nitrogen and phosphorus were correlated to observed patterns of forest structure in that system. The more fertile soils of the lower estuary were dominated by Laguncularia, and the less fertile soils of the intermediate and upper estuary were dominated by Rhizophora mangle. Similarly, soil pore water analyses conducted in a deltaic mangrove forest in the Dominican Republic showed that the distribution of Laguncularia was significantly correlated to total phosphorus, dissolved organic carbon, alkalinity, sulfate depletion and pyrite concentrations (Sherman et al. 1998). In contrast to our study, these other studies have not shown a clear correlation between soil physico-chemical characteristics and mangrove species distribution (Clarke and Hannon 1967, Naidoo 1980, Ukpong 1995).

### 3.6. CONCLUSIONS

The mangrove community associated with point bars and islands in the active sedimentary environments of the Tempisque-Bebedero system is characterized by a distinct species distribution across the intertidal gradient. Laguncularia racemosa always colonizes and dominates the lower intertidal region, and other species (Rhizophora racemosa, Avicennia germinans, Pelliciera rhizophorae and others) are found in the upper intertidal zone, forming more mature monospecific or mixed forests.

As a general characterization, and based on their physical characteristics, soils across the intertidal gradient of point bars and islands in the Tempisque-Bebedero estuarine system mainly differ in their consolidation. Increasing soil stability is observed in a landward direction, which is directly related to the gradient in the frequency and duration of flooding. Based on their chemical characteristics, MB soils are characterized by an accumulation of ammonium and lower levels of nitrate, probably as a result of higher reduced conditions in this zone. In general, higher nutrient concentrations characterize the more oxidized soils of LI and UI zones.

Soil parameters appear to be mainly controlled by the hydrology of the site and the presence of vegetation. Besides the above-mentioned gradient in frequency and duration of flooding, MB soils are the only ones left unvegetated. Flooding is important because it directly affects soil chemical

transformations and resource availability through material fluxes. In terms of nutrient concentrations, the high riverine influence in this environmental setting is important as a source of nutrient-rich sediments. As a result of different sedimentation rates between LI and UI zones, nutrient accumulation rates at LI are significantly higher than at UI. Vegetation, on the other hand, can influence soil physico-chemical characteristics through organic matter deposition, nutrient uptake, oxygen transport to the rhizosphere and by enhancing sediment binding and stability.

Therefore, based on the analyses of the soil physico-chemical characteristics, results from this study suggest that soil properties such the ones examined in this study are likely to influence the observed species distribution at point bars and islands. Laguncularia colonizes and dominates the lower intertidal zone, characterized by somewhat lower stability and “richer” soils. Rhizophora, Avicennia and Pelliciera, on the other hand, colonize the upper intertidal zone characterized by higher stability and “poorer” soils. Other characteristics, involving biological factors such as propagule dispersal, and establishment, crab herbivory, and inter-specific differences in flooding and sedimentation tolerance should also be considered to better explain the observed species distributional pattern across the intertidal gradient of point bars and islands in the Tempisque-Bebedero system.

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## **CHAPTER 4.**

### **THE IMPORTANCE OF PROPAGULE ESTABLISHMENT ABILITY AND PHYSICAL FACTORS IN MANGROVE DISTRIBUTIONAL PATTERNS OF A COSTA RICAN ESTUARY**

#### 4.1. INTRODUCTION

Different biotic and physico-chemical characteristics of the environment are known to affect propagule dispersal, survival and establishment, and the subsequent species distribution under different environmental settings (Thom 1967, Snedaker 1982, Louda 1989, Duke et al. 1998). Propagule buoyancy, period of obligate dispersal, anchoring time, and the action of tides and currents are primary factors determining dispersal and establishment of mangroves and other water-dispersed species (Rabinowitz 1978a, Foote and Kadlec 1988, Schneider and Sharitz 1988, Clarke and Myerscough 1991, Clarke 1993, McGuinness 1997a). Furthermore, when propagules reach a newly-formed habitat, other factors become important in determining establishment success and survival including: (1) predation (Louda 1982, Smith 1987b, 1987c, White 1993, McKee 1995a, Dahdouh-Guebas et al. 1998), (2) interspecific competition (Ball 1980, Kangas and Lugo 1990, Clarke and Myerscough 1993, Patterson et al. 1993), (3) frequency and duration of flooding (Jiménez and Sauter 1991, Clarke and Myerscough 1993), and (4) soil physical-chemical characteristics (Nickerson and Thibodeau 1985, Patterson and Mendelssohn 1991, Ukpong 1991, McKee 1993, White 1993, Sherman et al. 1998).

In the Gulf of Nicoya, a tropical estuary on the Pacific Coast of Costa Rica, the Tempisque and Bebedero rivers form a very active estuarine environment. Because of high riverine influence, low salinities and high sediment transport are important characteristics of this system. Both rivers are characterized by meandering channels, forming cut banks in the concave side of a river bend, and point bars in the opposite convex bank. Because of geomorphology and water downstream and lateral velocities, sediments are eroded from cut banks, but deposited in point bars (Coleman 1969). Considering the sedimentary nature of point bars and islands (which also represent areas of deposition) they form unstable environments, with specific hydrological and physical characteristics which influence mangrove establishment. In point bars and islands of the Tempisque-Bebedero system, Laguncularia racemosa (L.) Gaertn. f. is found as the pioneer species colonizing emergent mud bank deposits and the lower intertidal zone. Similar to other mangrove ecosystems, under similar geomorphic settings (Pool et al. 1977, Jiménez 1994, Cantera and Arnaud 1997, Fromard et al. 1998). In this environment, Laguncularia forms the largest monospecific stands found in the country. Rhizophora racemosa G.F.W. Meyer, Avicennia germinans (L.) L., A. bicolor Standley, and Pelliciera rhizophorae Triana y Planchon

are also found colonizing middle and upper intertidal zones and fringing cut banks. Rhizophora mangle, which is absent from this particular system is generally found colonizing low intertidal zones along the entire Pacific coast of Costa Rica (Jiménez and Soto 1985).

Very little is known about the actual physical and biological factors responsible for the apparent distribution of mangrove species along the mud bank – intertidal zone gradient in point bars and islands in such a tropical estuarine system. The main objective of this study is, therefore, to determine the importance of various biological and physical properties of mangrove propagules and the mangrove environment, which make Laguncularia a successful colonizer in this environmental setting. Based on observations of distributions, we hypothesize that Laguncularia is a more successful pioneer than Avicennia spp. because of propagule buoyancy characteristics, rapid rooting (fixation), insensitivity to shallow burial by sediment, and anchoring insensitivity to regular water movement and frequent flooding. Conversely, Laguncularia's distribution into upper intertidal zones might be limited due to predation that increases mortality prior to establishment.

#### 4.2. STUDY AREA

The study was conducted in mangrove forests of the Tempisque and Bebedero rivers, which flow into the Gulf of Nicoya, a tropical estuary on the Pacific coast of Costa Rica (Figure 4.1). Both rivers supply the largest contribution of freshwater to the upper Gulf (Voorhis et al. 1983), as well as sediments and nutrients to the estuary (Epifanio et al. 1983). This estuary represents the second most important region colonized by mangroves in the country, covering an area of approximately 15 176 ha (Jiménez and Soto 1985, Jiménez 1994). Climatically this area is a low-land dry tropical forest life zone (Holdridge 1967). Rainfall varies from less than 50 mm month<sup>-1</sup> during the dry season (December through April) to over 600 mm month<sup>-1</sup> during the rainy season (May through November). The annual precipitation for the region falls between 1 500 and 2 000 mm (Peterson 1960). The tidal regime is semi-diurnal, with an amplitude ranging 2-3 m (Peterson 1960).

A typical mangrove vegetational pattern across the intertidal gradient of point bars and islands in the Tempisque-Bebedero system (see Chapter 2) shows Laguncularia racemosa as the dominant species in the lower intertidal zone forming mono-specific patches 17 to 40m wide. In the middle intertidal zone it is also very abundant, but forms a more mixed forest with other species such as Avicennia spp.,

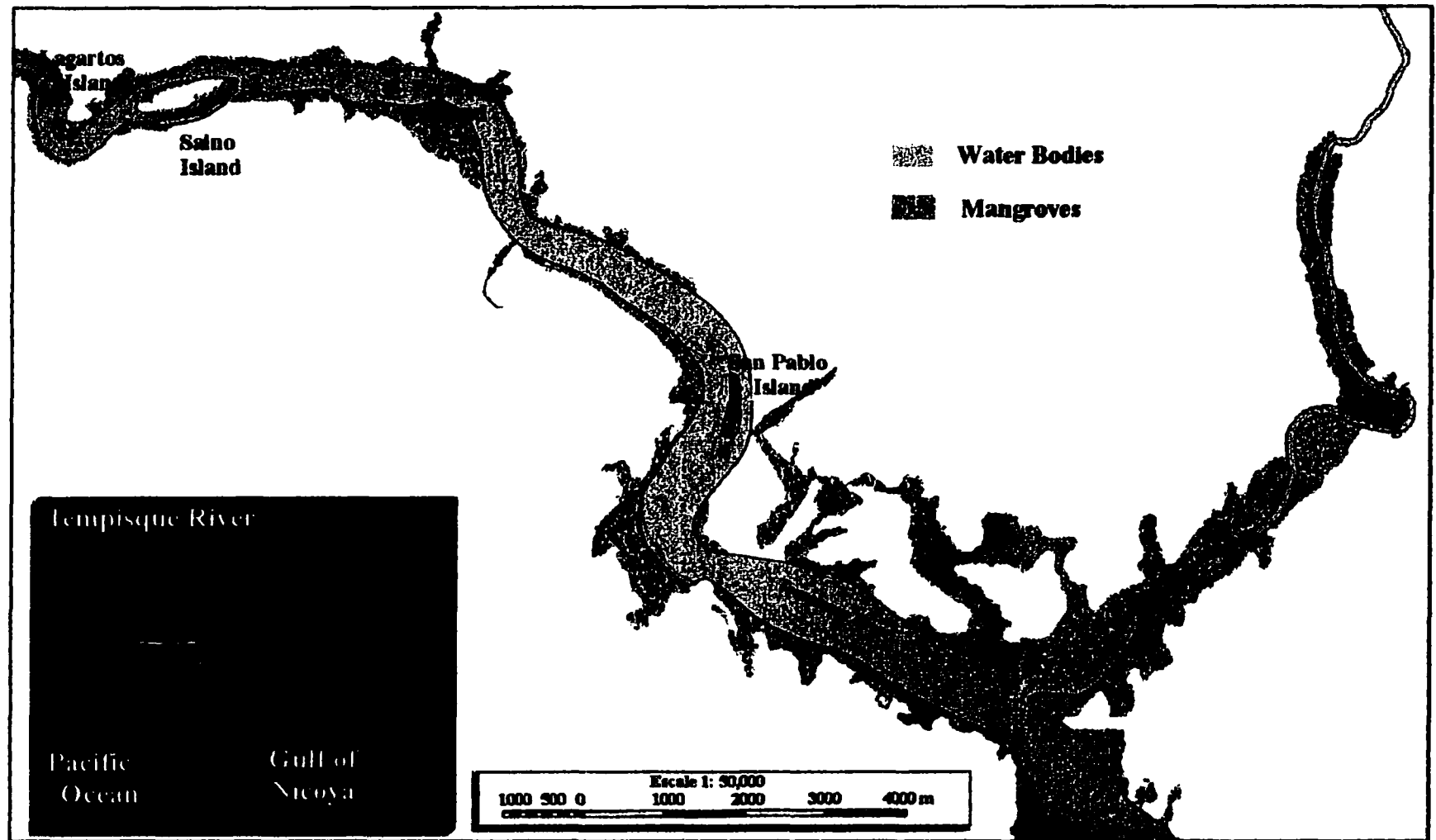


Figure 4.1. Map of the Tempisque-Bebedero estuarine system showing the study areas, numbered from one to six. Propagules in the field cross-planting experiment were placed across each area's intertidal gradient according to the following pattern: study area 1, MB, LI; study area 2, MB, LI, UI; study area 3, LI; study area 4, MB; study area 5, UI and study area 6, UI. Where MB, LI, UI correspond to mud bank, lower and upper intertidal zones.

Pelliciera and/or Rhizophora. Rhizophora and Avicennia spp. were the main species colonizing the upper intertidal zone, but with scattered occurrence of Laguncularia, Pelliciera and/or more upland vegetation.

The presence of marginal vegetation and facultative marginal vegetation (Jiménez and Soto 1985) such as Tabebuia palustris, Anona glabra, Cocoloba caracasana (trees and shrubs), Bactaris minor (palm), Crinum erubescens (lily), Echinochloa polystachya, Panicum maximum (grasses), is an indication of the low salinity conditions of the environment. Most of these species were distributed in the interior areas of the forest at higher elevations, with the exception of C. erubescens, T. palustris and the grasses, which could also be found in lower intertidal zones.

#### **4.3. METHODS**

Propagule establishment, development and mortality and seedling survival and growth were studied for Laguncularia and Avicennia spp. under two different experimental settings: a field cross-planting experiment and a controlled mesocosm experiment. Species selection for the study was based on several reasons: 1) because of Laguncularia dominance in the lower intertidal zone, this species was of main interest. 2) Because Avicennia spp., similar to Laguncularia, are characterized by small propagules and have also been reported as pioneer species elsewhere (Thom 1967, López-Portillo and Ezcurra 1989), these were the most appropriate for comparison reasons. 3) Because R. racemosa is rarely a pioneer species, and because of logistical constraints of adding a third species, this was not considered for the study. 4) R. mangle, which is commonly found colonizing unstable environments such as these (Tomlinson 1986, Jiménez 1994), was not considered since it is absent from the system.

For the field cross-planting experiment, propagules of A. germinans and A. bicolor were grouped together, due to the limited availability of intact propagules of either species during the time of the experiment. Because inter-specific differences in establishment, mortality and predation were not significant between them, and both showed the same relationship to Laguncularia; we referred to both species as Avicennia, in the text. For the mesocosm experiment only A. germinans propagules were used.

##### **4.3.1. Field Cross-Planting Experiment**

This first study was designed to measure differences in the ability of Laguncularia and Avicennia propagules to establish in point bars and islands, along the gradient from mud bank to lower

and upper intertidal zones. We hypothesize that differential success in propagule establishment will explain the observed pattern of mangrove distribution, with Laguncularia acting as the pioneer mangrove species.

Six study areas, located in point bars and islands, were selected along the Tempisque and Bebedero rivers (Figure 4.1). Each area included one or more of the three zones: mud bank (MB), lower (LI), and upper intertidal (UI), which were defined mainly by their differences in frequency and duration of tidal flooding, and vegetation. MB and LI zones are generally flooded daily, although during very low water levels, the LI zone may not be completely covered. Because of its higher elevation, during low water levels, the UI zone is only flooded during the highest tides of the month. For a twelve-hour tidal cycle approximate flooding durations per zone are MB, 4-5 hrs; LI, 2-3 hrs; and UI, 0-1 hr. Soil consolidation also changed across the intertidal zone increasing from MB to UI zone. The MB is generally un-vegetated, the LI zone is colonized by Laguncularia and the UI zone by a more mature and mixed mangrove forest.

Propagules of Laguncularia and Avicennia were collected from the field. Laguncularia propagules were taken directly from the trees, while Avicennia propagules with intact pericarps were taken from the forest floor, since propagules were hard to reach from the tall, mature trees. Propagule fresh weight and length measurements were taken from representative samples of all species. Before placing propagules in the field, a tethering system was used to keep the experimental propagules from leaving the study zones in which they were to be placed; with a sewing needle, a fine fishing line 30 cm long was pulled through the propagule cotyledons taking care not to damage the embryo. The propagule was then tied to a 30 cm wire stake. One hundred propagules of each species were thus prepared and placed in each of the three study zones (MB, LI, and U), and replicated a total of three times across the various areas (Figure 4.1), for a total of 900 propagules per species. Propagules were set 25 cm apart along four lines parallel to the main channel. In MB zones, a boardwalk parallel to the channel was built to avoid sediment disturbance, and propagules were placed 25 cm apart along four lines, two along each side of the board. Placement of propagules in the field was done at different times between September 8 and 20, due to logistical constraints and the lack of embryo dormancy. Once the propagules were placed in the field, radicle protrusion, establishment, expansion of first pair of leaves, mortality and survival

were recorded at different intervals for approximately 40 days. A propagule was considered established once anchoring and lifting of the cotyledons above the sediment surface took place. Mortality was differentiated by cause, desiccation, herbivory and other factors. A last reading of survival-mortality was recorded after 75 days for several of the study areas. Due to preliminary results showing crab propagule predation, the abundance and size of crab holes was estimated for LI and UI zones. Five plots of one square meter were randomly placed in each LI and UI zone across areas. Due to very low crab activity observed in MB's, crab abundance was not quantitatively estimated for these zones.

The experimental design consisted of a combination of a split plot design, with a completely randomized design (CRD) for study zone (MB, LI, UI), and a randomized block design (RBD) for species (L, A) with a nested error structure. Statistical tests (SAS Inst. 1992) were conducted to determine significant differences in the success of propagule establishment and mortality among study zones and between species. A chi-square test was performed to determine differences in the size class distribution of crab holes between LI and UI zones.

#### **4.3.2. Mesocosm Experiment**

This second study was designed to determine the importance of propagule buoyancy, time of establishment, hydroperiod and high sedimentation (shallow burial) in the establishment success of Laguncularia racemosa and Avicennia germinans propagules.

Twenty wooden mesocosms (boxes), approximately 51 cm x 38 cm and lined with a plastic bag, were placed in open sunlight at the Palo Verde Biological Station located at approximately 5 km from the first study area. All mesocosms were exposed to the same climatic conditions. Each box was filled with 7 cm of sediment collected from a Tempisque river mud bank, and was covered with 10 cm of Tempisque river water. Four different flooding treatments consisted of: (1) flooded according to tidal cycle (FT), (2) no flooding (NF), (3) continuous flooding (F), and (4) flooded according to tidal cycle with propagules buried at approximately 2-3 cm deep (FTB). Treatments were randomly assigned to the mesocosms, with five replicates per treatment. For those boxes assigned to the F treatment, water was replaced once a day. In boxes assigned to the NF treatment, sediments were maintained under saturated conditions, but with no water above the sediment surface. Boxes with treatments FT and FTB were flooded and non-flooded for alternate periods of six hours each, simulating a semi-diurnal tidal cycle.

Fifteen propagules each of Laguncularia and A. germinans, weighed and measured, were placed in every mesocosm. Observations of propagule buoyancy, radicle protrusion, time and success of establishment, expansion of first leaves, seedling growth, and response of propagules to buried conditions were recorded every day for 24 days. Once a propagule was established, height increment was measured every other day.

The experimental design consisted in a combination of a complete randomized design (CRD) for treatment (FT, NF, F, FTB), and a randomized block design (RBD) for species (L, A) with a nested error structure. Statistical tests were conducted to determine significant differences in the success of propagule establishment and seedling growth among treatments and between species.

#### **4.4. RESULTS**

##### **4.4.1. Field Cross-Planting Experiment**

###### **4.4.1.1. Propagule Radicle Protrusion**

Across intertidal zones, radicle protrusion for Laguncularia and Avicennia propagules after the fifth day in the field ranged from 66% to 81%, and 84% to 89%, respectively (Table 4.1). The variability was essentially due to increased radicle protrusion in MB. By the end of the experiment ( $\approx 40$  days) between 1% (UI) and 25% (MB) of the Laguncularia propagules that developed radicle and did not die were unable to establish, compared to 20% (LI) to 53% (MB) for Avicennia (Table 4.1).

###### **4.4.1.2. Propagule Establishment**

Laguncularia showed maximum establishment in the following order: LI (73%) > MB (52%) > UI (18%). Establishment in LI and MB was significantly greater than in UI ( $P < 0.05$  and  $P < 0.1$ , respectively). Highest establishment for Avicennia was also in LI (66%), followed by UI (51%) and MB (29%); establishment was significantly greater in LI than in MB ( $P < 0.05$ ). Avicennia had significantly higher establishment than Laguncularia in UI ( $P < 0.05$ ). Maximum cumulative establishment for Laguncularia and Avicennia started at approximately 11-15 days and extended until the end of the experiment (26-40 days, Figure 4.2). Both species had an early rapid establishment (days 6-10) in MB and LI. Most established propagules of both species expanded their first pair of leaves by 16-25 days in all three zones (Table 4.1). However, after 40 days 13%, 23% and 14% of established Laguncularia



propagules and 8%, 51% and 30% of *Avicennia* had not yet opened their leaves (for MB, LI and UI, respectively).

Table 4.1. Results of the *Laguncularia* and *Avicennia* propagule field experiment following the gradient: MB = mud bank, LI = lower intertidal, and UI = upper intertidal. Total percentage (%  $\pm$  standard error) of propagules is given for each of the conditions. Conditions were defined as: R = propagule with protruded radicle, ES = propagule established (including LE), LE = propagule with first pair of leaves expanded, D = propagule dead, missing or eaten, and B = propagule buried.

LAGUNCULARIA						
Site	Condition	Days				
		0 - 5	6 - 10	11 - 15	16 - 25	26 - 40
MB	R	81 $\pm$ 4	80 $\pm$ 9	64 $\pm$ 14	44 $\pm$ 16	25 $\pm$ 9
	ES	0 $\pm$ 0	6 $\pm$ 6	18 $\pm$ 8	36 $\pm$ 10	38 $\pm$ 6
	LE	0 $\pm$ 0	0 $\pm$ 0	4 $\pm$ 4	28 $\pm$ 9	33 $\pm$ 4
	D	1 $\pm$ 1	1 $\pm$ 1	1 $\pm$ 0	11 $\pm$ 6	25 $\pm$ 5
	B	2 $\pm$ 2	9 $\pm$ 3	10 $\pm$ 3	2 $\pm$ 2	4 $\pm$ 2
LI	R	66 $\pm$ 7	85 $\pm$ 8	38 $\pm$ 10	17 $\pm$ 6	7 $\pm$ 4
	ES	0 $\pm$ 0	7 $\pm$ 7	51 $\pm$ 12	61 $\pm$ 10	47 $\pm$ 9
	LE	0 $\pm$ 0	0 $\pm$ 0	2 $\pm$ 0	36 $\pm$ 11	36 $\pm$ 10
	D	1 $\pm$ 0	3 $\pm$ 2	7 $\pm$ 2	15 $\pm$ 4	42 $\pm$ 12
	B	0 $\pm$ 0	3 $\pm$ 2	2 $\pm$ 2	4 $\pm$ 4	1 $\pm$ 0
UI	R	73 $\pm$ 0	64 $\pm$ 2	30 $\pm$ 8	17 $\pm$ 6	1 $\pm$ 0
	ES	0 $\pm$ 0	0 $\pm$ 0	13 $\pm$ 5	12 $\pm$ 7	7 $\pm$ 3
	LE	0 $\pm$ 0	0 $\pm$ 0	1 $\pm$ 1	8 $\pm$ 4	6 $\pm$ 3
	D	10 $\pm$ 0	29 $\pm$ 0	42 $\pm$ 3	64 $\pm$ 8	90 $\pm$ 4
	B	2 $\pm$ 0	3 $\pm$ 3	5 $\pm$ 3	6 $\pm$ 2	0 $\pm$ 0
AVICENNIA						
Site	Condition	Days				
		0 - 5	6 - 10	11 - 15	16 - 25	26 - 40
MB	R	84 $\pm$ 7	76 $\pm$ 13	86 $\pm$ 3	58 $\pm$ 27	53 $\pm$ 22
	ES	0 $\pm$ 0	15 $\pm$ 15	2 $\pm$ 1	34 $\pm$ 33	25 $\pm$ 19
	LE	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	27 $\pm$ 27	23 $\pm$ 19
	D	0 $\pm$ 0	2 $\pm$ 2	5 $\pm$ 2	8 $\pm$ 7	15 $\pm$ 6
	B	0 $\pm$ 0	5 $\pm$ 1	5 $\pm$ 4	0 $\pm$ 0	2 $\pm$ 1
LI	R	89 $\pm$ 3	86 $\pm$ 2	52 $\pm$ 6	32 $\pm$ 1	20 $\pm$ 7
	ES	0 $\pm$ 0	12 $\pm$ 3	37 $\pm$ 15	64 $\pm$ 2	63 $\pm$ 14
	LE	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	17 $\pm$ 4	31 $\pm$ 13
	D	0 $\pm$ 0	2 $\pm$ 1	8 $\pm$ 5	4 $\pm$ 0	13 $\pm$ 5
	B	0 $\pm$ 0	0 $\pm$ 0	2 $\pm$ 2	0 $\pm$ 0	1 $\pm$ 0
UI	R	89 $\pm$ 4	88 $\pm$ 0	55 $\pm$ 18	16 $\pm$ 0	24 $\pm$ 9
	ES	0 $\pm$ 0	0 $\pm$ 0	21 $\pm$ 12	51 $\pm$ 0	46 $\pm$ 10
	LE	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	27 $\pm$ 0	32 $\pm$ 9
	D	2 $\pm$ 0	4 $\pm$ 0	10 $\pm$ 2	21 $\pm$ 0	25 $\pm$ 4
	B	1 $\pm$ 0	1 $\pm$ 0	4 $\pm$ 1	6 $\pm$ 0	1 $\pm$ 1

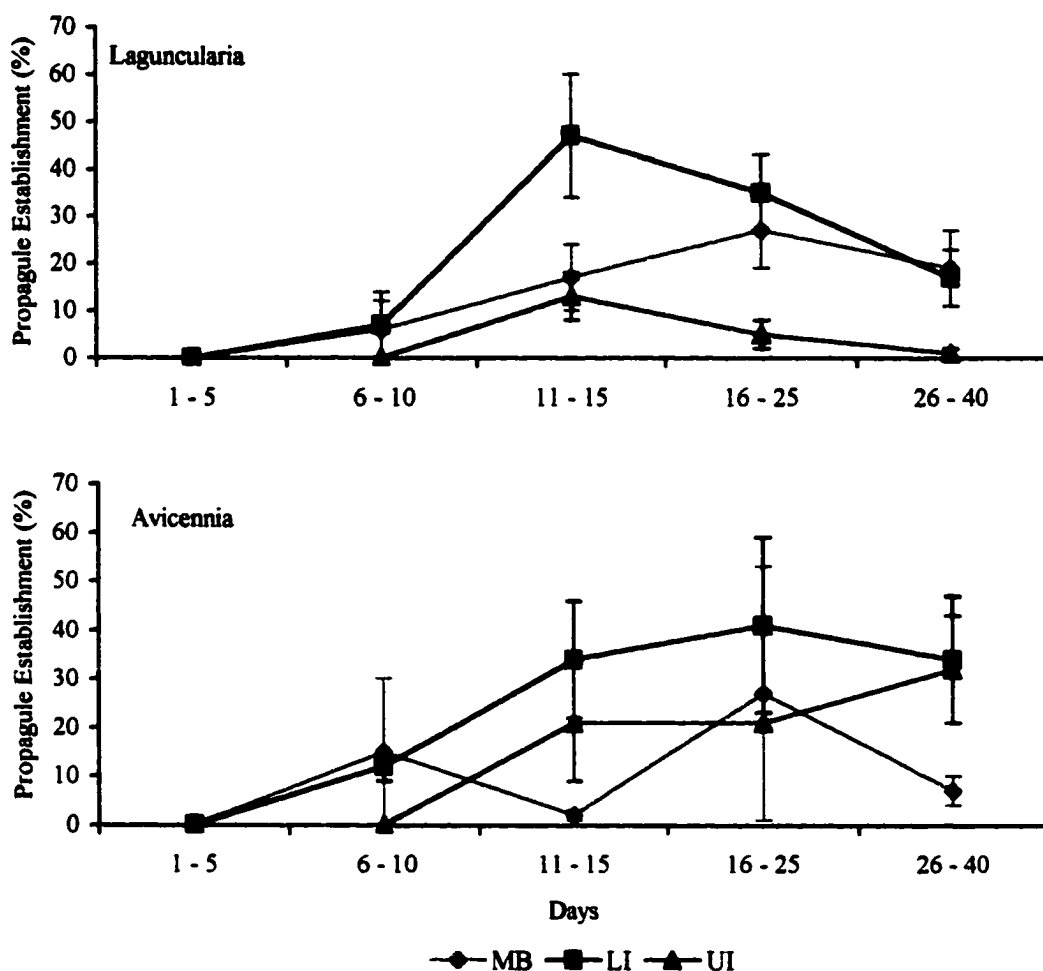


Figure 4.2. Establishment of *Laguncularia* and *Avicennia* propagules in the field experiment following the gradient: mud bank (MB), lower intertidal (LI), and upper intertidal (UI). Values at each time period are expressed as the average percent of established propagules calculated from the total number of non-established propagules remaining for that time period.

The maximum percentage of anchored *Laguncularia* propagules that were naturally buried in sediment was 10% and 6% for MB and UI, respectively, with 5% and 6% for *Avicennia* in the same zones, after a 40 day time interval (Table 4.1).

#### 4.4.1.3. Propagule Mortality and Survival

Average mortality of *Laguncularia* propagules, pooling across zones, was approximately 1.6 times greater than that of *Avicennia* ( $P < 0.05$ ). By zone (pooling species), mortality was significantly higher in UI (71%) compared to MB (17%,  $P < 0.05$ ) and LI (37%,  $P < 0.1$ ). Propagule mortality was also analyzed in two separate categories: dead-missing (D), and eaten (E, Figure 4.3). Differences in D

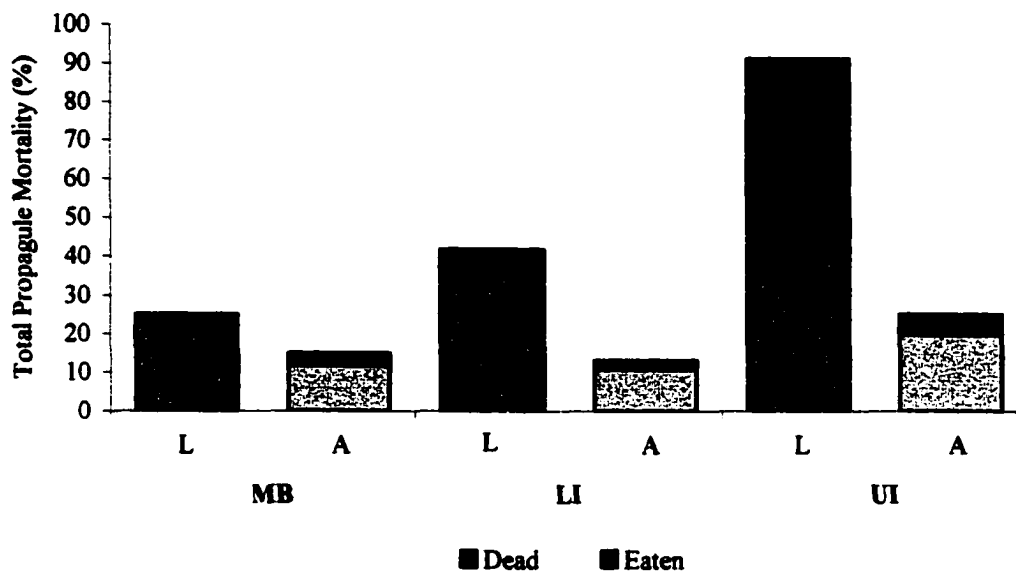


Figure 4.3. Total mortality of Laguncularia and Avicennia propagules in the field experiment. Mortality of propagules was divided in two categories: dead and eaten propagules; missing propagules were assumed to be dead. Values are given as the average percent of total number of propagules for the mud bank (MB), lower intertidal (LI), and upper intertidal (UI) zones.

propagules among zones was not significant, but overall Laguncularia had higher D propagules than Avicennia ( $P < 0.05$ ). Significantly higher predation (E) of Laguncularia propagules occurred in UI (52%) compared to MB (2%,  $P < 0.05$ ), and LI (5%,  $P < 0.05$ ). Laguncularia also had significantly higher propagule predation than Avicennia in UI ( $P < 0.05$ ). Laguncularia propagules were eaten 11 more times than Avicennia in the same period of time: in approximately 25 days 52% of Laguncularia propagules were eaten compared to 5% for Avicennia. LI and UI had similar abundance of crab burrows: 85 and 75 burrows  $m^{-2}$ , respectively. Size class distribution of crab burrows, however, was significantly different between zones ( $P < 0.001$ , Figure 4.4). Significantly more crab burrows of smaller size were distributed in LI ( $P < 0.001$ ), while significantly more crab burrows of larger size were distributed in UI ( $P < 0.001$ ). In LI, 87% of the total crab burrows measured corresponded to sizes between 1 to 10 mm in diameter, while in UI, 57% corresponded to sizes between 11 to 20 mm in diameter. Direct observations of crabs eating propagules were not conducted, but high abundance of the grapsidae Sesarma sulcatum (pers. obs.) on the upper intertidal zones suggests that this is likely to be the main species predated both species, mainly Laguncularia.

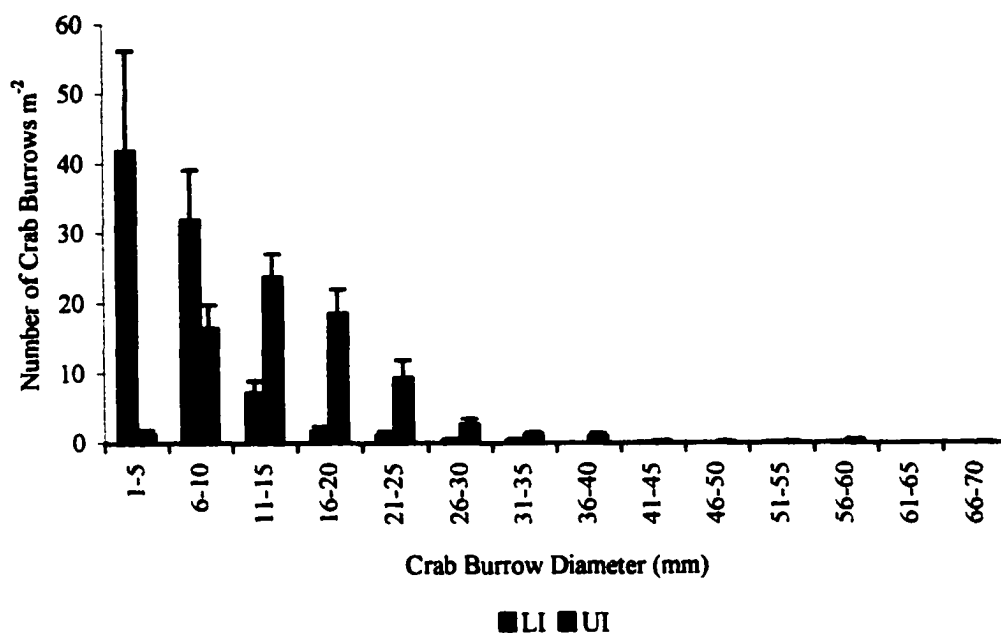


Figure 4.4. Distribution of crab burrows by diameter size in the lower intertidal (LI) and upper intertidal (UI) zones.

Laguncularia survivorship curves had more pronounced slopes ( $\delta$ ) compared to Avicennia for all three zones (Figure 4.5). Calculated half life ( $\ln 0.5/\delta$ , Pielou 1974) values for Laguncularia seedlings (MB = 45, LI = 40, UI = 37 days) were between 2.1 and 3.4 times less than those for Avicennia (MB = 117, LI = 84, UI = 126 days).

#### 4.4.2. Mesocosm Experiment

##### 4.4.2.1. Propagule Size and Buoyancy

Laguncularia had significantly smaller propagules than A. germinans ( $P < 0.05$ ). The average fresh weight and length of Laguncularia propagules was 0.35 g ( $\pm 0.01$  g standard error) and 19.1 mm ( $\pm 0.1$  mm standard error), respectively, compared to 1.90 g ( $\pm 0.04$  g) and 24.7 mm ( $\pm 0.2$  mm) for A. germinans. Under continuous flooding (F), Laguncularia propagules lost their buoyancy soon after radicle protrusion occurred. Propagules began to sink the second and third day of being in the mesocosm and between five and eight days, 83% to 100% of the propagules had already sunk. A. germinans propagules floated during the whole 25-day experiment even though long roots were developed.

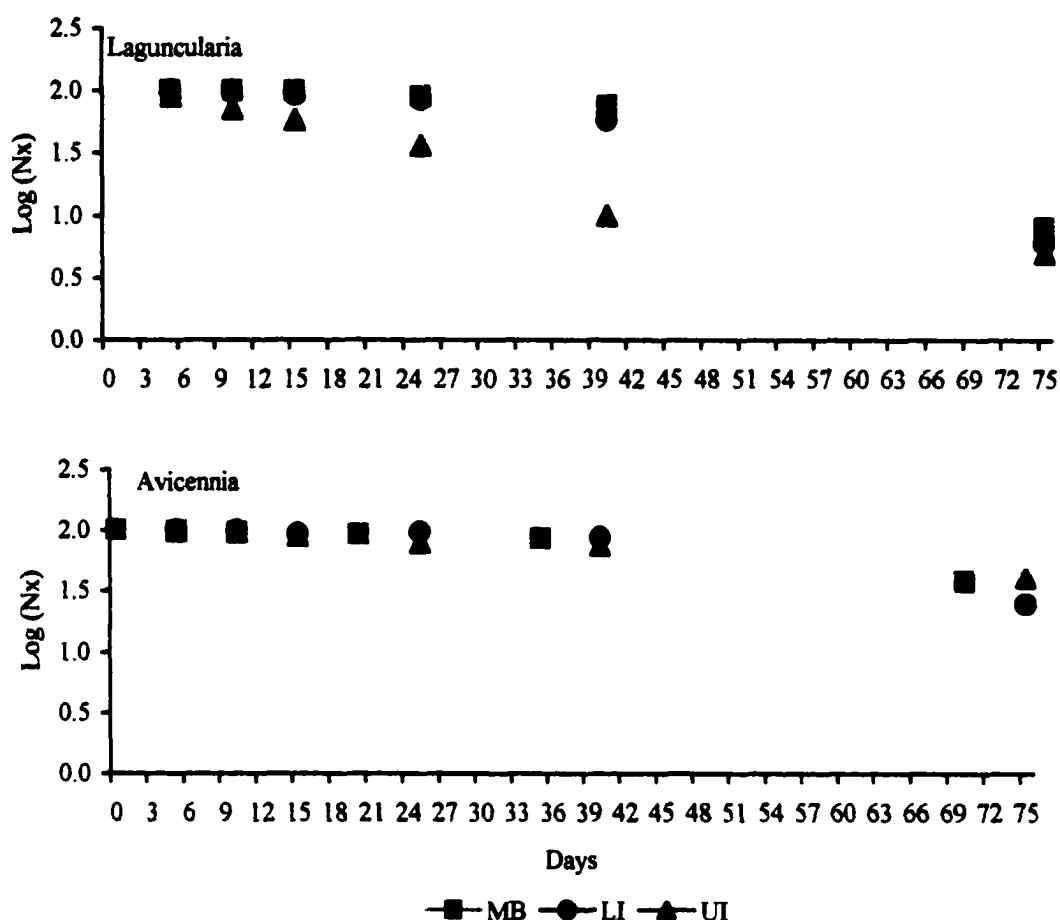


Figure 4.5. Survivorship curves log (Nx) for the cohorts of *Laguncularia* and *Avicennia* seedlings used in the field experiment, for the mud bank (MB), lower intertidal (LI), and upper intertidal (UI) zones. Nx = number of living seedlings.

#### 4.4.2.2. Propagule-Seedling Development

Under the treatment flooded according to tidal cycle (FT), *Laguncularia* propagules had 48% of radicle protrusion by the fifth day compared to 100% for *A. germinans*. By days 11-12 both species had less than 50% of establishment, and by day 17, 17% and 40% of *Laguncularia* and *A. germinans* propagules had opened their leaves. At the end of the experiment 29% and 31% of the *Laguncularia* and *A. germinans* propagules, respectively showing radicle protrusion were not able to establish (Figures 4.6 and 4.7). Under continuous flooding (F), both species had fast radicle protrusion, but only *Laguncularia* propagules lost their buoyancy and were able to establish. After eight days all *Laguncularia* propagules had sank and by day 11 they began to establish; however, it was not until day 22 that leaves began to expand (Figures 4.6 and 4.7). Under no flooding (NF) conditions both species had more than 70% of

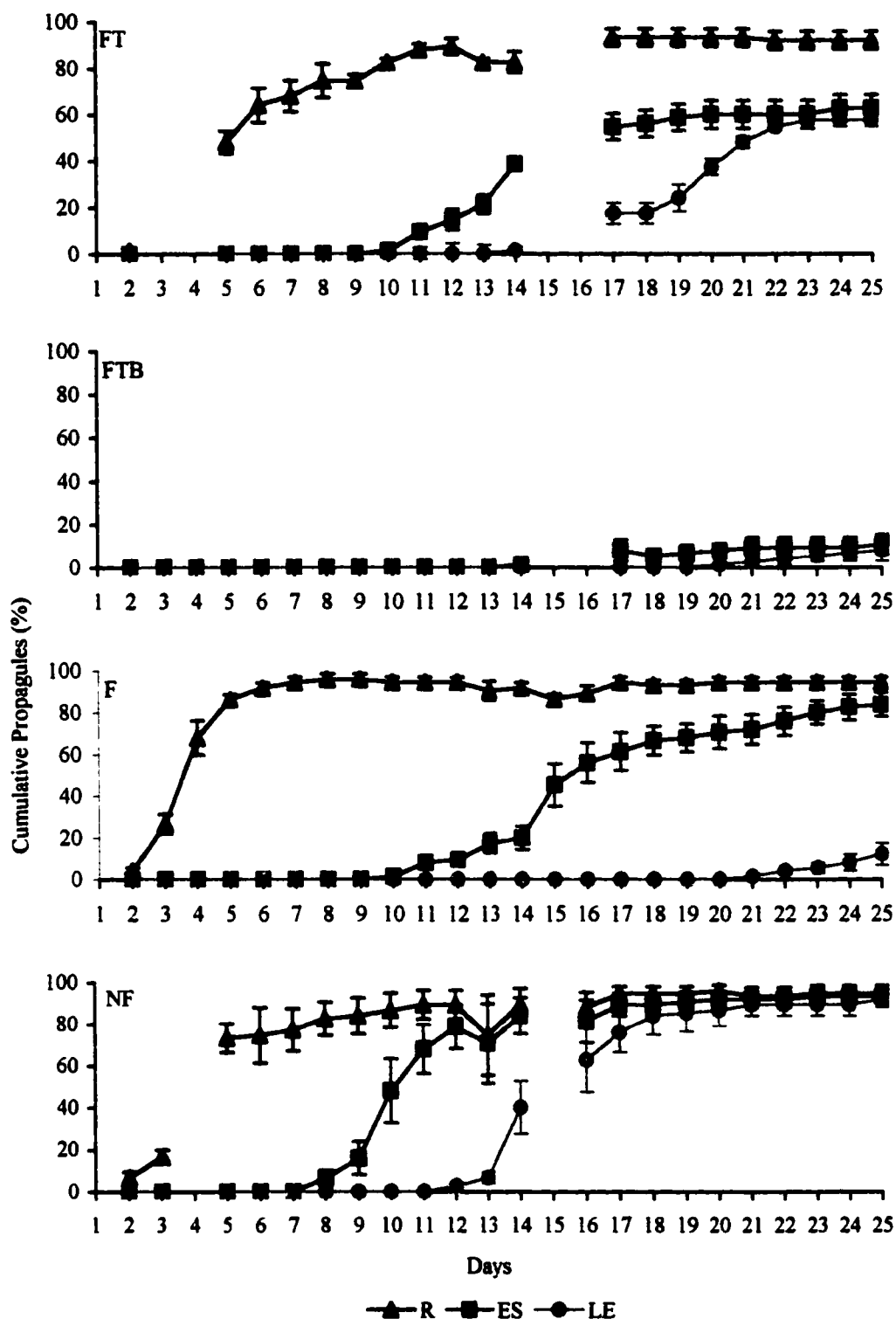


Figure 4.6. Development of *Laguncularia* propagules-seedlings in the mesocosm experiment. Radicle protrusion (R), establishment (ES), and leaves expansion (LE) is given as the average cumulative percent of the total number of propagules by treatment: flooded according to tidal cycle (FT), flooded according to tidal cycle with propagules additionally buried (FTB), continuous flooding (F), and no flooding (NF).

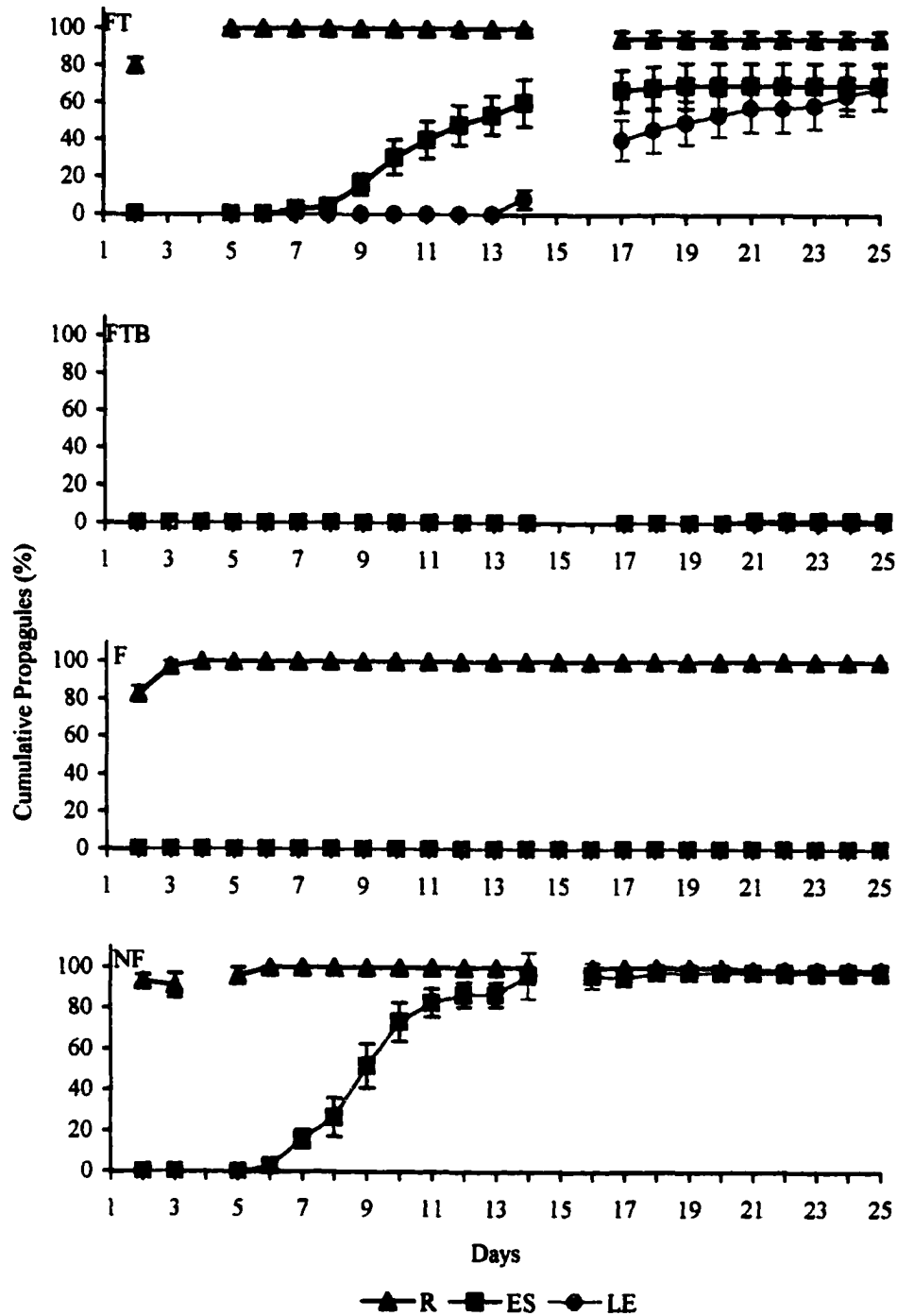


Figure 4.7. Development of *A. germinans* propagules-seedlings in the mesocosm experiment. Radicle protrusion (R), establishment (ES), and leaves expansion (LE) is given as the average cumulative percent of the total number of propagules by treatment: flooded according to tidal cycle (FT), flooded according to tidal cycle with propagules additionally buried (FTB), continuous flooding (F), and no flooding (NF).

radicle protrusion by day 5, and by days 11-12 more than 80% of propagules had established. Contrary to A. germinans, in which leaves began to open at about the same time as establishment, Laguncularia showed a lag of four days (Figures 4.6 and 4.7).

#### **4.4.2.3. Propagule Establishment**

Propagule establishment for both species was greater than 60% under NF and FT treatments. Success of Laguncularia establishment under NF (93%) and F (84%) was significantly greater than FT (63%,  $P < 0.05$ ). Success of A. germinans establishment under NF (97%) was significantly greater than FT (69%,  $P < 0.05$ ). Establishment of Laguncularia was significantly greater than A. germinans under F conditions ( $P < 0.05$ , Figures 4.6 and 4.7).

Laguncularia showed a faster rate of establishment under NF conditions. Propagules started to establish around day 8, and by day 17 approximately 89% of the total propagules were established; by day 23, 93% of propagules were established. Propagules growing in F and FT began to establish at day 11, reaching maximum establishment between 24-25 days with 80%-84%, and 60%-63% of establishment for F and FT, respectively. Similarly to Laguncularia, A. germinans establishment was faster under NF conditions. Propagules began to establish at day 6 and by day 19, 97% of all propagules had established. Propagules in FT began to establish at day 7, reaching 69% of establishment at day 19 (Figures 4.6 and 4.7). Laguncularia showed an approximate peak of establishment between days 14-17 for F and FT, and between 9-11 for NF. The peak of establishment for Avicennia for FT and NF was at approximately 9-12 and 7-10 days, respectively.

#### **4.4.2.4. Seedling Growth**

Growth of established Laguncularia seedlings was significantly different among treatments ( $P < 0.05$ ), following the gradient  $FT > NF > F$ . Height increment of A. germinans seedlings did not differ significantly among treatments, however A. germinans seedlings under NF conditions showed significantly greater height increment than Laguncularia ( $P < 0.05$ , Figure 4.8).

#### **4.4.2.5. Propagule Mortality**

Mortality of Laguncularia and A. germinans propagules was very low throughout the experiment therefore this factor was not analyzed in greater detail.



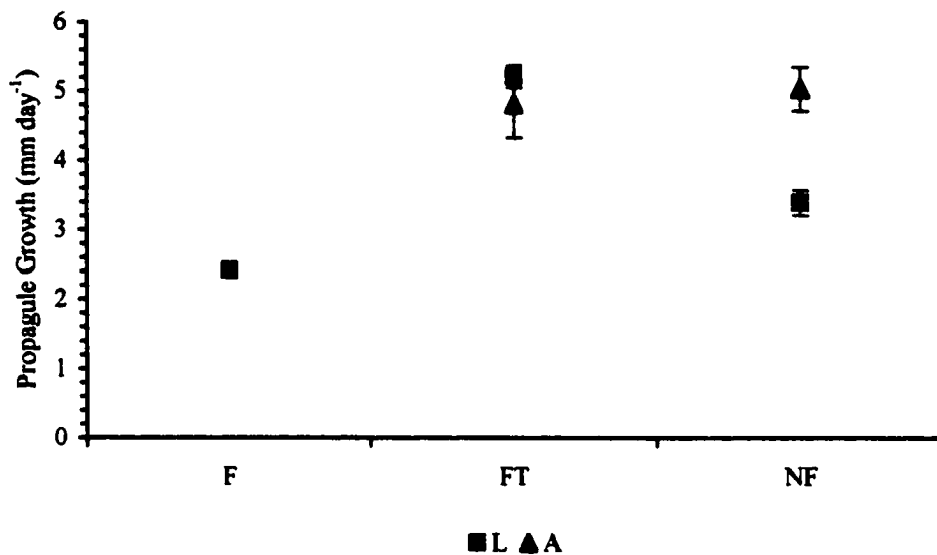


Figure 4.8. Height increment of *Laguncularia* (L) and *A. germinans* (A) propagules in the mesocosm experiment by treatment: continuous flooding (F), flooded according to tidal cycle (FT), and no flooding.

#### 4.4.2.6. Response of Buried Propagules

From all propagules buried under 2-3 cm of sediment, only 11% of *Laguncularia* and 1% of *A. germinans* were able to rise to the sediment surface and establish. By the end of the experiment, 8% of the *Laguncularia* propagules that were able to establish opened their first pair of leaves. It took 17 and 21 days for the first *Laguncularia* and *A. germinans* propagules, respectively, to emerge (Figures 4.6 and 4.7).

### 4.5. DISCUSSION

#### 4.5.1. *Laguncularia* Colonization and Distribution in Lower Intertidal Zones

The distribution of *Laguncularia* in the lower intertidal zone of point bars and islands sheds new light on the hypothesis proposed by Rabinowitz (1978c), which states that mangrove zonation is controlled by tidal sorting of propagules according to size and buoyancy capacities. Although *Avicennia* propagules are over 30% larger than *Laguncularia*, their greater buoyancy may restrict them to the middle and upper intertidal zones. Propagule size may therefore not be the more important characteristic. Indeed, the distribution of mangrove species with small propagules in the lower intertidal zone and

species with large propagules in the middle to upper intertidal zones is a common observation for Australian mangrove forests (Smith 1987a).

Laguncularia colonizes active sedimentary environments such as shoals and point bars in riverine mangrove forests of Mexico, Colombia and French Guiana (Pool et al. 1977, Cantera and Arnaud 1997, Fromard et al. 1998). Laguncularia as a pioneer of low intertidal zones is not, however, typical for other environmental settings. In Mecoacan Lagoon, Mexico, for example, A. germinans colonizes mud flats characterized by high salinities and anaerobic conditions (López Portillo and Ezcurra 1989). In the downstream region of estuaries or under more marine influence, R. mangle is generally found colonizing mud bank deposits and lower intertidal zones, mainly characterized by higher salinities and more vigorous water movement. Under these conditions Laguncularia is found in higher elevations forming mixed stands with Avicennia and/or other species (Thom 1967, Detweiler et al. 1975, Pool et al. 1977, Ball 1980, Soto and Jiménez 1982, Jiménez and Soto 1985, Day et al. 1987, Jiménez 1994, Cantera and Arnaud 1997). Throughout the Caribbean, Laguncularia has been observed as a dominant species in basin type mangrove forests (Jiménez pers. comm.).

#### **4.5.2. Dynamics of Mud Bank Colonization**

Mangrove establishment and colonization of new environments is initially dependent on the availability and successful dispersal of propagules to the sites of colonization (Ball 1980, Clarke 1993, Duke et al. 1998, Panapitukkul et al. 1998). High tree density increases the number of propagules that can be dispersed, and the closer the parent trees are to sites of colonization the higher the chances of successful dispersal. Both Laguncularia and Avicennia produce large quantities of small, water-dispersed propagules (Jiménez 1988), however, the current dominance of Laguncularia adjacent to mud banks certainly places this species at an advantage for continued dominance of this zone. The absence of A. germinans in some forests along Biscayne Bay, Florida was attributed to a limited source of propagules and to physical factors affecting propagule dispersal such as direction of winds and currents (Ball 1980). In Pak Bay, Thailand, a rapid colonization of accreting mud flats by Avicennia alba was attributed to high propagule availability and dispersal to sites of colonization (Panapitukkul et al. 1998).

Frequency and duration of flooding within the upper intertidal zone are important factors affecting propagule dispersal of Avicennia. Dispersal of A. marina propagules in southeastern Australia

was mostly restricted to a distance of 500 m from the point of release, with propagules under poor tidal flushing showing the least dispersal (Clarke 1993). In north Australia, propagules of Ceriops tagal, a common species of mid to high intertidal zones had limited dispersal due to reduced tidal inundation (McGuinness 1997a).

Propagule buoyancy is also an important factor affecting propagule dispersal and establishment in frequently flooded environments (Johansson et al. 1996, Danvind and Nilsson 1997). Propagules that can remain buoyant and viable for longer periods of time increase their effective range of dispersal (Steinke 1975, Rabinowitz 1978a, Steinke 1986, Johansson et al. 1996, Duke et al. 1998). Laguncularia propagules showed a floating period between two and seven days, and the ability to establish and grow under water. Avicennia, however, floated during the 25-day experiment. In contrast to our studies, in Panamanian mangroves Rabinowitz (1978a) reported for Laguncularia an average floating period of 23 days in freshwater and 31 days in salt water, while Avicennia floated during an 82-day period. Avicennia germinans propagules from Twin Cays, Belize showed a similar floating behavior as reported by Rabinowitz (McKee 1995b). Being a “floater”, Avicennia thus increases its chances for long distance dispersal but also its probability of being carried out of the system by tidal action. In mud banks Avicennia propagules would require a longer stranding period to establish (Rabinowitz 1978a). This process may occur during low tides, and if sediment becomes trapped within the cotyledons their weight increases and are more likely to remain sunken during succeeding tides (Rabinowitz 1978a). However, under natural conditions we did not find A. germinans or A. bicolor colonizing mud banks influenced by regular tidal action. This suggests that being a “floater” may ensure Avicennia dispersal to higher elevation zones where seedlings can better survive and grow once rooted (Rabinowitz 1978a, Jiménez and Soto 1985, Duke et al. 1998). Similarly, in a forested floodplain in South Carolina, bald cypress and water tupelo seeds, which remain buoyant up to three months, were dispersed during high water levels to elevated, less frequently flooded substrates where conditions were more favorable for seed germination (Schneider and Sharitz 1988). Propagules that sink rapidly, such as Laguncularia, may result in restricted dispersal away from parent trees. In a Belizean mangrove forest, relative densities of Laguncularia seedlings just after dispersal coincided with the region dominated by conspecific adults (McKee 1995b). Being a “sinker”, however, appears also to be an advantageous characteristic for a pioneer species with

small size propagules colonizing frequently flooded environments such as mud banks. Similar to Laguncularia, small propagules of Avicennia marina, sometimes found in the seaward edge of mangroves (Semeniuk 1985, Fujimoto and Miyagi 1993, Osunkoya and Creese 1997), sink within one to three day period (Steinke 1975, Clarke and Myerscough 1991, Clarke 1993). This process of propagule dispersal relating water level and buoyancy capacities seems to agree with the hypothesis of “directed dispersal” proposed by Howe and Smallwood (1982), which assumes that adaptations for dispersal increase the probability of seeds to reach suitable sites for germination.

Once propagules of Laguncularia and Avicennia reach a mud bank and become stranded, differential tolerance of physical-chemical characteristics of the environment affecting propagule establishment and seedling survival will become important. Results from this study showed, however, that artificially retained propagules of both species established and grew similarly in this environment, and Avicennia even survived better than Laguncularia during early establishment. Even though significant interspecific differences in establishment success were not found due to high variability, 23% more of Laguncularia propagules established in mud banks compared to Avicennia, and approximately 28% more Avicennia propagules remained non-established by the end of the 40-day experiment. Establishment of Avicennia appeared to be more influenced by tidal water movements than Laguncularia. Under the action of relatively strong water currents buoyant Avicennia propagules tended to remain above the soil surface making stranding more difficult. Those propagules that were able to stay on the bottom had to spend more energy and time reorienting their anchoring roots each time they were moved from their original position (pers. obs.). Similarly, A. germinans and R. mangle propagules had difficulty becoming established at a lower intertidal Rhizophora dominated zone, where tidal action regularly buoyed them away from the soil surface (McKee 1995b). McMillan (1971) demonstrated a negative relationship between water turbulence and A. germinans root development under laboratory experiments. Under field conditions mortality of A. germinans of clipped plots in a Spartina low marsh was attributed to the physical effects of the tides (Patterson et al. 1993, Patterson et al. 1997). The effect of water movement has also been shown on the establishment of other mangrove and wetland species (Foote and Kadlec 1988, Clarke and Allaway 1993, Clarke and Myerscough 1993).

Mortality of Laguncularia propagules was higher than Avicennia. Similarly, in Panamanian mangrove forests Laguncularia showed higher mortality rates than Avicennia, Rhizophora and Pelliciera (Rabinowitz 1978b). In our study, calculated half-life values for Laguncularia and Avicennia propagules were 45 and 117 days, respectively. Rabinowitz (1978b) reported for Laguncularia 50% propagule disappearance after 45 days, but after 85 days for Avicennia. Much higher calculated half-life values were obtained for A. bicolor in a monospecific stand (242 days), and in a mixed stand (732 days) in a mangrove forest in the Pacific coast of Costa Rica (Jiménez and Sauter 1991). It is important, however, to indicate that these experiments carried out by Rabinowitz and Jiménez and Sauter were conducted under different environmental conditions and using different cohort sizes. Similar to Rabinowitz (1978b), these results indicate a positive relationship between half-life values and propagule size. Primary causes of early propagule mortality in mud banks were lost of viability, decay, and loss of propagules by being washed out of the system. Herbivory and buried propagules were not important sources of mortality. Crab activity in mud banks was very low or absent, and when present corresponded to members of the genus Uca spp (pers. obs.), which are not known for predating mangrove propagules (Jiménez 1994, Sousa and Mitchell 1999). The percentage of buried propagules as a result of reworking and/or sediment deposition was lower than expected, especially since mud banks in this region are very active sedimentary environments. It appears that the same tidal action causing burial also lead to propagule uncovering. In Thailand, mortality of R. apiculata seedlings in an expanding mud flat increased linearly with increasing sediment accretion (Terrados et al. 1997). Under mesocosm conditions, both Laguncularia and A. germinans were, however, very sensitive to two or three centimeters of permanent burial, similar to other coastal plants (Maun and Lapierre 1986, Rybicki and Carter 1986, Jurik et al. 1994, Wang et al. 1994).

In point bars and islands of the Tempisque-Bebedero system, lower intertidal flooding conditions are not limiting Laguncularia establishment, which is evident through its present dominance in these zones. Avicennia, however, seems to require drier conditions for establishment (Johnston 1983). McMillan (1971) showed that this species requires five centimeters or less in water depth to become established. This is probably related to Avicennia's buoyancy characteristics since high water levels decrease the probability of propagule contact with the soil surface, which is necessary for establishment.

Once established, however, this species is able to grow under permanently flooded conditions (McKee 1993, Patterson et al. 1993).

In summary, results of the field experiment do not support our hypothesis that Laguncularia propagules will establish better than Avicennia in mud banks. Even though in natural conditions Avicennia does not colonize this environment, artificially planted propagules established and grew similarly to Laguncularia, and even survived better during early establishment. Both species showed similar time of establishment, and tolerance to the prevalent flooding regimes. These results indicate that in this environmental setting, propagule buoyancy characteristics, the effect of water mechanical action on propagule dispersal and establishment, density and intertidal distribution of reproductive trees appear to be important factors limiting Avicennia colonization of mud banks, conferring a competitive advantage to Laguncularia. Laguncularia's ability to quickly lose propagule buoyancy, in addition to a less sensitivity to tidal action and currents increases this species probability to remain in the site of colonization and then become established.

#### **4.5.3. Lower Intertidal Mangrove Distribution**

Under natural conditions this is a zone dominated by Laguncularia, however, if Avicennia propagules are artificially planted, they can establish and survive well. In fact, across the intertidal gradient, propagules of both species established best at this lower zone. This partially contradicts the hypothesis of physiological preference, where we expect establishment, seedling growth, and survival to be best under the adult conspecific forest. This is the case for Laguncularia but not for Avicennia. Similar results to our study were found by Rabinowitz (1978c) for Panamanian mangroves, where Rhizophora, Avicennia and Laguncularia seedlings generally survived best under the canopy of another mangrove species rather than their own. A reciprocal planting experiment carried on in the Pacific of Costa Rica, showed A. bicolor seedlings growing and surviving better in a R. racemosa monospecific stand, while R. racemosa grew and survived better in its own home stand (Jiménez and Sauter 1991). Therefore, if Avicennia can grow well in the lower intertidal zone, why is not naturally found in these areas? Similar to mud banks we suggest that propagule buoyancy characteristics, the effects of water movement on propagule anchoring and establishment, limited propagule supply, and limited dispersal, are important factors limiting Avicennia colonization of lower intertidal zones.

Establishment of retained Avicennia propagules in the lower intertidal zone was significantly higher than in mud banks. Lower intertidal zones offer more consolidated soils and reduced water scour due to the presence of tree trunks, roots and debris on the forest floor, increasing the probability of propagule establishment. The growth of Avicennia (4.8 mm day<sup>-1</sup>) and Laguncularia seedlings (5.2 mm day<sup>-1</sup>) under simulated flooding according to tidal cycle (FT in mesocosm experiment) was high and did not differ between species. These values, probably an overestimation of growth under natural conditions, are higher than those obtained for A. bicolor in a reciprocal field plating experiment in a mangrove forest in the Pacific of Costa Rica. In that experiment, A. bicolor grew 1.8 and 1.4 mm day<sup>-1</sup> when growing in monospecific R. racemosa and A. bicolor forests, respectively (Jiménez and Sauter 1991). Additionally, Avicennia germinans seedlings growing under three different zones (Avicennia, high-elevation Spartina and low-elevation Spartina), exhibited growth rates of 1.1, 0.9, and 0.9 mm day<sup>-1</sup>, respectively (Patterson et al. 1993). Laguncularia and Avicennia are shade intolerant (Ball 1980), thus we could expect light conditions to be a limiting growing factor for established seedlings under the forest canopy in lower intertidal zones. However, Teas (1974, cited by Ball 1980) reported that a higher percentage of incident light is transmitted through a Laguncularia canopy (70%) than it is through a Rhizophora canopy (20-30%).

Mortality in lower intertidal zones was primarily a consequence of propagule decay, loss of viability, and physical damage to established propagules; Laguncularia being the most affected. Mortality due to crab herbivory was not significant, probably related to the smaller size of crabs present in this zone (Sousa and Mitchell 1999).

#### 4.5.4. Upper Intertidal Mangrove Distribution

In the upper intertidal zone, artificially retained Avicennia propagules performed better than Laguncularia, which showed higher mortality and lower establishment. The high mortality of Laguncularia was due to an intensive and selective crab predation on propagules (52% compared to 5% for Avicennia). In contrast to our results, McKee (1995a) showed significantly higher A. germinans (60%) propagule predation than R. mangle (18%) and L. racemosa (28%) on a mangrove island range at Twin Cays, Belize. Also, Sousa and Mitchell (1999) showed higher crab predation on A. germinans propagules compared to L. racemosa and R. mangle in a mangrove forest at Punta Galeta on the

Caribbean coast of Panamá. These differences found among results are probably associated to the different predator guilds found at the different regions.

Differential propagule crab preference among different mangrove species has been correlated to propagule characteristics such as size and chemical composition (Smith 1987b, McKee 1995a, 1995c). Higher predation in upper intertidal zones could also be related to frequency of tidal inundation (which affects the amount of forage time, Osborne and Smith 1990), and dominant species and size of the crabs populating the area (Warner 1969, McKee 1995a). In this study, higher zones were flooded less regularly, and had significantly larger crab burrows than lower intertidal zones, which may partially explain the higher crab predation on these upper intertidal zones. Contrary to our observations, Sousa and Mitchell (1999) reported for a mangrove forest in the Caribbean coast of Panamá, higher crab propagule predation in lower intertidal zones. This zone was dominated by larger crab species such as Ucides cordatus and Goniopsis cruentata, while the upper intertidal zone was dominated by small species (Uca spp.). Even though crabs were not directly observed feeding on propagules in this study, a high abundance of the grapsidae Sesarma sulcatum (pers. obs.) suggests that this might be one of the main species predating Laguncularia and Avicennia propagules in this upper intertidal zone. Crabs of the same family and genus have also being reported responsible for propagule predation in other mangrove ecosystems (Smith et al. 1989, McGuinness 1997b, Dahdouh-Guebas et al. 1998, Steele et al. 1999).

Based on the pattern of propagule predation observed across the intertidal gradient of point bars and islands, the dominance-predation model does apply for Laguncularia. Predation was lowest where this species was dominant and highest where it was absent from the canopy. This model has been supported for some mangrove species (Smith 1987b, Smith et al. 1989, Robertson 1991) but not for others (McKee 1995a, McGuinness 1997b, Sousa and Mitchell 1999). In addition to predation, propagule desiccation and loss of viability were also causes of Laguncularia mortality in upper intertidal zones.

The growth of Avicennia under simulated no flooding conditions (NF, mesocosm experiment), was greater than Laguncularia, which suggests a performance advantage of Avicennia under less regularly flooded environments such upper intertidal zones. Avicennia propagules have more reserves in their cotyledons, which gives them the capacity to grow better under more stressed conditions, at least during the early establishment stage. For example, the success of R. mangle seedlings under high stress



and limited resources is partially due to its long hypocotyl that contributes to initial seedling height and to carbon reserves (Lin and Sternberg 1995, McKee 1995c).

In summary, limited propagule dispersal and selective crab predation of Laguncularia propagules are important factors limiting Laguncularia distribution in higher intertidal zones, favoring Avicennia performance in this environment. Similarly, the effect of crab predation on the distribution and zonation of mangrove species has been shown for other mangrove ecosystems around the world (Smith 1987b, 1987c, Robertson 1991, McKee 1995a, Steele et al. 1999). In other type of ecosystems such as coastal sage scrub vegetation and coral reefs, predation has also being related to community structure (Louda 1982, Hay 1984).

#### 4.6. CONCLUSIONS

A particular but common distribution of mangrove species is observed across the intertidal gradient of point bars and islands, active sedimentary environments, in the Tempisque-Bebedero estuarine system. Laguncularia, a species with small propagule size, colonizes rapidly emergent mud banks and lower intertidal zones. R. racemosa, A. germinans, A. bicolor, P. rhizophorae, and sometimes associated mangrove vegetation are observed colonizing middle and upper intertidal zones. Field and mesocosm experiments provided some insights about why Laguncularia is the pioneer species colonizing this type of environment. Propagule associated characteristics such as high propagule production, effective dispersal, short propagule floating period, and low propagule sensitivity to moderate tidal action and hydrologic regimes in anchoring and establishment, are important initial factors determining Laguncularia's successful colonization of emergent mud banks and lower intertidal zones. Laguncularia's limited distribution in upper intertidal zones, on the other hand, is closely related to restricted propagule dispersal, and to an intensive and selective crab propagule predation, which highly increased its mortality in this zone. Restricted dispersal and stranding requirements (buoyancy) are important factors limiting Avicennia establishment in lower intertidal areas, giving an advantage to Laguncularia in this environment.

This study suggests that factors affecting early processes on mangrove establishment such as dispersal, anchoring and actual propagule establishment are important determining mangrove species distribution in this environmental setting. In addition to propagule related characteristics, the role of

hydrology from the initial phase of dispersal through the final establishment stage is of great importance. How far a propagule can be dispersed is highly dependent of frequency and duration of flooding; likewise anchoring and establishment success is limited by flooding regimes and water mechanical effect. Therefore, Laguncularia dominance in lower intertidal zones of point bars and islands is initially determined by a combination of hydrological and propagule characteristics, which define this species ability of successfully establish in these environments. Recruitment from the seedling to the sapling stage constitutes a next important step for successful colonization, and should be addressed in future studies.

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## **CHAPTER 5.**

## **CONCLUSIONS**



## **5.1. THE CONCEPTUAL MODEL OF MANGROVE STRUCTURE DYNAMICS AND THE TEMPISQUE-BEBEDERO SYSTEM**

The structural dynamics of mangrove ecosystems are closely linked to the environmental setting of a particular coastal region, which is the reflection of the geomorphology and geophysical processes acting within the system (Thom 1967). Even though a species occurs in several different regions, the spatial distribution along the intertidal gradient, relative dominance, and structural development will often lead to the same species being classified as different ecological types (scrub, basin, riverine, fringe, Twilley 1998). Thus, the different biotic and physico-chemical factors characterizing each environmental setting play an important role defining the resulting mangrove community structure. In the Tempisque-Bebedero estuarine system, point bars and islands (active sedimentary environments), form an environment with specific characteristics that leads to a mangrove community dominated by Laguncularia racemosa in lower intertidal zones, and other species such as Rhizophora racemosa, Avicennia germinans, A. bicolor and Pelliciera rhizophorae in upper intertidal zones.

The conceptual model of mangrove structure dynamics developed in Chapter 1 (Figures 1.3 and 1.4) included several of the different biotic and physico-chemical factors, which have been identified as important factors determining mangrove forest structural characteristics under different environmental settings. The main objective of building the model was to conceptually establish the main relationships between those factors and the mangrove community. The model thus established the framework for conducting field studies to address the relative importance of the environmental factors in explaining mangrove structural characteristics at point bars and islands. Based on the results from field and mesocosm studies, I will now discuss the results in the context of the model.

### **5.1.1. Sedimentation Dynamics**

In the Tempisque-Bebedero system, irrigation activities in the river basin have modified the hydrology and sedimentation dynamics within the system. During the dry season, Tempisque river discharge decreases and sediment load increases. The high total suspended sediment (TSS) concentrations in the river during the dry season are also affected by winds (Figure 5.1). Strong dry season northeasterly winds reach velocities of 55-65 km hr<sup>-1</sup> and last from one to five days (Peterson 1960). As a result, there is wave-induced resuspension of bottom sediments. As a result, TSS during the dry season were much higher (12.88 g l<sup>-1</sup>) than during the rainy season (0.32 g l<sup>-1</sup>). Results from the

sedimentation study showed that spatial and temporal sedimentation patterns at point bars and islands were closely related to TSS concentrations.

#### Module 1

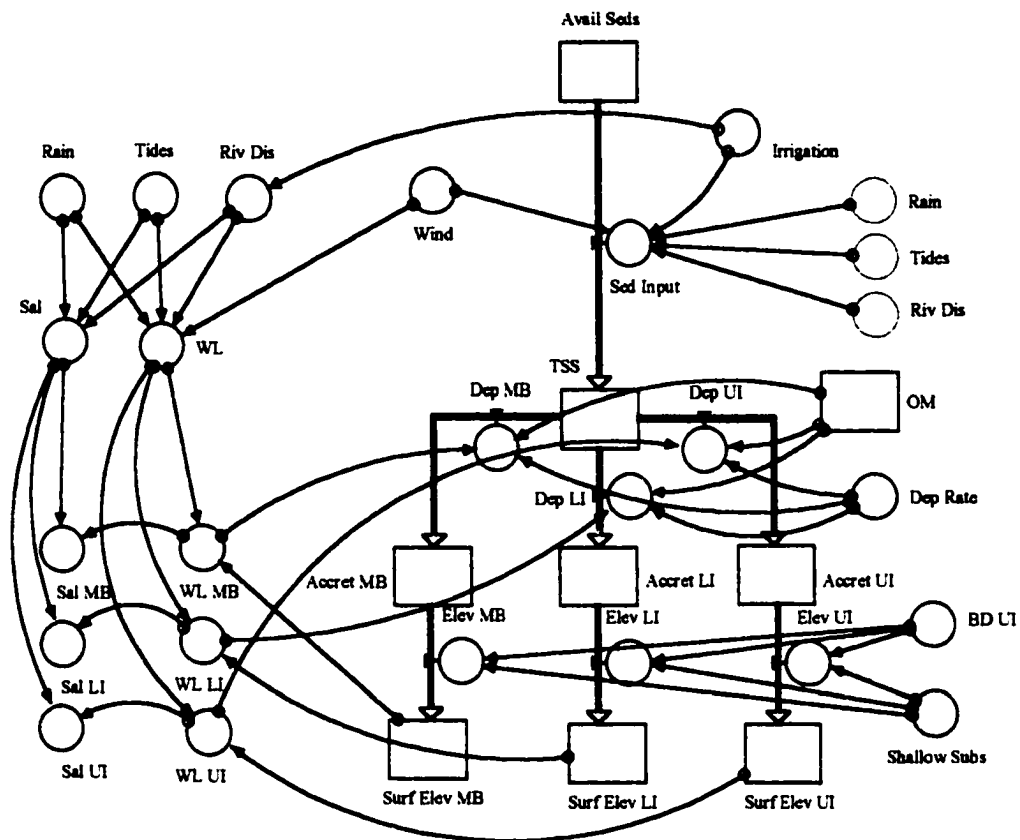


Figure 5.1. Conceptual model of mangrove structure dynamics (Stella® diagram) showing Module 1: sedimentation dynamics. State variables are rectangles, circles are forcing functions, pipes with circles attached are fluxes between state variables, and arrows are interactions. Other abbreviations are as follows: Avail Seds=available sediments, Riv Dis=river discharge, Sal=salinity, WL=water level, TSS=total suspended sediments, OM=organic matter, Accret=accretion, Surf Elev=surface elevation, Dep Rate=deposition rate, BD=bulk density, Shallow Subs=shallow subsidence, MB=mud bank, LI=lower intertidal, and UI=upper intertidal. Lines in blue indicate additions to the model, or highlighting of important factors based on experimental data.

Point bars and islands showed a clear spatial sedimentation gradient, with the highest rate of vertical accretion at the lower intertidal zone, ( $8.37 \text{ cm yr}^{-1}$  compared to  $1.85 \text{ cm yr}^{-1}$  for the upper intertidal zone). Differential sedimentation across the intertidal gradient was mainly controlled by the local hydroperiod (water level in the model, Figure 5.1). Significantly lower relative elevation and higher frequency and duration of flooding characterized the lower intertidal zone (see Chapter 2); conditions that favor sediment availability and deposition. Vertical accretion was higher during the dry season (4.53

cm yr<sup>-1</sup> compared to 2.52 cm yr<sup>-1</sup> for the rainy season) as a result of the extremely high TSS concentrations in the Tempisque River during this time of the year. The effect of increased sediment load on sedimentation dynamics in the Bebedero was less evident because it is less directly impacted by irrigation activities. The Bebedero sites did not show a significant seasonal effect in vertical accretion and vertical elevation change was low compared to the Tempisque during the dry season (4.31 cm yr<sup>-1</sup> and 5.07 cm yr<sup>-1</sup> for the dry and rainy seasons, respectively).

The lower intertidal zone had high rates of vertical accretion (8.37 cm yr<sup>-1</sup>), shallow subsidence and elevation change (3.76 cm yr<sup>-1</sup>). In the upper intertidal zone, there was positive vertical accretion (1.85 cm yr<sup>-1</sup>) but a loss in elevation (-0.44 cm yr<sup>-1</sup>) due to shallow subsidence. Several different processes contribute to shallow subsidence including decomposition, de-watering, compaction and erosion. Soil erosion was not significant in lower and upper intertidal zones meaning that in soil processes dominated shallow subsidence.

Soil formation in the study sites is a product of both mineral and organic matter deposition, both of which are affected by river discharge and tidal flooding. Short-term sedimentation and surface soils were dominated by inorganic sedimentation (see Chapter 2 and Chapter 3). Organic matter in recently deposited surface sediments was 31.5% and 35.1% in lower and upper intertidal zones, respectively. In contrast, the organic content of the superficial soil layer (after removal of recently deposited leaves, twigs, etc., Chapter 3) was 9.0 % for both lower and upper intertidal zones. This indicates an organic matter loss of approximately 73%, likely a result of decomposition and loss by tidal flushing. Further studies addressing these two factors are necessary for a better understanding of the organic matter dynamics of the system.

From the perspective of global climate change, the results help to determine if these mangroves are keeping pace with estimated rates of sea level rise. Mangroves of point bars and islands had an elevation change in the lower intertidal zone about one order of magnitude higher than the global mean sea level rise of 0.1-0.2 cm yr<sup>-1</sup> (Gornitz 1995). From a regional perspective, however, human induced alterations to the system are more relevant to mangrove population dynamics than sea level rise. For example, as a result of the increased sediment load, the Tempisque River seems to be experiencing channel filling. During the period of this study, there was an expansion of mud banks around islands and

point bars, and the exposure during low ebb tides, of sandbars being formed in the main river channel at several different sites. If the general geomorphology of the main river channel continues to change in this manner, it will greatly affect changes in mangrove community structure.

Currently, these changes in the hydrology and sedimentation dynamics of the Tempisque-Bebedero system are leading to increased vertical accretion and probably bringing nutrients to the system. This is leading to an increase in mangrove area. Long term monitoring and modeling should be carried out to evaluate and predict future responses of the system to current and projected increases in the use of the Tempisque river water for irrigation purposes.

#### **5.1.2. Propagule Dispersal and Establishment**

The ability of a mangrove species to colonize new environments initially depends on propagule dispersal and the capacity to establish successfully under the predominant physico-chemical characteristics of the environment (Ball 1980, Clarke 1993, Duke et al. 1998). Point bars and islands of the Tempisque-Bebedero system are currently colonized by a mangrove population, dominated by Laguncularia in the lower intertidal zone and other species, especially Avicennia germinans and Rhizophora racemosa in the upper intertidal zone. The expanding mud banks in islands and point bars are being mainly colonized by Laguncularia. Field and controlled mesocosm experiments were conducted to determine the relative importance of some of the factors involved in the dispersal and establishment processes that might give an advantage to Laguncularia over the other species in colonizing these types of environments.

Density and intertidal position of reproductive trees are important first factors influencing dispersal, by providing a propagule source and determining distance of travel to colonizing sites. The main source of propagules was in situ propagule production (Figure 5.2). This explains the maintenance of dominance of Laguncularia in the lower intertidal zone. Hydroperiod was the main factor controlling propagule dispersal (Figure 5.2), but which can also be affected by debris on the forest floor. The upper intertidal zone, characterized by less frequent flooding, has a lower dispersal of propagules to mud bank areas. Dispersal is also affected by propagule buoyancy characteristics. Laguncularia propagules, in contrast to Avicennia spp., had a reduced floating period (2-7 days), and the ability to establish and grow under water. While Laguncularia propagules sank soon after radicle protrusion, Avicennia spp.

## Module 2

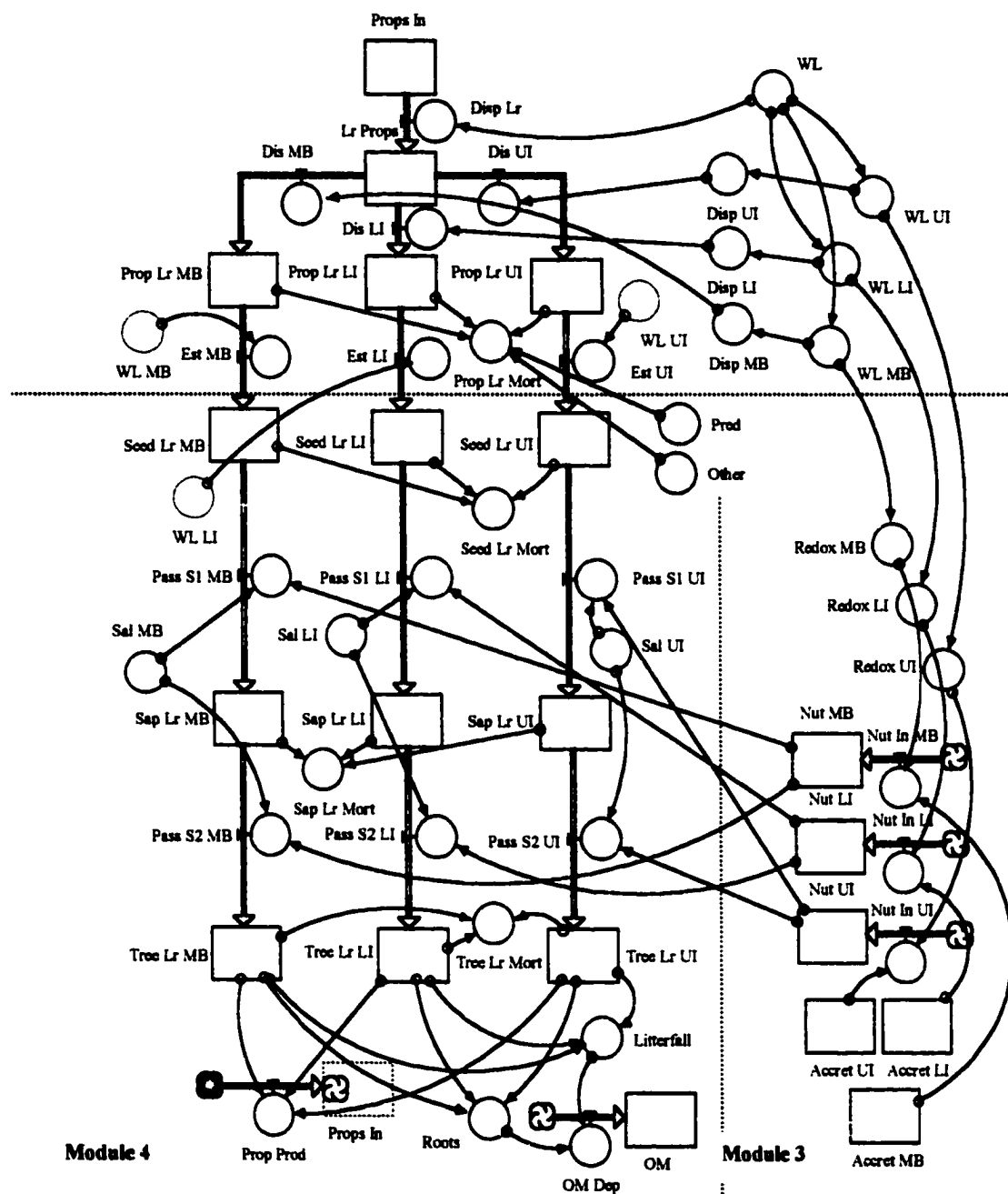


Figure 5.2. Conceptual model of mangrove structure dynamics (Stella® diagram) showing modules 2, 3 and 4: propagule dispersal and establishment, soil physico-chemical variables, and forest structure, respectively. State variables are rectangles, circles are forcing functions, pipes with circles attached are fluxes between state variables, and arrows are interactions. Other abbreviations are as follows: Lr=*Laguncularia racemosa*, WL=water level, Props=propagules, Disp=dispersal, Mort=mortality, Seed=seedling, Sap=sapling, Nut=nutrients, OM=organic matter, MB=mud bank, LI=lower intertidal, and UI=upper intertidal. Lines in blue indicate additions to the model, or highlighting of important factors based on experimental data.

propagules remained buoyant for longer periods of time. Under the higher frequency and duration of flooding experienced in mud banks and lower intertidal zones, Laguncularia by being a “sinker” as compared to Avicennia spp. being a “floaters” gives an advantage to Laguncularia in colonizing these environments.

Hydroperiod can also affect establishment, especially in mud bank zones, by making stranding more difficult due to the effect of tidal and wave action (McMillan 1971, McKee 1995). In point bars and islands, water currents and wave action are generally moderate, but seemed to cause a greater influence upon the establishment of Avicennia spp. propagules. Even though a significant difference was not found, results from the field cross planting experiment (see Chapter 4) showed that 25% more of Laguncularia propagules were able to establish in the mud bank zone compared to Avicennia; and about 28% more Avicennia propagules remained non-established by the end of the 40-day experiment.

Within the Tempisque-Bebedero system, an intensive and selective crab predation on Laguncularia propagules in the upper intertidal zone was an important source of mortality. Laguncularia propagules in the upper intertidal zone were eleven times more likely to be eaten than those of Avicennia spp. This factor probably limited the distribution of this species in this zone, thus giving an advantage for the colonization of Avicennia spp. and other species. Mortality can also result from lost of viability and decay, which were the main causes of mortality in the lower intertidal zone. In view of these results, the effect of crab predation on propagule mortality was included in the model (Figure 5.2).

#### **5.1.3. Soil Physico-Chemical Variables**

River discharge, tides and rain are the main forcing functions determining the system hydroperiod, which is an important modifying factor of the soil physico-chemical characteristics (Figure 5.2). River discharge lowers salinity in the system. Even during the dry season, average soil pore water salinity for the lower and upper intertidal zones was very low, with values of 1.67 ppt and 2.40 ppt, respectively. Salinity in this system, therefore, is not a limiting factor for mangrove growth and productivity. Low values, however, have influenced some structural aspects of the mangrove community. For example, less tolerant species have been able to establish in the mangrove community, especially in the less frequently flooded upper intertidal zone, increasing its species diversity. Also, mangrove expansion towards a landward direction has been limited by competition with more terrestrial vegetation.

The strong influence of river discharge and tides results in strongly mineral soils due to the high sedimentation rates. Based on several soil physico-chemical variables including permeability to air, soil shear strength, pH, exchange acidity, cation exchange capacity (CEC) and macronutrients (Ca, Mg, K, P, TN, NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>), soils characteristics changed across the intertidal gradient of point bars and islands. Mud bank soils or bare soils were characterized by a lack of consolidation, an accumulation of ammonium, and lower levels of nitrate as a result of higher reduced conditions. Higher soil consolidation and generally higher nutrient concentrations characterized the more oxidized soils of lower and upper intertidal zones.

Hydrology affects nutrient concentrations and the availability for plant uptake by acting on several soil physico-chemical parameters. This includes modification of soil redox, and vertical accretion rates which represents a source of both organic and inorganic sediments. In fact, as a result of a differential rate of sedimentation between the lower and upper intertidal zones, a significantly higher nutrient deposition rate characterized the former, which accumulated more sediments (nutrient associated) compared to the upper intertidal zone. The presence of vegetation also modifies the nutrient pool within the system (Boto and Wellington 1984). Nutrients are removed by plant uptake, some of which are re-incorporated in the soil through organic matter deposition and decomposition.

#### **5.1.4. Forest Structure**

Mangroves colonizing point bars and islands in the Tempisque-Bebedero system exhibited a characteristic species distribution across the intertidal gradient. Laguncularia racemosa was the dominant species in the lower intertidal zone, forming monospecific forests characterized by a high density of small diameter trees, which is characteristic of young immature forests in high sedimentary environments. Their contribution to the total basal area was high (approximately 23%). Rhizophora racemosa and Avicennia germinans were generally the dominant species, in terms of basal area, in the upper intertidal zone, forming more mature forests. Tree density of both species in this zone was low, but trees had larger diameters.

The occurrence of Laguncularia seedlings in the upper limit of mud banks indicated that a gradual colonization of this zone is taking place. In addition, the presence of seedlings, saplings, and trees from different diameter classes of the different nuclear mangrove species, suggested potential forest

recruitment across the intertidal gradient, and an active mangrove community development. Transition success from one life stage to the next is closely related to the environmental conditions, especially at the early stages of seedlings and saplings, which are in general more vulnerable to both flooding and salinity stress. In the Tempisque-Bebedero system low salinity conditions provide a non stressful environment for mangrove development. However, significant modifications to this factor because of human induced alterations to the system might lead to modifications in the forest structure. Salinity and flooding stressors affect plant growth and can cause mortality under extreme conditions. Since current changes in the system hydroperiod involve a decrease of river discharge, flooding probably will not likely represent a limiting factor for mangrove development. For model simplicity, the effect of the different factors determining mortality of saplings and trees was pooled within a single rate of mortality. High nutrient availability enhances plant growth, which favors transition to an upper structural class.

## **5.2. MANGROVE STRUCTURAL DYNAMICS IN POINT BARS AND ISLANDS OF THE TEMPISQUE-BEBEDERO ESTUARINE SYSTEM**

The Tempisque and Bebedero rivers are an active meandering system, with the formation of point bars on aggrading banks of a river bend (convex bank) and erosive cut banks on the opposite side (concave bank). Maximum current velocities and turbulence occur near the cut bank decreasing towards the point bar. This flow pattern causes erosion in the cut bank zone and deposition of eroded materials on the point bar of the next river bend, leading to downstream migration of meander loops (Coleman 1969). These erosive and depositional dynamics result in constant changes in the system, where the presence of Rhizophora racemosa in the fringe zone of cut banks probably represents a point bar that has been eroded away.

Point bars and islands (which also represent areas of deposition), therefore, constitute unstable low energy environments characterized by a dynamic sedimentation pattern, which changes across the intertidal gradient. In the mud bank and lower intertidal zone higher sediment deposition, frequency and duration of flooding and water movement create conditions of soil instability and more stress, favoring establishment of species well adapted to these characteristics. Laguncularia racemosa dominates these environments and exhibits properties that makes it suitable to growth in these lower intertidal zones as compared to other species such as Avicennia spp and Rhizophora racemosa, which dominate the more stable and less frequently flooded upper intertidal zones.



Laguncularia propagules show limited buoyancy characteristics giving an advantage to this species under frequently flooded environments, by decreasing removal from the system, and indirectly by accelerating the establishment process. Propagule anchoring is not significantly affected by water movement and can take place under water. Once propagules establish and pass to the seedling stage, rapid height increment helps overcome stress by flooding. Once established, Laguncularia exhibits a special prostrated growth form with high aerial root density that enhances stability in unconsolidated soil. Laguncularia forms a type of horizontal branching at the level of the soil surface with abundant secondary root growth on the lower part of stems and lower branches, simulating extensive root systems, which cover the substrate efficiently while augmenting sediment stability. Therefore, addressing the first hypothesis in Chapter 1, this study has shown that in point bars and islands of the Tempisque-Bebedero system sedimentation dynamics and hydroperiod do create specific conditions in the lower intertidal zone which favor the establishment and dominance of Laguncularia.

Other factors influencing mangrove species distribution and other structural characteristics are related to soil physico-chemical variables. In point bars and islands, soils variables seem to play an important role affecting species distribution and mangrove development across the intertidal gradient, as expressed in the second hypothesis of the study. Even though soils of lower and upper intertidal zones were fairly homogeneous for certain characteristics (bulk density, soil texture, organic matter and salinity); the lower intertidal zone had higher frequency and duration of flooding, somewhat lower stability and higher nutrient deposition rates (Ca, Mg, K, P, TN, NH<sub>4</sub>), which seem to favor the establishment and dominance of Laguncularia in this zone. Therefore, in addition to offer an adequate environment for mangrove growth and development, reflected by the high basal areas and distribution of diameter classes observed across the intertidal gradient, soil characteristics of point bars and islands seem to also affect the species distributional pattern. High mangrove development in these environments thus seems to be the response of the significant input of freshwater and sediments to the system.

The last hypothesis of the study addressed the effect of biotic factors influencing species distribution. In point bars and islands, distribution of Laguncularia in the upper intertidal zone appears to be limited by a selective crab predation of its propagules as compared to Avicennia. Under these

conditions, propagules that get dispersed to upper zones have a reduced chance of survival because of predation, giving an advantage to *Avicennia* spp. and other species in colonizing this zone.

### **5.3. BROADER PERSPECTIVES**

Within a regional perspective, the Tempisque and Bebedero river systems are a very important resource to socio-economic activities of local communities. The Tempisque River, especially, is a source of freshwater for irrigation, and a natural resource being exploited for tourism and small-scale fisheries. Currently, irrigation activities have modified the system by decreasing river discharge and increasing sediment load during the dry season. In spite of these changes, mangrove communities bordering the riverbanks have not shown signs of negative impacts. However, this does not seem to be the case for other populations. According to local fishermen (pers. comm.), shellfish populations occurring in the Tempisque River have decreased during past decade, probably the result of increased suspended sediments in the river.

Considering that changes to the system are going to continue and probably increase as a result of current and projected irrigation activities, management strategies should strive for an efficient use of the river water to avoid severe alterations to the system. In addition to a continuation of the monitoring of the mangrove community responses to these changes, a more comprehensive study might reveal more insidious impacts across these and other populations. In other systems in which agricultural irrigation has significantly altered hydrology, cumulative impacts have affected the coastal system on the larger geomorphological scale (Stanley 1988).

The conceptual model of mangrove forest structure dynamics developed for this environmental setting has revealed some important relationships between the mangrove community colonizing point bars and islands in the Tempisque-Bebedero systems and the larger estuarine environment. There are still many unknowns concerning these relationships and how human impacts may affect them at larger spatial and temporal scales. The ubiquity of these impacts in the tropics warrants a better understanding of these relationships between the mangrove forest, its soils, and the water from which it arises.

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## **VITA**

**Patricia Delgado Sánchez was born to Víctor Hugo Delgado and Norma Sánchez on November 03 1968, in San José, Costa Rica. Early in her high school studies, Patricia showed interest for science. To pursue her interests Patricia went on to attend the Universidad Nacional de Costa Rica, from which she graduated in 1991 with a bachelor in Marine Biology. As an undergraduate, Patricia worked for three years in the Laboratory of Mangrove Ecology and Management in the same University, under the direction of Dr. Jorge A. Jiménez, to whom she attributes her early interest in mangrove ecology. In 1992, Patricia earned an US-AID scholarship to pursue graduate studies at Louisiana State University, from which she graduated in 1995 with a master of science degree. Her master's thesis was entitled "Effects of Longterm Wastewater Discharge in the Cyprière Perdue Forested Wetland at Breaux Bridge, Louisiana", which she conducted under the tutelage of Dr. John W. Day, of the Department of Oceanography and Coastal Sciences. During this period, Patricia met Philippe, also student of Dr. Day, who she married in Costa Rica in 1995; in 1996 both were blessed with a son François Nicolas. Soon after Patricia obtained her master's degree, Dr. Day offered to her the opportunity to continue her studies towards the doctorate, also under his direction, which she did. In 1998, Philippe was awarded a Fulbright grant to conduct post-doctoral research in Costa Rica. Wanting to go back to mangrove ecology, Patricia, used this opportunity to conduct her doctoral research in the mangroves of the Palo Verde National Park, Guanacaste, Costa Rica, where she and Philippe worked together in a same project. Patricia, Philippe and Nicolas lived in the Palo Verde Biological Station of the Organization of Tropical Studies (OTS) for two years while they were studying aspects related to mangrove structure. Patricia will receive the degree of Doctor of Philosophy in 2001 from the Department of Oceanography and Coastal Sciences at Louisiana State University, with a dissertation entitled "Factors Affecting Community Structure of Mangroves Associated with Point Bars and Islands in a Costa Rican Estuary".**

# DOCTORAL EXAMINATION AND DISSERTATION REPORT

**Candidate:** Patricia Delgado-Sanchez

**Major Field:** Oceanography and Coastal Sciences

**Title of Dissertation:** Factors Affecting Community Structure of Mangroves Associated with Point Bars and Islands in a Costa Rican Estuary

Approved:

  
Major Professor and Chairman

  
Dean of the Graduate School

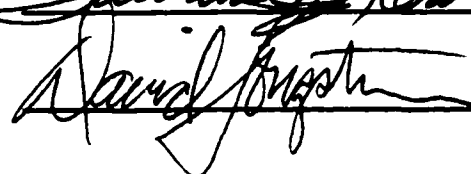
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**Date of Examination:**

March 16, 2001