

Center for Tropical Marine Ecology
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Investigations of mangrove forest dynamics in Amazonia, North Brazil

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Abstract

The north coast of the Brazilian states of Pará and Maranhão, presents a large continuous belt of mangroves, covering an area of about 700 000 ha. Although mangroves in this region are relatively well preserved, expanding tourism, intensification of fisheries and of urban growth in the region may endanger this important coastal ecosystem. In spite of the immense area covered by mangrove forest, very few is known about species distribution and forest ecology in the region.

The present study focuses on the growth dynamics of the mangrove species *Rhizophora mangle* L. under different conditions of inundation frequency, salinity and rainfall regime on the north coast of Brazil. The study concentrates on: 1) evidence of seasonality in primary production, reflected in phenology, litter fall and interactions with herbivores; 2) application of dendrochronological methods on *R. mangle*, including determination of tree age and influence of climatic and site-specific factors on tree growth; 3) applying these findings in an analysis of forest structure and dynamics on Ajuruteua Peninsula. Wood samples for dendrochronology were taken at three points along the coast of Pará: Viseu, São João de Pirabas and Bragança. Detailed studies of phenology and litter fall, herbivory, forest structure and forest evolution were developed at different sites on Ajuruteua Peninsula, Bragança district.

A study on litter fall and phenology demonstrated that rainfall seasonality is reflected in mangrove tree primary production. The description of a severe infestation by moth larvae in mangrove forests demonstrated that, besides climate and site-specific conditions, herbivory can be substantially influence the primary production.

The wood of all studied specimens of *R. mangle* showed distinct rings. The rings were formed by a light and a dark layer. The light layer, formed at the end of the rainy season, is the result of a higher density of vessels; the dark layer, formed at the end of the dry season. The increase or decrease of vessels may be a reaction to seasonal salinity variation.

Radiocarbon analysis showed that growth rings are annual. This allowed to the determination of tree age. The oldest tree was 111 years old.

Growth curves revealed a linear growth (absence of trend-age). Growth rates varied strongly. The highest (however, not significantly different) rates were found at the sector of the Pará coast with the highest tidal amplitudes, suggesting an influence of the tide on tree growth. The relationship between rainfall and growth was not easily interpretable, however, growth was positively correlated to rainfall in some areas. A presumed influence of rainfall may have been superimposed by the impact of other factors as salinity and input of fresh water.

Growth rates on Ajuruteua Peninsula were highly variable. Trees were tentatively divided in three groups (fast, medium and slow growth). Although trees from each study site could occur in more than one group, there is an obvious trend that trees from frequently inundated areas dominate the group with the highest growth rate. Considering that all sites are submitted to similar climatic conditions, the absence of fast growing trees at certain sites may be due to the influence of local factors (e. g. salinity, inundation frequency or also neighbourhood competition among trees). It is assumed that neighbourhood competition is an important source of within-site variability of growth rates.

The determination of the age of forest stands in combination with a classical study of forest structure allowed to propose a model of forest succession.

This study demonstrated that the combination of forest structure surveys and dendrochronological methods provided informations concerning trees growth and forest development that were up to now not available. The application of these informations in mangrove forest management and preservation is suggested. In spite of the weak correlations between tree growth and climatic factors, dendrochronology may also help to understand changes of coastal vegetation within the past decades.

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Chapter 1 Introduction

Introduction

1.1 The scope of the thesis

Mangroves are coastal forests of sheltered tropical and subtropical coastlines. They feature trees with a capacity to survive in a saline or brackish environment under tidal influence (Tomlinson, 1986). There are more than 50 mangrove species described in the literature, but in new world mangroves, only 8 tree species occur (Tomlinson, 1986). In Amazonia there are 6 mangrove species: *Rhizophora mangle* L., *Rhizophora racemosa* G.F.W. Meyer, *Rhizophora harrisonii* Leechman, *Avicennia germinans* (L.) Stearn 1958, *Avicennia schaueriana* Stapf and Leechman ex Moldenke 1939, and *Laguncularia racemosa* L. (for more details see section *Floristic composition and species distribution*, Chapter 2). Mangroves offer a variety of economically important resources exploited by the coastal human population, and are important as fish nursery (Macnae, 1968; Sasekumar et al., 1992) as well as for coastal protection (Ewel et al., 1998). Their primary production is fundamental for estuarine and coastal food chains (Alongi et al., 1989). Nevertheless, this ecosystem has been destroyed by construction of shrimp farms, by deforestation, overfishing, pollution and urban development (Spalding et al., 1997).

Very few is known about temporal changes of mangrove forest structure, that is, forest dynamics. Mangrove trees present a high plasticity in growth with respect to diameter, height and tree architecture (Hallé et al., 1974). This plasticity seems to be a consequence of the specific abiotic conditions determined by nutrients, salinity and tidal regime frequency in their highly variable coastal environment (Tomlinson, 1986; Suarez et al., 1998). The same factors are held responsible for the great variety of mangrove forest types found along tropical coastlines. Important tools for understanding the dynamics of forests are assessments of forest structure (trees size, species distribution, and biomass) and stand demography (tree establishment, mortality, life span) under different levels of the relevant environmental factors as pore water salinity and tidal

regime. The dynamics of mangrove forests have been accessed by simulation models (Chen and Twilley, 1998; Berger and Hildenbrandt, 2000) or conceptual models (Jiménez and Lugo, 1985; Duke, 2001). However, their success has been limited by the lack of information about demographic processes, as data on species-specific growth rates, mean age of individuals, or the age of whole stands are extremely scarce (e.g. Fromard et al., 1998). A valuable tool to provide this kind of information is dendrochronology (tree ring analysis). The growth and consequent formation of wood structure depends on ambient conditions, and if seasonal changes in these conditions lead to traceable, periodical modifications of wood structure (growth rings), morphological, physical or chemical analysis of wood samples may allow the chronological reconstruction of the tree's life. Counting growth rings allows the determination of the age of trees, while measuring ring width provides information concerning the growth and the conditions affecting it (Schweingruber, 1988; Worbes, 1999; Worbes, 2004). The knowledge about forest dynamics resulting from dendrochronological studies is of great importance also for the development of sustainable management of tropical tree species (Worbes et al., 2003). However, this kind of approach has not been applied to mangrove forests yet.

The study of forest dynamics includes the determination of tree growth. For tree growth studies, an integrated approach of investigation of growth patterns is required (Worbes, 1995). It includes the observation of cambial activity and phenological events. Phenological investigations give an indication of the growth pattern of the species, of a single tree or a forest stand. These growth patterns may depend on external factors; an increase in leaf production of a tree species during a certain time of the year, for example, can indicate a change of external factors specific for the respective season (e.g. rainfall; Worbes, 1995). While phenology has to be observed in real-time, changes in cambial activity can be assessed by means of dendrochronological analysis also for the past. The concept of combining several aspects important for the determination of

growth patterns was fundamental to the design of this study, which tries to answer the following main questions:

1. Is mangrove growth along the north coast of Brazil seasonal?
2. Which factors influence the seasonality?
3. Are there different patterns of cambial growth in mangrove trees along the north coast?
4. How old are mangrove trees and mangrove forests?
5. What is the impact of the observed growth patterns for forest dynamics?

This thesis consists of six chapters in form of individual scientific papers. The first article (Chapter 2) starts with a review of the available literature concerning the vegetation of mangrove forests of the states of Pará and Maranhão on the north coast of Brazil. The review demonstrates that the status of knowledge about mangrove vegetation in the region is still scarce. The available information supports the choice of *Rhizophora mangle*, which is the dominant tree species in mangroves along the coast of Pará and Maranhão, as main object of this study. Concerning the questions 1 and 2, the review suggests a strong influence of seasonal rainfall regime and salinity variations both, on phenology and litter production. Chapter 3 presents a study of tree phenology and amount of litter fall in a mangrove forest under influence of an inundation/salinity gradient, assessing the questions 1 and 2. Additionally, a rare case of massive defoliation of the mangrove tree *Avicennia germinans* by the moth *Hyblaea puera* is described (Chapter 4). This is used for evaluating how such “catastrophic” events can influence tree growth and, consequently, forest structure (question 2).

The other three articles focus on the growth dynamics of *Rhizophora mangle* trees under both saline and brackish conditions. To study the periodicity of cambial growth of adult trees, dendrochronological tree ring analysis is used. In Chapter 5, this methodology is successfully tested to determine the occurrence and periodicity of ring formation

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(question 1), the age of trees (question 4) and aspects of tree growth (question 3). To verify whether the growth patterns described in Chapter 5 are local or regional (question 3), dendrochronological investigations are extended to *R. mangle* trees from different regions of the coast of Pará State (Chapter 6). Finally, the findings from Chapter 5 and 6 concerning growth rates and age of trees are examined in combination with forest structure and the influence of inundation frequency and competition among individual trees on the trees' growth (question 3) in a case study of Ajuruteua Peninsula. The results of this analysis were used to interpret changes in forest structure (question 5). Based on these results, new suggestions to a model of forest dynamics are proposed (Chapter 7). The different questions covered in each chapter are summarized in Figure 1.1.

The present study was developed within the frame of the Brazilian-German Cooperation project MADAM (Mangrove Dynamics and Management) initiated in 1995 to study the mangrove ecosystems of northern Brazil with emphasis on the estuary of the Caeté River near Bragança (Pará). The principal aim of the project was to generate multi-disciplinary scientific knowledge of the spatial-temporal patterns characteristic of the mangrove ecosystem of the Caeté mangrove estuary (Berger et al., 1999).

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Brazil, Amazonia**

Questions	Related chapters
Does seasonality of mangrove tree growth exist on the north coast of Brazil?	2, 3, 5, 6
Which factors influence the seasonality?	2, 3, 5, 6, 7
Are there different patterns of cambial growth along the coast?	6
How old are mangrove trees and mangrove forests?	5, 6, 7
What is the consequence of the observed growth patterns for forest dynamics?	7

Figure 1.1: Overview of the main questions and the related chapters.

1.2 Study area

The area of interest comprises the north coast of the Brazilian states of Pará and Maranhão, extending over 600 km from Marajó Bay (Pará State) to the estuary of the Preguiças River (Maranhão State) between 0°13'45"S, 48°33'19"W and 2°29'32"S, 43°27'44"W. This region is part of the world's

largest continuous belt of mangroves, covering an area of about 700 000 ha, that is, almost 85% of the Brazilian mangroves (Herz, 1991; Lacerda, 1999). In this region, mangroves can extend more than 40 km landward following the course of numerous small estuaries and bays. The area is characterised as macro tidal. Tidal amplitudes vary between 4 m and 7.5 m. The tidal regime is semi-diurnal (DHN, 2004). The climate is tropical warm and humid. The registered mean annual precipitation is about 2300 mm. Dry and rainy season are well defined. Mean annual precipitation is 26°C. The mangroves are still well preserved, probably due to the difficulty of access (Lara, 2003). Nevertheless, these forests are under pressure from the growing population, deforestation for a variety of purposes and increasing demand for wood and other mangrove products (Senna et al., 2002; Szlafsztein, 2003).

Dendrochronological samples were taken at three points along the coast: Viseu (1°12'18"S, 46°08'19"W), São João de Pirabas (0°46'18"S, 47°10'33"W) and Bragança (1°03'34"S, 46°45'55"W). Detailed studies of phenology and litter fall, herbivory, forest structure and forest evolution were developed at different sites on Ajuruteua Peninsula, Bragança district.

1.3 Methods overview

1.3.1 Phenology and litter fall

The patterns of litter fall and tree phenology were assessed by means of litter traps along an inundation/salinity gradient on Ajuruteua Peninsula. Litter was collected fortnightly. The litter material was sorted by species and components. Linear mixed-effects models were used to characterise litter fall with respect to position along the gradient and to collection date as well as their interaction (Chapter 3).

1.3.2 Forest structure

Forest structure was assessed by means of the point centred quarter method (PCQM, e.g. Cintrón and Schaeffer-Novelli, 1984) and the plot method (Chapters 5; 7).

1.3.3 Assessing cambial activity by means of tree ring analysis

To analyse the existence of growth rings in *R. mangle*, wood discs (stem cross sections) were collected (Chapters 5; 6; 7). In some cases, core samples were taken with a 5 mm increment corer (Chapter 5). All samples were polished to increase visualization of rings. Rings were counted and measured with a stereo microscope (Chapters 5; 6; 7).

The annual periodicity of rings was assessed by means of ^{14}C isotope contents (Chapter 5). The age of felled trees was directly assessed by counting the number of growth rings (Chapters 5; 6; 7). Growth rates were calculated by dividing the cumulative radius increment by the number of rings of each wood disc. The age of living trees could then be estimated from stem diameter at breast height and the mean growth rate obtained from the wood discs (Chapters 5; 7).

Ring width curves were transformed into index curves and, after trend removal, correlated with precipitation time series (annual total, totals for specific seasons and extension of dry season; Chapters 5; 6).

1.3.4 Estimates of competition among trees

The competition among the trees was evaluated via the Field-of-Neighbourhood (FON) approach (Berger and Hildenbrandt, 2000). A FON is defined as a size-dependent circular scalar field around a tree. It has its maximum directly at tree's stem and decreases exponentially towards its boundary. A FON describes phenomenologically the competition strength which a tree exerts on its neighbourhood. Trees with overlapping FONs are neighbours. The FONs of neighbouring trees sum up to an aggregate field strength which is taken as the proxy for the intensity of competition a tree suffers at its specific position (Berger and Hildenbrandt, 2000). The neighbourhood of trees was mapped during the forest structure survey, and aggregate field strength was calculated according to Berger and Hildenbrandt (2000). Competition intensity was then tested for relevance as factor influencing mean growth rates (Chapter 7).

1.4 Results and discussion summary

1.4.1 The state of the art

Concerning mangrove vegetation in the study region, socio-economic studies reveal that wood is used as fuel, timber and for medicinal purposes (Glaser, 2003; Glaser et al., 2003). Studies of forest structure and species richness revealed the presence of three typical mangrove species: *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* (Thüllen, 1997; Matni et al., 2005; Abreu et al., 2005). Litter fall studies showed a high primary production (Mehlig, 2001; Carvalho, 2002; Reise, 2003). A rich associated fauna uses mangrove vegetation as habitat and food source (Barletta, 1999; Koch, 1999), especially the crab *Ucides cordatus* (Diele, 2001; Nordhaus, 2004; Nordhaus et al., 2006) that has a high economic importance (Glaser, 2003; Glaser and Diele, 2004). The mangroves in the region have been described as exporter of organic material (Dittmar, 1999). Studies of leaf gas exchange (Brabo, 2004) and chlorophyll fluorescence (Hu, 2004) of *A. germinans*, *A. schaueriana* and *L. racemosa* trees indicate that salt stress reaches critical levels in seldom inundated areas. However, no comparable stress response was detected at a moderately saline, well-inundated site (Brabo, 2004; Hu, 2004). Essential for the following parts of this study are the findings regarding mangrove structure, documenting the dominance of *R. mangle* in mangroves of the Pará and Maranhão coast, and the indications for seasonal climatic changes with effects on tree growth (Chapter 2).

1.4.2 Phenological patterns and primary production

Seasonality in tree growth can be assessed by observing phenology and by measuring litter fall dynamics as proxy for primary production. In this study (Chapter 3) as well as in others from the literature survey (see section *Phenology of mangrove trees* in Chapter 2), both phenology and litter production are influenced by the rain fall regime. In general, mangrove species in the studied area are evergreen with a well defined reproductive phase. Variation in site-specific abiotic conditions (inundation, salinity) is made responsible for

differences in productivity. While a trend to lower litter production under high salinity conditions was observed in the present study, seasonal phenological patterns (fruition, flowering and leaf production) were more or less consistent along an inundation/salinity gradient. This demonstrates that periodical changes in growth induced by the seasonal rain fall regime are still traceable in superposition with a general pattern of primary production governed by site-specific conditions (Chapter 3).

An exceptionally strong infestation of one of the principal mangrove tree species in the area, *A. germinans*, by moths of the species *Hyblaea puera* as recorded in Chapter 4 demonstrates its significant impact on tree growth, besides or in addition to climatic and geochemical factors, or of competition between trees (see below). Interviews with locals gave evidence that similar infestation events have occurred in the past, possibly with an unknown, supra-annual periodicity. This fact would have to be considered when studying the long-term growth history of stands. It is, however, not known whether *R. mangle*, the main study object of this text, is affected in a similar way by herbivore attacks or comparable diseases. Dendrochronological studies do not provide evidence for occasional events reducing the growth of whole stands of *R. mangle* so far (see below).

1.4.3 Cambial activity and age of trees

Seasonality was also found in cambial activity, as expected after analysing tree phenology. *R. mangle* trees produce distinguishable annual wood rings. The annual character was proved using ^{14}C dating; this was the first time that annual growth rings could be confirmed for a mangrove tree species (Chapter 5). The growth rings were formed by a light and a dark layer. Dark layers present low density of vessels, while light layers present higher density of vessels. Production of dark layers begins at the end of the dry season, while the light layer production are formed at the end of the rainy season (Chapter 6). With the help of the annual rings, it was possible to determine the maximum age of *R. mangle* trees. Based on the findings that a single growth ring is produced per year, it

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can be confirmed that *R. mangle* trees reach an age of approximately 100 years; the oldest tree analysed was 111 years old (Chapters 5, 6). The combination of forest structure and mean forest age indicates that the oldest *R. mangle* trees do not reach much more than 130 years (Chapter 7). The life span is short when compared to other tropical trees which can reach an age of about 400 years (Worbes and Junk, 1999).

Correlations between different rainfall-related time series and growth increment of *R. mangle* trees from different sites along the coast did not reveal clear pattern. At a few sites, a positive correlation of rainfall and growth could be detected. An analysis of individual trees revealed strong variability of growth rates even under similar local conditions (Chapter 5; 6). At each site, a broad spectrum of individual growth rates was observed.

The mean radial growth of *R. mangle* varied between 2.5 and 4.9 mm·y⁻¹ (Chapters 5; 6). The highest values were found in areas subject to higher tidal amplitudes (Chapter 6; 7). The cumulative curve of the radial growth increment revealed a linear trend (Chapters 5; 6). This implies constant radial growth over the life span of the tree. Field observations (Chapter 7) documented that height growth of trees stagnates when they surpass a breast height diameter of approximately 30 cm, while stem diameter still increases after approaching maximum height (Chapter 7).

In the case study of Bragança, trees were tentatively assigned to growth groups (“fast”, “medium”, “slow”) with growth rates of 3.6 mm·y⁻¹, 2.9 mm·y⁻¹ and 1.8 mm·y⁻¹ for each group, respectively. While at some sites a greater number of trees belonged to one or the other growth group, mixed assemblages of slow and fast growing trees were found at most locations. Considering that all study sites are submitted to similar climatic conditions, the absence of fast growing trees at certain sites suggests an influence of local factors (e. g., salinity and inundation) or also competition among individual trees. Regression analysis revealed that the most important factor influencing the growth of trees in the different growth groups is the small scale variation of inundation frequency.

Trees more frequently inundated by the tide presented higher growth rates. In areas inundated less frequently, the neighbourhood competition plays an important role for the growth of trees (Chapter 7). According to Cordeiro et al. (2003), areas more frequently inundated present higher amounts of bioavailable phosphorus essential for plant growth.

1.4.4 Dynamics of mangrove forests

The forest structure survey on Ajuruteua Peninsula together with the estimates of stand age based on dendrochronological findings allows a detailed analysis of existing forest types and their developmental stage. For example, the impact of clear cutting, fuel wood and timber extraction by humans (site Acarajó) is clearly reflected in diameter and age structure. The exploited forest presents a continuous rejuvenation characterised by a broad distribution of diameter classes, while unexploited forests present a bell-shaped diameter class distribution. An inverse J-shaped diameter distribution at one of the forest stands may indicate a stage of forest succession after an impact caused by changes in the hydrographic regime (Chapter 7). Exponential regression lines described the relationship between stem diameter and height of *R. mangle* trees and manifested a size-limitation of height growth while diameter growth continues (Chapter 7).

After combining the results of mean forest age and forest structure to data of species succession obtained by Berger et al. (2006), a good agreement with the general succession model for neotropical mangroves introduced by Jiménez and Lugo (1985) was obtained. The model describes four stages of development of a forest stand: colonisation, early stage, maturity and senescence. However, according to this study the early development stage is much longer than proposed by Jiménez and Lugo (1985). Therefore, this stage was subdivided in an “early development” and a “young forest stage”, leading to a model of mangrove forest development with 5 stages (Chapter 7):

Chapter 1

Stage 1 – colonisation: starts with gap creation. High density due to number of seedlings. This stage lasts for about 4 years (Berger et al., 2006).

Stage 2 – early development: the number of individuals decreases in function of self-thinning. This stage lasts 5 years (Berger et al., 2006).

Stage 3 – young forest: two trajectories are identified, depending on environmental conditions: under benign conditions, the forest develops towards a mature forest; under adverse conditions, the development stagnates. In this stage trees are between 20 and 30 years old.

Stage 4 - mature stand: tree density and neighbourhood competition are reduced to low or moderate values. The mean age of trees varies from 30 to 60 years.

Stage 5 - senescent forest: No senescent forest was identified in this study. This can be interpreted as absence of such a forest stage in the study area, or in function of the short life span of trees. Alternatively, as hypothesised by Duke (2001), gap formations may lead to continuous rejuvenation of the forest without entering a stage of general senescence. However, Fromard et al. (1998) describe senescent or “cemetery” forests in French Guyana. Their descriptions suggests similarities with certain areas of Ajuruteua Peninsula which were not subject of this study; however, tree mortality at those sites could be high due to geomorphological changes rather than due to senescence.

1.5 Concluding remarks and research perspectives

This study documents the existence of seasonality in mangrove tree phenology, cambial growth and primary production. Factors affecting phenology and primary production (litter fall) patterns as pore water salinity and tidal inundation are linked with the strong seasonality of rain fall regime. Dependence of cambial growth on climate and on site-specific abiotic factors as well as on competition among trees certainly exists, but correlation between any of these factors and growth rates are weak.

1.5 Concluding remarks and research perspectives

The high importance of inundation is reflected by the highest growth rates in areas subject to a macro tidal regime (Viseu); also high growth rates were recorded in frequently inundated areas (Furo Grande, Ajuruteua Peninsula). The positive influence of inundation frequency can be related to the input of nutrients and the moderate levels of salinity. Equally, inundation influences primary production positively, as shown in the litter fall study.

Individual competition is an important factor affecting the growth of trees only in areas inundated infrequently. It seems that due to reduced water exchange and, consequently, lower availability of nutrients, competition of the individuals for the same scarce resource has more pronounced effects.

R. mangle trees present a size-limited height growth while diameter growth is continuous.

Based on dendrochronological data, this study improved insights from classical analysis of forest structure and could thus enhance a conceptual model of forest dynamics. According to this model a mature equatorial Brazilian mangrove forests is about 50–80 years old.

Further investigations of phenological responses of *R. mangle* trees to climatic factors can help to refine dendrochronological analyses of this species. However, dendrochronology already can help to understand changes of the coastal vegetation within the past decades, filling the gap between palaeobotanical assessments (e. g. Behling et al., 2001) and short-term analysis by satellite image analysis (Cohen and Lara, 2003).

Understanding the dynamics of ecotone shifts in the coastal region is becoming very important in the context of the discussion of global change. Further application of the findings presented in this study should be considered in mangrove forest management and preservation initiatives: 1) The continuous growth of diameter and the absence of senescent forests are important for planning forest exploitation. 2) The time to reach the harvesting size (e. g., 20 cm stem diameter at breast height) varies according to local conditions. This

stresses the necessity of local evaluation of mangrove growth rates. 3) The cutting of trees leads to changes in trees size distribution. It specifically causes the depletion of big trees.

The *Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis* (IBAMA) has been creating co-management reserves (*reservas extrativistas* – RESEX) in mangrove areas along the coast of Pará state (see Glaser and Oliveira, 2004). This kind of initiative focuses mainly on sustainable use of resources important for the human population and on preserving traditional forms of resource extraction. Traditional forms of resource usage include wood extraction for subsistence purposes (Glaser, 2003). On a small scale, impacts by harvesting trees are certainly not dangerous, but with the increase of the coastal population (Szlafsztein, 2003) extraction activities can become predatory. In this case, the use of mangrove trees has to be restricted to certain areas, possibly in the neighbourhood of the villages, and has to be accompanied by a reforestation program to guarantee the preservation of the forest and its associated biodiversity. Loss of mangrove area may otherwise have profound effects on the dependent food chains of the marine ecosystems in its vicinity, and, finally, thus affect the human population living on these resources.

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Chapter 2

Amazonian mangrove forest along the coast of Pará and Maranhão States: a review



Amazonian mangrove forest along the coast of Pará and Maranhão States: a review*

Menezes, M. P. M. and U. Berger

Abstract The present study is a compilation of the literature about mangrove forests of the north coast of Brazil. It synthesises the knowledge about this vegetation and lists the currently available literature. The study focuses on the coast of Pará and Maranhão states, where there is a continuous belt of mangroves covering a total area of approximately 700 000 ha. The literature indicates the occurrence of six mangrove species and many other associated species. Tree height and stem diameter vary as a function of local parameters. Seasonal variation in rainfall and salinity affect species phenology and litter fall. Local people use mangrove flora for different purposes (e. g. fuel and medicine). The increase in the coastal population has given rise to conflicts, which impact on mangrove forest.

Key words: Amazonian mangroves, forest structure, species distribution, phenology, litter fall, herbivory, human impacts, Brazil

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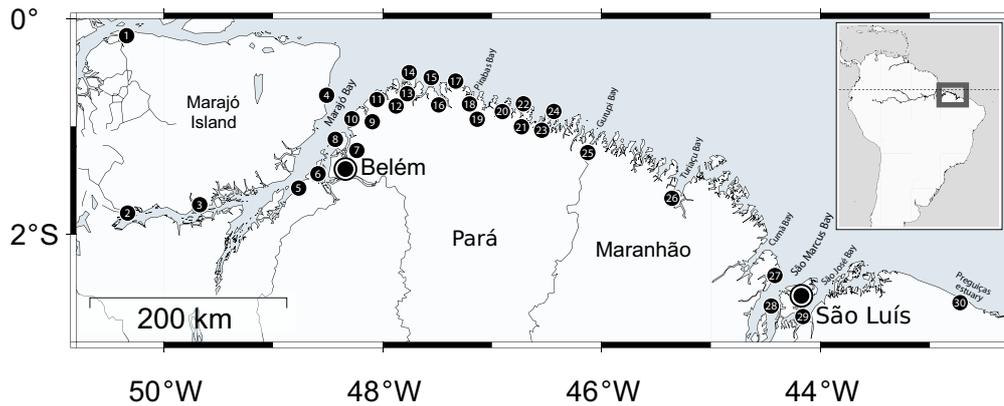


Figure 2.1: Study area on the North Coast of Brazil, states of Pará (with the Marajó Island) and Maranhão. Localities with informations about mangrove forests are indicated by numbers (1: Afuá; 2: Breves; 3: São Sebastião da Boa Vista; 4: Soure, Salvaterra; 5: Barcarena; 6: Ilha das Onças; 7: Ananindeua, Marituba and Benevides; 8: Ilha do Mosqueiro, Santa Bárbara; 9: Vigia; 10: Colares; 11: São Caetano de Odivelas; 12: Curuçá; 13: Mapanim; 14: Marudá, Praia do Crispim; 15: Ilha de Algodoal; 16: Maracanã; 17: Salinas (Salinópolis); 18: São João de Pirabas; 19: Primavera; 20: Quatipuru; 21: Bragança; 22: Ilha de Canelas; 23: Augusto Corrêa; 24: Urumajó; 25: Viseu; 26: Turiaçu; 27: Alcântara; 28: Baía de São José; 29: Baía de São Marcus, Parnaucu e Rio Mearim 30: Rio Preguiças).

2.1 Introduction

The present work synthesises the current literature on the mangrove forests along the coast of Brazilian states of Pará and Maranhão (Figure 2.1). This is the world's largest continuous belt of mangroves, covering a total area of about 700 000 ha and comprising nearly 85% of Brazilian mangroves (Herz, 1991; Lacerda, 1999). In recent years, integrated research into coastal ecosystems has been initiated (Berger et al., 1999; Prost et al., 2001) and has provided most of the currently available information on mangrove vegetation of the region. However, no summary of the information is available. In this review, we present a synthesis of the current publications on mangrove forests of the region, including grey literature. Additional observations on mangrove specimens from the collection at the João Murça Pires Herbarium at the

Paraense Emilio Goeldi Museum (MG) in Belém complete our survey.

2.2 Data Collection

The current scientific literature analysed includes papers published in peer reviewed journals, books, conference proceedings, internal reports of university programs as well as graduate, master and doctorate theses. Additionally investigations of the mangroves collection of the Herbarium João Murça Pires from Museu Paraense Emílio Goeldi at Belem (MPEG) and personal observations complete the information.

2.3 Study area

We concentrate on the coast of the north-Brazilian states of Pará and Maranhão, extending over 650 km from Marajó Bay (Pará State) to the estuary of river Preguiças (Maranhão State) between 0°13'45"S, 48°33'19"W and 2°29'32"S, 43°27'44"W (Figure 2.1). In this region, mangroves can extend more than 40 km landward following the course of numerous small estuaries and bays (P. W. Souza-Filho, unpublished data). The area is characterised as macrotidal; tidal amplitude varies between 4 m and 7.5 m. The tidal regime is semi-diurnal (DHN, 2004). The climate is tropical, warm and humid. The annual mean precipitation is approximately 2300 mm (Fisch et al., 1998). The mean air temperature is about 26°C. The region presents a well defined dry season with mean monthly precipitation less than 50 mm, lasting from July to December (Fisch et al., 1998).

2.4 Results and Discussion

2.4.1 Floristic composition and species distribution

Major elements of the mangrove forest (sensu Tomlinson, 1986)

Rhizophora mangle L. (Rhizophoraceae) is the most widely distributed mangrove tree species (Prance et al., 1975), and is dominant in estuaries more exposed to the ocean (Almeida, 1996a). A second, less widely distributed *Rhizophora* species is

R. racemosa G.F.W. Meyer, which occurs in Marajó Bay (Almeida, 1996a). Further south, there is only one other report of *R. racemosa*, from the Preguiças estuary, Maranhão (Santos, 1986). The third species is *R. harrisonii* Leechman, which is less frequently reported than the other two species (Figure 2.2) and dominates a single forest area in the Preguiças estuary (Santos, 1986). According to Breteler (1969), the salt tolerance of these species increases from *R. racemosa* through *R. harrisonii* to *R. mangle*. This characteristic might explain the restriction of *R. racemosa* and *R. harrisonii* to the Marajó bay region and the Preguiças estuary (Figure 2.2). However, no detailed investigations have been carried out into the salt tolerance of these species.

Avicennia germinans (L.) Stearn 1958 is the commonest species of the family Avicenniaceae (Figure 2.3). According to Luz et al. (2000), *A. germinans* is more frequent in elevated, less inundated areas and under more saline conditions.

Avicennia schaueriana Stapf and Leechman ex Moldenke 1939 (Figure 2.3) has been recorded at several locations along the coast, principally near sandy beaches (Amaral et al., 2001; Santos, 2005). This species has nowhere been reported as a major constituent of the mangrove forest in our study area.

Laguncularia racemosa L. (Combretaceae) occurs along the entire coast in saline as well as in brackish water mangroves (Figure 2.3). This species mostly occupies forest edges, large gaps, riparian sites, and other open areas. There are no records of *L. racemosa* dominated forests.

Minor elements of mangrove forest and associated species (sensu Tomlinson, 1986)

Among the species cited as mangrove associated (Table 2.1), only a few occur under high salinity conditions. Most of these are halophytic herbs more frequently found at channel borders or in other open areas; a few are salt marsh species (Carlton, 1975). The only woody plant in this group is *Conocarpus erectus* L. (Combretaceae), which mainly colonises ecotones of mangroves and salt marshes where the soil is sandier and less frequently inundated. A few shrubs and vines (*Muellera*, *Rhabdadenia*) have been observed by the authors in saline environments on Ajuruteua Peninsula, Bragança. However, most of the woody mangrove associates, as well as herbs like *Crinum* and the mangrove fern *Acrostichum*, seem to be unable to thrive without significant freshwater influence. A number of species cited in the literature might in fact be of terrestrial origin (e.g., *Astrocaryum*, *Cassipourea*) and thus belong to adjacent ecosystems like *restinga* (dune vegetation).

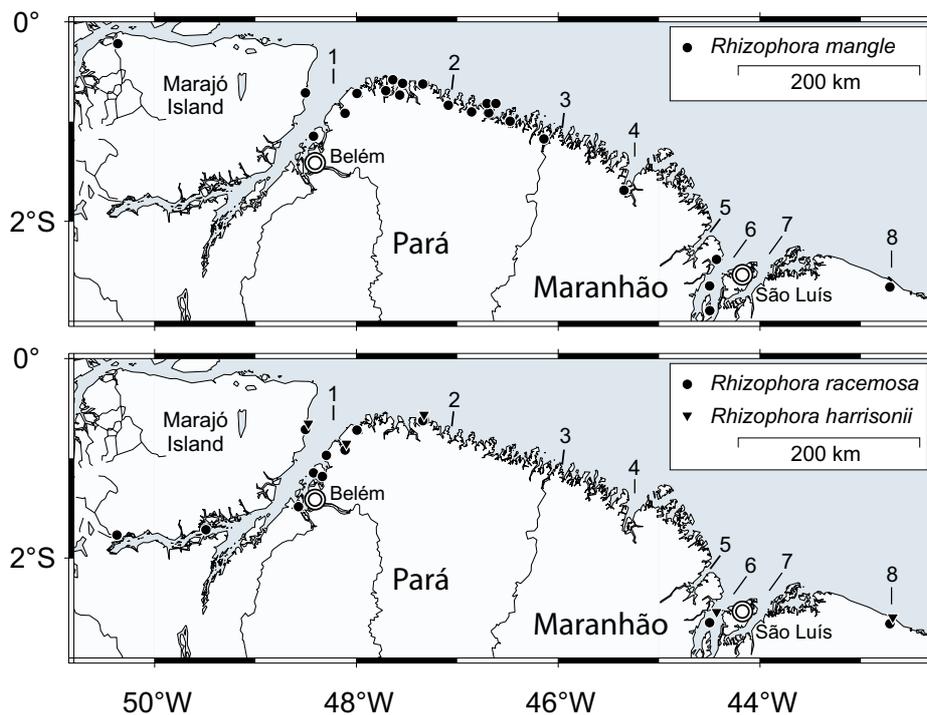


Figure 2.2: Distribution of *Rhizophora* species in the study area. Bays are indicated by numbers (1: Marajó bay; 2: Pirabas bay; 3: Gurupi bay; 4: Turuiçu bay; 5: Cumã bay; 6: São Marcus bay; 7: São José bay; 8: Preguiças estuary). Data source: Appendix.

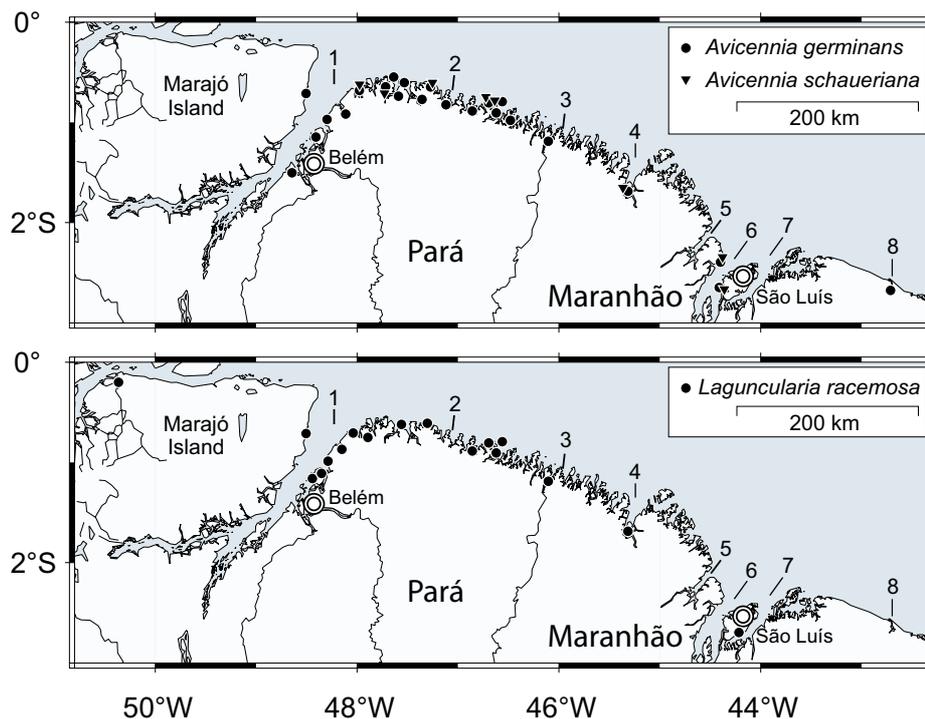


Figure 2.3: Distribution of *Avicennia* species (above) and *L. racemosa* (below) on the study area. Bays are indicated by numbers (1: Marajó bay; 2: Pirabas bay; 3: Gurupi bay; 4: Turuaçu bay; 5: Cumã bay; 6: São Marcus bay; 7: São José bay; 8: Preguiças estuary). Data source: Appendix.

2.4.2 Forest structure

Schaeffer-Novelli et al. (1990) divide the Brazilian coast in 7 segments. The mangroves of our study area (“segment III”) are classified as *Rhizophora*-dominated “fringe forests”, reaching 20 m in height. Nevertheless, our review reveals considerable heterogeneity in species composition and forest structure and indicates that this classification is too coarse. Unfortunately, the majority of studies is merely descriptive and does not provide quantitative data based on an adequate sampling area. Furthermore, the methods used to describe forest structure include a variety of plot-based methods and distance-based methods (point-centred quarter method), as well as “rapid assessment” estimation techniques. This means that comparisons of the results of the studies (summarised in Table 2.2) should be viewed with caution.

2.4 Results and Discussion

Table 2.1: Minor elements and species associated to mangrove flora. *Locality*: site of occurrence on the coast (1 Marajó bay; 2 Pirabas bay; 3 Gurupi bay; 4 Turiaçu bay; Cumã bay; 6 São Marcus bay; 7 São José bay; 8 Preguiças estuary); *bs* brackish mangrove; *hs* saline mangrove; ? no information available.

Family	Species	Locality								Sal.		Reference
		1	2	3	4	5	6	7	8	br	hs	
Aizoaceae	<i>Sesuvium portulacastrum</i>											● 6; pers. obs.
Amaranthaceae	<i>Alternanthera</i> sp.											● 1
	<i>Blutaparon</i> sp.											● 6
Amaryllidaceae	<i>Crinum</i> sp.											● 10; 2; 11
Annonaceae	<i>Annona palustris</i>											● 15
Apocynaceae	<i>Mesechites trifidus</i>											● 1
	<i>Echites valenzuelanus</i>											● 1
	<i>Rhabdadenia biflora</i>											● ● pers. obs.
	<i>Forsteronia</i> sp.											● 18; 19
	<i>Mandevilla</i> sp.											● 18; 19
Araceae	<i>Montrichardia arborescens</i>											● 1; 2
Arecaceae	<i>Euterpe oleracea</i>											● 13
	<i>Mauritia flexuosa</i>											● 13
	<i>Astrocaryum vulgare</i>											● 18
Bataceae	<i>Batis maritima</i>											● 6; pers. obs.
Bombacaceae	<i>Bombax</i> sp.											● 12
	<i>Bombax aquaticum</i> (= <i>Pachira aquatica</i>)											● 13; 15
Cecropiaceae	<i>Cecropia</i> sp.											● 6
Clusiaceae	<i>Symphonia globulifera</i>											● 13
Combretaceae	<i>Conocarpus erectus</i>											● 3; 4; 5; 6; 7; 8; 17
Costaceae	<i>Costus arabicus</i>											● 1
Cyperaceae	<i>Cyperus giganteus</i>											● 1
	<i>Bulbostylis paraensis</i>											● 1
	<i>Cyperus distans</i>											● 1
	<i>Cyperus ligularis</i>											● 1
	<i>Fimbristylis</i> sp.											● 6
	<i>Eleocharis caribaea</i> sp.											● 6; pers. obs.
	<i>Eleocharis geniculata</i>											● 19
	<i>Eleocharis intersita</i>											● 6
	<i>Eleocharis geniculata</i>											● 19
Dennstaedtiaceae	<i>Pteridium aquilinum</i>											● 1
Euphorbiaceae	<i>Alchornea brevistyla</i>											● 1
Fabaceae	<i>Desmodium canum</i>											● 1
	<i>Machaerium lunatum</i>											● 9
	<i>Pterocarpus</i> spp.											● 12
	<i>Macherium lunatum</i>											● 13
	<i>Pterocarpus rohrii</i>											● 15
	<i>Drepanocarpus lunatus</i>											● 15
	<i>Inga</i> sp.											● 15
	<i>Muelleria frutescens</i>											● 1
Lythraceae	<i>Crenea maritima</i>											● pers. obs.
Malvaceae	<i>Pavonia spicata</i>											● 6
	<i>Hibiscus</i> sp.											● 19; 18
	<i>Hibiscus tiliaceus</i>											● 1
Melastomataceae	<i>Mouriri angulicosta</i>											● 12
	<i>Miconia</i> sp.											● pers. obs.
Orchidaceae	<i>Epidendrum ciliare</i>											● pers. obs.
	<i>Epidendrum</i> sp.											● pers. obs.
Poaceae	<i>Sporobolus virginicus</i>											● 2; 6
	<i>Spartina alterniflora</i>											● 2; 6
	<i>Spartina brasiliensis</i>											● 14; 19
	<i>Cynodon</i> sp.											● 1
	<i>Paspalum</i> sp.											● 6
Pteridaceae	<i>Acrostichum aureum</i>											● 2; 6; 5; 14; 16; 18; 19; 18
Rhizophoraceae	<i>Cassipourea guianensis</i>											● 15

References: 1 Tourinho (1998); 2 Menezes et al. (2003); 3 Medina et al. (2001); 4 Medina et al. (2000); 5 Lisboa et al. (1993); 6 Rebelo-Mochel, (1997); 7 Rebelo-Mochel et al. (2001); 8 Carreira et al. (2002); 9 Adams & Berger (2002); 10 Berger et al. (2005); 11 Matni (2003); 12 Gama et al. (1996); 13 Almeida (1996a); 14 Prost et al. (2001); 15 Ferreira (1989); 16 Sales (2000) 17 Santos et al. (2003); 18 Almeida et al. (2002); 19 Damasio (1980b)

Table 2.2: Mangrove forests structure. *Height* mean height; *dbh* mean stem diameter; *BA Rhz* basal area *Rhizophora*; *BA Av*: basal area *Avicennia*; *BA Lg* basal area *Laguncularia*; *Ag %* relative density *Avicennia germinans*; *As %* relative density *Avicennia schaueriana*; *Rm %* relative density *Rhizophora mangle*; *Rr %* relative density *Rhizophora racemosa*; *Rh %* relative density *Rhizophora harrisonii*; *Lg %*: relative density *Laguncularia racemosa*

Locality	Height m	dbh cm	BA Rhz m ² ·ha ⁻¹	BA Av m ² ·ha ⁻¹	BA Lg m ² ·ha ⁻¹	Ag %	As %	Rm %	Rr %	Rh %	Lg %	Reference
Salvaterra	20.0	-	13.2	11.9	-	47.4	-	-	52.6	-	-	Lisboa et al. (1993)
Bragança AC1	11.8	17.8	12.7	4.0	0.04	16.4	-	68.8	-	-	14.7	Menezes et al. (2003)
Bragança FG1	11.8	19.2	4.7	13.1	-	66.7	-	33.3	-	-	-	Menezes et al. (2003)
Bragança FdM1	13.0	32.5	14.6	15.1	-	21.6	-	75.7	-	-	-	Menezes et al. (2003)
Bragança dwarf	2.4	0.5	-	0.6	-	100	-	-	-	-	-	Reise (1999)
Bragança DA	0.8	0.5	-	-	-	46.7	-	-	-	-	53.3	Schories and Reise (2000)
Bragança AV1	4.0	0.7	0	0.7	-	100	-	-	-	-	-	Schories and Reise (2000)
Bragança AVII	1.9	3.1	0.03	1.7	-	98.0	-	2.0	-	-	-	Schories and Reise (2000)
Bragança AV&RH	5.8	7.4	0.5	0.74	0.03	67.9	-	24.4	-	-	7.7	Schories and Reise (2000)
Bragança	8.9	13	1.7	0.3	0.008	3.2	-	95.5	-	-	1.3	Abreu (2004)
Marapanim I	18.1	30.6	14.5	19.9	-	13.7	-	86.2	-	-	-	Costa-Neto et al. (2000)
Marapanim II	14.9	27.6	9.1	17.3	-	17.5	-	82.5	-	-	-	Costa-Neto et al. (2000)
Marapanim III	21.3	31.4	18.9	10.1	-	10.0	-	90.0	-	-	-	Costa-Neto et al. (2000)
Marapanim IV	9.8	30.5	1.3	7.2	5.8	30.0	0	32.5	0	0	37.5	Costa-Neto et al. (2000)
Marapanim V	13.4	23.1	2.3	0.2	0.01	11.6	-	86.1	-	-	2.3	Sales (2005)
Marapanim VI	16.5	27	4.5	0.01	-	0.2	-	99.8	-	-	1.3	Sales (2005)
Crispim	7.2	4.8	0.5	0.4	3.3	4.3	0	50.5	0	0	4.3	Bastos and Lobato (1996)
Curuça	13.5	42.2	10.1	15.6	-	-	0	0	0	0	0	Menezes (1994)
Algodoal	8.1	12.4	26.6	1.6	2.2	22.8	0	75.4	0	0	1.7	Bastos and Lobato (1996)
Preguiças	19.8	21.2	14.3	5.1	-	27	0	9.0	9.0	54.0	0	Santos (1986)
Parnauaçu	6.0	15.0	-	-	-	-	25	25	-	-	50.0	Rebello-Mochel et al. (1997)
Benevides	7.3	18.1	0	0	-	0	-	0	0	0	0	Ferreira (1989)
Ananindeua	13.2	25.4	0	0	-	0	-	0	0	0	0	Ferreira (1989)
Mosqueiro	11.7	24.2	0	0	-	0	-	0	0	0	0	Ferreira (1989)
Vigia	24.7	28.5	0	0	0	-	0	0	-	-	0	Ferreira (1989)
São Caetano	19.6	23.0	0	0	-	0	-	0	0	0	0	Ferreira (1989)
Turiáçu	10.0	15.2	-	-	-	-	-	-	-	-	-	Rebello-Mochel (2000)
Viseu	20.0	35.0	-	-	-	-	-	-	-	-	-	Menezes et al. (2003b)

1) *Avicennia germinans* dwarf forest (tree height <2.5 m; Reise, 1999; 2003) at highest elevations (above mean spring tide level, inundation frequency <28 d·y⁻¹); pore water salinity 90–100.

2) Low *A. germinans* forest (average tree height 6 m, mean dbh 5 cm; Reise, 1999) in areas inundated only during normal spring tides (28–78 d·y⁻¹); pore water salinity 90–50.

3) *A. germinans*-dominated, tall mixed forests (mean height 11.8 m, mean dbh 19.2 cm Menezes et al., 2003); inundated for about 175 d·y⁻¹; pore water salinity 23–58.

4) Tall, mixed *R. mangle*/*A. germinans* forests (mean height 12 m, mean dbh 31 cm Menezes et al., 2003), composed of *R. mangle*, *A. germinans* and *Laguncularia racemosa*, but dominated by *R. mangle*; at mid-tide level, normally well inundated (up to 233 d·y⁻¹); pore water salinity 20–60.

5) A variety of the forest type “tall, mixed *R. mangle*/*A. germinans* forest” (type 4) occurs under brackish conditions; it has similar structural properties, but features a greater number of associated understorey species (Menezes et al., 2003; Berger et al., 2006). The pore water salinity ranges from 10 to 17 and inundation frequency is about 140 d·y⁻¹. These forests occupy inner parts of the estuary with pronounced influence of fresh water runoff.

In addition to the forest types described so far, other forest types can be identified as: 1) regenerating forests consisting of seedlings and/or young trees of *L. racemosa* and *A. germinans*; 2) degraded areas with total or partially dead vegetation (due to damage caused by human activities or changes in local conditions).

All types of forests occur side by side on the peninsula, as can be seen clearly in aerial photographs (Reise, 2003) and satellite images (Souza-Filho and Paradella, 2002; Cohen et al., 2003). The forest types so far described indicate that in spite of the low species richness, there is a great deal of variation in mangrove forest structure, according to topographical and hydrological conditions. Since the geomorphological settings and hydrographic conditions in other regions of the Brazilian

north coast are comparable to those on Ajuruteua Peninsula (Souza-Filho and Paradella, 2002), vegetation patterns observed here can be expected to be typical of the region as a whole. No detailed investigations of other areas have been undertaken so far, however.

2.4.3 Phenology of mangrove trees

Information on mangrove phenology is derived from studies of litter fall (Mehlig, 2001; Reise, 2003; Mehlig, 2006; all Ajuruteua Peninsula), direct observation of phenophases of whole trees (Carvalho, 2002; Ajuruteua Peninsula), and periodic monitoring of individually marked shoots (Menezes, 1997, Curuçá; Silva, 2005; Santos, 2005; Mehlig, 2006, Ajuruteua Peninsula). Information on the phenology of *R. racemosa* is based on an analysis of specimens from the João Murça Pires Herbarium at the Paraense Emilio Goeldi Museum (MG) in Belém. There are no data on phenology of *R. harrisonii*.

Avicennia germinans leaf fall is seasonal and precedes flowering (Mehlig, 2001; Carvalho, 2002). New leaves appear mainly during the transition from rainy to dry season when the salt stress is lower (Mehlig, 2001; Santos, 2005: direct observation). Median leaf life time is 275 days (Santos, 2005). Flowering is restricted to the dry season (Mehlig, 2001; Carvalho, 2002; Santos, 2005). Ripe fruits are released in the rainy season (Table 2.3; Carvalho, 2002). The time span between peak of flowering and fruit fall is 4–5 months (Mehlig, 2001).

Information on the phenology of *Avicennia schaueriana* is based on observations by Santos (2005) on Ajuruteua Peninsula. Leaves are produced throughout the year but higher production rates were observed during the rainy season. No clear pattern in leaf fall is discerned. The median life span of leaves is 115 days (Santos, 2005). Flowering takes place from April to October; ripe fruits are observed during the rainy season (Table 2.3; Santos, 2005).

Laguncularia racemosa sheds leaves throughout the year (Table 2.3; Mehlig, 2001). New leaves are produced throughout the year at well-inundated sites but production rates are higher during the rainy season. Median leaf life time is 100 days (Silva, 2005).

Table 2.3: Phenology of Amazonian mangrove species. ● = new leaves/flowers/fruits present; ■ = peak period; ? = no information available

Species	J	F	M	A	M	J	J	A	S	O	N	D
<i>A. germinans</i> ^{1,2,5}												
leaves	●	●	●	●	●	●	●	●	■	■	■	●
flowers	●							●	■	●	●	●
fruits	●	●	■	■								●
<i>A. schaueriana</i> ^{3,5}												
bud						●	●	●				
flowers				●	●	■	■	●	●	●		
fruits	●	■	■	●		●	●		●			●
<i>R. mangle</i> ^{1,2,4,7}												
leaves	■	■	■	■	■	■	●	●	●	●	●	●
flowers	●	●	●	●	■	■	■	■	●	●	●	●
fruits	●	●	●	●	●	●			■	■	■	●
propagules	■	■	■	●								
<i>R. racemosa</i> ³												
buds		●	●		●	●			●	●		●
flowers	?											
fruits	●	●	●	●	●	●	●	●	●	●	●	●
propagules			●	●					●	●		●
<i>L. racemosa</i> ^{1,6}												
leaves	●	■	●	●	●	■	●	●	●	●	●	
flowers	●	●	●	●	●							●
fruits	■	■	■	■	●							

References: ¹Mehlig, 2001; ²Carvalho, 2002; ³MPEG Herbarium (MG); ⁴Menezes, 1997; ⁵Santos, 2005; ⁶Silva, 2005; ⁷Mehlig, 2006

L. racemosa starts flowering at the beginning of the rainy season. Fruits develop quickly and are shed in the rainy season (Mehlig, 2001; Silva, 2005).

Rhizophora mangle sheds leaves throughout the year and new leaves are also produced continuously. Leaf production is higher in the rainy season (Table 2.3), when soil salinity is lower. Leaf age is variable but rarely exceeds one year (Mehlig, 2006). *R. mangle* also produces flowers throughout the year, but flowering peaks at the end of the rainy season (Menezes, 1997; Mehlig, 2001; Carvalho, 2002; Mehlig, 2006). Propagule release is mostly restricted to the rainy season (Menezes, 1997; Mehlig, 2006; Carvalho, 2002). The time span between

pollination and maturation of propagules is about 8 months (Menezes, 1997; Mehlig, 2006). According to Mehlig (2001) the comparison of propagule production between brackish and saline mangroves suggests that differences in salinity regime might play a role in premature abscission of flowers and fruits.

Buds and immature propagules are present in almost all examined herbarium specimens of *Rhizophora racemosa*. It is thus probable that flowering and propagule development in *R. racemosa* take place throughout the year (Table 2.3).

Generalisations based on the currently available phenological data should be avoided due to the small geographic range covered so far. However, differences in patterns of rainfall (for example in the duration of rainy and dry seasons) probably influence the extension and intensity of the phenophases.

2.4.4 Litter fall

Information about mangrove litter fall is available from Ajuruteua Peninsula (Schories and Reise, 2000; Mehlig, 2001; Carvalho, 2002; Reise, 2003; Nordhaus, 2004; Table 2.4). In all studies, leaves are the most abundant component of the litter (about 70% of total litter). Litter fall rates range between $4.1 \text{ ton}\cdot\text{ha}\cdot\text{y}^{-1}$ in *A. germinans* dwarf forest (Schories and Reise, 2000) and $16.3 \text{ ton}\cdot\text{ha}\cdot\text{y}^{-1}$ in tall, mixed *R. mangle/A. germinans* forest (Nordhaus, 2004; Nordhaus et al., 2006). Comparing mangroves with similar structural characteristics on the Ajuruteua Peninsula, Schories and Reise (2000) identify salinity as the principal factor affecting the total litter production; the most productive forests are frequently inundated and are characterised by lower salinity. Schories et al. (2003) estimate that less than 31% of the litter production of a mangrove stand at Furo do Meio on Ajuruteua Peninsula is exported to the estuary by tidal flushing.

Table 2.4: Annual litter fall rates ($t \cdot ha^{-1} \cdot y^{-1}$) from Ajuruteua Peninsula, Bragança.

<i>Local</i>	<i>Litter dry matter ($t \cdot ha^{-1} \cdot y^{-1}$)</i>	<i>Reference</i>
Furo do Meio	12.8	Mehlig (2001)
Acarajó	13.1	Mehlig (2001)
Furo Grande I	7.9	Carvalho (2002)
Furo Grande II	15.4	Reise (2003)
Dwarf Forest	4.1	Reise (2003)
Furo Grande III	16.3	Nordhaus (2004)
Dwarf Forest	4.1	Reise (2003)
Bosque de <i>Avicennia</i>	9.5	Batista (2003)

2.4.5 Leaf decomposition

Leaf decomposition was analysed through mesh bag exposure experiments by Sales (2000), at São Caetano de Odivelas east of the Marajó Bay ($0^{\circ}44'50''S$, $48^{\circ}01'16''W$), and Schories et al. (2003) at Furo do Meio on Ajuruteua Peninsula. In both studies, *A. germinans* leaves decomposed faster than those of *R. mangle* and *L. racemosa*. Decomposition of 50% of the exposed material lasted 34 and 90 days for *A. germinans* and *R. mangle*, respectively (Sales, 2000). Schories et al. (2003) found slightly faster decomposition rates at frequently inundated than at rarely inundated sites (23–34 vs. 29–41 days, respectively). Sales (2000) unfortunately does not specify the inundation regime at his experimental site.

2.4.6 Herbivory

A. germinans is described as the tree species most affected by herbivores, while *R. mangle* is considered the least affected species (Pontes and Mochel, 2000; Rebelo-Mochel, 1997; Ohana et al., 1996; Praxedes and Mello, 1998; Praxedes et al., 1998). The most common predators of mangrove vegetation are Hymenoptera (Praxedes and Mello, 1998; Pontes and Mochel, 2000), crustaceans, Isoptera, Hemiptera (Pontes and Mochel, 2000) and Lepidoptera (Pontes and Mochel, 2000; Menezes and Mehlig, 2005). According to Pontes and Mochel (2000), *L. racemosa* is severely affected by herbivores in areas polluted by waste-water discharges. Pontes and Mochel (2000) attribute herbivore activity on *L. racemosa* trees to increased nitrogen concentration in the leaves caused by sewage. A

massive infestation of *A. germinans* by caterpillars of the moth *Hyblaea puera* (Hyblaeidae) was documented on Ajuruteua Peninsula in 1998 (Mehlig and Menezes, 2005), leading to complete defoliation of *A. germinans*-dominated stands. This phenomenon contributed to a decrease in litter fall (Mehlig, 2001). Similar observations were made in the same area in 2000 (Reise, 2003) and in São Caetano de Odivelas (Sousa, 2001; Prost et al., 2001).

2.4.7 Spatial dynamics of mangrove vegetation

Loss and gain of mangrove vegetation along the coast line of Pará has been monitored by means of satellite images (Souza-Filho, 2001; Souza-Filho and Paradella, 2002; Cohen and Lara, 2003). Mangrove losses are associated with erosion or are the result of sand deposits asphyxiating mangrove roots (Souza-Filho, 2001; Souza-Filho and Paradella, 2002; Cohen and Lara, 2003). New mangroves can develop following the colonisation of emerging mud banks by *Spartina* grass or *Laguncularia racemosa* (Prost et al., 2001; Menezes et al., 2003b).

Analyses of Landsat images and pollen profiles from soil cores by Behling et al. (2002) document a long-term expansion of mangroves on Ajuruteua Peninsula towards higher elevation salt flats with herbaceous vegetation. This expansion may be due to rising sea levels (Lara and Cohen, 2002).

2.4.8 Anthropic uses of mangrove flora

Mangrove wood is utilized as fuel and as material for rural construction; poles are extracted for the construction of fish traps (Bastos, 1995; Almeida, 1996b; Rebelo-Mochel, 1997; Glaser and Grasso, 1998; Santana, 2001; Senna et al., 2002; Glaser et al., 2003). *Rhizophora* bark is used for tannin extraction. Glaser et al. (2003) identify two types of timber extraction: “basic needs” extraction and extraction for commercial purposes. “Basic needs” extractors utilize mangrove products for subsistence (domestic fuel, fish traps). Commercial extraction of wood and bark is an activity not talked about openly because it is illegal under Brazilian law. However, the commercial use of the mangrove trees contributes to the income of a considerable number of households (Glaser et al., 2003). *R. mangle* is the most

exploited species. Almeida (1996b) explains the apparent preference for *R. mangle* wood over that of the *Avicennia* species as reflecting the greater abundance of the former species, but considers wood of *Avicennia* as equally suitable or even better for construction. Large *Rhizophora* trees can be felled quite easily by cutting their stilt roots. Large *A. germinans* trees are often hollow and thus not suitable for certain uses. However, large trees of either species are rarely extracted because the transport of logs through the mangrove swamp is usually not viable (they do not float) and stems cannot always be sawn into transportable pieces *in situ* (pers. obs.).

Bark, leaves and young roots from *R. mangle*, *Conocarpus erectus* and the grass *Spartina alterniflora* are used in traditional popular medicine (Bastos, 1995; Almeida, 1996b). During its flowering period, *A. germinans* attracts honeybees kept by locals. "Mangrove honey" is an appreciated product in the region, but its commercial potential has not been assessed so far. To collect the honey of feral honey bees, locals occasionally cut down trees (Rebelo-Mochel, 1997).

2.4.9 Impacts of human activities and perspectives of mangrove recovery

The coastal zone is subjected to diverse anthropogenic pressures due to exploitation and human occupation (Szlafsztein, 2003). Mangrove areas are impacted by clay extraction, aquaculture, agriculture, salt extraction and industrial activities (Senna et al., 2002), and may also be affected by recreational activities (Szlafsztein, 2003). Near urban centers, pollution can affect the ecosystem; Rebelo-Mochel et al. (2001) describe oil spillages and waste dumping as responsible for mangrove destruction around the city of São Luis. On the other hand, mangroves are important for subsistence of the coastal population. For example, in coastal villages of Bragança district, 80% of the population depends on mangrove products for a variety of subsistence uses (Glaser, 2003). Tourinho (1998) reports the establishment and subsequent abandonment of rice paddy fields in freshwater-influenced mangroves near Acarajó in the Caeté estuary. Rice cultivation failed because farmers were unable to control

invasive weeds. Secondary succession of abandoned areas started with colonisation by salt marsh and swamp vegetation, then by *L. racemosa* and finally by *A. germinans*. However, regenerating areas are still distinctly different from the original *R. mangle* dominated forest, which is preserved in the surrounding areas. This case study shows that, even under benign environmental conditions, the recovery of deforested or degraded areas to the original ecosystem state is not straightforward (Berger et al. 2006).

Changes of the hydrographic regime caused by construction of a causeway through mangrove forests on Ajuruteua Peninsula have led to die-back of more than 2 km² of mangrove forest along a 25 km section of the PA 458 highway. The new road blocked several tidal channels, reducing the inundation frequency in some areas and leading to prolonged or permanent inundation in others (Souza-Filho, 2001; Carvalho, 2000; Krause et al. 2001). A natural resilience is observed in parts of the area, where *L. racemosa* trees are successfully colonising the bare mudflat. According to Cohen and Lara (2003), the degraded area decreased by 6.6% per year during 1986-1988 and 0.04% in 1991-1997.

2.5 Conclusion and outlook

In spite of the fact that mangroves seem to form a homogeneous system along the north coast of Pará and Maranhão, a closer look reveals their structural diversity in function of local variations in inundation frequency, salinity and species distribution. There is evidence that seasonal variation in environmental factors like rainfall regime, salinity and inundation frequency influence litter fall and tree phenology. The distribution of *Rhizophora* species indicates the occurrence of three units of mangroves: those localized in the Marajó bay (dominated by *R. racemosa*) and those localized on the northern coast of Pará and Maranhão state (dominated by *R. mangle*) and those localized in the Preguiças estuary (dominated by *R. harrisonii*). This distribution corresponds to variations in salinity, suggesting that the higher salinity in coastal areas, more exposed to the Atlantic, prevents the dispersion of *R. racemosa* and *R. harrisonii* into this region.

However, this statement is still speculative because the underlying mechanisms are still not understood due to the absence of research into this aspect of mangrove physiology. More studies of species distribution and physiological patterns should be encouraged, especially in the low salinity areas of Marajó bay and Maranhão coast.

The mangroves of the study area remain well preserved, probably due to the difficulty of access (Lara, 2003). Nevertheless, these forests are under pressure from the growing population, deforestation for a variety of purposes and increased demand for wood and other mangrove products (Senna et al., 2002; Szlafsztein, 2003).

Policy initiatives are required for the preservation and conservation of the mangrove forests in the region. To this end, the Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis (IBAMA) has been creating co-management reserves (*reservas extrativistas* – RESEX) in mangroves on the coast of Pará state (see Glaser and Oliveira, 2004). This kind of initiative focuses mainly on sustainable use of resources important for the human population and on preserving traditional forms of resource extraction. To complement this, the authors would emphasise the importance of current and future research. Continued investigation, focusing on topics such as species distribution, plant growth, adaptation to environmental factors and plant associations, is essential for the preservation of mangroves in the region.

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Chapter 2

2.6 Annex: Mangrove tree species distribution

Rhizophora manilge (Rm), *R. racemosa* (Rr), *R. harrisonii* (Rh)

Local	Rm	Rr	Rh	References
<i>Pará State</i>				
Afuá	●			Maciel & col. 1842 (MG 144453)
Ananindeua		●		Ferreira (1989)
Augusto Correa – Urumajó	●			Carreira & col. 1462 (MG 165749), Bastos et al. (2000); Bastos et al. (2002)
Barcarena – Rio Caripi, Vila São Vicente		●		Lins & col. 338 (MG 115416)
Benevides – Benfica Bragança – Península de Ajuruteua, Ilha de Canelas	●			Rosa & Renner (MG 0147650); Ferreira (1989) Almeida (1996b); Thüllen and Berger (2000); Krause et al. (2001); Amaral et al. (2001); Menezes et al. (2003); Matni, (2003); Seixas (2003); Abreu (2004)
Colares		●		Almeida (1996a)
Curuçá	●			Mello et al. (1995); Carvalho et al. (1995); Almeida (1996a)
Ilha das Onças, Ilha da Tatuoca – Belém	●	●		Prance et al (1975); Almeida & Lobato 376 (MG 135338)
Ilha de Algodoal; Praia do Crispim; Ilha de Maiandeuá – Marudá	●			Bastos & Lobato (1996), Carreira et al. (2002)
Ilha de Mosqueiro, Praia do Maraú, Praia do Paraíso		●		Prance et al. (1975)
Marajó – Breves, Salvaterra, Soure, São Sebastião da Boa Vista	●	●		Lisboa et al. (1993); Rosa & col. 5469 (MG 143964); Rosa & col. 5547 (MG 144042)
Marituba	●	●		Almeida (1996a)
Marapanim – Rio Marapanim, Rio Mojuim, Rio Cajutuba	●			Prost and Loubry (2000); Costa-Neto et al. (2000); Prost et al. (2001); Sales (2005)
Primavera	●			Almeida (1996a)
Quatipuru	●			Huber 1899 (MG 1766); Almeida et al. (2002)
Salinas – Rio Sampaio	●	●	●	Prance et al. (1975); Ferreira (1989)
Santa Bárbara		●		Santos et al. 2 (MG 172748)
São Caetano de Odivelas	●			Prance et al. (1975); Ferreira (1989); Sales (2000)
São João de Pirabas	●			Prost & Loubry (2000); Luz et al. (2000); Menezes et al. (2003)
Vigia	●	●		Ferreira (1989); pers. obs.
Viseu – Jabotitiua-Jatium	●			Santos et al. (2003) Menezes et al. (2003b)
<i>Maranhão State</i>				
Baía de São Marcos	●			Silveira and Mochel (2000)
Golfão Maranhense	●	●	●	Santos (1986)
Rio Mearim	●			Behling et al. 1997.
Rio Preguiças	●	●	●	Santos (1986)
São Luis	●	●		Prance et al. (1975); Damasio (1980a); Rebelo-Mochel (1997); Rebelo-Mochel et al. (2001);
Turiçu	●			Rebelo-Mochel (2000)

Avicennia germinans (Ag), *A. schaueriana* (As)

Local	Ag	As	Reference
<i>Pará State</i>			
Algodoal, Maiandeuá, Maracanã	●		Bastos & Lobato (1996); Carreira et al. (2002)
Ananindeua – Maguarizinho, Rio Seco, Curuçambá	●		Ferreira (1989)
Augusto Correa –	●		Carreira & col. 1449 (MG 165737); Bastos et al. (2002)

2.6 Annex: Mangrove tree species distribution

<i>Local</i>	<i>Ag As Reference</i>
Urumajó	
Barcarena	● Lins & col. 103 (MG 113223)
Belém – Ilha das Onças	● Huber 1903 (MG 3832)
Benevides – Igarapé Estaleiro	● Ferreira (1989)
Bragança – Península de Ajuruteua, Ilha de Canelas, Praia de Ajuruteua	● ● Almeida (1996a); Thüllen (1997); Amaral et al. (2001); Matni (2003); Seixas (2003); Brabo (2004); Abreu (2004); Santos (2005)
Curuçá	● ● Menezes (1994); Carvalho et al. (1995); Almeida (1996a); Mello et al. (1995)
Colares	● Almeida (1996a)
Estreito de Coqueiros	● Santana (MG 69921)
Igarapé do Japim	● Duke, 1895 (MG)
Marajó – Pacorral; Salvaterra	● Gress 1899, 1915 (MG); Lisboa et al. (1993);
Marapanim- Rio Marapanim, Rio Cajutuba	● Prost & Loubry (2000); Costa-Neto et al. (2000); Sales (2005)
Marituba, Mosqueiro	● Almeida (1996a); Ferreira (1989)
Marudá - Crispim	● Bastos & Lobato (1996)
Primavera	● Almeida (1996a)
Quatipuru – Boa Vista	● Rodrigues 5072 (MG 35584); Almeida et al. (2002)
Salinas – Rio Sampaio	● ● Ferreira (1989)
São Caetano de Odivelas – Rio Araciteua, Ilha Nova, Rio Mojuim	● ● Ferreira (1989); Luz et al. (2000); Prost & Loubry (2000); Prost et al. (2001)
São João de Pirabas	● ● Sales et al., 2004
Vigia	● Ferreira (1989); Mello et al., 1995
Viseu	● Santos et al. (2003); Menezes et al. (2003b)
<i>Maranhão State</i>	
Alcântara	● ● Rosa & Silva 2509 (MG 132535); pers. obs
Baía de São Marcos	● ● Silveira and Mochel (2000)
Parnauçu	● ● Rebelo-Mochel et al., (2001)
São Luis	● Fern & Rob 96 (MG 129408); Damasio (1980a); Rebelo-Mochel (1997); Rebelo-Mochel et al. (2001)

Laguncularia racemosa

<i>Local</i>	<i>Reference</i>
<i>Pará State</i>	
Ananindeua – Igarapé Curuçamba	Fereira (1989); Mello et al. (1995);
Bragança	Almeida (1996a); Tourinho (1998); Amaral et al. (2001); Menezes et al. (2003); Menezes & Compton (2003)
Curuçá	Menezes (1994); Mello et al. (1995)
Colares	Almeida (1996a)
Ilha de Algodoal	Bastos & Lobato (1996)
Maracanã – Algodoal	Carreira et al. (2002)
Marituba	Almeida (1996a)
Marapanim	Luz et al. (2000); Costa-Neto et al. (2000); Sales (2005)
Mosqueiro	Almeida (1996a)
Primavera	Almeida (1996a)
Salinas – Rio Sampaio	Fereira (1989); Mello et al. (1995)
São Caetano de Odivelas – Rio Araciteua	Fereira (1989); Mello et al. (1995); Cruz et al. (2000); Prost et al. (2001)
Viseu – Jabotitua-Jatium	Santos et al. (2003); Menezes et al. (2003b)
Vigia	Pers. Obs.
<i>Maranhão State</i>	
Ilha de São Luis	Damasio (1980a); Rebelo-Mochel (1997); Rebelo-Mochel (2000); Rebelo-Mochel et al. (2001)
Parnauçu	Rebelo-Mochel (2000)

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Chapter 3

Litter fall and phenology patterns in a mangrove forest along a gradient of inundation in equatorial Brazil



Litter fall and phenology patterns in a mangrove forest along a gradient of inundation in equatorial Brazil*

M. P. M. Menezes, U. Mehlig and B. S. Batista

Abstract Litter fall and tree phenology were measured in an Amazonian mangrove forest along an inundation gradient. The study site was divided into 3 zones, one drier and hyper saline area (Z1) and two more frequently inundated, saline zones (Z2 and Z3). The total litter fall amounted to about $9.1 \text{ t}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$. The smallest amount of litter was recorded from the most saline zone. Leaves accounted for the majority of the litter. The amount of *Rhizophora mangle* litter was higher than from the other species. Phenological patterns varied between the species. *Avicennia germinans* showed a well defined seasonality while *R. mangle* and *Laguncularia racemosa*, while presenting peak flowering and leaf fall periods, produced leaves and flowers throughout the year. Nevertheless, fruition of all species occurred during the rainy season. Few differences between phenological patterns in the three zones were observed.

Key words: *Rhizophora mangle*, *Avicennia germinans*, salinity gradient

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3.1 Introduction

The northern coast of Brazil contains nearly 85% of the country's tidal forests, including a continuous belt of mangroves covering >7000 km² along the coast of Pará and Maranhão States (Lacerda, 1999; Lacerda et al., 2001). Mangroves in this region occupy an environment characterised by a high precipitation regime (>2000 mm per year) and high tidal amplitudes. Although the diversity of mangrove species is low, important differences exist with respect to species distribution and forest structure (Santos, 1986; Almeida, 1996; Prost and Rabelo, 1996). These both vary in response to freshwater input as well as to inundation frequency and correlated factors like salinity (Menezes et al., 2003), which in turn vary according to tidal elevation and are influenced by seasonal climatic changes (Dittmar, 1999; Schwendenmann, 1998). The above mentioned environmental factors could be expected to affect forest productivity and be reflected by indicators of productivity such as litter production. However, few studies have considered litter production of equatorial Brazilian mangroves (Fernandes, 1997, Maraca Island/Amapá state; Mehlig, 2001; Carvalho, 2002; Reise, 2003, Ajuruteua Peninsula/Pará state); the majority of these do not analyse the relationship between litter fall and inundation regime. The aims of this study are: 1) to characterise temporal and spatial variation of mangrove litter fall and 2) to document phenological patterns along an inundation gradient in a mangrove stand on the north coast of Brazil.

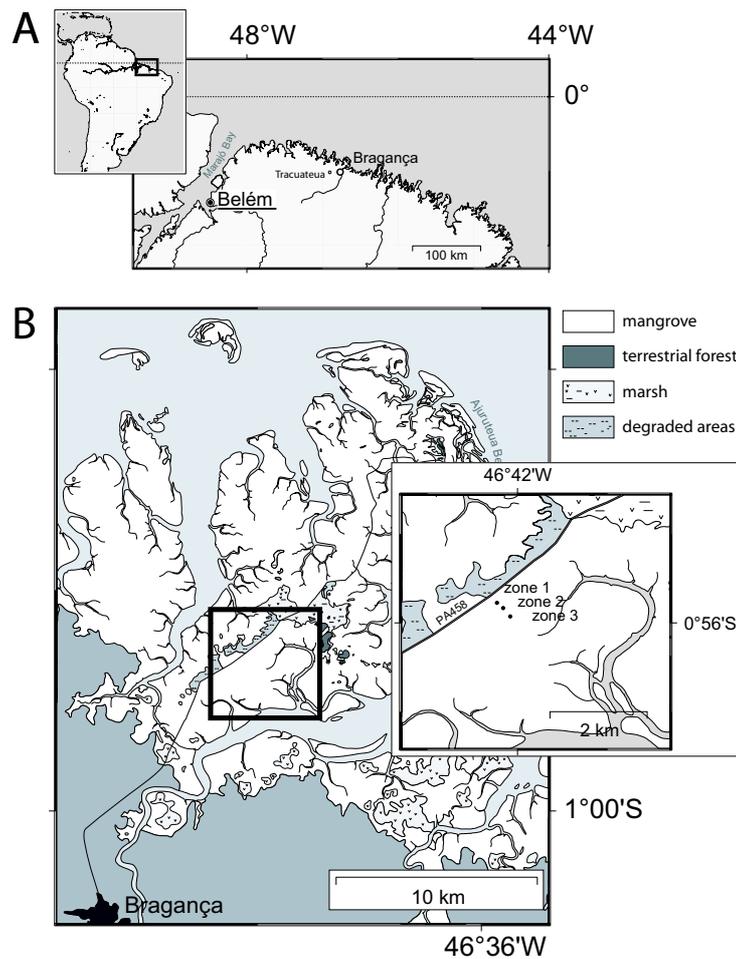


Figure 3.1: Localization of the study area. (A) Ajuruteua peninsula; inset: position of zones (B).

3.2 Material and Methods

3.2.1 Study area

The study area is situated on the Ajuruteua Peninsula, Bragança District, Pará, Brazil (Figure 3.1). The regional climate is humid and warm, with a well-defined dry season between July and November. The mean temperature is about 26°C and annual precipitation amounts to 2500 mm. Approximately 80% of the peninsula is covered by mangrove forests, which are composed of *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia germinans* (L.) Stearn (Avicenniaceae) and

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Laguncularia racemosa Gaertn. f. (Combretaceae) (Thüllen and Berger, 2000; Mehlig, 2001; Menezes et al., 2003).

The Ajuruteua Peninsula is cut in a northeast-southwest direction by a paved road, built along the most elevated, central part of the peninsula. In the study area, ground level decreases from the highest and least inundated point next to the road towards the River Caeté estuary. Following a transect perpendicular to the road, three zones with different inundation regimes were defined: Zone 1 (Z1) is nearest the road and inundated 60 d·y⁻¹. Zone 2 is inundated (Z2) 61–80 d·y⁻¹ and zone 3 (Z3) 81–100 d·y⁻¹. As a consequence of this inundation gradient, the zones present different soil pore water salinity conditions. Z1 is hyper saline, and both Z2 and Z3 are strongly saline. In addition, soil pore water salinity decreases during the wet season (Table 3.1). The structural parameters of the forest vary according to these environmental conditions (Table 3.2).

Table 3.1: Soil pore water salinity in 0.1 and 0.5 m depth of zones 1-3 in wet and dry season (Menezes et al., unpublished data).

zone	dry season		rainy season	
	0.1 m	0.5 m	0.1 m	0.5 m
Z1	78.7	46.3	50.2	61.4
Z2	72.6	43.6	56.2	52.0
Z3	51.0	40.4	36.4	31.0

Table 3.2: Forest structure in zones 1-3. dbh: mean stem diameter; height: mean height; density: number of individual trees ≥ 2.5 cm dbh per unit ground area; basal area: sum of stem cross-sectional area per unit ground area; relative dominance: species-wise percentage of basal area (Rh: *Rhizophora mangle*; Av: *Avicennia germinans*; Lg: *Laguncularia racemosa*). Menezes et al., unpublished data.

zone	dbh, cm	height, m	density, ind·ha ⁻¹	basal area, m ² ·ha ⁻¹	rel. dominance Lg, %	rel. dominance Rh, %	rel. dominance Av, %
Z1	6.8	7.3	2475.0	26.4	0.0	1.0	99.0
Z2	9.3	7.3	1600.0	23.8	1.8	17.9	80.4
Z3	19.7	10.2	517.0	37.0	12.9	61.3	25.8

3.2.2 Methodology

In each zone, 4 litter traps were installed in equidistant intervals along straight lines of 60 m length perpendicular to the salinity/inundation gradient. Litter traps consisted of 1 mm mesh bags mounted below square wooden frames with a 1 m² opening. All traps were suspended above the highest high water level. Litter was collected fortnightly between December 2001 and December 2002. The litter material from each trap was separated by species and sorted into components (leaves, flowers, fruits etc.). Twigs and bark, together with unidentifiable material and debris, were classified as “miscellaneous”. Material was dried to constant weight at 70°C.

3.2.3 Statistical analysis

Statistical analyses were performed with GNU R, version 2.1.1 (R Development Core Team, 2004). For litter fall data, linear mixed-effects models (Pinheiro and Bates, 2000) were used to characterise litter fall with respect to the fixed factors “zone” and “collection date” as well as their interaction; a random factor associated with litter traps was included to account for repeated measurements at the same spot. The quality of the fit was assessed using diagnostic plots of the residuals. Models were compared using likelihood-ratio tests and their Akaike Information Criterion (AIC; Pinheiro and Bates, 2000). Statistical tests were not done for litter components which were recorded sporadically or only occurred during restricted periods of the year.

3.3 Results

A. germinans was the only species producing considerable amounts of litter in all three zones. Both *R. mangle* and *L. racemosa* were rare in Z1; consequently, they contributed only negligible quantities of litter in this zone. Leaves were the most important litter component, followed by miscellaneous and reproductive material. The mean annual litter fall rates in Z1, Z2 and Z3 and their standard errors were $7.2 \pm 0.6 \text{ t} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$, $10.8 \pm 0.6 \text{ t} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ and $10.0 \pm 0.8 \text{ t} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$, respectively. Almost

equal amounts of litter were collected in Z2 and Z3; however with different relative contributions of the single species (Figure 3.2).

A. germinans leaf fall was low in the beginning of the year and then increased to a broad peak in the dry season. The maximum leaf fall in Z1 and Z2 was observed in August and in Z3 shortly afterwards in September (Figure 3.3). Almost no reproductive material of *A. germinans* appeared in litter collections between April and the onset of flowering in August/September. Shedding of immature fruits was most intense in November/December. Few fully developed fruits were found in litter samples (data not shown).

R. mangle showed no distinct peak leaf fall period common to all zones (Figure 3.4). Reproductive material in *R. mangle* litter consisted mainly of flowers and propagules, while flower buds and fruits made only small contributions. A distinct peak of flower litter was observed at the start of the transition from wet to dry season (end of May) synchronously in both Z2 and Z3. Propagules showed a number of distinct peaks during the wet season. Flower production continued at a decreased rate into the dry season in Z2 but virtually ceased in Z3.

Preliminary analysis of the leaf litter fall data indicated strong heteroscedasticity for both *A. germinans* and *R. mangle* material. Allowing heteroscedasticity among collection dates in the linear mixed-effects models (Pinheiro and Bates, 2000) led to significantly better fits for *A. germinans* and *R. mangle* leaves as well as for *R. mangle* stipules (likelihood-ratio test of homo- and heteroscedastic models: $p < 0.001$; lower AIC of heteroscedastic model). The interaction between collection date and zone was significant for both *A. germinans* leaves and for *R. mangle* leaves and stipules (Table 3.3), indicating that the timing of leaf and stipule fall was not fully synchronised between zones, in spite of the common seasonal trend described for *A. germinans* above. Differences between zones were significant for *A. germinans* leaves ($p = 0.01$; Table 3.3). *R. mangle* leaf fall did not differ significantly between zone 2 and 3 ($p = 0.18$; Table 3.3); however, stipule fall did ($p = 0.04$; Table 3.3).

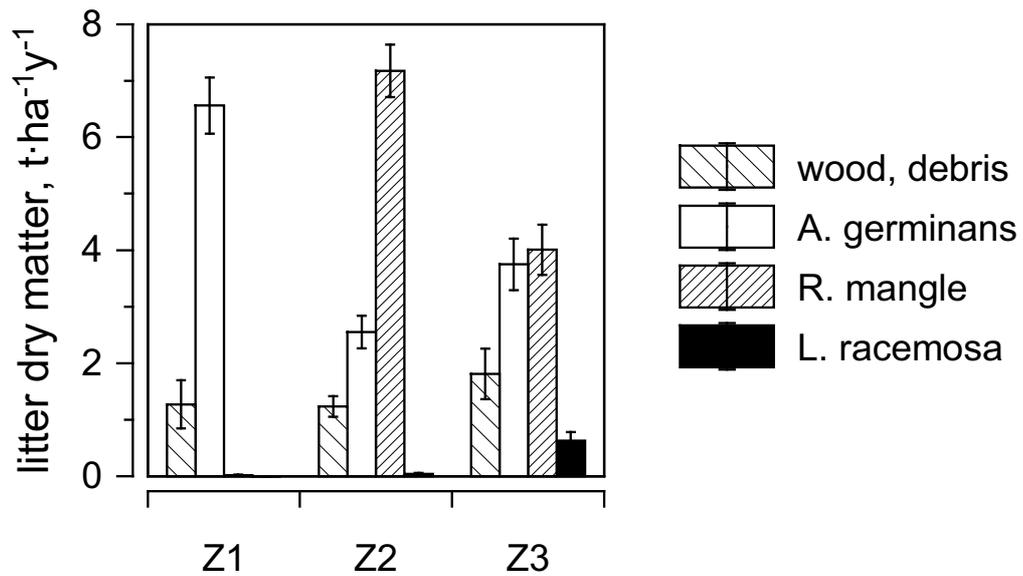


Figure 3.2: Average annual litter production of single species at zones 1-3. Error bars represent standard errors.

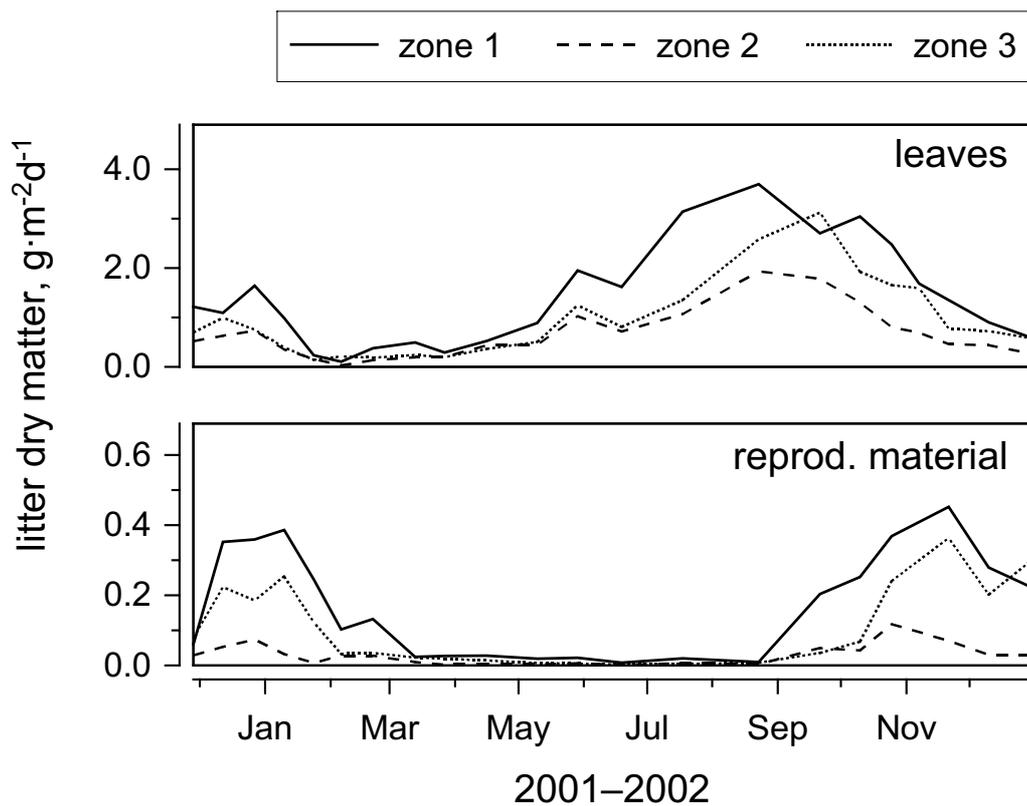


Figure 3.3: *A. germinans* litter fall (leaves and reproductive material). Reproductive material includes flowers and fruits.

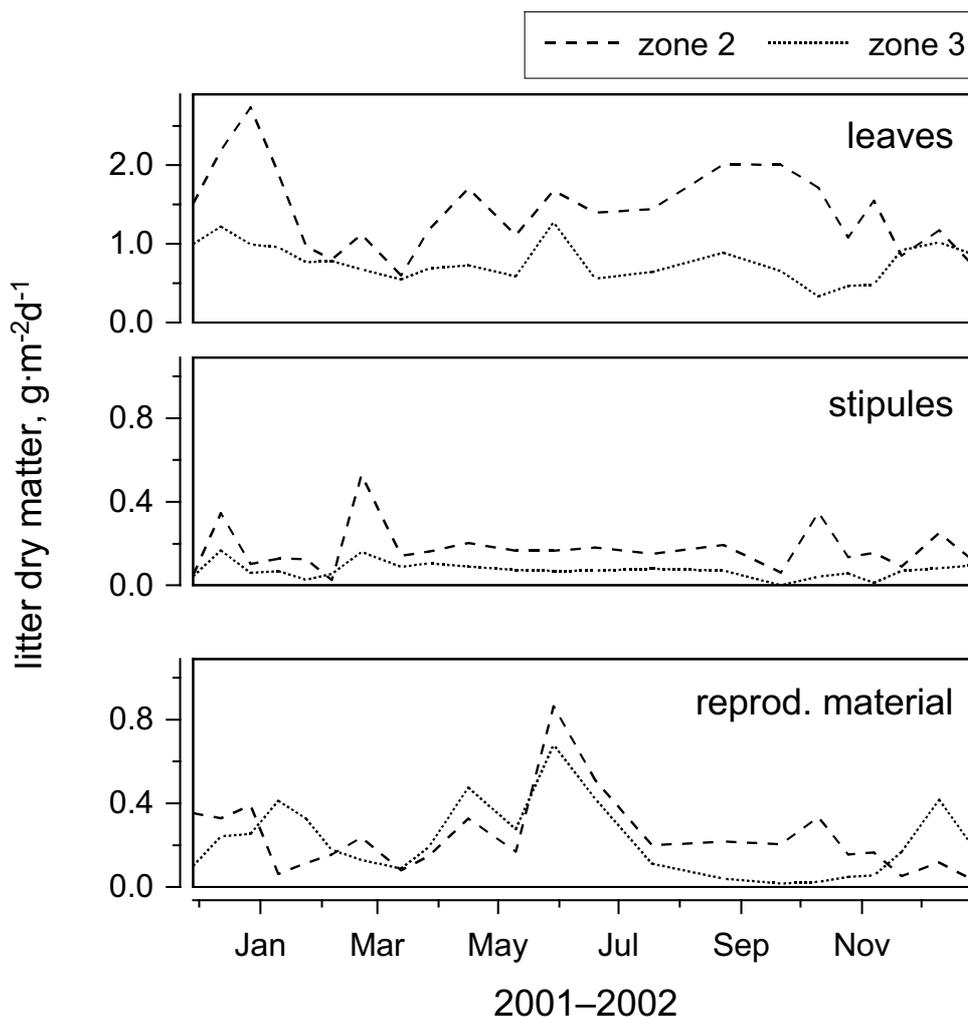


Figure 3.4: *R. mangle* litter fall (leaves, stipules and reproductive material). Reproductive material includes flowers, fruits and propagules.

Small amounts of *L. racemosa* leaf litter were found throughout the year in Z2 and Z3 (Figure 3.5). Due to its scarcity and sporadic occurrence, this litter component was not analysed statistically. However, the amount of *L. racemosa* leaf litter shed in Z3 was distinctly higher. *L. racemosa* leaf fall reached a maximum in the wet season, while little or no *L. racemosa* leaf fall was recorded during the transition from dry to wet season (December/January). Reproductive material of *L. racemosa* was collected mainly in Z3 (Figure 3.5). Flowers appeared in March, while fruits were found principally in May/June. The material shed in dry season was composed of *L. racemosa* inflorescence axes.

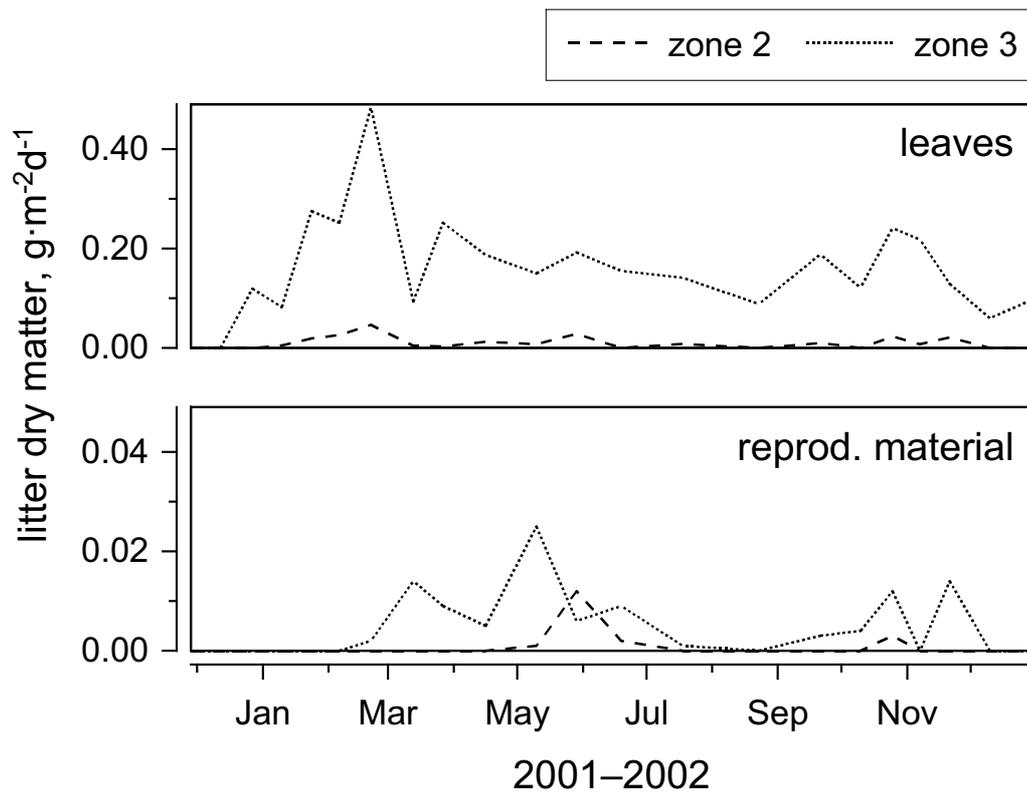


Figure 3.5: *L. racemosa* litter fall (leaves and reproductive material). Reproductive material includes flowers and fruits.

Table 3.3: Analysis of Variance tables for linear mixed-effects models. num DF: numerator degrees of freedom, den DF: denominator degrees of freedom (Pinheiro and Bates, 2000).

		num DF	den DF	F	p
<i>A. aerminans</i> , leaves	intercept	1	181	201.268	<0.001
	collection date	21	181	21.399	<0.001
	zone	2	9	14.797	0.001
	collection date:zone	42	181	2.380	<0.001
<i>R. manale</i> , leaves	intercept	1	119	24.125	<0.001
	collection date	21	119	9.399	<0.001
	zone	1	6	0.183	0.183
	collection date:zone	21	119	3.434	<0.001
<i>R. manale</i> , stipules	intercept	1	66	0.824	0.367
	collection date	11	66	12.408	<0.001
	zone	1	6	0.005	0.947
	collection date:zone	11	66	3.432	<0.001

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Table 3.4: Published records of litter fall, forest type and soil pore water salinity (PSU) along the coast of equatorial Brazil. Litter fall data in $t \cdot ha^{-1} \cdot y^{-1}$.

Local	Litter fall	Type	Salinity (PSU)	Reference
Maracá Island (Amapá)	14.1	Rh ⁺	-	Fernandes,1997
Maracá Island (Amapá)	7.3	Av ⁺	-	Fernandes,1997
Maracá Island (Amapá)	5.1	Lq ⁺	-	Fernandes,1997
Braçançã-FdM* (Pará)	12.8	M/Rh ¹⁺	26–52 ¹	Mehliq (2001)
Braçançã-Ac* (Pará)	13.1	M/Rh ¹⁺	10–17 ¹	Mehliq (2001)
Braçançã-FG* (Pará)	7.9	M ¹⁺	23–58 ¹	Carvalho (2002)
Braçançã-FG* (Pará)	15.4	M/Av ¹⁺	23–58 ¹	Reise (2003)
Braçançã-Dwarf* (Pará)	4.1	Av ⁺	100 ³	Reise (2003)
zone 1	7.2	Av ²⁺	46–79 ²	Present study
zone 2	10.8	M/Av	44–73	Present study
zone 3	10.0	M/Rh	31–51	Present study

*FdM Furo do Meio; Ac Acarajó; FG Furo Grande; Dwarf dwarf mangrove. ⁺ Rh *Rhizophora mangle* dominated forest; Av *Avicennia germinans* dominated forest; Lg= *Laguncularia racemosa* dominated forest; M mixed forest. ¹ Menezes et al, (2003). ² Menezes et al. (unpublished data). ³ Reise (1999).

3.4 Discussion

Our results reveal two important characteristics of litter production: 1) the total amount of litter produced differs between inundation/salinity zones; 2) litter fall varies throughout the year in amount and composition.

The average total annual litter production for all three zones was $9.1 t \cdot ha^{-1} \cdot y^{-1}$. This is within the range of American mangroves with similar floristic composition (Rico-Gray and Lot, 1983; Twilley et al., 1986; Day et al., 1987; Silva et al., 1998) but is lower than totals recorded from some other parts of the Amazon region (Table 3.4).

Several parameters are known to be connected with the amount of litter produced by mangrove forests, including rainfall, salinity, inundation frequency and forest structure (Lugo and Snedaker, 1974; Twilley et al., 1986; Saenger and Snedaker, 1993).

In the present study, the zone with the highest soil pore water salinity produced the lowest amount of litter. There was a significant, negative correlation between salinity and litter

production in all three zones on Ajuruteua Peninsula ($r = -0.89$; $R^2 = 0.74$). The same pattern was observed along a salinity gradient in Florida (Twilley et al., 1986). However, the authors of this study considered this apparent inverse relation to be due to species-specific differences in productivity between *R. mangle* and *A. germinans* stands. In our Z2, *R. mangle* litter production is distinctly higher than that of *A. germinans* in spite of the larger basal area of the latter. However, in Z3 (lowest salinity) *R. mangle* produces a smaller amount of litter compared to *A. germinans*, despite the dominance of the former species in this zone. One possible explanation for this apparent contradiction could be higher leaf turnover, caused by salt accumulation in *R. mangle* leaves, which do not possess salt glands and lack the salt exudation capability possessed by the other species. Evidence for increased leaf production at higher salinities is given by Day et al. (1996). The differences in production may, however, also be related to the different successional structure of the stands in Z2 and Z3. In Z2, *A. germinans* trees are numerous but present comparatively low stem diameters. The decreasing density and increasing average diameter in the transition from Z1 to Z3 might be related to a successional shift from an almost pure, *A. germinans* dominated forest to a mixed forest dominated by *R. mangle*. In Z2, the situation would then be that 1) the *A. germinans* population is undergoing a self-thinning process and 2) *R. mangle* is expanding vigorously. By contrast, the mature forest in Z3 would contain a few, large *A. germinans* specimens which, in spite of their low density (and possibly favoured by the lower salinity), would contribute significantly to total litter production in the zone. The hypothesis that shifts in species composition, structure and productivity, as observed along our inundation gradient, also have a successional component was recently supported by Berger et al. (2005).

Species-specific phenological patterns did not show large differences among the zones and confirm the findings of Mehlig (2001); Carvalho (2002); Reise (2003) and Mehlig (2006) from different mangrove stands on the Ajuruteua Peninsula. Nevertheless, at Maracá Island (Amapá State, about

500 km NE of our study area) propagules of *Rhizophora* ssp. are shed throughout the year, and no synchronisation of the phenophases was found among study sites (Fernandes, 1999).

A. germinans presented strongly seasonal leaf fall and also seasonal flowering and fruiting. In Z1, leaf fall began earlier than in Z2 and Z3. *R. mangle* leaf fall and leaf production took place throughout the year.

Peak flower fall took place at the end of the rainy season. However, flower production was not limited to that period. According to Menezes (1997), it might be advantageous for *R. mangle* to increase flower production in a comparatively dry period as flowers of this species are wind pollinated. Fruits and propagules of *R. mangle* were shed during the rainy season. Similarly, in *L. racemosa*, fruit fall was observed in the rainy season.

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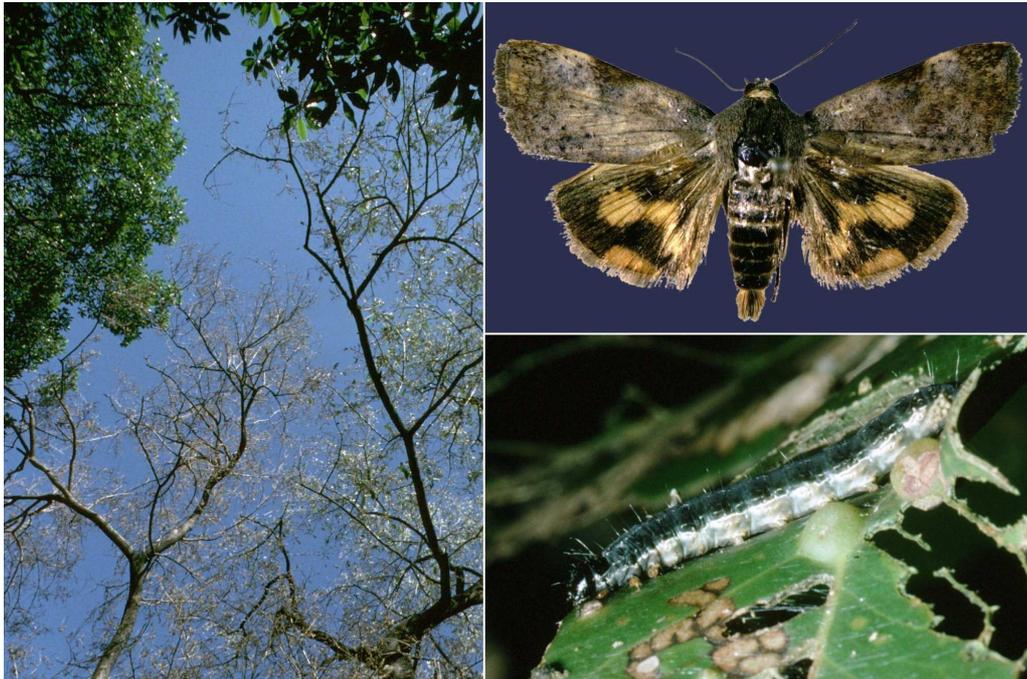
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Chapter 4

Mass defoliation of the mangrove tree *Avicennia germinans* by the moth *Hyblaea puera* (Lepidoptera: Hyblaeidae) in equatorial Brazil



**Mass defoliation of the mangrove tree
Avicennia germinans by the moth *Hyblaea
puera* (Lepidoptera: Hyblaeidae) in equatorial
Brazil***

U. Mehlig and M. P. M. Menezes

Key words: herbivory, mangrove, Brazil

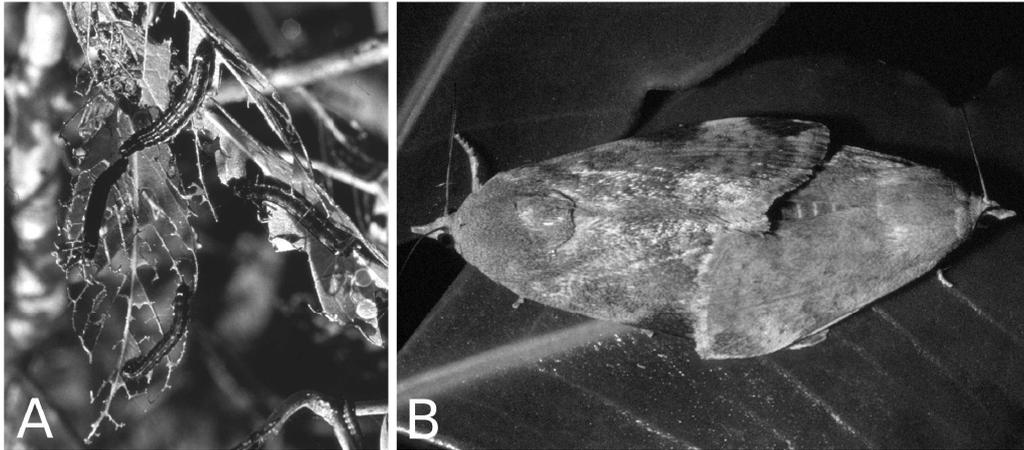


Figure 4.1: Larvae (A) and adult individuals (B) of *Hyblaea puera* on *Avicennia germinans*.

This note reports mass defoliation of *Avicennia germinans* (L.) Stearn (Avicenniaceae) trees by larvae of the moth *Hyblaea puera* (Lepidoptera: Hyblaeidae; Figure 4.1) in mangrove forests of Ajuruteua peninsula near Bragança, Pará state, Brazil (1°03'26"S , 46°45'45"W). Ajuruteua peninsula lies within a continuous mangrove belt of approximately 7000 km², extending from Marajó Bay south of the Amazon mouth to St. Marcos Bay, Maranhão (Lacerda et al., 2001). Mangrove forest on the peninsula covers an area of >170 km²; 5% of this forest are almost pure *A. germinans* stands. *A. germinans* is further a major constituent of the remaining, mixed forest (Menezes et al., 2003).

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To the best of our knowledge, there is no published account on insect herbivory in this region. However, Saur et al. (1999) recorded defoliation of *A. germinans* by *H. puera* and larvae of the butterfly *Junonia evarete* after a hurricane on Guadeloupe. Infestation of Asian *Avicennia* species by *H. puera* has further been observed in Thailand (Murphy, 1990) and India (Pirojshanagar; V. Kulkarni, personal communication). Factors controlling *H. puera* outbreaks are unknown, as are the consequences of infestation for the mangrove ecosystem.

On Ajuruteua peninsula, infestation of *A. germinans* by *H. puera* was observed during transition from the rainy to dry season between March and July 1998. The other occurring mangrove tree species, *Rhizophora mangle* L. and *Laguncularia racemosa* Gaertn. f., were not affected. Leaves of *A. germinans* were skeletonised; defoliated twigs died. The accumulation of frass on the forest floor beneath infested trees produced a distinct smell of ammonia. New shoots were produced directly on large branches and stems 4-5 weeks after defoliation. Further attacks on this fresh foliage were observed during subsequent waves of infestation. Monospecific *A. germinans* stands were completely defoliated, whereas in mixed forest several *A. germinans* trees remained unaffected, even in the immediate neighbourhood of infested trees. During a survey from the air in July 1998, defoliated mangrove trees were observed not only on Ajuruteua peninsula, but also along the coastline between Bragança and Marajó Bay.

In our study area, *A. germinans* leaf litter fall shows a distinct peak between May and October. The attack in 1998 led to comparatively early shedding of *A. germinans* leaf material and to a significant reduction of the total amount of leaves shed during this year compared to the years 1996 and 1997 (Mehlig, 2001).

According to locals, *H. puera* infestations occur every year. However, massive development with repeated waves of infestation was considered a rare event. The years with intense infestation are locally called "shrimp years" because fishermen found that *A. germinans* defoliation was coupled with higher shrimp catches. Unfortunately, due to lack of local fishery statistics, we cannot document any change of the shrimp

production in 1998. Nevertheless, based on the litter fall observations, we may assume that in this year large amounts of *A. germinans* leaf material bypassed the normal benthic food chain of leaf-eating land crabs (Ocypodidae: *Ucides cordatus* L.; Nordhaus, 2004) and detritus-feeding organisms like fiddler crabs (*Uca* spp.; Koch, 1999). In form of easily degradable material like frass, faeces and dead *H. puera* larvae, this part of the annual *A. germinans* leaf production was rapidly removed from the forest by tidal flushing, possibly leading to enhanced nutritional conditions for aquatic organisms like shrimp.

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Chapter 5

Annual growth rings and long-term growth patterns of mangrove trees from the Bragança peninsula, North Brazil



Annual growth rings and long-term growth patterns of mangrove trees from the Bragança peninsula, North Brazil*

Menezes, M. P. M., U. Berger and M. Worbes

Abstract Ring analysis was carried out on 39 *Rhizophora mangle* trees from two saline and one brackish forest sites on a peninsula in north Brazil. Even if all trees showed constant growth over their entire life span, the distinctiveness of growth rings was greater in trees from a saline area than in trees from a brackish forest. The mean radial increments form a pattern of three distinct groups. Although trees from each study site occur in each group, the trend is obvious that trees from a brackish and from a frequently inundated saline area dominate the group with the highest growth rate ($3.3 \text{ mm}\cdot\text{y}^{-1}$) whereas trees from a saline, seldom inundated area more often have low growth rates. Radiocarbon analysis showed that *R. mangle* forms annual rings in the region. The mean ages of the three forests were calculated based on mean stem diameter and site distribution in each growth group. They were correlated with forest density and basal area of the study sites. For the trees from a saline area belonging to the medium growth group (mean increment $2.5 \text{ mm}\cdot\text{y}^{-1}$), the cambial growth correlates significantly with the precipitation in the transition months between the dry and the rainy season. The slowest growing trees ($1.2 \text{ mm}\cdot\text{y}^{-1}$) showed close relations between ring width and the number of months with rainfall $<50 \text{ mm}$. Based on these results, we propose that the local abiotic factors influence the individual growth rates but their effect on the forest structure is modified by biotic factors like neighborhood competition.

Key Words: age determination, dendrochronology, mangrove forest dynamic, *Rhizophora mangle*

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5.1 Introduction

Mangrove trees of the same species can show a high plasticity in growth, e.g. height, stem diameter, and tree architecture, depending on specific environmental factors like nutrients, salinity or inundation frequency (Tomlinson, 1986; Suarez et al., 1998). A detailed analysis of mangrove forest dynamics is therefore complex and still not covered by a general theory (Fromard et al., 1998). Several researchers have tried to investigate the development of mangrove forests by means of simulation models (Chen and Twilley, 1998; Berger and Hildenbrandt, 2000). However, their success has been limited since key data of demographic processes are still unavailable, e. g. site- and species-specific growth rates, or medium age of individuals and stands. It has been generally assumed that datable growth rings do not exist in mangrove trees (Ash, 1983; Tomlinson, 1986; Gill, 1971). This assumption is partially linked to the general assumption that annual growth periodicity does not occur in the tropics (Lamprecht, 1959; Hallé et al., 1978, Uhl, 1980). Nevertheless, a number of investigations have shown that tropical trees exposed to distinct rainy/dry seasons or to extended periods of flooding form annual rings (Coster, 1927,1928; Mariaux, 1967; Worbes, 1985). In these cases, ring analysis enables the determination of tree age (Jacoby, 1989; Worbes, 1989; Worbes and Junk, 1989, Worbes and Junk, 1999) and provides the base for an appraisal of the age of forest stands. This is important for identifying and understanding successional sequences (Worbes et al., 1992) and, thus, a key factor for an analysis of forest dynamics.

The present work focuses on the analysis of differences in mangrove forest structure based on the growth dynamic of the trees. We present data on forest structure and tree rings of *Rhizophora mangle* from forests differing in the ranges of pore water salinity and inundation frequency. The relationship between these factors and seasonal wood increments was discussed. We also assessed the influence of precipitation on growth rates in the different sites. Ring counts, ¹⁴C analysis,

data on growth rates and data on forests' species composition were used to determine tree and stand age.

5.2 Methods

5.2.1 Study Area

Three different mangrove forests on the Bragança peninsula, north Brazil, were investigated (see Lara, this volume, and porewater salinity and inundation data in Table 1). One site at Acarajó (AC) is a brackish mangrove, and one of the last intact mangrove forests in this part of the peninsula. The low pore water salinity enables agricultural utilization, e. g. rice and manioc cultivation, in the higher parts of this area. For field reclamation, many of the mangroves were clear cut. In consequence, the former crab collection region has changed its character. The crab stocks are now too low to be exploited economically.

The second area at Furo do Chato (FC)¹ is a saline mangrove. The forest is crossed by numerous creeks and receives water from a tidal channel being significantly more influenced by seawater than AC. The forest is well preserved and used for subsistence and commercial crab collection. The third study site is also saline. It is situated at the main channel Furo Grande (FG) of the peninsula. The most important difference between the two saline sites is the higher inundation frequency in FG.

Lara (2001) provides an overview of the study area and climatic conditions, including a map showing site locations. In brief, the region is characterized by a defined dry season of 3–5 months (August/September to November/December), and a pronounced rainy season (January–July). Thus, the salinity gradient of the Caeté river and the contiguous creeks varies seasonally. Mainly this gradient and the differences in inundation frequency cause the differences in pore water salinity between the study sites (Cohen et al., 2000; Tab. 1).

¹ The tidal channel Furo do Chato is identical to the Furo do Meio mentioned in other chapters of this text.

5.2.2 Forest structure

Usual structure data were obtained in 10 m x 10 m plots (at least 10 plots in each site). The stem diameter was determined at the main trunk above the last intersection of the prop roots (or, if possible, in 1.37 m height) according to Schaeffer-Novelli and Cintrón (1986). All individuals greater than 2.5 cm stem diameter were measured, identified and recorded in the plots. Smaller trees were counted as saplings (Thuellen and Berger, 2000). To evaluate the forest type on the basis of species composition, the importance value was calculated according to Cintrón and Schaeffer-Novelli (1984). As an indicator for the spatial distribution of species within the forest, the frequency of occurrence was used, expressed as the percentage of investigated plots in which a given species is present.

5.2.3 Tree ring analysis

In general the existence of annual rings in tropical trees is not widely accepted despite numerous instances recorded since the beginning of the 20th century (Coster, 1928; overview in Worbes, 1996). In particular the existence of annual rings in mangrove tree species is discussed controversially (Duke et al., 1981, Ash, 1983). The discussion is complicated by the finding of Gill (1971) who stated that *A. germinans* forms up to six rings of uniform width in a branch during one year. Unfortunately this species shows a rare but well described type of wood formation with alternating phloem and xylem bands induced by a successive cambium growth (Carlquist, 1988). The very distinct rings merge frequently and could not be used for age determination. By contrast, there were distinct and complete rings in *R. mangle* which were considered suitable for age determination in this study. The rings are characterized by a varying vessel distribution. Small rows of vessels form a bright band around the entire stem disc at the boundaries. This type of growth zone structure are reminiscent of semi porous ring structure of *Tectona grandis* (Coster, 1928). The number of wood *R. mangle* discs and core samples collected from each site are shown in Table 2. The cores were taken with an increment corer of 5 mm in diameter and a length of 40 cm. All cores and discs were air-dried and polished to increase the

visualization of the growth zones. Rings were counted in all cores and discs using stereomicroscopy at the International Dendrochronological Laboratory, Institute of Forest Botany, University of Goettingen, Germany. Ring width was measured to the nearest 0.1 mm using a binocular microscope. This is only possible in the wood discs since the ring width in the cores can be compressed during the drilling process.

The annual periodicity of rings was assessed from chemical time markers left in wood structure from atmospheric fallout of atomic and nuclear testing during the latter part of the twentieth century. After 1950, the radiocarbon content in the air almost doubled within a few years. Wood formed at the time therefore contains a carbon-14 content which reflects the radiocarbon content of the atmosphere for respective years from 1950 to the present (Worbes and Junk, 1989). By comparing these markers with the date when the tree was felled, we were able to correlate the number of growth rings with the number of years between two dates and thus to determine doubtless the nature of the periodical growth zones as annual or not.

From one wood disc of AC and one disc from FC, 3 isolated growth rings were tentatively dated by ring counting and then removed using a fine saw. The radiocarbon content of sawn blocks were measured with an AMS (Accelerator Mass Spectrometer) at the Institute of Physics, University of Erlangen, Germany.

Ring-width curves were transformed in index curves with the program V-FORMAT (Riemer, pers. com.) and compared with precipitation data in a regression analysis. Raw data were divided by a trend value obtained from a Hegershoff curve to remove all long term trends in growth while preserving the climatically induced year-to-year variations. This provided normal distribution of values for a regression calculation. We used long-term (1973-1998) precipitation data available from the meteorological station Tracuateua (1°05'S, 47°10'W; INMET, 2000) about 23 km from Bragança, and calculated eight different time-series based on the sum of the precipitation in the following periods:

- whole year (TOTAL),
- rainy season (RAINY: January–July),
- dry season (DRY: September–November),
- transition months (TRANS: August + December),
- transition months + dry season (DRY–TRANS),
- months with more than 50 mm rainfall (THR–RAIN),
- months with less than 50 mm rainfall (THR–DRY), and, additionally,
- the number of months with less than 50 mm rainfall (D–MONTH).

The value of 50 mm is assumed as threshold for tree growth (Worbes 1995).

5.3 Results

Three species (*Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*) dominate the mangrove forests on the Bragança peninsula. However, whereas *L. racemosa* is relatively abundant within the AC area, it only occurs at the forest edges in FC and FG, (Thuellen and Berger, 2000). In the brackish mangrove AC, an understory is present which consists of mangrove associated species: *Crinum* spp., *Montrichardia arborescens* (Araceae) and the fern *Acrostichum aureum*. A further characteristic of that forest is the existence of two strata. The difference between the mean height of the three highest trees ($29.33 \pm .89$ m) and the highly varying mean height of the forest (17.8 ± 16.2 m) is a sign for this feature (Schaeffer-Novelli and Cintrón 1986). However, the area presents also a re-colonization stand of about 3–4 m height. It is a mono-specific *L. racemosa* spot located at the front edge of the forest. According to information provided by local people, the stand is about 10 years old.

Table 5.1 contains the forest structure data. Considering the importance value, *R. mangle* is the most important species in the brackish area AC and in the saline, less inundated area FC.

Table 5.1: Porewater salinity, inundation frequency, and structure data of the investigated forests. The code letters given in the first column mark Acarajó (AC, a brackish mangrove forest), Furo do Chato (FC, a saline, seldom inundated area), and Furo Grande (FG, a frequently inundated saline site).

Inundation Site	Inundation Frequency (days/year)	Salinity Range (PSU) Rainy .. Dry Season	Species	Stem Diameter (cm)	Height (m)	Basal Area (m ² /0.1ha)	Density (ind./0.1ha)	Frequency of Occurrence (%)	Importance Value
AC	140	~10 .. 17	Total	17.8 ± 16.2	11.8 ± 8.0	1.52	61	-	-
			<i>R. mangle</i>	19.6 ± 16.3	12.7 ± 8.0	1.27	42	100	195
			<i>A. germinans</i>	22.6 ± 18.1	16.2 ± 8.6	0.40	10	60	69
			<i>L. racemosa</i>	7.9 ± 5.4	5.4 ± 3.0	0.04	9	40	36
FC	76	26 .. 52	Total	32.5 ± 28.1	13.0 ± 5.0	3.04	37	-	-
			<i>R. mangle</i>	25.8 ± 11.3	12.4 ± 4.2	1.46	28	100	180
			<i>A. germinans</i>	49.0 ± 47.1	12.8 ± 8.1	1.51	8	42	120
FG	175	23 .. 58	Total	19.2 ± 9.3	11.8 ± 3.8	1.82	63	-	-
			<i>R. mangle</i>	16.9 ± 9.9	11.7 ± 4.1	0.47	21	85	113
			<i>A. germinans</i>	19.9 ± 7.6	11.7 ± 3.7	1.31	42	92	187

Trees of this species are distributed homogeneously in both areas (see frequency of occurrence), while the more frequently inundated, saline FG forest is dominated by *A. germinans*, and a slight species clustering can be observed. In terms of tree density and basal area, AC and FG are similar, whereas FC shows the lowest density and the highest basal area per hectare. Nevertheless, the mean height of the most frequent species *R. mangle* and *A. germinans* is highest in AC. A similar feature of FC and FG is the contribution of *A. germinans* to more than a half of the total basal area. These forests present an uniform strata. We did not register individuals having a stem diameter smaller than 2.5 cm. There was also no understorey of mangrove associated plants.

The distinctiveness of the growth rings of *Rhizophora mangle* varies between the study areas. Trees from AC show less distinct growth rings than those of FC (Figure 5.1a and b).

Rhythmic tree growth was induced by seasonal fluctuations in growth conditions. In the tropics, the alternation of the dry and the rainy seasons can induce such a growth rhythm (Worbes, 1995). The investigated region has seven rainy months with an averaged monthly precipitation of 328 mm, and three months with little or without rain (43 mm/month in mean, INMET, 2000). Assuming a monthly precipitation of 50 mm as minimum being necessary for a tree growth (Worbes 1995), it is interesting that no month with less than 50 mm precipitation was registered during the rainy seasons of the years 1973-1998.

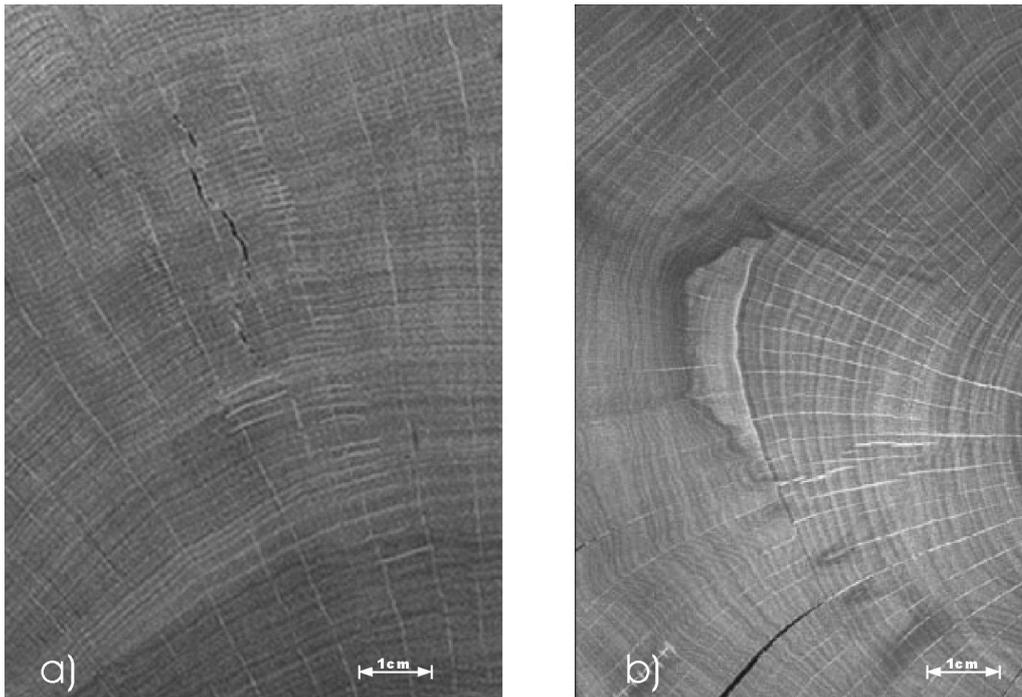


Figure 5.1: Stem discs from a) the brackish area Acarajó (AC) and b) from the saline, less frequently inundated forest Furo do Chato (FC)

On the other side, there was only one dry period (1986) interrupted by a month (November) with a higher precipitation (67.2 mm) (INMET, 2000). This pronounced seasonality leads to the hypothesis that the growth rings in this system are annual in nature. We could verify this hypothesis by radiocarbon analysis. The ^{14}C amount of the isolated tree rings in tree fc3 corresponds well with the standardized curve of the atmospheric ^{14}C concentration at the Southern Hemisphere (Hua et al., 1999; Figure 5.2). In tree ac1, the initial pre-dating determined by ring counting showed obviously one year too much. The ^{14}C results match the atmosphere curve after correcting our pre-dating and shifting the results for one year towards the present. This result shows the existence of annual rings in the investigated species at the given sites.

Table 5.2 lists the stem diameters and the corresponding ring numbers of all sampled trees. We registered the oldest tree (111 years) in AC followed by FC (97 years), and FG (45 years). The youngest trees were 36, 14, and 9 years old, respectively.

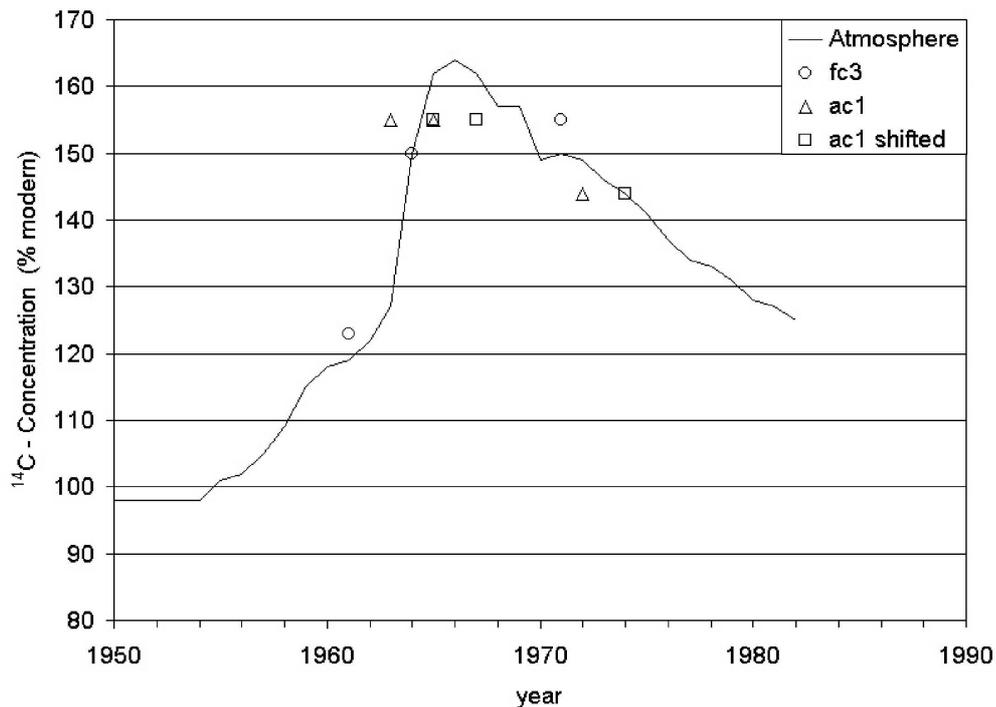


Figure 5.2: Results from the ^{14}C analysis (this work) and radiocarbon atmosphere concentration (after Hua et al., 1999).

It is interesting that FC trees having a similar mean stem diameter as trees from FG are older than them (compare, e. g. FC: fmd2, fmd2a, rhsfc11, rhsfc14, s1, s2, s3 with a mean stem diameter of 22.96 cm and a mean age of 58.57 years with FG: fgb2, rhs2g2, rhs2g4 with 22.27 cm and 38.00 years; or compare FC: rhsfc2, rhsfc3, rhsfc8, rhsfc10, rhsfc12, rhsfc15, rhsfc18 with 10.64 cm and 20.71 years with FG: rhs2g3, rhs2g7, rhsfg2, rhsfg4 with 11.08 cm and 15.05 years). The small sample size from AC does not allow such a direct comparison.

Figure 5.2 shows the cumulative radial increment (CRI) in the wood discs. A general characteristic is the constancy in the individual mean growth rate of all sampled trees. While these rates differ between individuals and areas, this seems to be attributable to the existence of three distinct groups. A linear regression line was calculated for each group between CRI and time for discs and the core data.

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Table 5.2 Data list of all sampled trees. The column 'Type' indicates whether core samples or wood discs were taken from the tree, and from which discs ^{14}C -analysis were carried out. Key: AC: Acarajó, FC: Furo do Chato, FG: Furo Grande. The last column shows tree's affiliation to one of the three growth rate groups identified. The group code '1' marks the highest mean radial increment ($3.3 \text{ mm}\cdot\text{y}^{-1}$, see Figure 5.3).

Sample Name	Type	Stem Diameter (cm)	No. of Rings	Site	Growth Group
103b	core	49.10	61	AC	1
201a		10.10	36		3
202b		23.20	52		2
rhiza1		43.00	63		1
ac2 (rhiza2)	disc	61.40	111		2
ac3 (rhiza3)		28.12	63		2
ac1 (104d)	(^{14}C)	38.07	61		1
fmc3	core	47.00	97	FC	2
fmd2		19.10	65		3
fmd2a		25.80	58		2
rhsfc10		10.90	22		2
rhsfc11		22.00	31		1
rhsfc12		11.10	14		1
rhsfc14		21.10	42		2
rhsfc15		12.80	29		2
rhsfc18		8.30	18		2
rhsfc2		13.00	29		2
rhsfc20		18.80	36		2
rhsfc3		9.25	17		1
rhsfc7		7.50	16		2
rhsfc8		9.10	16		1
fc4	disc	21.70	97		3
fc5		16.58	65		3
fc6		16.56	58		3
fc1 (sn1)		25.00	57		2
fc2 (sn2)		26.00	60		2
fc3 (31c)	(^{14}C)	27.49	60		2
fgb2	core	24.40	43	FG	1
rhs2g1		7.70	11		1
rhs2g2		20.70	45		2
rhs2g3		11.30	11		1
rhs2g4		21.70	26		1
rhs2g5		36.00	45		1
rhs2g7		11.10	16		1
rhsfg1		4.90	9		1
rhsfg2		11.10	18		1
rhsfg3		17.60	33		2
rhsfg4		10.80	17		1
rhsfg5		4.00	28		3

The slopes (B), their standard errors of B, and the regression coefficients R are also given in Figure 5.3. Although all forest sites are present in each 'growth rate group', trees of AC and FG are more frequent at group 1, i. e. the fastest growing group. On the other hand, trees from FC dominate group 2 and 3.

The frequency of the sites' occurrence in each growth rate group allows an approximation of the mean age of the respective forests, assuming that the *R. mangle* trees approximately represent the age distribution of the whole forest according to:

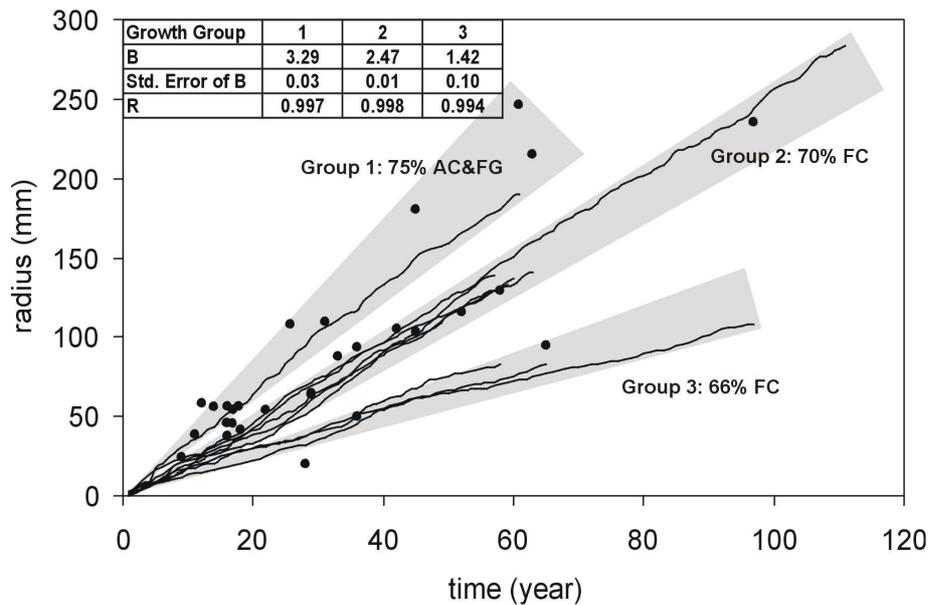


Figure 5.3: Cumulative radial increment obtained from the wood discs from the brackish area Acarajó (AC), from the frequently inundated, saline area Furo Grande (FG), and from the seldom inundated, saline area Furo do Chato (FC). The lines mark the radial increment in time taken from the wood discs. Circles show the final radii and the corresponding tree age taken from core samples. The gray sectors mark the three ranges which we have assigned to different growth groups. The mean radial increment B ($\text{mm}\cdot\text{y}^{-1}$), the error of B , and the regression coefficient R were calculated for each group based on the sample data belonging to them (see table given within this figure). The values are valid on a significance level $p < 0.0001$. Since trees from different forest sites can belong to the same growth group (see table 2), the statement 'Group 3: 66% FC' signifies, e. g., that 66% of all trees assigned to this group with the lowest growth rate are from Furo do Chato.

$$age = \overline{radius} \cdot \sum_{i=0}^n \frac{TAG_i}{B_i}$$

where \overline{radius} is the mean radius in the study site, TAG_i is the tree affiliation to the i^{th} growth group and B_i is the growth rate of the i^{th} growth group (given in Figure 5.3). Since the mean stem diameter of *R. mangle* in FG is 16.9 cm, and the tree affiliation of this site to the growth groups is 75%:17%:8% (last column Figure 5.3), the mean age of that forest can be calculated to 31 years. The approximated ages for AC and FC are 41 and 60 years, respectively.

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Table 5.3: Correlation coefficients ($p < 0.05$) between trend clarified annual growth increment of the trees analyzed by wood discs and between different precipitation time series (whole year (TOTAL), rainy season (RAINY), dry season (DRY), transition months (TRANS), transition months + dry season (DRY-TRANS), months with more than 50 mm rainfall (THR-RAIN), and the number of months with less than 50 mm rainfall (D-MONTH). The sample codes identify the 9 wood discs which were extracted from the brackish mangrove Acarajó (ac1-ac3) and from the saline, seldom inundated area Furo do Chato (fc1-fc6). The first row shows that trees from the brackish area as well as trees from the saline area belong to the growth group "2" (mean radial increment = $2.5 \text{ mm} \cdot \text{y}^{-1}$).

<i>Growth Group</i>	1			2			3			
	<i>Sample</i>	ac1	ac2	ac3	fc1	fc2	fc3	fc4	fc5	fc6
TOTAL	-	-	-	0.44	0.59	0.53	0.40	-	-	-
RAINY	-	-	-	0.43	0.58	0.49	-	-	-	-
DRY	-	-	0.40	-	-	0.45	-	-	-	-
TRANS	-	-	-	-	-	-	-	-	-	0.50
DRY-TRANS	-	-	0.42	-	-	-	-	-	-	0.46
THR-RAIN	-	-	-	-	0.58	0.50	0.40	-	-	-
D-MONTH	-	-	-	-	-0.41	-	-0.47	-0.40	-	-

According to our original hypothesis that the study sites differ significantly in their growth conditions depending on pore water salinity and inundation frequency, one could assume that the trees from AC, FC, and FG also differ in their growth response to the precipitation regime. There was, however, no correlation between the annual radial increment averaged for each forest and the eight calculated precipitation time series. Nevertheless, considering that the detected growth rate groups consist of samples from different areas, it was of interest whether the annual increment within these groups is correlated to the rainfall. Table 5.3 shows the low, but significant correlation coefficients (significance level $p < 0.05$) between the "disc" trees and the calculated precipitation time series (the series THR-DRY is not listed since there was no correlation between it and the stem increase of any tree considered). The trees fc1, fc2, and fc3 from the saline areas belonging to the second growth group show significant correlations, to the total rainfall and the rainfall within the rainy season only. Furthermore, the growth of fc2 and fc3 is correlated with rainfall in all these months with a total

precipitation >50 mm (THR-RAIN). It is interesting that these trees are additionally linked in their growth with a correlation coefficient of 0.80 ($p < 0.05$). However, further correlations can be found between the rain in the dry season and trees (ac3, fc2, and fc3) in this growing group. Only one 'Furo do Chato' tree (fc4, growth group 3) shows a correlation with total rainfall, and with rainfall during the 'truly' rainy months (TR-RAIN). Moreover, the trees of group 3 show significant correlations to the rainfall in the transition months, the rain in the transition months + dry season (fc6), and the number of dry months with less than 50 mm precipitation respectively (fc4, fc5).

5.4 Discussion

Radiocarbon datings of isolated growth zones match our age predictions in one case, and were shifted only one year in the second tree. This variation probably can be traced back to the fact that the felling date of this tree was not very well documented. The results show that the trees formed one ring every year between the mid sixties and the present. It can be reasonable assumed, that this is also true for the time prior to the bomb peak, allowing the number of visible rings as proxies for the age as it is accepted in temperate zones.

The wood formation in *Rhizophora mangle* is regular. The varying density of vessels between the center and the margins of the growth zones points to a varying water supply throughout the growth period. Wood structure in this species therefore record growth responses reflecting fluctuations in climate. The seasonality in precipitation is also reflected by the leaf fall behavior although there is no direct relation between the latter and the tree growth response to the precipitation regime. Leaf fall in *Rhizophora mangle* was lowest in the beginning of the rainy season after increased leaf shedding in the dry period, but elevated leaf fall rates were also observed towards the end of rainy season in FC and AC (Mehlig, 2001). Differences in the values of pore water salinity and inundation frequency seem to cause differences in wood formation and tree growth. The rings in the *R. mangle* from the FC saline site

are more distinct than those from the brackish one. The higher soil salinity results in a more negative water potential and a higher water stress for the plants during the dry period. This may result in a sharper decrease of the cambial activity at the end of the rainy period followed by distinct structures at the end of the growth zones.

The existence of mangrove associated plants is also controlled by the salinity. Plants being indicators for low salinity conditions occur in AC, but not in FC and FG. The differences in tree species composition can, however, not be explained by this factor nor by the variation of inundation frequency. Considering that *A. germinans* shows the best salt tolerance, the highest occurrence of that species would be expected in FC. However, the structure analysis shows the lowest frequency of this species at this site. This apparent contradiction can be clarified by considering that the ranking of salinity tolerance between *A. germinans*, *L. racemosa* and *R. mangle* becomes just significant for salinities >50 PSU. Furthermore, *R. mangle* has the lowest salinity tolerance of all these species, with about 70 PSU (Chen and Twilley, 1998). Thus pore water salinity should have no or at least a small influence on the tree species composition on the forest level. Nevertheless, the higher salinity stress combined with the lower inundation frequency should be reflected in more unfavorable growth conditions in FC. The low forest density and the high basal area seem to demonstrate the opposite. However, trees with similar stem diameters from FG are on average younger than trees from FC. Moreover, trees from the brackish site and those from the often inundated forest dominate the group with the highest annual stem increment whereas most of the trees belong to the group with the lowest growth rate occurs in the saline, seldom inundated area. This shows that a higher inundation frequency leads often to a higher growth rate.

There is very little information on maximum tree age in the tropics. However, there is some evidence that giant trees can reach a maximum age of around 500 years (Worbes and Junk, 1999). In comparison with that, the age of our oldest trees

seems to be low. A comparison of the forest ages approximated with the maximum age of *R. mangle* of about 250 years assumed by Chen and Twilley (1998) consolidates the hypothesis that the investigated forests are young. Furthermore, the age differences between sites can explain why the saline, less frequently inundated forest shows the lowest tree density and the highest basal area. Since the investigated forests typify different stages of development, the differences in density and basal area could be comparatively more affected by the self-thinning process than by abiotic factors. The constancy of growth rates supports this hypothesis. The results agree with data from natural terrestrial forests where trees tend to have no distinct 'age trend' as known from plantations (Worbes, 1999; Schweingruber, 1988). The annual growth rates varying between 1.2 and 3.3 mm diameter increment per year (this work) are similar to those from other natural forest stands in the tropics. Manokaran and Kochummen (1987) found in a Malaysian Dipterocarp forest a mean radial increment over all species of $2.6 \text{ mm}\cdot\text{y}^{-1}$. The mean for the published data in an Ecuadorian rain forest was $2.6 \text{ mm}\cdot\text{y}^{-1}$, too (Korning and Balslev, 1994). Nevertheless the high mean increment of $4.2 \text{ mm}\cdot\text{y}^{-1}$ measured for canopy species in a Costa Rican rain forests by Lieberman et al. (1985) are also interesting in comparison to our data since they demonstrate that there is a high variation potential of the growth rates even through the small scale variance of individuals' neighborhood conditions.

Statistical comparisons between ring-width patterns and rainfall data are possible (Worbes 1999) but seem to be complicated for mangrove species (Duke et al., 1981; Ash, 1983). Our results show that correlations can be detected if the growth of the trees is considered on the individual scales and not on the scale of a wide area. The influence of rainfall is superimposed by the impact of other factors like neighborhood competition or, particularly in mangrove forests, by inundation frequency or groundwater table. Hence, a correlation between the annual stem increment and precipitation can only be detected in locations where the freshwater input by rain is one

of the most important factors. Although our results show that precipitation is most important in less frequently inundated areas with higher pore water salinity, the spatial resolution of our information about these environmental factors is insufficient for a full explanation of the presence or absence of growth versus precipitation correlations and of the growth rate grouping. Finally, it should be noted that the importance of local competition does not explain why the growth rate grouping is so distinct. Differences in neighborhood competition should lead to a growth rate variation in general but should not lead to a significant separation. The search for the answers to these questions might be the key to future investigations of the dynamic of mangrove forests.

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Chapter 6

***Rhizophora mangle* growth in response to rainfall seasonality in Amazonian North Brazil**



Rhizophora mangle growth in response to rainfall seasonality in Amazonian North Brazil*

Menezes, M.P.M, U. Berger and M. Worbes

Abstract The growth rings in the wood of *Rhizophora mangle* trees were investigated by dendrochronological methods. Samples were taken along the coast of Pará state, north Brazil. All specimens showed distinct rings. Each ring is formed by a light and a dark layer. The light layer, formed at the end of the rainy season, is the result of a higher density of vessels. The dark layer, formed at the end of the dry season, shows lower vessel density. The increase or decrease of vessel density is probably caused by seasonal variation in soil pore water salinity due to rainfall. Linear growth curves revealed linear growth, implicating the absence of a trend-age. The highest (however, not significantly different) growth rates were found at the sector of the Pará coast with the highest tidal amplitudes, suggesting an influence of the tidal range on tree growth. Annual growth increment and corresponding data on precipitation were only partly correlated. The relationship between growth and rain fall was thus not easily interpretable. This may indicate that the presumed influence of rainfall is superimposed by the impact of other factors, e. g. general, site-specific salinity and fresh water input from rivers.

Key words: dendrochronology, tree rings, age determination, *Rhizophora mangle*, Amazonian mangroves.

* in preparation.

6.1 Introduction

Growth rings result from alternating cambium activity and dormancy periods induced by seasonal changes in environmental conditions (Fahn, 1967; Worbes, 1989). There is a general assumption that tropical trees lack annual growth rings because of the absence of seasonal climatic variation. Consequently it is widely assumed that determination of the age of tropical trees by ring counting is not possible (Hallé et al., 1978). Nevertheless, dendrochronological investigations have revealed that many tropical trees do have periodic radial growth as a result of seasonal variations in temperature, rainfall regime or day length (Coster, 1927; Mariaux, 1967; Worbes and Junk, 1999; Worbes, 1999) or in response to extended periods of flooding, as is the case in the Amazon basin region (Worbes, 1985). The formation of growth bands may indicate that the age of these species can be determined by counting the rings (Jacoby 1989; Worbes, 1989; Worbes and Junk, 1999).

In mangroves, the age of *Rhizophora mangle* seedlings has so far been determined by counting the number of leaf scar nodes and internodes (Duke and Pinzon, 1992), providing important informations for studies of ecology, dynamics and growth rate of mangrove seedlings (e. g., *Rhizophora mangle*: Thüllen and Berger, 2000; *Rhizophora apiculata*, *Sonneratia caseolaris* and *Avicennia alba*: Duarte et al., 1999; Padilla et al., 2004). However, attempts to investigate the occurrence of growth rings in mangrove trees have yielded controversial results. Mangrove trees of the species *Avicennia germinans* have anomalous secondary growth with rings consisting of xylem, phloem and conjunctive tissue (Gill, 1971; Carlquist, 1988). It has been shown that these rings cannot be used for dendrochronological analysis. The presence of growth rings was confirmed for other trees in mangrove forests (Duke et al., 1981; Davis, 1940, cited by Tomlinson, 1986); however their value for dendrochronological studies is discussed controversially (Ash, 1983; Tomlinson, 1986). Nevertheless, recent dendrochronological studies have revealed the annual

periodicity of growth rings in the mangrove *R. mangle* in North Brazil, based on ^{14}C analysis (Menezes et al., 2003) and in *Rhizophora mucronata* in Kenya, based on cambial markings (Verheyden et al., 2004). Menezes et al. (2003) related the annual periodicity of ring formation to variations of rainfall and pore water salinity. Based on the assumptions of the studies cited above, the present work focuses on four questions:

1. Do *R. mangle* trees show similar growth patterns as those described by Menezes et al. (2003) along the entire coast of Pará State?
2. How does the seasonal variation of precipitation influence the growth of *R. mangle* trees under different salinity conditions?
3. Are there significant differences in *R. mangle* growth rates along the coast of Pará?
4. How old are the *R. mangle* trees?

6.2 Material and Methods

6.2.1 Study areas

The region studied is located on the northeast coast of Pará State and forms part of a large belt of mangroves covering an area of about 8,894 km² (Lara, 2003; Figure 6.1). In this region, mangroves develop under semidiurnal, macro tidal conditions. The tidal amplitude varies between approximately 4 m and 7.5 m (DHN, 2004). The climate is tropical warm and humid. Annual precipitation varies between 2500 and 3500 mm (Fisch et al., 1998). Three areas on the coast were chosen for this study:

1. São João de Pirabas (0°46'17.8"S, 47°10'32.7"W; short: Pirabas). Mangrove forests around Pirabas are dominated by *R. mangle* (Menezes, unpubl. data). The mean annual precipitation is 2603 mm (based on data from 1990–2000; data source: INMET). Two study sites were selected in this area. At both sites, punctual measurements of soil pore water salinity were done (June 2002, September 2003). The first site, “Frente de Pirabas” (P1), is situated

directly opposite the city of São João de Pirabas (salinity: 12 PSU in June, 24 PSU in September). The second area is located next to the tidal channel Areião (P2; salinity: 26 PSU in June, 48 PSU in September).

2. Bragança Peninsula (1°03'33.7"S, 46°45'55.0"W; short: Bragança). The forests are dominated by *R. mangle* and *A. germinans* (Berger and Thüllen, 2000; Menezes et al., 2003; Matni et al., 2005). The mean annual precipitation is 2470 mm (based on data from 1973–2004; INMET, Tracuateua meteorological station, about 23 km from Bragança). On the peninsula, two sites in saline mangrove forest and one in brackish mangroves were chosen for study. At Furo do Meio (B1), the maximum and minimum values of pore water salinity are 17 and 36 PSU; at Furo Grande (B2), the salinity varies between 29 and 37 PSU. In the brackish mangrove Acarajó (B3), the maximum and minimum values of salinity are 2 and 22 PSU (Menezes et al., 2003).
3. Viseu (1°12'18.2"S, 46°08'18.8"W). The mangroves around Viseu are dominated by *R. mangle* (Santos et al., 2003). The mean annual precipitation is 1383 mm (based on data from 1966–1976; INMET). Two sites were selected in this area. At both sites, punctual measurements of soil pore water salinity were done. The first site is located on Jabotitiua Island (V1; salinity 8 PSU July; 28 PSU September). The second site is located next to the tidal channel Furo do Gato (V2, salinity: 20 PSU, July 2002; 34 PSU, September 2003).

Historical and recent precipitation data from the region show that all areas present well defined dry and rainy seasons (INMET/DHN). In Bragança and Pirabas, the dry season lasts from August to December, in Viseu it persists until January. Thus each of the study areas present at least five months with precipitation <100 mm (Figure 6.2).

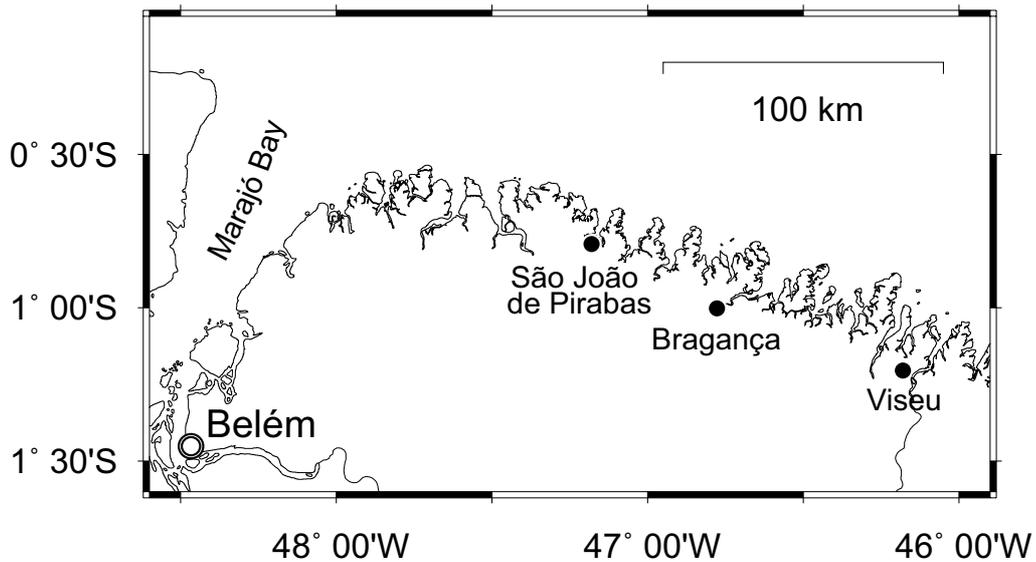


Figure 6.1: Localisation of the study sites.

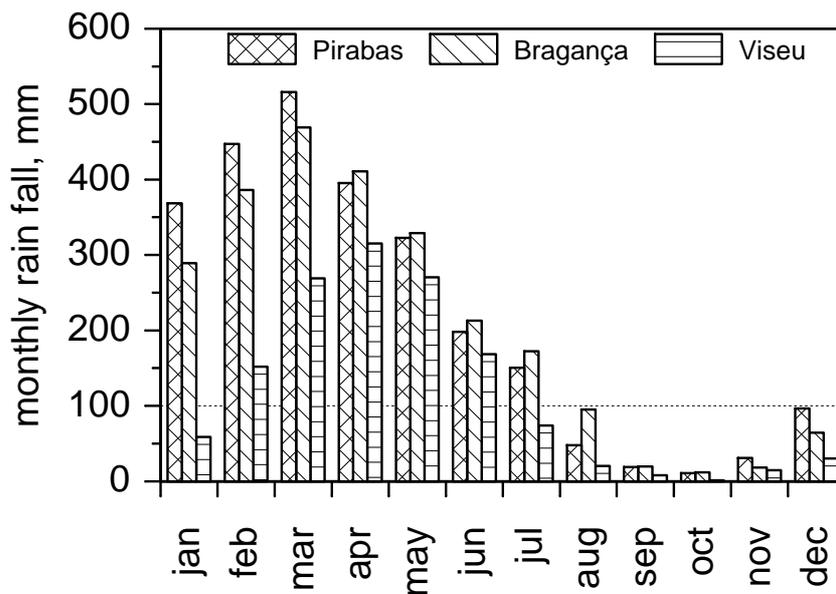


Figure 6.2: Rainfall regime on the coast of Pará State, North Brazil. Dry period: <100 mm monthly precipitation.

6.2.2 Tree ring analysis

27 wood discs (orthogonal stem cross-sections) of *R. mangle* trees were collected (Table 6.1). Most of the trees were felled in July 2003 (end of the rainy season) and August 2003 (transition to dry season). Samples from site B3 (Bragança) had been collected previously during the transition from dry to rainy season (December 2001).

Table 6.1: Growth rate, age and diameter of wood disc samples.

<i>Sample</i>	<i>Local</i>	<i>Growth rate (mm·y⁻¹)</i>	<i># of rings</i>	<i>Diameter (cm)</i>
352	V1	4.2	70	33.2
244		4.2	66	34
247		2.1	44	17
273		4.1	59	16.2
<i>mean</i>		3.9		
309	V2	4.7	40	18.5
363		5.1	67	41.6
<i>mean</i>		4.9		
825	P1	2.7	70	27.3
806		3.5	68	24
807		4.0	68	7.8
<i>mean</i>		3.4		
sn-1	P2	3.3	90	
492		4.2	52	21.3
571		3.1	48	23
992		3.6	70	28.6
sn1-6		2.9	17	7.5
sn2-6		3.0	20	8
<i>mean</i>		3.4		
4278	B1	3.0	34	17.5
4092		4.1	90	43.3
4244		4.6	50	21
4275		4.8	40	38.8
4264		3.1	26	8.3
<i>mean</i>		3.9		
4042	B2	3.1	100	38.2
4346		4.7	47	28
4331		4.9	52	25.5
4343		2.9	34	19.4
<i>mean</i>		3.9		
v21	B3	2.5	33	11.8
v20		2.9	53	19.4
v22		2.4	39	9.8
<i>mean</i>		2.6		

Discs were cut above the highest stilt root from a part of the stem without externally visible irregularities. All discs were air-dried and polished to increase the visibility of the growth zones. Rings were counted in all discs, and ring width was measured to the nearest 0.1 mm using a binocular microscope. Ring-width curves were transformed into index curves (Cook et al., 1992) using the program TSAP-Win, version 0.3 (Rinntech, 2003). Raw data were divided by a trend value obtained from a

Hugershoff curve to remove all long-term trends in growth while preserving the climatically induced year-to-year variations. The index curves were calculated for each site and for each tree.

Long-term precipitation data from the nearest meteorological station (INMET/DHN) at each study site was used to calculate eight different time-series (Menezes et al., 2003) based on the sum of precipitation during the following periods: Whole year (TOTAL), rainy season (RAINY: January–July); core dry season (DRY: September–November), transition months (TRANS: August + December), transition months + dry season (DRY-TRANS), months with >50 mm rainfall (THR-RAIN), months with <50 mm rainfall (THR-DRY).

Additionally, one more time series was constructed with the number of months per year with <50 mm rainfall (D-Month). The value of 50 mm is assumed as threshold for tree growth in terrestrial trees (Worbes, 1995). Each precipitation time series was compared with the joint index curves for each site, and separately with the individual index curve of each tree using a simple correlation analysis. Correlations were also calculated between index curves and the rainfall time series shifted by one year, thus analysing possible effects of the previous year's precipitation on growth increment. In the following text, "index curve" will also be referred to as "growth curve".

Growth rates were calculated dividing the wood disc radius by the number of its rings. The difference of growth rates between the sites was verified by means of a single-factor ANOVA.

6.2.3 Terminology

Stem cross sections of *R. mangle* show alternating layers of lighter and darker wood; the combination of a dark and a light layer constitutes a single annual growth ring (Menezes, 2003). We use the term "layer" exclusively to describe one of these visually different portions of a single growth ring, and reserve "ring" for the combination of the two characteristic layers.

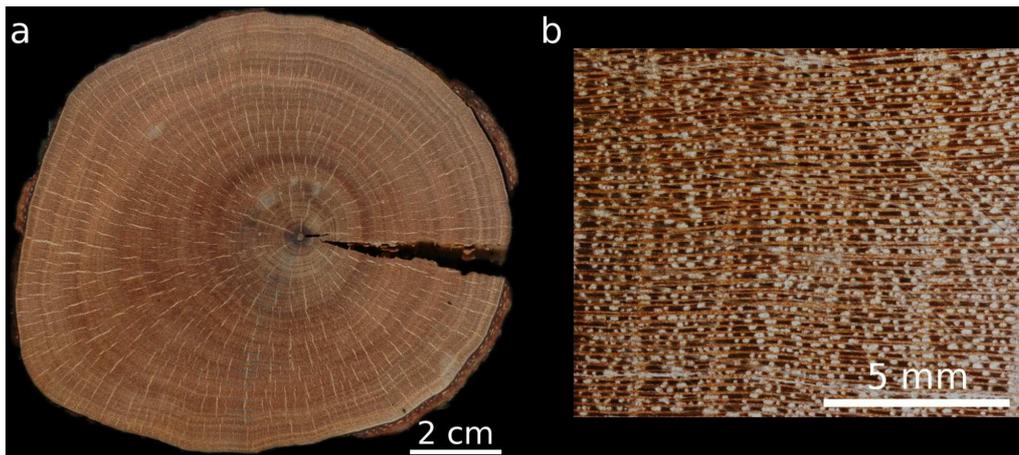


Figure 6.3: a Polished disc of *R. mangle* showing the dark heartwood and the occurrence of rings. b Microscopic view of rings revealing the occurrence of zones with higher and lower vessel density.

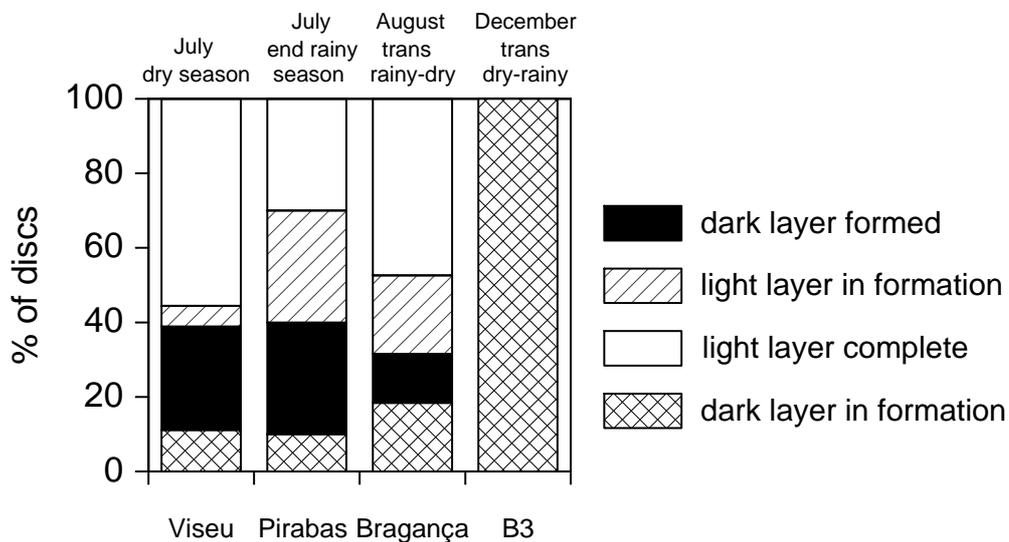


Figure 6.4: Stage of formation of the outermost layer of each disc.

6.3 Results

6.3.1 Ring characteristics

The heartwood has a distinct colouration of dark, reddish brown (Figure 6.3a). Sequences of dark and lighter-coloured layers can be distinguished macroscopically. Wood discs from the most saline areas present more distinct rings than those from the other areas (not shown).

Microscopic examination reveals that the lighter colour results from of a higher density of vessels; darker layers have low

vessel density. There are no distinct boundaries but a gradual change in vessel density between the layers (Figure 6.3b).

6.3.2 Layer formation during the year

Whether ring formation was complete at the time of felling can be roughly guessed from comparisons of the width of the outermost layer with the corresponding layers of previously formed, inner rings; comparatively narrow rings are probably still in formation (Verheyden et al., 2004). However, examination of the outermost, last-formed layer did not reveal a clear timing pattern of layer formation. Some of the outermost, “complete” layers from discs collected in July–August were dark, while others were light. Also, narrow, possibly incomplete dark and light layers were identified. Interestingly, all discs collected in the transition from dry to rainy season (December) in B3 were just starting the formation of the dark layers (Figure 6.4).

6.3.3 Measurements of ring width

Mean growth rates varied considerably between the areas, (2.6–4.9 mm; overall mean: 3.6 mm; Table 6.1). Nevertheless, there was no significant difference between growth rates of the different study sites. Cumulative growth curves reveal linear growth (Figure 6.5), indicating a continuous increase in diameter over the entire life span of the trees. The oldest tree in the samples was 100 years old (Table 6.1).

6.3.4 Response to rainfall regime

The relationship between growth curves and the calculated time series of rainfall regime was not clear. The site's growth curves correlated significantly with the time series only at B3 (time series: TOTAL, RAINY and THR-RAIN) and V2 (positive for the time series: THR-RAIN; negative for: THR-DRY and D-Month; Figure 6.6a). The correlation between growth rate and rainfall time series from the previous year showed a significant correlation at B3 (negative for TOTAL, RAINY and THR-RAIN) and V1 (negative for TOTAL, RAINY, THR-RAIN; positive for THR-DRY and D-Month; Figure 6.6b). No significant correlations were found at the other sites.

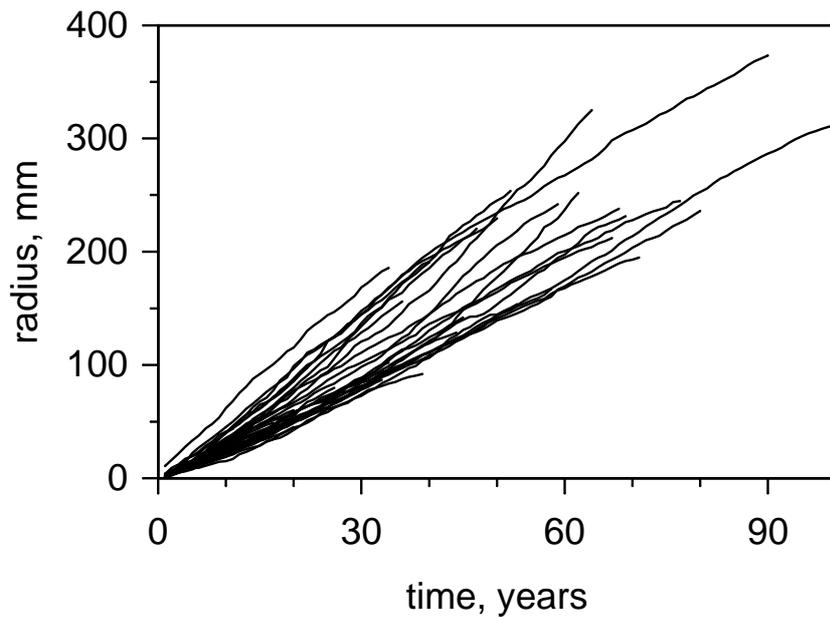


Figure 6.5: Cumulative radial increment obtained from wood discs.

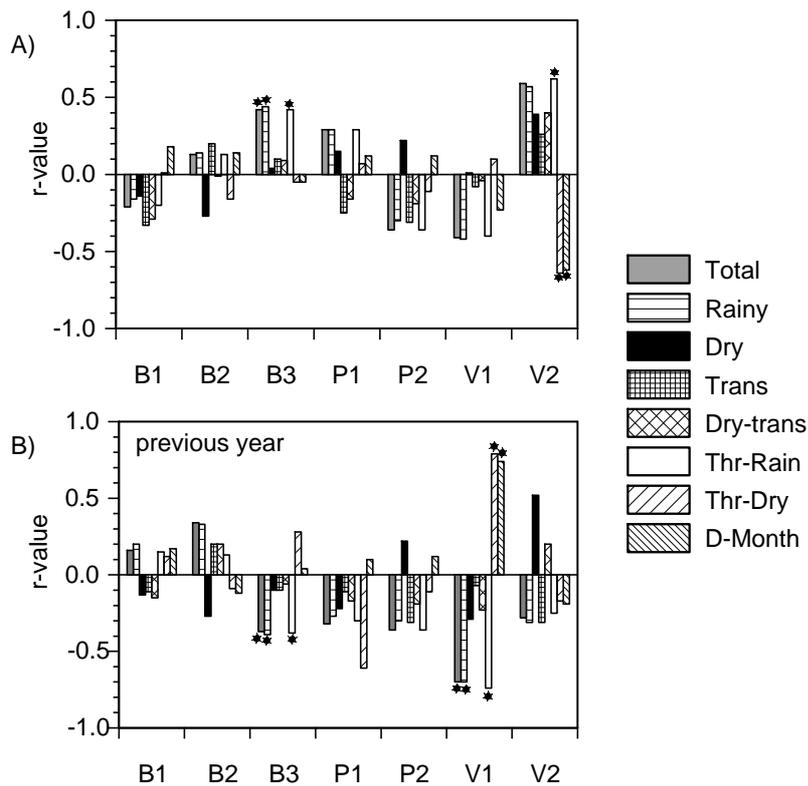


Figure 6.6: Correlation of *R. mangle* growth curves of each study sites (B1, B2, B3, P1, P 2, V1, V2) with rainfall regime time series TOTALI, DRY-TRANS, Thr-RAIN, Thr-DRY, D-Month (see Material and methods). Stars indicate significant correlations ($p > 0.05$).

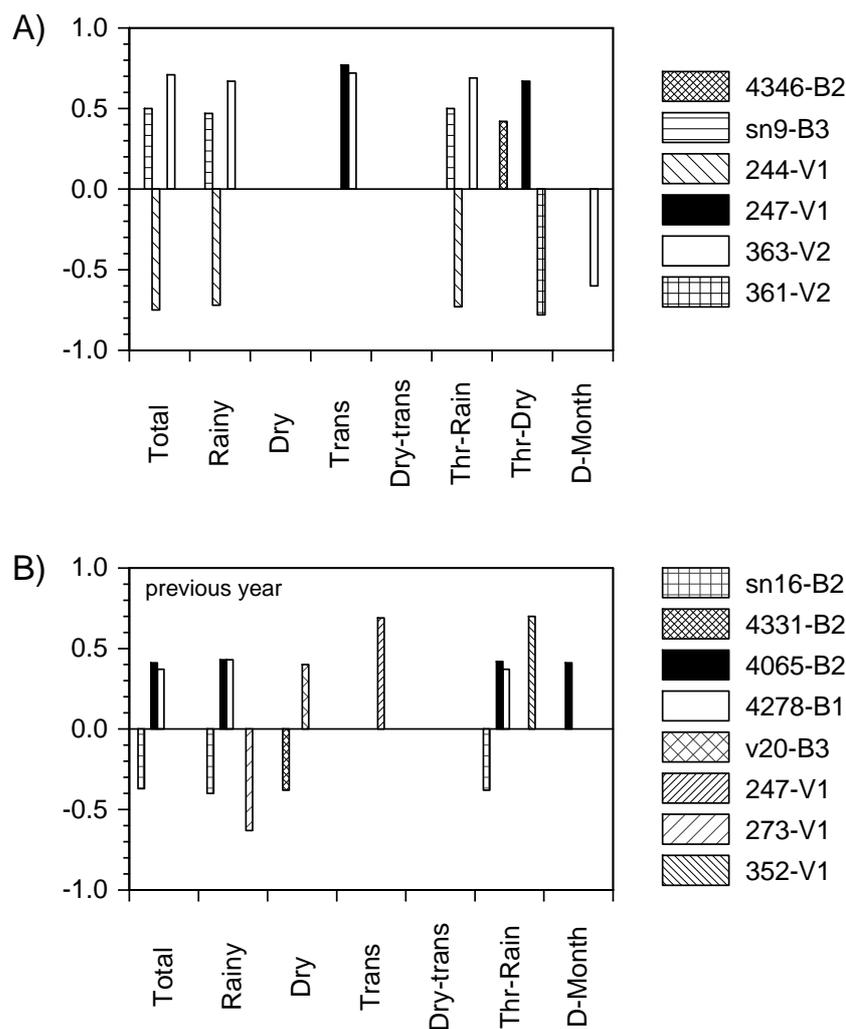


Figure 6.7: Correlation of *R. mangle* growth curves of individual trees with rainfall regime time series TOTAL, Dry-TRANS, Thr-RAIN, Thr-DRY, D-Month. All showed correlations are significant at $p > 0.05$.

The individual correlations for each tree between growth curve and rainfall regime showed different patterns among sites. Only one tree from the saline sites had a significant correlation (4346-B2). Several trees from brackish mangroves showed significant correlations, but in some cases positive and in other cases negative (Figure 6.7a). The correlation of the individual chronologies with rainfall from the previous year showed significant correlations for a number of time series, without indicating a consistent pattern (Figure 6.7a).

6.4 Discussion

6.4.1 Ring formation

The visual characteristics of rings (dark and light layers) of *R. mangle* are similar to those described by Verheyden et al. (2004) for *R. mucronata*. Nevertheless, in our study the periodicity of layer formation (dark and light) is not clear. The high percentage of discs with light and narrow light outermost layers in Viseu, Pirabas and Bragança shows that many trees start formation of layers with high vessel density during the rainy season and in the transition to the dry season; however, a few trees also presented outermost narrow dark layers. The fact that discs from trees felled at Bragança in December 2001 had exclusively narrow, dark outermost layers indicates that at this time trees were starting the formation of wood with low vessel density. The timing of layer formation has been interpreted as a response to seasonal variations in pore water salinity (Verheyden, 2004). At the end of the rainy season, salinity and water stress increase (Ball, 1988), and this in turn results in an increase in vessel density (light layer). In *R. mucronata*, the higher density of vessels is in fact the result of the production of larger numbers of smaller vessels (Verheyden et al, 2005), which prevents cavitation (Zimmermann, 1983).

6.4.2 Responses to rainfall

The annual periodicity of *R. mangle* growth rings was proven by Menezes et al. (2003) using ¹⁴C dating. Recently, preliminary measurements with permanent girth increment tapes support the finding that radial growth in *R. mangle* decreases during the dry season (U. Mehlig, pers. comm.). Menezes et al. (2003) related the annual periodicity to the influence of seasonal rainfall and changes in pore water salinity. Seasonal rainfall in the Amazonian mangroves also influences phenological patterns. Under a distinctly seasonal rain fall regime, *R. mangle* produces flowers and leaves continuously but, e. g., with flower production peaks at the end of the rainy season; mature propagules are released predominantly during the rainy season (Menezes, 1997;

Mehlig, 2006). On the other hand, in areas without defined dry and rainy seasons, *Rhizophora* species do not present distinct seasonal phenological patterns (Fernandes, 1999). It is, however, not known whether distinct growth rings exist in the respective region.

Correlations between annual rainfall and the corresponding growth increment did not reveal easily interpretable patterns. Drought induces embolism which may cause 10–15% loss of hydraulic capacity in *R. mangle* (Sperry et al., 1988). Salinity stress also affects the intrinsic photosynthetic capacity of leaves and results in reduced growth (Feller, 1995; Ball and Sobrado, 1998; Ball, 2002). Soil pore water salinity can be mitigated by freshwater discharge of rivers, which depends on rain fall in the river's catchment area, and by direct influence of rainfall in the mangrove, where water with low salinity may accumulate in the ground water table (Dittmar and Lara, 2001). We thus would expect positive correlations between growth and amount of rainfall, and negative correlations e. g. with the duration of the dry season. Effects of last year's precipitation could originate from better constitution of trees after a year of low salt stress, and possibly from higher freshwater supply from groundwater reserves built up over the past rainy season. The low correlations of growth and rainfall indicates, however, that the presumed influence of rainfall is superimposed by the impact of other factors like local inundation frequency or neighbourhood competition; correlations with climatic patterns are therefore difficult to detect (Ash, 1983; Menezes et al., 2003).

Further investigations into the physiological reactions of *R. mangle* to rainfall are needed to understand these phenomena.

6.4.3 *R. mangle* growth rates and tree age

The constant growth of trees revealed by the linear cumulative growth curve implicates absence of a trend-age. The same was found by Menezes et al (2003) and Verheyden (2004). In the present study, the mean growth rate of *R. mangle* varied between 2.6 and 4.9 mm·y⁻¹; the mean growth rate was

3.6 mm·y⁻¹. The highest (however, not significantly different) growth rates were found at Viseu, the sector of the Pará coast with the highest tidal amplitude (DHN, 2006). Viseu mangroves are associated with the estuary of the Gurupí, the largest river of the southeastern coast of Pará. It is conceivable that these factors are beneficial to tree growth.

The range of growth rates is much wider than previously described by Menezes et al (2003) for *R. mangle* trees from Bragança. The oldest tree in our sample was 100 years old. Menezes et al. (2003) analysed *R. mangle* rings of trees which had fallen down naturally in the forest and found the oldest tree to be 111 years old. A similar lifespan is inferred for *R. mucronata* in Mombasa (Kenya; 106 years; Verheyden et al., 2004). This lifespan is shorter than estimates for other tropical tree species (Worbes and Junk, 1999)

Conclusion

Answering the four main questions of this study, one can conclude that:

1. *R. mangle* trees present a similar linear pattern of growth in all studied areas.
2. The weak correlations between tree growth and rainfall regime are not clear. The apparently different response of tree growth in brackish and saline mangroves to rainfall and the production of vessels in response to pore water salinity changes indicate rather a direct influence of salinity. Higher growth rates in mangroves submitted to the macrotidal regime (Viseu) and those from the more frequently inundated sites in Bragança suggest that tidal regime is another important factor to increase tree growth. We conclude therefore that the influence of rainfall regime is superimposed on salinity variations and inundation frequency.
3. The linear growth of *R. mangle* is similar in all studied areas.
4. Counting of *R. mangle* rings suggests that trees do not attend much more than 100 years.

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Chapter 7

From age determination to the dynamics of *R. mangle* dominated mangrove forests: a case study of Ajuruteua Peninsula, Amazonia, North Brazil



From age determination to the dynamics of *R. mangle* dominated mangrove forests: a case study of Ajuruteua Peninsula, Amazonia, North Brazil*

Menezes, M.P.M. and U. Berger

Abstract This article presents a new approach of explaining mangrove forest dynamics by combining forest structure surveys, dendrochronology of *Rhizophora mangle* trees and analysis of neighbourhood competition. Sites were chosen on Ajuruteua Peninsula, North coast of Brazil. Regressions between height and stem diameter showed that height growth of trees stagnates surpassing a breast height diameters of approximately 30 cm, while stem diameter still increases after approaching maximum height. Based on diameter size classes and growth ring analysis, we identified mature forests (between 50 and 60 years old) as well as younger forests (about 20 to 30 years old). Anthropogenic influences on forest structure were detectable. At each site, a broad spectrum of individual growth rates was observed. Cumulative radial growth curves revealed the existence of three “growth groups” (“fast”, “medium”, “slow”) with growth rates of 3.60, 2.94 and 1.75 mm·y⁻¹, respectively. Fast and slow growing trees were found at the same sites, however, fast growing trees were rarely found or absent at sites with highest and lowest soil pore water salinities. Regression analysis demonstrated that inundation frequency as well as competition among trees had high influence on tree growth. We propose a model of mangrove forest evolution based on the age of stands and density of trees.

Key words: dendrochronology, long-term growth, KiWi model, neighbourhood competition, stand age, inundation frequency

* in preparation

7.1 Introduction

Although numerous studies exist which focus on selected aspects of mangrove forest ecology, general analyses of forest dynamics are rare due to limited information on growth, age, and mortality of mature trees. Restrictions imposed by logistic difficulties make these features hard to study. The majority of investigations are based on repeated inventory surveys providing data on stand level like tree density, basal area, leaf area index, and estimations of above ground biomass. Remote sensing studies of temporal changes in vegetation cover complete such analyses. In comparison, investigations on seedlings and saplings are frequent. They suggest that pore water salinity, nutrient and light availability, as well as soil redox potential and sulphide level affect strongly the performance of mangroves (e. g., Snedaker, 1982; McKee, 1993; McKee, 1995; Ellison and Farnsworth, 1993; Padilla et al., 2004). All these factors are directly or indirectly linked to the inundation regime and, therefore, to the geomorphological settings of a given site. The determination of age of seedlings from internodal counts is also well established (e. g., Duke and Pinzon, 1992). This method facilitates the study of recruitment dynamics (e. g., *Rhizophora mangle*, Berger and Thüllen, 2000; *Rhizophora apiculata*, *Avicennia alba* and *Sonneratia caseolaris*, Duarte et al., 1999; Padilla et al., 2004).

Jiménez and Lugo (1985) developed a conceptual succession model for neotropical mangrove forests. It describes four succession stages (colonisation, early stage, maturity, and senescence) based on tree density. Fromard et al. (1998) identify all four stages in mangrove stands of French Guyana using empirically obtained biomass data and forest age approximations based on sediment age and information about mud bank formation. Duke (2001) improves this approach by considering gap dynamics explicitly. This idea forms the basis of the available simulation models for mangrove forests, the FORMAN model (Chen and Twilley, 1998), and the KiWi model (Berger and Hildenbrandt, 2000). Both models are spatially explicit and individual-based but differ in their description of

tree competition and the spatial scale they are suitable for. They are able to analyse succession phenomena and forest dynamics in various environmental scenarios. However, the success of such models is still limited due to the scarce data for adult trees, as mentioned above. Few studies (Menezes et al., 2003; Verheyden et al., 2004) apply successfully dendrochronological methods and measure the annual growth rates and mean age of *Rhizophora* trees.

Menezes et al. (2003) reveal that growth rate variations of *R. mangle* trees can not only be explained by differences in abiotic conditions among study sites. Annual growth rates of trees vary also significantly within study sites and even among trees in immediate neighbourhood under similar abiotic conditions. The authors suggest that other local factors, particularly neighbourhood competition among trees, may explain such patterns.

This study focuses on the verification of this hypothesis. The following questions will be assessed: 1) Do abiotic factors, as inundation regime, explain differences in annual growth rates and age distribution of *R. mangle* trees? 2) Do resource competition among the individual trees as well as their local constellation have a significant effect on growth rates? 3) What are the consequences of growth rate variation on forest dynamics? The study finally suggests a modification of the conceptual succession model mentioned above.

7.2 Material and Methods

7.2.1 Study area

The study area investigated is part of a large mangrove belt extending from the northeast coast of Pará State to the Paraíba river estuary, Maranhão/Piauí, in northern Brazil (Lara, 2003). The study sites are located in the Caeté estuary and on the Ajuruteua Peninsula, which features >160 km² of mangrove forest (Krause et al., 2001). Several large tidal channels cut the peninsula and guarantee inundation of the mangrove area at least during spring tides. Tidal amplitudes range between 3 and 6 m (Cohen et al., 1999). The climate is wet and warm.

Precipitation varies throughout the year. A dry season and a rainy season are well defined. Besides mangroves, salt-marshes, salt-flats, and restinga (vegetation on sandy areas) occur (Krause et al., 2001). Four study sites were chosen which represent different settings of species composition, salinity, and inundation frequency:

1. Acarajó (AC) is a brackish mangrove forest, localised in the internal part of the Caeté River estuary (1°00'42"S, 46°45'30"W). Pore water salinity varied between 3 PSU during the rainy season and 22 PSU during the dry season. These conditions permitted the establishment of rice cultivation which required the clear cut of large mangrove plots (Tourinho, 1998; Berger et al. 2005). The study site itself is also man-used for harvesting fire wood and timber for house constructions.
1. Bosque de Avicennia (BAV) is localised in a relatively high and less inundated part of the central peninsula (00°55'65"S, 46°40'09"W). The distance to the nearest tidal channel is 1 km. The topography induced a pronounced gradient of inundation and pore water salinity. Pore water salinity varied between 28 and 76 PSU (Menezes et al., unpublished data).
2. Furo do Meio (FdM; also: Furo do Chato) is localised in the seaward part of the peninsula (0°52'28"S, 46°38'59"W). Numerous tidal creeks cross the forest and receive water directly from the tidal channel. Pore water salinity varied between 17 and 42 psu (Menezes et al., 2003).
3. Furo Grande (FG) is situated next to the Furo Grande channel (0°50'25"S, 46°38'20"W). Pore water salinity varies between 34 and 42 PSU (Menezes et al., 2003).

7.2.2 Inundation frequency

Topographic elevation was measured by means of PVC tubes with small bottles attached in regular intervals. Several of these devices were installed in the field before spring high tide (Figure 7.1; Cohen et al., 2001). When checked at subsequent low tide, water filled bottles marked the level of inundation at the respective spot.

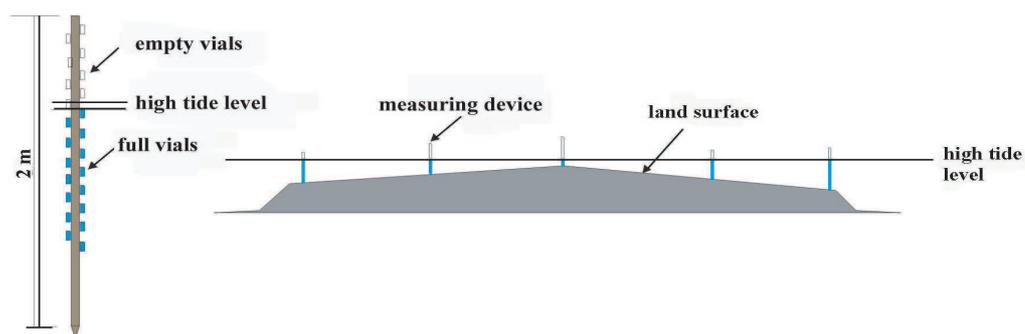


Figure 7.1: Devices utilised to measure the height of inundation during spring high tide. Modified from Cohen et al. (2000).

Relative inundation height was matched to maximum Furo do Meio water level measured at the same tide. Using a set of water level data for the complete annual cycle at Furo do Meio (Cohen and Lara, 2003), inundation frequency was predicted for each transect.

7.2.3 Forest structure

Forest structure was surveyed according to the point centred quarter method (PCQM, e. g., Cintrón and Schaeffer-Novelli, 1984) at AC, FdM and FG. At each site, a transect of 400 m was equidistantly subdivided, yielding 20 measurement points. At all points, the distance to the nearest tree with a stem diameter >2.5 cm was recorded in each of four quadrants. From the measured distances, a density estimate is derived (Cintrón and Schaeffer-Novelli, 1984). Further, tree species, stem diameter and height were registered. At BAv, forest structure was assessed in eleven plots of 10x10 m size positioned along a 900 m transect.

The relationship between tree stem diameter and tree height were analysed by means of linear and non-linear regression. Importance value, basal area and stem density were calculated for the whole forest and for each species.

For the analysis of neighbourhood effects on tree growth, *R. mangle* trees were chosen as references according to the following principles: the trees located closest to each measurement point in the PCQM transects were selected. In the plot transect, one *R. mangle* tree was randomly chosen from each plot. Each tree whose crown contacted the crown of

the reference tree was considered as a neighbour; the distances of all neighbours to the reference tree were measured.

7.2.4 Assessment of competition

The competition among the trees was evaluated using the so called Field-of-Neighbourhood (FON) as a proxy. The FON was introduced for the description of individual trees in the mangrove forest model KiWi (Berger and Hildenbrandt, 2000). The FON is defined as a size dependent circular scalar field around the stem position. It has its maximum at the stem and decreases exponentially to the boundary. It describes phenomenologically the competition strength which a tree exerts in its neighbourhood. Trees with overlapping FONs are neighbours. The FON intensity a tree “receives” from its neighbours within the overlapping area was taken as the proxy of competition.

7.2.5 Dendrochronology

At each study site, six trees selected from the group of reference trees were cut and stem cross-sections were taken above the highest stilt root. The 24 wood discs were air-dried and polished to increase the visibility of the growth zones. Some discs (particularly from Acarajó) were damaged during drying or polishing and could not be used for all parts of the dendrochronological analysis. We declined to use wood cores because compression during the drilling process can bias growth rate estimation. Rings were counted and ring width was measured to the nearest 0.1 mm using a binocular microscope. The rings were assumed to be annual, based on previous studies of ^{14}C contents of samples from Ajuruteua Peninsula (Menezes et al., 2003). From ring width/annual radial growth and the number of rings/tree age, growth rates could be calculated. The relationship of stem diameter (dbh) and age were analysed by linear regression; based on this regression, the age of living trees from the forest structure survey was estimated.

Importance of both inundation frequency and competition for tree growth were tested using a Generalized Linear Model (GLM).

To determine the mean age of *R. mangle* stands was calculated according to Menezes et al. (2003).

To estimate the age of *Laguncularia racemosa* and *Avicennia germinans* from stem diameters recorded in the field, we assumed continuous growth and used the growth rates provided by Chen and Twilley (1998).

7.3 Results

7.3.1 Forest structure

The mangrove tree species *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* occurred at all study sites (Table 7.1). *L. racemosa* was the least frequent species and occurred mainly near tidal creeks and forest gaps. *R. mangle* and/or *A. germinans* formed the forest upper strata. At Bosque de Avicennia (BAv), *L. racemosa* also occurred in the highest stratum (Figure 7.2). At the same site, *A. germinans* dominated the drier and more saline zones. At all other sites, *R. mangle* was the dominating tree species.

The diameter at breast height (dbh) class distribution varied between the sites. At Furo Grande (FG), the distributions are bell-shaped showing a dominance of *R. mangle* trees belonging to the stem diameter size classes 7.5–27.5 cm (Figure 7.3). Acarajó (AC) presented a broader distribution which tended to be uniform (Figure 7.3). At Furo do Meio (FdM), the dbh distribution was also bell-shaped but showed a broader maximum than at FG. Here, trees of *R. mangle*, *A. germinans*, and *L. racemosa* occurred in three dominant size classes which ranged from 7.5 to 37.5 cm. BAv presented an inverse-J pattern distribution. Most trees were *A. germinans* and belonged to the smallest diameter size class (Figure 7.3).

Exponential regression lines described the relation between stem diameter and height of *R. mangle* trees and documented a size-limitation of height growth well known for woody plants (Figure 7.4).

Table 7.1: Forest structure data. IV: importance value. Study sites: AC Acarajó; FdM Furo do Meio; FG Furo Grande; BAv Bosque de Avicennia. Height and diameter: mean±standard deviation.

Site/species	Mean diameter, cm	Mean height, m	Density, stems·ha ⁻¹	Basal Area, m ² ·ha ⁻¹	IV
AC, total	30.8±21	13.4±6	101.6	107.0	-
<i>L. racemosa</i>	2.3±7	4.2±0.4	7.6	0.3	8
<i>A. germinans</i>	27.5±26	11.9±6	15.1	16.0	30
<i>R. mangle</i>	33.8±21	14.7±5	78.3	91.0	163
FdM, total	26.4±18	11.5±4	146.0	111.0	-
<i>L. racemosa</i>	13.6±8	8.4±3	18.0	3.0	16
<i>A. germinans</i>	43.2±22	13.8±3	34.7	64.0	82
<i>R. mangle</i>	21.8±11	11.1±4	93.1	44.0	104
FG, total	23.9±14	13.6±4	79.4	47.0	-
<i>L. racemosa</i>	14.5±9	10±4	4.0	1.0	7
<i>A. germinans</i>	33.4±16	14.7±4	7.9	8.0	28
<i>R. mangle</i>	23.3±13	13.7±4	67.5	38.0	166
Bav, total	9.7±8	7.9±3	1417.7	17.4	-
<i>L. racemosa</i>	7.0±1	5.6±1	120.0	0.5	6
<i>A. germinans</i>	8.9±8	7.5±3	1293.3	14.8	220
<i>R. mangle</i>	14.3±5	9.7±3	800.0	14.3	120

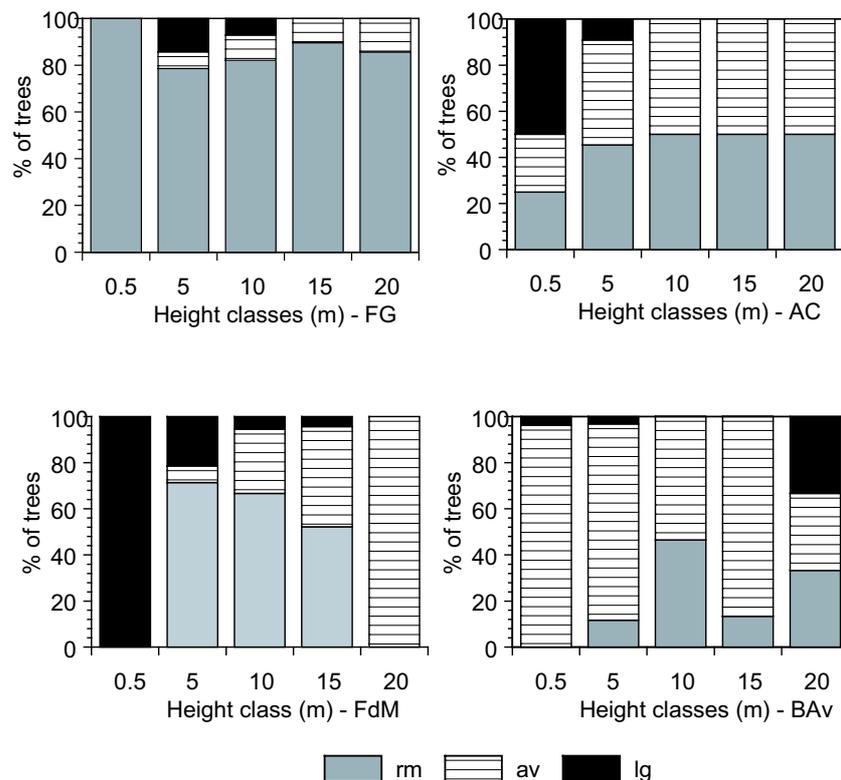


Figure 7.2: Height class distribution of trees at the studied sites. Ticks of X axis represent the lower boundary of each size class. rm: *R. mangle*; ag: *A. germinans*; lg: *L. racemosa*

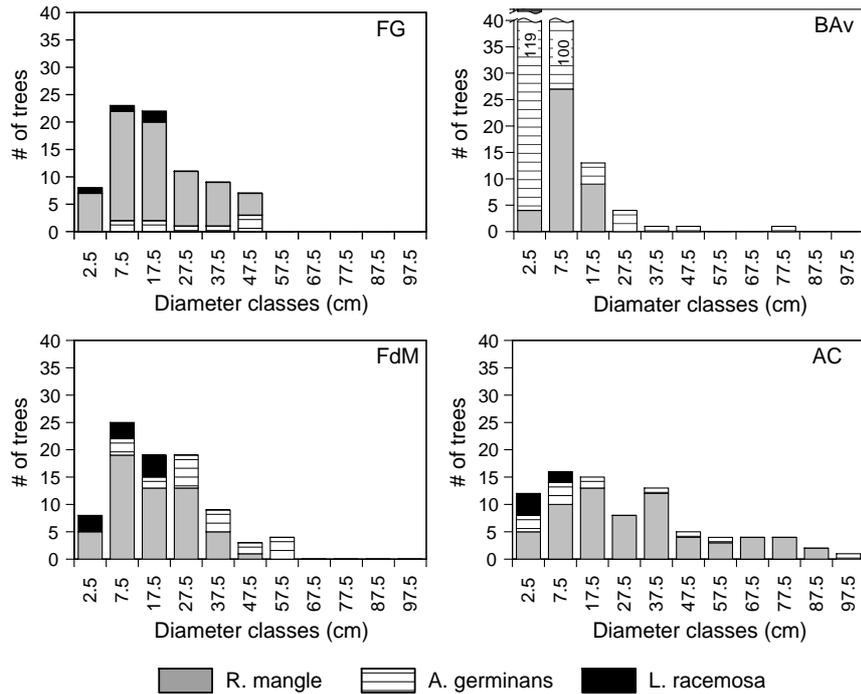


Figure 7.3: Stem diameter class distribution of trees at the study sites. FG Furo Grande; FdM Furo do Meio; BAv Bosque de *Avicennia*; AC Acarajó

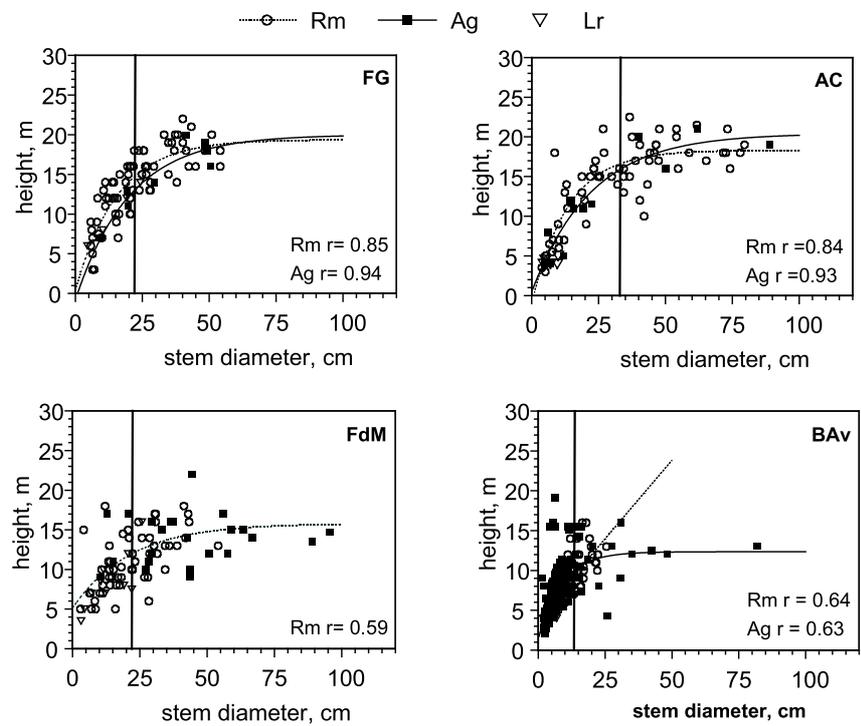


Figure 7.4: Regression of height and stem diameter of trees at each study site. Vertical lines indicate the mean stem diameter of *R. mangle*. rm: *R. mangle*; ag: *A. germinans*; lg: *L. racemosa*

At FG, FdM and AC, height growth of trees stagnated when their diameters had reached 38, 31 and 36 cm, respectively (Figure 7.4). However, the trees continued to grow in stem diameter after reaching maximum heights. At BAv, the relation between stem diameter and tree height was better described by a linear regression due to the dominance of smaller trees (Figure 7.4).

7.3.2 Growth rings

Relationship between tree age and stem diameter

Based on the assumption that tree rings are annual, the oldest *R. mangle* tree at FG was 100 years old. In the other areas FdM, BAv and AC the maximum registered tree ages were 9, 71 and 53 years, respectively (Table 7.2). For all study sites, the correlation between number of rings and stem diameter was significant ($r=0.71$, $p=0.05$). The correlation coefficient r varied among the areas (FG $r=0.96$; FdM $r=0.64$; AC $r=0.95$; BAv $r=0.80$; $p=0.05$ for all sites).

Forests age

The mean stand age differed between the sites: FdM (62.30 years) > AC (56 years) > FG (31 years) > BAv (24 years). The same was true for the mean age of each species: FG *A. germinans* (83 years) > *R. mangle* (30 years) > *L. racemosa* (28.96 years). FdM: *A. germinans* (86 years) > *R. mangle* (51 years) > *L. racemosa* (27 years). AC: *A. germinans* (69 years) > *R. mangle* (43 years) > *L. racemosa* (5 years). BAv: *R. mangle* (26 years) > *A. germinans* (22 years) > *L. racemosa* (14 years)

Growth rates and growth conditions

All wood discs presented a linear radial growth of the trees (Figure 7.5). Mean growth rates varied between $2.5 \text{ mm}\cdot\text{y}^{-1}$ (BAv) and $4.9 \text{ mm}\cdot\text{y}^{-1}$ (FG), in the order FG>FdM>BAv>AC. The average for the whole data set was $2.9 \text{ mm}\cdot\text{y}^{-1}$. As already discussed in Menezes et al. (2003), according to the growth curves trees were tentatively divided into three groups for “fast”, “medium” and “slow” growth.

Chapter 7

Table 7.2: Wood disc samples. Study sites:BAv Bosque de *Avicennia*; FG Furo Grande; AC Acarajó; FdM Furo do Meio. Number of rings=tree age. FON Field of Neighbourhood (neighbourhood competition strength). Groups: 1 fast; 2 medium; 3 slow growth.)

Site	Sample	Growth rate	# of rings	FON	Diameter	Group
BAv						
	892	3.6	50	0.32	19.1	2
	884	2.1	40	0.01	13.1	2
	797	3.0	71	0.04	27.4	2
	792	3.4	27	0.62	11.8	2
	903	3.1	44	-	3.5	2
	433	2.7	18	0.02	6.7	2
	432	2.6	81	0.09	24.2	2
	648	2.9	38	0.34	16.6	2
FG						
	4042	3.1	100	0.18	38.2	2
	4065	4.4	22	-	9.9	2
	4331	4.9	52	0.05	25.5	1
	4343	2.9	34	0.35	19.4	1
	4346	4.7	47	0.15	28.0	1
	sn9	3.2	15	-	-	1
	sn16	3.2	77	-	-	2
Ac						
	v22	2.4	39	-	9.9	2
	v20	2.9	53	-	19.4	2
	v21	2.5	33	-	11.8	2
	sn9	2.3	20	-	-	2
	Rhiza1*	2.3	63	-	43	2
	Rhiza2*	2.6	111	-	61.4	2
	Rhiza3*	3.1	63	-	28.1	2
FdM						
	4264	3.1	26	0.00	8.3	2
	4092	4.2	90	0.00	43.3	1
	4244	4.6	50	-	21.0	1
	4275	4.8	40	0.02	38.8	1
	4278	3.0	34	0.17	17.5	2
	Rhidf1*	1.7	65	-	19.1	3
	Rhidf2*	1.6	58	-	25.8	3
	Rhifc1*	2.4	51	-	25.0	2
	Rhifc2*	1.9	57	-	26.0	3
	Rhifc3*	1.0	60	-	27.5	3
	Rhifc4*	1.2	97	-	21.7	3
	Rhifc5*	1.4	65	-	16.6	3

* data source: Menezes et al. (2003)

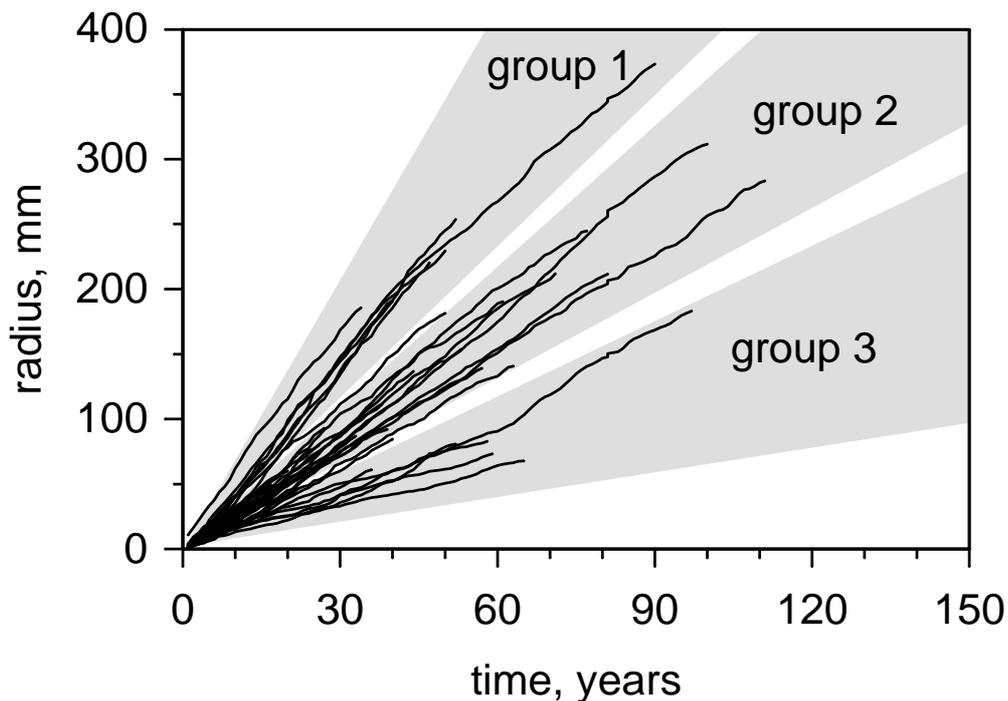


Figure 7.5: Relationship between density of individuals and mean age of trees from forests with different stages of development.

Trees in the “fast” group were only found FG (50% of the trees in this group) and FdM (50%). Trees in the medium group were from BAv (32%), AC (37%), FdM (21%) and FG (10%) trees. The “slow” group was formed exclusively by FdM trees. The mean growth rates were 3.6 , 2.9 and $1.7 \text{ mm}\cdot\text{y}^{-1}$ for group 1, 2 and 3, respectively.

Inundation frequency and neighbourhood competition

FG was the most frequently inundated area with about $332.1 \text{ d}\cdot\text{y}^{-1}$ (inundation days per year), while FdM was inundated $264.6 \text{ d}\cdot\text{y}^{-1}$ and AC $229.9 \text{ d}\cdot\text{y}^{-1}$. BAv was the least frequently inundated area ($73.9 \text{ d}\cdot\text{y}^{-1}$).

The calculation of the Field-Of-Neighbourhood (FON) as proxy for neighbourhood competition revealed a high variation of the FON for single trees at each study site (Table 7.2). The highest values for the FON were found in BAv and FG, while FdM presented the lowest values.

Table 7.3: Influence of parameters inundation frequency (a) and competition (b) on the growth rate of trees, tested by GLM. "Peninsula" considers all sites as one single forest. Bav Bosque de *Avicennia*, FG Furo Grande, FdM Furo do Meio. The column "Factor" indicates the parameters analysed: a inundation frequency; b competition; c competition*inundation frequency interaction.

<i>Site</i>	<i>Factor</i>	<i>r²</i>
Peninsula	a+b+c	0.59
Peninsula	a+b	0.58
Peninsula	a	0.47
BAv	a+b+c	0.69
FdM	a+b+c	1.00
FG	a+b+c	0.94
BAv	a+b	0.56
FdM	a+b	0.41
FG	a+b	0.94
BAv	a	0.02
FdM	a	0.11
FG	a	0.89

Importance of inundation frequency and competition

The analysis of local parameters (inundation frequency and FON) was carried out only for FG, FdM and Bav due to loss of samples from Ac (see above). The analyses were done by means of a General Linear Model (GLM) which provided a regression coefficient (r^2) as a measure of the proportion of variability explained by the two factors. Considering the whole peninsula as a single forest (joining all sites), inundation frequency was the most important factor (Table 7.3). In FG, inundation frequency was most important ($r^2=0.89$) but the regression coefficient increased to $r^2=0.94$ when competition was associated or combined. For trees from FdM and BAv, inundation frequency alone was not important but when combined with competition, the regression became highly significant ($r^2=1.0$; $r^2=0.69$, respectively; Table 7.3).

7.4 Discussion

The present study used dendrochronological analyses of *Rhizophora mangle* to assess the importance of abiotic factors (roughly described by inundation frequency) and neighbourhood competition (via Field-of-Neighbourhood, FON). In combination with forest structure data, the measurement of growth rates and tree age provides further insights into mangrove forest dynamics which we want discuss in the following.

7.4.1 Forest structure and age of trees

R. mangle and *A. germinans* dominate the upper strata at all study sites. Trees of all three species occurred also in the lower stratum but, depending on their shade tolerance, their location (inner forest, forest boundary or gap) varied. The diameter class distribution provides information on forests rejuvenation through the diameter-age relationship analysed by dendrochronology.

In Acarajó, diameter distribution is broad and tends to be uniform. This distribution corresponds to a wide range of tree age of *R. mangle* (mean age=50 years, maximum age=111 years). Our approximation of average tree age for the whole forest shows nevertheless that Acarajó is a relatively old forest (the second oldest stand investigated). It should be noted that age always refers to the mean age of the trees and is not meant as an absolute forest age counted from the colonisation of an empty area. The data on tree height and stem diameter relation support this hypothesis since they reveal that the forest canopy has reached its maximum height. Acarajó is a well developed, mature *R. mangle* dominated forest under continuous rejuvenation. This can be explained by benign abiotic conditions combined with high light availability in gaps, facilitating the development of seedlings or young trees. Gaps have been created not only by natural tree fall (Rebelo-Mochel and Façanha, 2002), but also by wood extraction for timber and charcoal production (Glaser et al., 2003; Berger et al., 2006). The existence of a well developed understorey consisting of *Crinum* sp., *Montrichardia arborescens* and

Acrostichum aureum is probably another effect of these dynamics (Menezes et al., 2003).

Furo Grande forest is also *R. mangle* dominated. The stem diameter distribution shows that the majority of trees belong to only two size classes. *R. mangle* trees of these size classes are about 23 years old. Under consideration of the age estimates for the eight *A. germinans* trees which occurred in our PCQM transect, the average stand age was approximated to 31 years. The stem diameter/tree height relation shows, furthermore, that the majority of trees has not yet reached the maximum height. Thus, we hypothesise that there was a colonisation peak not more than three decades ago, and that the forest itself is still in transition between a young and a mature succession stage.

The broader, bell shaped stem diameter distribution confirms that the Furo do Meio site is a mature forest. The majority of trees are between 18 and 64 years old. The stem diameter/tree height relation suggests that the oldest trees have already reached their maximum heights. Old trees frequently have a broken apex at this study site, causing considerable scatter and a comparatively low medium height.

At BAv, the inverse J-pattern of the stem diameter distribution reflects mainly the heterogeneity in abiotic conditions. This site may be strongly affected by construction of a road passing through the peninsula in the early 1980's. Our 900 m transect starts at the road and follows a gradient of increasing inundation towards the Caeté River. At its highest elevation, inundation frequency is low and pore water salinity is high. This plot is dominated by small *A. germinans* trees forming dense vegetation. At the opposite end of the transect, inundation frequency is high and the resulting pore water salinity low. In addition, phosphorous availability is much higher than in the parts dominated by *A. germinans* (Cordeiro et al., 2003). Here, the transect is dominated by tall *R. mangle* trees. Our data suggest that these trees have established before construction of the road. This fact and the existence of dead trunks of large *R. mangle* trees found at the *A. germinans* dominated part of the transect support analyses

of satellite images which suggest that forest composition was more homogeneous at Bosque de Avicennia before the road construction (Mehlig and Salzmann, unpublished data).

7.4.2 Factors influencing tree growth

The dependency of an individuals' growth rate on genetic, environmental, competitive, phenological or random factors has been investigated for different tropical tree species (Adlard, 1977 cited by Primack et al., 1985). Menezes et al., (2003) relate the variation of *R. mangle* growth rates to abiotic factors which are determined by the inundation regime, but hypothesise a strong influence of neighbourhood competition. The presented study supports these assumptions.

In our work, highest growth rates were measured at Furo Grande where the inundation frequency is high and pore water salinity is high but quite stable. Trees of this study site represent 50% of the first growth group (fast growth). It indicates that in spite of the high pore water salinity, the low variation of the latter combined to the frequent inundation favour growth. This is why the inundation frequency (as proxy for pore water salinity in the GLM) explains already 89% of growth rate variation. Frequent inundation also induces a higher transport of external nutrients into a forest (Feller et al., 2003) which may lead to higher levels of bioavailable phosphorous important for tree growth (Boto and Wellington, 1984; Feller et al., 1999, Cordeiro et al., 2003). Most studies demonstrating this relationship are carried out with mangrove seedlings and not with young or mature trees in the field. For example, in Kenyan mangroves, the growth of seedlings is higher in well inundated areas (Kairo, 1995, cited by Verheyden, 2004). Hong (1997) reports similar results for a *Rhizophora apiculata* plantation in Can Gio, Vietnam. However, although inundation frequency is so important at Furo Grande, neighbourhood competition has still a detectable effect on the trees' growth rate since a consideration of this factor in the General Linear Model increases the degree of explained growth rate variation.

At FdM, BAv and AC, no significant effect of inundation frequency on growth rate could be found. These results are similar to those of Verheyden (2004) for *Rhizophora mucronata* in Kenya. Thus, depending on the topography and the overall hydrological system, the importance of inundation frequency and the resulting pore water salinity on tree growth varies. Interestingly, the importance of neighbourhood competition is particularly pronounced at these forest sites. Whereas trees from BAv and AC belonged all to the medium growth group, trees from FdM occurred in all three groups. It is noteworthy, that the trees with the lowest neighbourhood competition belong to the “fast” growth group, and trees with the highest neighbourhood competition to the “slow” growth group. Consequently, a consideration of neighbourhood competition in the GLM increases the level of explained growth rate variation at FdM. It is reasonable that the emergence of the three growth groups is mainly caused by competition. It should be noted that the use of the Field of Neighbourhood (FON) approach considers the effect of resource competition phenomenologically but does not provide an explanation of the processes behind. Nevertheless, competition for light and space is, however, a likely candidate. Lieberman et al. (1985) attributes growth rate variations of tropical trees to an opportunistic response to light level changes during an individual’s lifetime. Worbes (1999) verifies that higher light availability during earlier succession stages of natural forests as well as in plantations results in higher growth rates. Trees established under closed canopies grow slower than those established in gaps (Worbes, 1999). Verheyden (2004) observed similar effects of better light conditions in Kenyan mangroves where trees grow slower in natural forests than in plantations.

7.4.3 Forests evolution

Merging the data of the study presented with data obtained by Berger et al. (2006) at AC, we arrive at a good agreement with the general succession model for neotropical mangroves introduced by Jiménez and Lugo (1985) and modified by Fromard et al. (1998).

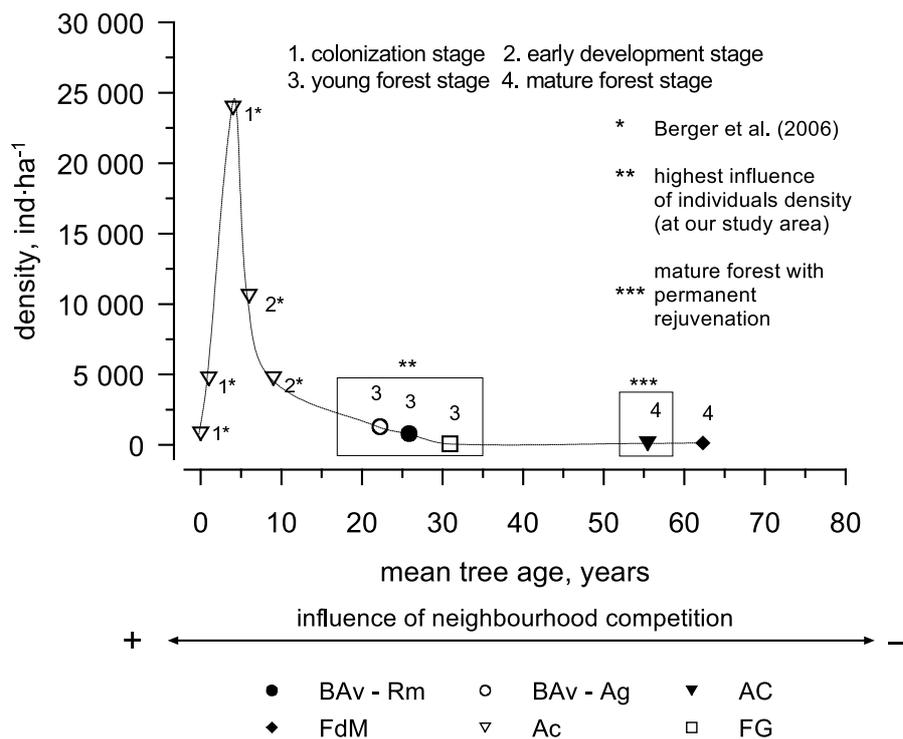


Figure 7.6: Relationship between density of individuals and mean age of trees from forests with different stages of evolution.

However, according to the data presented here, the early development stage is much longer than assumed in the original model. Thus, we subdivide this stage into “early development” and “young forest stage” and propose, therefore, a five stage classification which might be valid under optimal growth conditions (Figure 7.6):

State 1 - Colonisation stage: starts with gap creation and a dominance of *L. racemosa*. This stage lasts about 4 years (Berger et al., 2006).

State 2 - Early development stage: the number of individuals decreases due to self-thinning. *R. mangle* and/or *A. germinans* appear in the plot. This stage lasts about 5 years (Berger et al., 2006).

State 3 - Young forest stage: the number of individuals still decreases. Two trajectories are likely: either a dominance change from *L. racemosa* to *R. mangle* (Ball 1980) or a dominance change from *L. racemosa* to *A. germinans* (Berger et al. 2006). However, depending on the abiotic

conditions, the further development might be disturbed. While the forest develops towards a mature stand under benign conditions, the forest might stagnate under adverse conditions. The high saline plot of BAv is an example for the latter.

State 4 - Mature stand: tree density is reduced and neighbourhood competition varies between low and/or moderate values. The majority of trees have reached the maximum height. The mean age of the trees varies between 30 and 60 years.

State 5 - Senescent forests: Jimenez and Lugo (1985) define this stage as dominated by few old and large trees; forests present wide gaps in the canopy and lack of regeneration. None of our study sites correspond to that description, because all of them are subject to weaker or stronger regeneration. These findings agree with Duke (2001) who argues that a frequent gap creation leads to a permanent forest turnover which usually prevents mangrove forests from senescence. However, Fromard et al. (1998) describes senescent or “cemetery” forests in French Guiana. While similar areas exist on Ajuruteua Peninsula (not subject of the present study), we do not consider these as senescent stands but hold external destructive forces such as erosion, sand deposits, or alterations in inundation regime (Souza-Filho, 2001) responsible for the degradation of the forest. This “senescence” cannot be explained in the original sense by an internal development of the system. In these cases, the whole forest “collapses” (Duke, 2001).

Concluding, this study shows three important points: 1) the pattern of three different growth groups first described for *R. mangle* by Menezes et al (2003) can be verified and explained by a combined effect of inundation frequency and neighbourhood competition. 2) The general succession model for neotropical mangrove species explains very well the decreasing importance of neighbourhood competition with tree density. But, more interestingly, our results demonstrate that this statement does not necessarily count for abiotic conditions like pore water salinity and inundation frequency. This brings

an old challenge to mind: finding a model which is suitable to describe mangrove forest succession over a broad range of environmental settings.

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