

A COMPARATIVE EXAMINATION OF ENVIRONMENTAL FACTORS AT PATCHY MANGROVE SEEDLING STANDS ON THE PENINSULA OF BRAGANÇA, NORTHERN BRAZIL

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Resumo. O objetivo deste estudo foi esclarecer se amostragens estocásticas ou heterogeneidade ambiental em pequena escala poderiam explicar a ocorrência de manchas de plântulas no manguezal de Bragança, norte do Brasil. Outro objetivo foi comparar diferenças significantes encontradas entre manchas de plântulas das três espécies de mangue ocorrentes na área estudada (*Rhizophora mangle*, *Avicennia germinans* e *Laguncularia racemosa*) com outros resultados encontrados na literatura. Foram analisados vários parâmetros edáficos (salinidade, pH, concentração de nutrientes, conteúdo de água, etc.), além da luminosidade em áreas com plântulas e áreas controle (sem plântulas). A partir dos 50cm, o solo da península de Bragança consiste de uma fina camada de argila e em muitas alocações, o solo apresenta uma série de propriedades estressantes para a planta. Algumas vezes apresenta também depósitos de areia em pequena escala, na maioria das áreas com plântulas. Como resultado, as condições do solo em áreas com plântulas diferem em alguns aspectos importantes como argila e volume dos poros entre as áreas controle. Outro fator importante para o crescimento da planta (salinidade da água intersticial, pH e nutrientes) foram medidas em ambas as áreas. Estas são características básicas que permitem o estabelecimento das plantas de mangue nas áreas estudadas. A influência de condições físicas do solo, requeridas pelas plantas são também discutidas neste artigo.

Abstract. The aim of this study was to find out whether simple stochastic or small-scale heterogeneity of environmental conditions could explain the patchy occurrence of mangrove seedling stands in the northern Brazilian tidal forest of Bragança. Another aspect of interest was whether significant differences between seedling locations of the three mangrove species occurring in the area studied (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*) were detectable, and to what extent such differences correspond to other results known from the research literature. Various edaphic parameters (salinity, pH-value, nutrient concentrations, water content, etc.) as well as shading were examined at the seedling locations and at control sites without seedlings. Since the upper 50 cm of the soil on the Bragança peninsula consists of a fine clay layer, the soil at many of the locations displays a number of properties that are stressful to plants. However, there are also small-scale sand deposits at most of the seedling stands. As a result, soil conditions at the seedling stands differed in some decisive aspects, such as clay fraction and pore volume, from those at the control sites. Other factors important for plant growth (e.g., pore water salinity, pH, nutrients) were roughly within the same range at both location types. These characteristics basically permitted mangrove establishment at both the seedling and control locations under investigation. The influence of these physical soil conditions on seedling requirements is discussed in the present paper. *Accepted 3 November 1999.*

Key words: Mangroves, seedlings, *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*, environmental factors, northern Brazil.

INTRODUCTION

The analysis of seedling establishment is an essential step towards an understanding of distribution patterns in mangrove forests. Field studies related to this topic frequently address the underlying causes of mangrove

forest zonation. This usually engenders the question as to why seedlings of different species grow in distinct zones. Hence several factors which are postulated as causes for mangrove zonation have been well investigated, e.g. the influence of seed predators (Smith

1987, Smith *et al.* 1989, Clarke & Myerscough 1993), or the influence of physicochemical factors on seedling establishment (e.g., Thomas & Smith 1987, Clarke & Myerscough 1993, Ellison & Farnsworth 1993, McKee 1995a). In contrast, the causes of the patchy occurrence of mangrove seedlings in mixed forests has rarely been investigated (but see Clarke & Allaway 1993).

Our work addresses this topic and asks why no mangrove seedlings at all grow in certain locations, even though the latter may seem favorable for seedling establishment. To answer that question a comparison of abiotic and biotic factors at locations with and without seedlings was performed. In order to investigate locations without seedlings, an experimental strategy was chosen that had not been used frequently hitherto. As mentioned above, a simple reason for this might be that most investigations on seedling establishment have been carried out in zoned mangrove forests, where a differentiation between locations with and without seedlings is not a relevant issue. The following questions were addressed:

- (1) Are differences in environmental factors detectable between locations with and without seedlings that would explain the occurrence or absence of seedling recruitment at these sites?
- (2) Are there significant differences in environmental factors detectable between seedling patches of the mangrove species studied, and do they provide information about varying ecological requirements of the seedlings in the mixed forest?

STUDY AREA

The research area is part of a mangrove-dominated peninsula adjacent to the Caeté river estuary, near the north Brazilian municipality of Bragança (State of Pará). The area is located on the Atlantic coast, south of the Amazon delta, in the coastal section between Belém and São Luis (Fig. 1). The coordinates are 46°32'10"W to 46°55'10"W and 00°43'20"S to 01°04'20"S. Geologically, the soils in the region result from the formation of the "Barreiras" (barrier), consisting of Tertiary marine sediment deposits originating from the crystal line rock of the inner Brazilian highlands (Grabert 1991). These are covered with a non-homogeneous clay layer, interrupted by small-scale sand deposits (Souza Filho & El-Robrini 1997).

The region has a tropical climate, with two distinct seasons. The wet season, which lasts from December to May, and the dry season, extending from June to November. The mean temperature varies be-

tween 25.1°C (July) and 26.6°C (November). The amplitude between the maximum and minimum temperatures measured amounts to 14.9°C (Departamento Nacional de Meteorologia 1992). In the dry season the duration of sunshine is about 247.5 hrs/month, and in the wet season about 99.8 hrs/month.

Relative humidity is high, averaging between 77% (in October, November) and 91% (April, May). The region is among the wettest in Brazil. The mean annual total rainfall is 2545 mm, with mean annual evapotranspiration of about 813 mm. Since the difference in precipitation between the wet and dry season is very distinct (there is almost no rain at all in the dry season), the salinity of the rivers and creeks of the Caeté estuary is subject to seasonal variations. In June, an average salinity of 16‰ was measured, whereas in December salinities as high as 38‰ are common (Cohen *et al.* 1998).

According to criteria provided by Lugo & Snedaker (1974), the area under investigation can be described as a basin mangrove forest. Apart from a few small creeks and channels affected by the daily tides, the major part of the area is flooded at spring tides only. Consequently, the soils dry out in the dry season, and cracks occur in places exposed to the sun. During the wet season, by contrast, the soils become very soft, and a mud layer up to 1 m in depth can form.

The forest studied is a mixed stand without distinct zones of the three species present: *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*. The mean height of the trees was 12.6 m (Menezes 1998), the tallest tree registered was an *A. germinans* measuring 34.5 m (Thüllen 1997).

Although *R. mangle* occurs in the area with the highest relative density (83%), *A. germinans* shows the highest relative dominance (67%) (Thüllen 1997). The stand structures of the three species also differ from one another. Whereas the *R. mangle* and *L. racemosa* populations are characterised by logarithmic population curves, the size classes of *A. germinans* are more or less equally distributed, with virtually no recruitment.

The few seedling stands which existed in the study occurred in clustered form, (predominantly) in species-specific patches.

MATERIAL AND METHODS

Field research was undertaken between the end of August and the end of December 1996. In the eastern Amazon this period represents the peak of the dry season and causes severe stress for the seedlings.

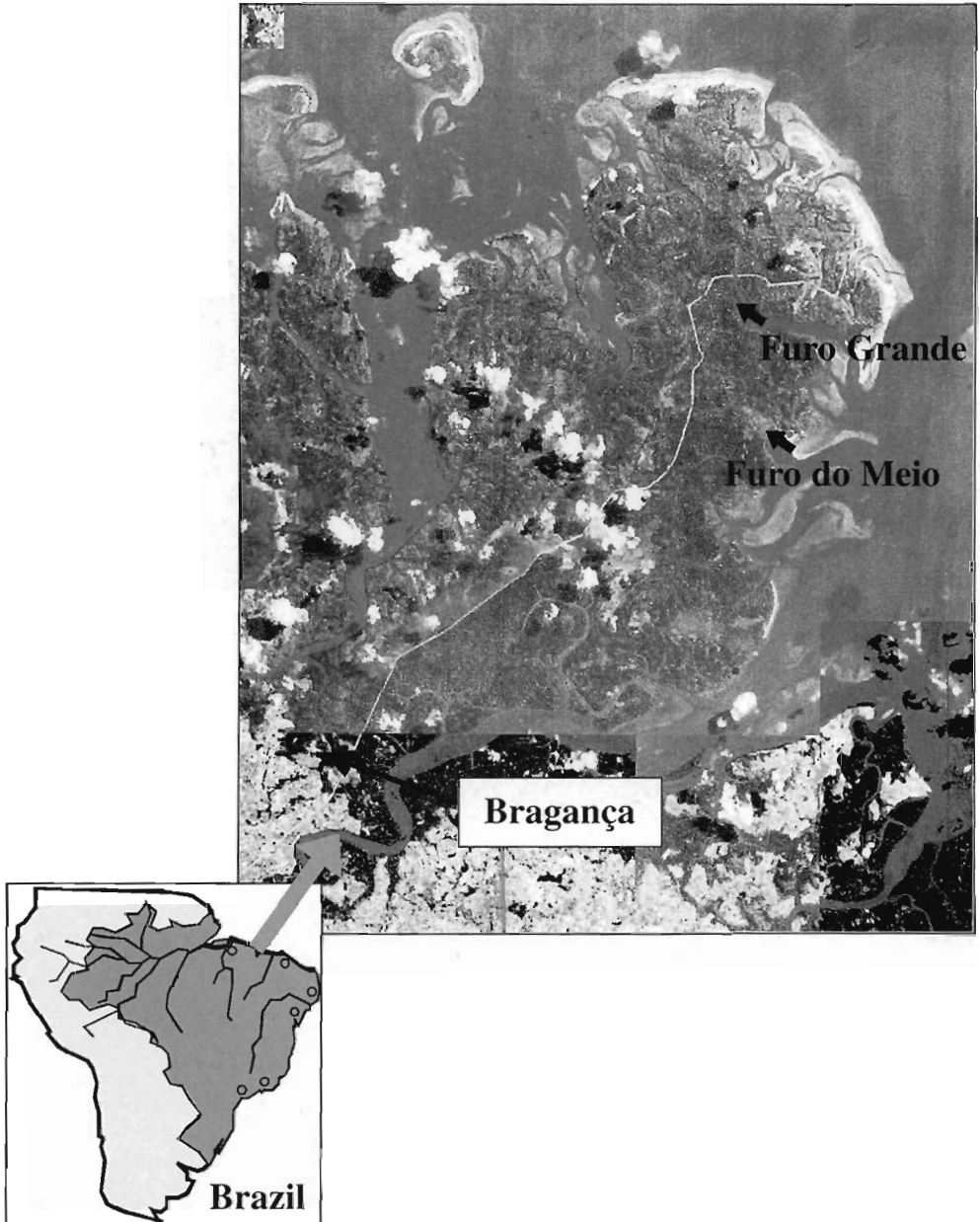


FIG.1. Location of the study area. Satellite image (16.8.1988; bands 3,4,5; courtesy of CPRM Serviço Geológico do Brasil Superintendência Regional de Belém; on a scale of 1 : 100.000).

It was initially intended to regard all unbranched plants as seedlings. However this idea was revised because preliminary investigations had shown that *A. germinans* and *L. racemosa* seedlings occasionally branch very early due to the high feeding activity of crabs on their tips; in many cases branched plants were only about 5 cm tall. Thus it was decided to take 45 cm, the size where *R. mangle* seedlings started to branch naturally, as the maximum seedling size. In order to get an idea of the approximate age of the seedlings (see, e.g., Duke & Pinzon 1992) the number of leaf nodes of each seedling was counted.

Seedlings appeared in small, isolated patches. For each of the three species, six patches with high seedling densities were examined. These patches were selected according to the criterion that a minimum of 20 seedlings of the respective species were visible from a given position. Accordingly, the sizes of the selected plots ranged from 0.5 m² to 36 m², depending on the specific density of the seedlings. Five of the 18 seedling sites were located at the forest margin or in smaller gaps, nine of them on the banks of larger drainage channels, their levees or nearby. The rest of the seedling sites were situated in the inner forest. As control sites, 18 locations without seedlings were randomly chosen within a transect defined perpen-

dicularly from the river "Furo do Meio" (Fig. 2). These were situated in the inner forest, eight of them on or in small drainage channels.

The general characteristics (e.g., flooding frequency, surrounding vegetation) of all locations investigated are listed in Table 1. Most of the seedling locations were flooded during spring tides only. Once flooded, the seedlings were covered completely for up to 3 hours. The exact height and duration of the flood was not measured at the different sites.

At all of the 36 sites the percentage shadow cover was estimated at noon using an area 2 m x 2 m in size marked in the middle of each location. This reference area was subdivided into quadrants. For each of these quadrants, the percentage shadow cover was estimated while the sun was at its zenith (between 11.30 h and 12.30 h). According to light measurements by Schories & Mehlig (pers. comm.), the irradiation was maximal during this period. The estimations were made only when the sun was not covered.

In order to characterize the locations, soil cores were taken with a sediment sampler (Hydro-Bios, Kiel). Black- and -white photographs were taken of the cores while still in the (transparent) sediment sampler and referenced to a dipstick. When the water level had stabilized, salinity (instrument type WTW

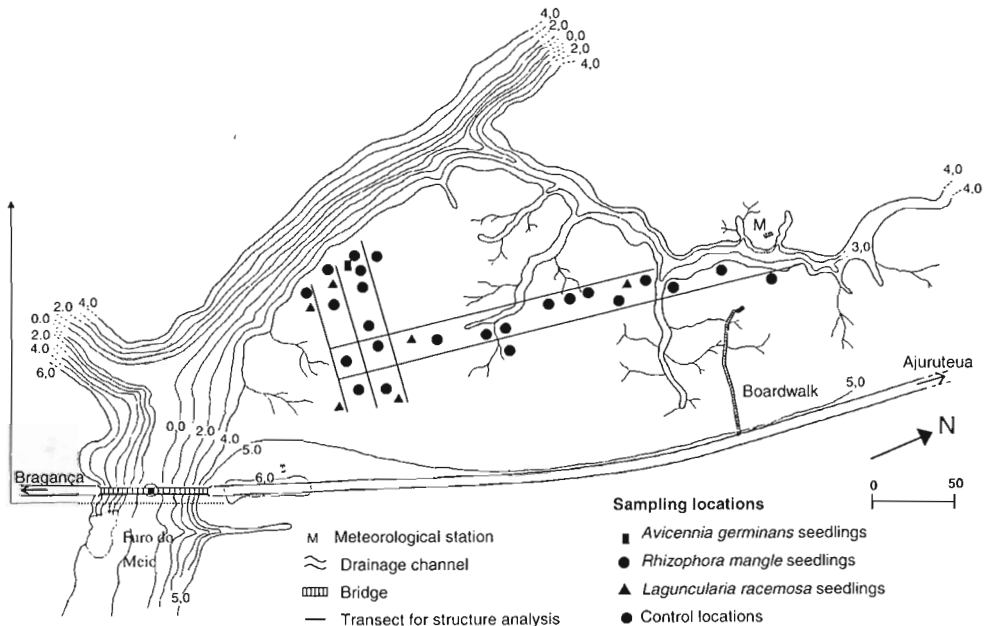


FIG.2. Seedling locations and control sites at the "Furo do Meio".

TABLE 1. Descriptions of the seedling locations and the locations without seedlings used for control purposes.

Location	Description
<i>Laguncularia</i> 1	On the bank of a large creek, fully exposed to sunlight for the greater part of the day, open to the south. Flooded at every high tide. Very soft substrate.
<i>Laguncularia</i> 2	On the bank of a large creek, fully exposed to sunlight for the greater part of the day, open to the north. Flooded at every high tide, with very soft, muddy substrate. <i>A. germinans</i> roots.
<i>Laguncularia</i> 3	In a small clearing, heavily influenced by crab feeding, dry, adult <i>L. racemosa</i> in the surrounding area. Near road.
<i>Laguncularia</i> 4	On river bank, fully exposed to sunlight for the greater part of the day, open to the north, flooded at every high tide. Seedlings partly on stony substrate covered by a thin layer of mud, partly on very soft, deep substrate.
<i>Laguncularia</i> 5	<i>A. germinans</i> roots, dry, on the bank of a small creek. Many <i>L. racemosa</i> seedlings in the surrounding area. Partly shaded.
<i>Laguncularia</i> 6	Very dry, sandy, shaded by <i>R. mangle</i> , much leafage, flooded infrequently in the course of a year.
<i>Rhizophora</i> 1	Situated on a river bank surrounded by adult trees of all three species. Ground covered with <i>A. germinans</i> roots, relatively firm substrate. Shaded for most of the day.
<i>Rhizophora</i> 2	With flat-leaved succulents. <i>R. mangle</i> roots, clearing near river bank. Located along a path that is regularly used.
<i>Rhizophora</i> 3	<i>A. germinans</i> roots, <i>R. mangle</i> roots, flat-leaved succulents. On the bank of a small creek.
<i>Rhizophora</i> 4	Many <i>R. mangle</i> roots. Adult <i>R. mangle</i> and <i>A. germinans</i> in the surrounding area, dry.
<i>Rhizophora</i> 5	Dry, sandy soil. Few <i>A. germinans</i> roots, <i>R. mangle</i> roots.
<i>Rhizophora</i> 6	Like <i>Laguncularia</i> 6, neighboring location. Winds, dry, <i>R. mangle</i> roots, very shaded under parent tree.
<i>Avicennia</i> 1	All three species in the surroundings of the location, total of five seedlings of the other species in the area taken, as well as succulents. On the bank of a small creek, few a <i>A. germinans</i> roots, much debris and deposited material. Fully exposed to sunlight for most of the day.
<i>Avicennia</i> 2	Near the bank of a large creek, under parent tree, <i>A. germinans</i> roots, location open to the west. <i>A. germinans</i> seedlings in the surroundings.
<i>Avicennia</i> 3	<i>A. germinans</i> roots, flat-leaved succulents, beside road, many <i>A. germinans</i> seedlings in the surroundings. Location open to the east.
<i>Avicennia</i> 4	Directly under parent tree. <i>A. germinans</i> roots, many <i>A. germinans</i> seedlings in surroundings, shady.
<i>Avicennia</i> 5	Many <i>A. germinans</i> roots, wet location, many crab holes, open.
<i>Avicennia</i> 6	Beside road, <i>A. germinans</i> roots, open.
T1Q3	<i>R. mangle</i> and (more) <i>A. germinans</i> roots. Adult <i>R. mangle</i> and <i>A. germinans</i> in surroundings. Oxidized spots in root zones.
T1Q4	Dense <i>R. mangle</i> shrubs, many <i>R. mangle</i> roots, many crab holes, wet, muddy.
T1Q5	<i>R. mangle</i> roots, dry, dense soil, oxidized spots in root zones.
T1Q6	Some <i>A. germinans</i> roots, very muddy with small creek, black, heavily reduced soil.
T2Q6	<i>R. mangle</i> roots. Very soft substrate, high sulfide concentration in soil.
T4Q3	Dense soil, many <i>A. germinans</i> roots, under large <i>A. germinans</i> .
T4Q5	On the bank of a creek, <i>R. mangle</i> roots. Very soft, reduced substrate, deep horizon, muddy.
T4Q7	Soft substrate, <i>R. mangle</i> clusters, muddy.
T4Q9	Near creek, approx. 50% of the area covered with <i>A. germinans</i> roots, <i>R. mangle</i> roots, dense, loamy soil, partly soft.
T5Q2	Intersected by a small creek, few <i>R. mangle</i> roots, shady.
T5Q5	<i>R. mangle</i> shrubs on a small island enclosed by two creeks.
T5Q6	Very soft, muddy substrate, intersected by a small creek, few <i>R. mangle</i> roots.
T5Q7	Many <i>R. mangle</i> roots, some <i>A. germinans</i> roots, relatively firm substrate.
T5Q8	<i>A. germinans</i> and <i>R. mangle</i> roots, soft substrate, intersected by a small creek.
T5Q9	<i>R. mangle</i> roots, soft muddy substrate, shady.
T5Q10	<i>R. mangle</i> roots, small creek, soft muddy substrate, shady. Near creek.
T5Q11	<i>R. mangle</i> roots, small creek, soft substrate.
T5Q14	Soft, muddy substrate, <i>R. mangle</i> roots.

LF 197) and pH (instrument type Portames 752, Calimatic) were measured in the interstitial water that gathered in the holes formed by taking the soil cores. The cores were air-dried and afterwards crushed with a hammer. Large organic material, such as leaves and twigs, was removed. The following parameters were subsequently analysed: inorganic nitrogen (with potassium chloride, according to Fleige *et al.* 1971), plant-accessible phosphate (with ammonium lactate, according to Bassler 1991); particle size (percentage of sand, silt, clay) by pipette analysis in sedimentation cylinders and moist sieving with different mesh sizes (Bassler 1991). Organic carbon was measured by glowing the soil at 550°C for 12 hours in a muffle furnace. Use of this latter method was possible because tests with hydrochloric acid had shown that carbonate concentrations were negligible in the soils being studied.

In order to determine the physical characteristics of the soil, samples of constant volume were taken with a syringe cut open at the front. The fresh and

dry weight (after drying at 100°C to a constant weight) of the samples were determined, thus permitting the calculation of bulk density, substance and pore volume, water, and air content of the soil (Schachtschabel & Scheffer 1984, Kuntze *et al.* 1988). To determine significant differences in the physico-chemical parameters between locations with and without seedlings and/or between seedling locations of the different species, one-way ANOVAs were carried out. If significant differences were detected additional Bonferroni tests were performed. If there was no homogeneity of variances a Kruskal-Wallis test was carried out instead, followed by a Nemenyi test. Data given in percent were arcsine transformed prior to testing. The tests were done in accordance with the descriptions by Sachs 1974 and Köhler *et al.* 1992.

RESULTS

R. mangle seedling locations. The *R. mangle* locations were situated near drainage channels, on levees as well as on sites distant from watercourses. Mature trees

TABLE 2. Means and standard deviations of the biotic and abiotic factors at the seedling locations (n = 6) and control locations (n = 18). In the last column the performed test type is given.

	<i>R. mangle</i>	<i>A. germinans</i>	<i>L. racemosa</i>	Control	Statistical test performed
Sand [% weight]	55,6 ± 3243	51,5 ± 27,06	46,2 ± 26,61	9,1 ± 7,84	ANOVA
Silt [% weight]	17,7 ± 12,98	19,2 ± 11,37	15,2 ± 7,87	26,0 ± 7,56	ANOVA
Clay [% weight]	25,8 ± 19,12	34,8 ± 23,82	37,2 ± 20,65	69,0 ± 14,87	ANOVA
Raw density dry [g/cm ³]	1,00 ± 0,22	0,99 ± 0,36	0,97 ± 0,25	0,59 ± 0,14	ANOVA
Substance volume [% vol.]	39,2 ± 7,67	39,3 ± 13,36	38,5 ± 9,16	24,5 ± 5,51	See pore volume
Pore volume [% vol.]	60,8 ± 7,67	60,7 ± 13,36	61,5 ± 9,16	75,5 ± 5,51	ANOVA
Air volume [% vol.]	25,5 ± 8,68	13,1 ± 5,47	16,1 ± 9,06	15,6 ± 8,16	ANOVA
Water cont. [% vol.]	35,3 ± 13,82	47,7 ± 11,19	45,4 ± 17,29	59,8 ± 8,51	ANOVA
Tot. inorg. N [mg/100g dry soil]	0,82 ± 0,85	1,21 ± 0,52	1,52 ± 1,52	1,89 ± 0,79	ANOVA
NH ₄ -N [mg/100g dry soil]	0,82 ± 0,85	1,20 ± 0,52	1,52 ± 1,52	1,89 ± 0,79	Nor tested
NO ₃ -N [mg/100g dry soil]	0,00047 ± 0,00045	0,00078 ± 0,00068	0,00146 ± 0,00242	0,00049 ± 0,00057	Nor tested
P [mg/100g dry soil]	1,34 ± 0,53	3,76 ± 4,26	3,26 ± 2,57	2,78 ± 1,14	ANOVA
Carbon content [% weight]	3,2 ± 2,10	3,9 ± 2,03	3,7 ± 1,88	6,4 ± 1,15	ANOVA
Organic carbon content [% weight]	5,5 ± 3,62	6,6 ± 3,49	6,5 ± 3,17	11,0 ± 1,99	Nor tested
pH	5,8 ± 0,41	6,5 ± 0,72	6,6 ± 0,52	6,4 ± 0,28	sign
Salinity [‰]	42,0 ± 4,37	43,8 ± 3,98	36,2 ± 1,76	37,4 ± 2,17	ANOVA
Shading [%]	45,5 ± 17,32	23,5 ± 26,37	37,1 ± 22,68	73,8 ± 17,03	ANOVA
Distance to nearest adult [m]	0,0 ± 0,00	0,6 ± 1,51	6,4 ± 3,43	–	Kruskal-Wallis

Values marked with are significantly lower than values marked with ($P < 0.05\%$)

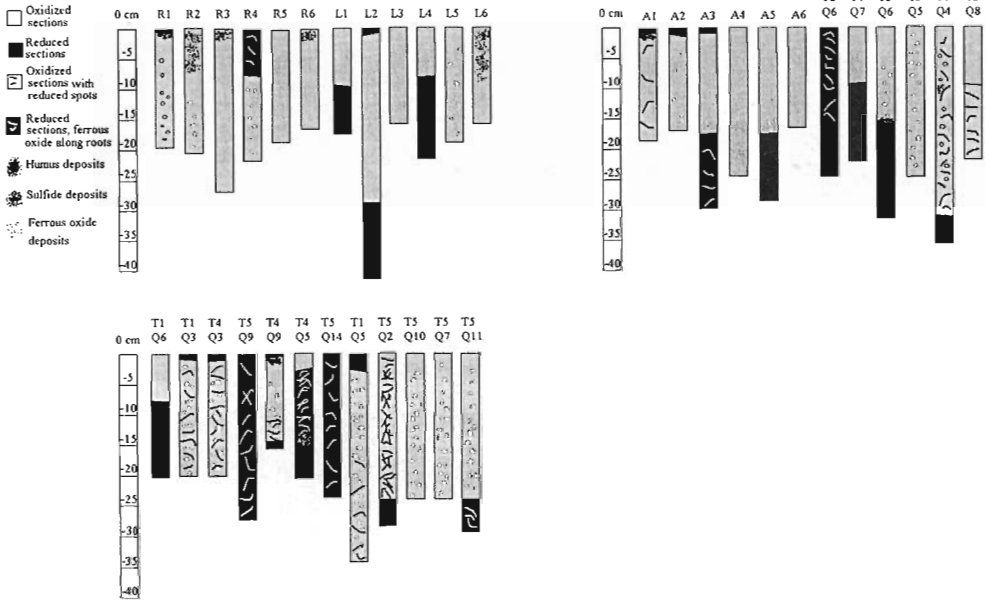


FIG. 3. Graphic representation of the slides taken of the soil cores from the seedling and control locations. L1 to L6 represent the *L. racemosa* seedling locations, A1 to A6 the *A. germinans* locations and R1 to R6 the *R. mangle* locations. TxQx are the transect and quadrat number of the screen transect.

were always present within study sites. Consequently, the distance to the nearest conspecific tree was low, significantly lower than for the *L. racemosa* seedling sites (see Table 2).

A pronounced humus layer consisting of barely decomposed leaves and small sticks was present in four of the six *R. mangle* cores (Fig. 3). The mean soil composition was dominated by a high percentage of sand and a relatively low proportion of clay. As shown in Table 2, the values of these components, as well as of the raw density and the pore and water volume of the soil, differed significantly from the control sites. The mean air volume of the soil was the highest of the four location types (three species and control). The difference from the *A. germinans* sites was significant. The amount of plant-accessible phosphate and inorganic nitrogen in the soil was lower than at all other sites. However these differences were not significant.

The mean pH-value of the interstitial water at the *R. mangle* locations was significantly lower than at the *L. racemosa* seedling locations. These sites also differed in terms of the interstitial water salinity, which was significantly higher at the *R. mangle* locations.

The mean node numbers of the *R. mangle* seedlings were higher (but also showed significantly higher standard deviations) than at the *A. germinans* and *L. racemosa* locations (see Table 3), whereas seedling density was significantly lower than at the *A. germinans* locations.

A. germinans locations. The *A. germinans* seedlings occurred predominantly at open locations, for example

TABLE 3: Mean leaf node number of each species at the six locations.

Location number	Mean node number <i>R. mangle</i> locations	Mean node number <i>A. germinans</i> locations	Mean node number <i>L. racemosa</i> locations
1	15 ± 12,2	12 ± 3,67	10 ± 3,34
2	5 ± 3,9	7 ± 2,50	10 ± 1,42
3	14 ± 7,3	7 ± 1,64	7 ± 2,34
4	15 ± 7,0	5 ± 1,55	11 ± 2,43
5	15 ± 6,7	6 ± 0,91	3 ± 1,36
6	9 ± 7,4	9 ± 4,21	2 ± 0,87

on creek banks or at roadsides. Although the mean distance of the sites to the nearest adult tree was low, the mean percentage shade cover was the lowest of all locations investigated. It was significantly lower than at the controls (Table 2). The areas were characterized by pure clay soils, extending to loamy sand. The mean proportion of sand, the raw density and the pore volume of the soil differed significantly from the figures at the control sites.

The mean salinity of the interstitial water was the highest of all location types, being significantly higher than at the *L. racemosa* and control locations.

L. racemosa seedling locations. The *L. racemosa* seedling locations showed high variability depending on environmental conditions. Half of the locations were situated directly on the banks of large drainage channels and were flooded daily. The soils at these bank locations were soft and characterized by a high water content. The plants were exposed to full sunlight most of the day. The other *L. racemosa* seedling sites were on dry, sandy soils, which were rarely flooded. Two of these locations were rather shady and dry.

Since the *L. racemosa* seedlings grew on moist and dry locations, the mean water content of the soil exhibited high a variation (Table 2). Fig. 3 shows that all soil cores of the bank locations (L1, L2, and L4) are characterized by a large reduced horizon. Differences in seedlings node numbers were also clearly detectable. At two locations, mean node numbers were very low (between two and three), whereas at the other four locations, they were between 7 and 11.

In general, the *L. racemosa* locations were characterized by the highest mean pH-value and the lowest interstitial water salinity. The salinity differed significantly from the *R. mangle* and the *A. germinans* locations. The *L. racemosa* seedling sites showed the greatest distance to the next conspecific adult. The difference between these and the *R. mangle* locations was significant.

Unlike the *R. mangle* and *A. germinans* sites there was no significant difference between the proportions of sand at these locations and those at the non-seedling sites. Nevertheless, the raw density of the soil was significantly higher, and the pore volume significantly lower than at the control sites.

Control sites. Firstly, the control sites differed from the seedling locations by virtue of their relatively fine-grained soils. The soil composition was dominated by a high proportion of clay (soil type: clay to silt) and a small sand fraction of 1.7% to a maximum 23% (in

contrast, the lowest sand proportion at the seedling locations was 10%). The soil cores in Fig. 3 show that completely and predominantly reduced cores with sulfide deposits occurred at the control locations. Furthermore, it is interesting that ferrous oxide is present in 11 of the 18 cores of the control sites. At the seedling sites it appeared in small amounts only.

The mean pH-value of the interstitial water was not significantly different from the values at the seedling locations. The salinity was significantly lower than at the *A. germinans* locations. The mean shading was the highest of all sites; none of the locations was unshaded. The difference between these and shading levels at the *A. germinans* locations was significant.

DISCUSSION

Differences between the seedling sites and the control sites. The control sites differed from the seedling locations with respect to several parameters important for plant growth, most prominent among them being soil composition. At most of the seedling locations the clay soil was covered by small-scale sand deposits. However, the hypothesis that sand deposits are favorable locations for seedling establishment is not straightforward.

Various authors have pointed out that *Rhizophora*, *Avicennia*, and *Laguncularia* grow poorly on sandy soils (Coutinho 1980, Zapata 1980, Cintrón & Schaeffer Novelli 1983). Clay soils, on the other hand, are characterized by salinities, pH-values, and nutrient concentrations that impose less strain on plant growth (Ball 1988, Boto 1988). Considering that salinities, pH, and nutrient values were in about the same range at the seedling sites as at our controls, one could expect that the control sites would also be suitable for seedling establishment. Hence there must be other characteristics preventing recruitment at these locations.

As the pore volume was higher, i.e., the raw density was lower at the controls than at all of the seedling sites, it is suggested that these are decisive factors prohibiting the establishment of seedlings at such locations. The high pore volume of the clay soils at the control sites may be unfavorable for plants for a variety of reasons. Due to their substantial water content, clay soils are unstable; when water is withdrawn they contract significantly, swelling strongly in response to a renewed water supply. This process harms the fragile roots of the seedlings. At Furo do Meio, this is promoted in two ways – by the limited flood-

ing regime and by the extreme precipitation difference between wet and dry seasons. The soil in the inner forest becomes so compact during the dry season that the spring tide water is able to dissolve the soil surfaces only and can not enter the soil to supply the roots in the uppermost soil horizons. We suggest, therefore, that pore volume is a decisive factor prohibiting seedling establishment at the control sites.

The pore space structure seems to be another stress factor. The fine pores of clay soils cause high capillary tension and thus a low permeability to water and air. As a result, plants at such locations have difficulty accessing water.

Besides these physical properties, the high density of ferrous oxide spots at the control sites could also be unfavorable to seedling establishment, given that iron is a phytotoxine in its reduced FeII form (Jones & Etherington 1970, Boto 1984). This could be important at our control sites, where reduced conditions occur at relatively low depths. We did not measure FeII directly, but it is known from the literature that, under dry conditions, iron dissolved from the reduced horizons rises with the groundwater and precipitates as ferrous oxide in oxidized horizons (Schachtschabel & Scheffer 1984). Thus, the high density of ferrous oxide spots in the oxidized horizons could indicate a high concentration of ferrous oxide in the reduced horizons and hence a possible factor inhibiting plant growth at the locations with reduced layers in the upper soil strata.

The high shading at the control sites was probably another important factor accounting for their lack of seedlings. The species occurring in the region are known for their low light requirements during seedling development (Tomlinson 1986). Although the difference between the control and the *A. germinans* locations was the only significant one, the shading at the controls was the highest of all location types examined (most of the seedling stands were located under canopy gaps).

Our findings support the hypothesis that, under the extreme climatic and hydrographic conditions present in the study area, the physical properties of the nearly pure clay soils effectively prohibit the establishment of mangrove seedlings. Instead, the establishment of seedlings is more successful at locations characterized by a mixed clay-sand structure.

Differences between the seedling locations. The differences between the respective locations of the three species were not nearly as distinct as those between

the controls and the seedling sites. The most striking differences between the locations of the three species were the pore water salinities. The significant difference of the values at the *R. mangle* and the *A. germinans* sites compared with the ones at the *L. racemosa* sites confirm observations that *L. racemosa* shows little tolerance of high salinities (e.g., McKee 1995a, 1995b; Elster & Schnetter 1998). This may also explain the occurrence of *L. racemosa* seedlings on the drainage channel banks, if one considers that the regular soil water exchange keeps the pore water salinities in drainage channel banks low (see, e.g., Rey *et al.* 1989).

Another factor that varied between seedling sites was the pH values of *R. mangle* and *L. racemosa* locations. Investigating mature trees, Lacerda & Schaeffer Novelli (1992) detected an accumulation of organic material in soils on *R. mangle* stands that was preserved in its original form. From raw humus layers, acid humic substances are transferred into the soil by seep water, which can cause a strong acidic soil reaction (Kuntze *et al.* 1988, Dierßen 1990). Due to the fact that at least one mature *R. mangle* tree was present at each of the seedling locations of this species, and accumulated organic debris was found at four of the six *R. mangle* soil cores, the process described above might explain the relatively low pH-values at the *R. mangle* locations investigated.

Although in many cases the *R. mangle* seedlings were growing under the most stressful conditions to which the three species were exposed (lowest pH, highest shading, lowest water content, lowest nutrient values, second highest salinity), the differences were significant in a few cases only. Thus the requirements of three species differed little, if at all, in respect of the abiotic factors examined in the study. However, the figures obtained suggest that they may have different preferences, i.e., *R. mangle* may be more adapted to stressful conditions than *L. racemosa* and *A. germinans* when there are no locations more suitable. This hypothesis is also supported by results obtained by other research workers who found, for example, that *R. mangle* has better growth capability at low nutrient concentrations than *A. germinans* and *L. racemosa* (McKee 1995b). A higher shade tolerance of *R. mangle* has been mentioned by Ellison & Farnsworth (1993) and by McKee (1995a), whereas the genus *Avicennia* has been described as completely shade intolerant by Smith (1999). However, it is not possible on the basis of the present study to provide a conclusive answer to the question as to whether these species show different preferences. The range of

factors examined was less important for the establishment of the seedlings than the physical properties of the soils at the control sites. This is at least the case in the area investigated and is apparently caused by the strength of the common stress factors.

The seedling stands of the various mangrove species differed clearly in their age structure. The high standard deviations of the *R. mangle* mean node number show that the examined stands had an heterogeneous age structure. In contrast the relatively low standard deviation of the *A. germinans* and *L. racemosa* stands signify a homogeneous age structure. This conforms to findings by Rabinowitz (1978a) and Ellison & Farnsworth (1993) who noted that mangroves with larger propagules (*Pelliceria* and *Rhizophora*) frequently form overlapping cohorts even beneath the canopy. By contrast, mangroves with smaller propagules (*A. germinans* and *L. racemosa*) turn over annually at such locations.

The reason for the homogeneous age structure at the *A. germinans* locations was certainly not that these were cohorts from the recent wet season being replaced in the next one. Although values linking age and node numbers of this species are not provided in the literature, stature, height and node numbers prompted the conclusion that they were a minimum of one year old. The age of the *A. germinans* and *L. racemosa* seedlings could not be determined with greater precision because the method described in Duke & Pinzon (1992) using seasonally varying lengths of the internodal sections to identify the age of seedlings, was examined but found not suitable in the study area because the lengths of the internodal sections varied in an irregular, non-cyclical manner.

For *R. mangle*, values are provided in the literature which link the node number to age: the mean node number at four of the six *R. mangle* locations was 15. Duke & Pinzon (1992) give node production values between 3.5 and 7.6 nodes per year for *R. mangle*, which according to the *R. mangle* seedlings were a minimum of two years old on average.

These different stand structures support the hypothesis that the resources of the large *R. mangle* propagules increase the likelihood, relative to the other two species, of the seedlings surviving, especially under stressful environmental conditions. Another difference between the three species was the *R. mangle* seedlings' proximity to the nearest conspecific adult tree. This short distance can be explained by two factors: 1) Their relatively large weight, which makes it more difficult for the propagules to be carried away by the slow

currents typical of the inner forest than the small *A. germinans* and *L. racemosa* propagules. 2) The way the arrow-shaped *R. mangle* propagules hit the ground when falling from the mother tree has been shown by the recent study of McKee (1995a) as being decisive for seedling survival. The survival rate of seedlings established with a vertical hypocotyl axis is much higher than that of the seedlings established with a horizontal hypocotyl axis (about 70%:5%, according to McKee 1995a).

The short distance of the *A. germinans* seedlings to the nearest adult tree is probably caused by the combination of the relatively short time-span which they need to establish themselves since they start rooting after seven days (Rabinowitz 1978b, Elster & Perdomo 1999), the low flooding frequency in the study area, and the geomorphology of the ground. Hence the propagules were not transported far from the mature tree by one single flood event and had enough time to establish before the next flooding took place.

The variable distance of the *L. racemosa* seedlings to the nearest adult tree can be explained by the low weight of the propagules and their mean rooting time of 13 days, (Rabinowitz 1978b, Elster & Perdomo 1999), which is longer than the time lapse of 10 days between two tidal flood events. Hence some of the propagules were transported by two consecutive tidal floods until they established.

CONCLUSION

In this study, the locations of mangrove seedling establishment in the research area were determined by a number of factors. The most decisive seemed to be the physical characteristics of the soil and/or the high proportion of clay at the control sites. These gave rise to conditions that are unsuitable for seedling establishment under the present climatic and hydrographic regimes. This set of conditions seems to be of greater importance than requirements and preferences reported by other researchers. Probably for that reason, different abiotic conditions at the locations of the three seedling species were detectable in a few cases only. The size and the distribution characteristics of the propagules proved to be further factors important for seedling establishment.

Our results are therefore an indication that the occurrence of the seedling clusters in the research area seems to be driven by a combination of propagule dispersal and common susceptibilities to stress factors.

Varying preferences for certain conditions may play a minor role in the distribution of the different species. The study underlines the importance of small-scale soil heterogeneities for the establishment of mangrove seedlings.

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