The importance of propagule establishment and physical factors in mangrove distributional patterns in a Costa Rican estuary


Abstract

Establishment of *Laguncularia racemosa*, *Avicennia germinans*, and *A. bicolor* was measured along intertidal gradients (mud bank (MB), lower intertidal (LI), and upper intertidal (UI)) on point bars and islands in a Costa Rican tropical estuary. Successful establishment showed the following order — *Laguncularia*: LI (73%) > MB (52%) > UI (18%), with UI significantly lower than LI and MB; *Avicennia* spp.: LI (66%) > UI (51%) > MB (29%), with LI significantly higher than MB. Establishment of *Laguncularia* in UI was significantly lower than *Avicennia* spp. due to selective crab herbivory. After 25 days, 52% of *Laguncularia* propagules were eaten compared to 5% for *Avicennia* spp. Total mortality of *Laguncularia* propagules and seedlings was significantly higher than that of *Avicennia* spp. in all three zones.

The hydrological regime affected propagule establishment under controlled mesocosm conditions. Four hydrological treatments included flooded according to tidal cycle (FT), no flooding (NF), continuous flooding (F), and flooded according to tidal cycle with propagules additionally buried (FTB). *Laguncularia* establishment under NF (93%) and F (84%) was significantly greater than under FT (63%). *A. germinans* establishment under NF (97%) was greater than under FT (69%). *Laguncularia* showed significantly higher establishment than *A. germinans* under F conditions. *Laguncularia* propagules sank soon after their radicles protruded (5–8 days), and subsequently established under water. *A. germinans* propagules floated during the 25-day experiment and never established. Propagule establishment under FTB was greater for *Laguncularia* than for *Avicennia* (11 and 1%, respectively). Height increase of established *Laguncularia* seedlings was significantly
Growth of established A. germinans seedlings did not differ between FT (4.8 mm per day) and NF (5.0 mm per day), but it was significantly higher than Laguncularia under NF.

These results show that both genera can successfully establish on the lower intertidal zone when artificially retained. However, propagule buoyancy, availability, dispersal, and the effect of water movement on propagule anchoring limit Avicennia spp. establishment in this regularly flooded environment. In the upper intertidal zone, however, differential predation on Laguncularia propagules favors Avicennia spp. establishment and dominance. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Costa Rica; Point bars; Mangrove; Propagule establishment; Colonization; Laguncularia racemosa; Avicennia germinans; Avicennia bicolor; Crab predation

1. Introduction

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

In the Gulf of Nicoya, a tropical estuary on the Pacific coast of Costa Rica, the Tempisque and Bebedero rivers form a very dynamic estuarine environment. Because of high riverine influence, this system is characterized by low salinities and high sediment transport. High tides (2–3 m) are also responsible for sediment resuspension and deposition. Both rivers are characterized by meandering channels, in which sediments are eroded from the concave side of a river bend (cut bank) and deposited on the adjacent accreting convex bank (point bar; Coleman, 1969). Islands are also accretionary surfaces due to riverine and tidal current asymmetries in the lower estuary. Due to their accretionary nature, point bars and islands are unstable sedimentary environments with specific hydrological and physical characteristics which may influence mangrove establishment.

In point bars and islands of the Tempisque–Bebedero system, Laguncularia racemosa (L.) Gaertn. f. acts as the pioneer species colonizing emergent mud bank deposits and the lower intertidal zone. This is similar to other mangrove ecosystems under similar geomorphic settings (Pool et al., 1977; Jiménez, 1994; Cantera and Arnaud, 1997; Fromard et al., 1998). In this environment, Laguncularia forms the largest monospecific stands found in
the country. *Rhizophora racemosa* G.F.W. Meyer, *Avicennia germinans* (L.) L., *A. bicolor* Standley, and *Pelliciera rhizophorae* Triana and Planchon are also found colonizing middle and upper intertidal zones and fringing cut banks. *R. mangle*, which is absent from this particular system is generally found colonizing low intertidal zones along the entire Pacific coast of Costa Rica (Jiménez and Soto, 1985).

In the New World, *R. mangle* is the dominant pioneer mangrove species colonizing emergent substrates (Thom, 1967; Pool et al., 1977; Jiménez and Soto, 1985; Tomlinson, 1986; Jiménez, 1994). The absence of this species from this area and the dominance of *Laguncularia* as the pioneer mangrove remains unexplained. In an effort to understand the processes behind this mangrove distribution pattern, the main objective of this study is to assess the importance of various biological and physical properties of mangrove propagules and the mangrove environment, which make *Laguncularia* a successful colonizer in this environmental setting. Based on the observed distributions, we hypothesize that *Laguncularia* is a more successful pioneer than *Avicennia* spp. because of propagule physical characteristics, rapid rooting (fixation), insensitivity to shallow burial by sediment, and anchoring insensitivity to moderate water movement and frequent flooding.

1.1. Study area

The study was conducted in mangrove forests of the Tempisque and Bebedero rivers, which flow into the Gulf of Nicoya, a tropical estuary on the Pacific coast of Costa Rica (Fig. 1). Both rivers together supply the largest contribution of freshwater to the upper Gulf (Voorhis et al., 1983), as well as sediments and nutrients to the estuary (Epifanio et al., 1983). This estuary represents the second most important region colonized by mangroves in the country, covering an area of approximately 15 176 ha (Jiménez and Soto, 1985; Jiménez, 1994). Climatically this area is considered a lowland dry tropical forest life zone (Holdridge, 1967), characterized by a long dry season (December through April) with a monthly average rainfall of 50 mm or lower, and a rainy season (May through November) with a monthly average rainfall of up to 600 mm or higher. The annual precipitation for the region falls between 1500 and 2000 mm (Peterson, 1960). The tidal regime is semi-diurnal, with an amplitude ranging 2–3 m (Peterson, 1960).

*L. racemosa* is the dominant species in the lower intertidal zone forming monospecific patches 17–40 m wide. In the middle intertidal zone (13–40 m wide) it is also very abundant, but forms a more mixed forest with other species such as *Avicennia* spp., *Pelliciera* and/or *R. racemosa*. *Rhizophora* and *Avicennia* spp. were the main species colonizing the upper intertidal zone, but with some contribution of *Laguncularia, Pelliciera* and/or more upland vegetation. The presence of marginal vegetation and facultative marginal vegetation (Jiménez and Soto, 1985) such as *Tabebuia palastris, Anona glabra, Cocoloba caracasana* (trees and shrubs), *Bactaris minor* (palm), *Crinum erubescens* (lily), *Echinochloa polystachya, Panicum maximum* (grasses), is an indication of the low salinity conditions of the environment (salinity ranged between 0 and 8 ppt). Most of these species were distributed in the interior areas of the forest at higher elevations, with the exception of *C. erubescens, T. palastris* and the grasses, which could also be found in lower intertidal zones.
Fig. 1. Map of the Tempisque-Bebedero estuarine system showing the study areas, numbered from 1 to 6. Propagules for the field cross-planting experiment were placed across each area’s intertidal gradient according to the following pattern — study area 1: MB, LI; study area 2: MB, LI, UI; study area 3: LI; study area 4: MB; study area 5: UI; study area 6: UI. Here MB, LI, UI correspond to mud bank, lower and upper intertidal zones.
2. Methods

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

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

2.1. Field cross-planting experiment

This study was designed to measure differences in the ability of *Laguncularia* and *Avicennia* propagules to establish in point bars and islands along the gradient from mud bank to lower and upper intertidal zones. We hypothesize that differential success in propagule establishment will explain the observed pattern of mangrove distribution, with *Laguncularia* acting as the pioneer mangrove species.

Six study areas, located in point bars and islands, were selected along the Tempisque and Bebedero rivers (Fig. 1). Each area included one or more of the three zones: mud bank (MB), lower intertidal (LI), and upper intertidal (UI), which were defined mainly by their differences in frequency and duration of tidal flooding, and vegetation. MB and LI zones are generally flooded daily, although during very low water levels, the LI zone may not be completely covered. Because of its higher elevation the UI zone is only flooded during the highest tides of the month. For a 12 h tidal cycle approximate flooding durations per zone are as follows: MB, 4–5 h; LI, 2–3 h; UI, 0–1 h. Soil consolidation also changed across the intertidal zone increasing from MB to UI zone. The MB is generally unvegetated, the LI zone is colonized by *Laguncularia* and the UI zone by a more mature and mixed mangrove forest.

Propagules of *Laguncularia* and *Avicennia* were collected from the field in September 1998. *Laguncularia* propagules were taken directly from the trees, while *Avicennia* propagules with intact pericarps were taken from the forest floor, since propagules were hard to reach from the tall, mature trees. Propagule fresh weight and length measurements were taken from representative samples of all species. A tethering system was used to keep the experimental propagules from leaving the study zones in which they were to be
placed; a fine fishing line 30 cm long was pulled through the propagule cotyledons with a sewing needle, taking care not to damage the embryo. The propagule was then tied to a 30 cm wire stake. One hundred propagules of each species were thus prepared and placed in each of the three study zones (MB, LI, and U), and replicated a total of three times across the various areas (Fig. 1), for a total of 900 propagules per species. The elapsed time between propagule collection and deployment in the field was between 1 and 2 days. Propagules were set 25 cm apart along four lines parallel to the main channel. In MB zones, a boardwalk parallel to the channel was built to avoid sediment disturbance, and propagules were placed 25 cm apart along four lines, two along each side of the board. Placement of propagules in the field was done at different times between September 8 and 20, due to logistical constraints and the lack of embryo dormancy. Once the propagules were placed in the field, radicle protrusion, establishment, expansion of first pair of leaves, mortality and survival were recorded at different intervals for approximately 40 days. A propagule was considered established once the radicle was anchored and the cotyledons lifted above the sediment surface. Mortality was differentiated by cause (e.g. desiccation, herbivory and other factors). A last reading of survival–mortality was recorded after 75 days for several of the study areas. Due to preliminary results showing crab propagule predation, the abundance and size of crab holes was estimated for LI and UI zones. Five plots of 1 m² were randomly placed in each LI and UI zone across areas. Due to very low crab activity observed in MBs, crab abundance was not quantitatively estimated for these zones.

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

2.2. Mesocosm experiment

This second study was designed to determine the importance of propagule buoyancy, time of establishment, hydroperiod and high sedimentation (shallow burial) in the establishment success of \textit{L. racemosa} and \textit{A. germinans} propagules. Twenty wooden mesocosms (boxes), approximately 51 cm × 38 cm and lined with a plastic bag, were placed in open sunlight (airstrip) at the Palo Verde Biological Station located at approximately 2 km northeast from the first study area. All mesocosms were exposed to the same climatic conditions. Each box was filled with 7 cm of sediment collected from a Tempisque river mud bank, and was covered with 10 cm of Tempisque river water. Four different flooding treatments consisted of (1) flooded according to tidal cycle (FT), (2) no flooding (NF), (3) continuous flooding (F), and (4) flooded according to tidal cycle with propagules buried at approximately 2–3 cm deep (FTB). Treatments were randomly assigned to the mesocosms, with five replicates per treatment. For those boxes assigned to the F treatment, water was replaced once a day. In boxes assigned to the NF treatment, sediments were maintained under saturated conditions, but with no water above the sediment surface.
Boxes with treatments FT and FTB were flooded and non-flooded for alternate periods of 6 h each, simulating a semi-diurnal tidal cycle. Water within the boxes was never reused; replacement water was taken from the Tempisque immediately before use.

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

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

### 3. Results

#### 3.1. Field cross-planting experiment

**3.1.1. Propague radicle protrusion**

Across intertidal zones, radicle protrusion for *Laguncularia* and *Avicennia* propagules after the fifth day in the field ranged from 66 to 81, and 84 to 89%, respectively (Table 1). At this time, *Laguncularia* propagules in MB had 15% more radicle protrusion than LI and 8% more than UI. *Avicennia* propagules in LI and UI had 5% more radicle protrusion than MB. By the end of the experiment (≈40 days) between 1% (UI) and 25% (MB) of the *Laguncularia* propagules that developed radicle and did not die were unable to establish, compared to 20% (LI) to 53% (MB) for *Avicennia* (Table 1).

**3.1.2. Propague establishment**

*Laguncularia* showed maximum establishment in the following order: LI (73%) > MB (52%) > UI (18%). Establishment in LI and MB was significantly greater than in UI ($P < 0.05$ and $P < 0.1$, respectively). Highest establishment for *Avicennia* was also in LI (66%), followed by UI (51%) and MB (29%); establishment was significantly greater in LI than in MB ($P < 0.05$). *Avicennia* had significantly higher establishment than *Laguncularia* in UI ($P < 0.05$). Maximum cumulative establishment for *Laguncularia* and *Avicennia* started at approximately 11–15 days and extended until the end of the experiment (26–40 days, Fig. 2). Both species had an early rapid establishment (days 6–10) in MB and LI. Most established propagules of both species expanded their first pair of leaves by 16–25 days in all three zones (Table 1). However, after 40 days, 13, 23, and 14% of established *Laguncularia* propagules and 8, 51 and 30% of *Avicennia* had not yet opened their leaves (for MB, LI and UI, respectively).

The maximum percentage of anchored *Laguncularia* propagules that were naturally buried in sediment was 10 and 6% for MB and UI, respectively, with 5 and 6% for *Avicennia* in the same zones, during a 40-day time interval (Table 1). Most of this burial was related to crab activity.
Table 1
Results of the *Laguncularia* and *Avicennia* propagule field experiment following the gradient*

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*MB: mud bank; LI: lower intertidal; UI: upper intertidal. Total percentage (% ± S.E.) of propagules is given for each of the conditions. Conditions were defined as follows — R: propagule with protruded radicle; ES: propagule established (including LE); LE: propagule with first pair of leaves expanded; D: propagule dead, missing or eaten; B: propagule buried.

### 3.1.3. Propagule mortality and survival

Average mortality of *Laguncularia* propagules, pooling across zones, was approximately 1.6 times greater than that of *Avicennia* (*P < 0.05*). By zone (pooling species), mortality was significantly higher in UI (71%) compared to MB (17%, *P < 0.05*) and LI (37%, *P < 0.1*). Propagule mortality was also analyzed in two separate categories: dead-missing (D), and eaten (E, Fig. 3). Differences in D propagules among zones was not significant, but
Fig. 2. Establishment of *Laguncularia* and *Avicennia* propagules in the field experiment following the gradient: MB, LI, UI. Values at each time period are expressed as the average percent of established propagules calculated from the total number of non-established propagules remaining from the previous time period.

Fig. 3. Total mortality of *Laguncularia* and *Avicennia* propagules in the field experiment. Mortality of propagules was divided into two categories: dead and eaten propagules; missing propagules were assumed to be dead. Values are given as the average percent of total number of propagules for MB, LI, and UI zones.
overall, *Laguncularia* had higher D propagules than *Avicennia* \( (P < 0.05) \). Significantly higher predation (E) of *Laguncularia* propagules occurred in UI (52%) compared to MB (2%, \( P < 0.05 \)), and LI (5%, \( P < 0.05 \)). *Laguncularia* also had significantly higher propagule predation than *Avicennia* in UI \( (P < 0.05) \). *Laguncularia* propagules were eaten 11 more times than *Avicennia* in the same period of time: in approximately 25 days 52% of *Laguncularia* propagules were eaten compared to 5% for *Avicennia*. LI and UI had similar abundance of crab burrows: 85 and 75 burrows m\(^{-2} \), respectively. Size class distribution of crab burrows, however, was significantly different between zones \( (P < 0.001, \text{Fig. 4}) \). Significantly more crab burrows of smaller size were distributed in LI \( (P < 0.001) \), while significantly more crab burrows of larger size were distributed in UI \( (P < 0.001) \). In LI, 87% of the total crab burrows measured corresponded to sizes between 1 and 10 mm in diameter, while in UI, 57% corresponded to sizes between 11 and 20 mm in diameter. Direct observations of crabs eating propagules were not conducted, but high abundance of the grapsidae *Sesarma sulcatum* (personal observation) on the upper intertidal zones suggests that this is likely to be the main species predaing both species, mainly *Laguncularia*.

*Laguncularia* survivorship curves had more pronounced slopes (\( \delta \)) compared to *Avicennia* for all three zones (Fig. 5). Calculated half-life (ln(0.5/\( \delta \)), Pielou, 1974) values for *Laguncularia* seedlings (MB = 45 days; LI = 40 days; UI = 37 days) were between 2.1 and 3.4 times less than those for *Avicennia* (MB = 117; LI = 84; UI = 126 days).

### 3.2. Mesocosm experiment

#### 3.2.1. Propagule size and buoyancy

*Laguncularia* had significantly smaller propagules than *A. germinans* \( (P < 0.05) \). The average fresh weight and length of *Laguncularia* propagules was 0.35 g (±0.01 g S.E.)
Fig. 5. Survivorship curves $\log(N_x)$ for the cohorts of *Laguncularia* and *Avicennia* seedlings used in the field experiment, for MB, LI, and UI zones. $N_x$: number of living seedlings.

and 19.1 mm (±0.1 mm S.E.), respectively, compared to 1.90 g (±0.04 g S.E.) and 24.7 mm (±0.2 mm S.E.) for *A. germinans*. Under continuous flooding (F), *Laguncularia* propagules lost their buoyancy soon after radicle protrusion. Propagules began to sink by the second and third day of being in the mesocosm and between 5 and 8 days, 83–100% of the propagules had already sunk. *A. germinans* propagules floated during the whole 25-day experiment even though long roots developed.

### 3.2.2 Propagule seedling development

Under the treatment flooded according to tidal cycle (FT), *Laguncularia* propagules had 48% of radicle protrusion by the fifth day compared to 100% for *A. germinans*. By days 11 and 12 both species had less than 50% of establishment, and by day 17, 17 and 40% of *Laguncularia* and *A. germinans* propagules had opened their leaves. At the end of the experiment 29 and 31% of the *Laguncularia* and *A. germinans* propagules, respectively, showing radicle protrusion were not able to establish (Figs. 6 and 7). Under continuous flooding (F), both species had fast radicle protrusion, but only *Laguncularia* propagules lost their buoyancy and were able to establish. After 8 days all *Laguncularia* propagules
had sunk and by day 11 they began to establish; however, it was not until day 22 that leaves began to expand (Figs. 6 and 7). Under no flooding (NF) conditions both species had more than 70% of radicle protrusion by day 5, and by days 11 and 12 more than 80% of propagules had established. Contrary to A. germinans, in which leaves began to open at about the same time as establishment, Laguncularia showed a lag of 4 days (Figs. 6 and 7).
3.2.3. Propagule establishment

Propagule establishment for both species was greater than 60% under NF and FT treatments. Success of *Laguncularia* establishment under NF (93%) and F (84%) was significantly greater than FT (63%, \( P < 0.05 \)). Success of *A. germinans* establishment under NF (97%) was significantly greater than FT (69%, \( P < 0.05 \)). Establishment of *Laguncularia* was significantly greater than *A. germinans* under F conditions (\( P < 0.05 \), Figs. 6 and 7).
Laguncularia established faster under NF compared to other conditions. Propagules started to establish around day 8, and by day 17 approximately 89% of the total propagules were established; by day 23, 93% of propagules were established. Propagules growing in F and FT began to establish at day 11, reaching maximum establishment between 24 and 25 days with 80–84, and 60–63% of establishment for F and FT, respectively. Similarly to Laguncularia, A. germinans establishment was faster under NF conditions. Propagules began to establish at day 6 and by day 19, 97% of all propagules had established. Propagules in FT began to establish at day 7, reaching 69% of establishment at day 19 (Figs. 6 and 7). Laguncularia showed an approximate peak of establishment between days 14 and 17 for F and FT, and between days 9 and 11 for NF. The peak of establishment for Avicennia for FT and NF was at approximately 9–12 and 7–10 days, respectively.

3.2.4. Seedling growth

Growth of established Laguncularia seedlings was significantly different among treatments ($P < 0.05$), following the gradient FT > NF > F. Height increment of A. germinans seedlings did not differ significantly among treatments, however, A. germinans seedlings under NF conditions showed significantly greater height increment than Laguncularia ($P < 0.05$, Fig. 8).

3.2.5. Propagule mortality

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

3.2.6. Response of buried propagules

A very low percentage of buried propagules were able to rise to the sediment surface and establish (Laguncularia: 11%; Avicennia: 1%). It took 17 and 21 days for the first Laguncularia and A. germinans propagules, respectively, to emerge. By the end of the
experiment, 8% of the *Laguncularia* propagules that were able to establish opened their first pair of leaves (Figs. 6 and 7). The propagules that did not establish during the study period had died.

4. Discussion

4.1. *Laguncularia* colonization and distribution in lower intertidal zones

The distribution of *Laguncularia* in the lower intertidal zone of point bars and islands sheds new light on the hypothesis proposed by Rabinowitz (1978c), which states that mangrove zonation is controlled by tidal sorting of propagules according to size and buoyancy capacities. Although *Avicennia* propagules are over 30% larger than *Laguncularia*, their greater buoyancy may restrict them to the middle and upper intertidal zones. Propagule size may therefore not be the more important characteristic. Indeed, the distribution of mangrove species with small propagules in the lower intertidal zone and species with large propagules in the middle to upper intertidal zones is a common observation for Australian mangrove forests (Smith, 1987a).

*Laguncularia* colonizes active sedimentary environments such as shoals and point bars in riverine mangrove forests of Mexico, Colombia and French Guyana (Pool et al., 1977; Cantera and Arnaud, 1997; Fromard et al., 1998). *Laguncularia* as a pioneer of low intertidal zones is not, however, typical for other environmental settings. In the downstream region of estuaries or under more marine influence, *R. mangle* is generally found colonizing mud bank deposits and lower intertidal zones, where higher salinities and more vigorous water movement exist. Under such conditions *Laguncularia* is found in higher elevations forming mixed stands with *Avicennia* and/or other species (Thom, 1967; Pool et al., 1977; Ball, 1980; Jiménez and Soto, 1985; Jiménez, 1994; Cantera and Arnaud, 1997). Throughout the Caribbean, *Laguncularia* has been observed as a dominant species in basin type mangrove forests (Jiménez, personal communication).

4.2. Dynamics of mud bank colonization

Mangrove establishment and colonization of new environments is initially dependent on the availability and successful dispersal of propagules to the sites of colonization (Ball, 1980; Clarke, 1993; Duke et al., 1998; Panapitukkul et al., 1998). High tree density increases the number of propagules that can be dispersed, and the closer the parent trees are to sites of colonization the higher the chances of successful dispersal. Both *Laguncularia* and *Avicennia* produce large quantities of small, water-dispersed propagules (Jiménez, 1994), however, the current dominance of *Laguncularia* adjacent to mud banks certainly places this species at an advantage for continued dominance of this zone. The absence of *A. germinans* in some forests along Biscayne Bay, FL, was attributed to a limited source of propagules and to physical factors affecting propagule dispersal such as direction of winds and currents (Ball, 1980). In Pak Phanang Bay, Thailand, in contrast, a rapid colonization of accreting mud flats by *Avicennia alba* was attributed to high propagule availability and dispersal to sites of colonization (Panapitukkul et al., 1998).
Frequency and duration of flooding within the upper intertidal zone are important factors affecting propagule dispersal of *Avicennia*. Dispersal of *A. marina* propagules in southeastern Australia was mostly restricted to a distance of 500 m from the point of release, with propagules under poor tidal flushing showing the least dispersal (Clarke, 1993). In north Australia, propagules of *Ceriops tagal*, a common species of mid to high intertidal zones had limited dispersal due to reduced tidal inundation (McGuinness, 1997a).

Propagule buoyancy is also an important factor affecting propagule dispersal and establishment in frequently flooded environments (Johansson et al., 1996). Propagules that can remain buoyant and viable for longer periods of time increase their effective range of dispersal (Steinke, 1975, 1986; Rabinowitz, 1978a; Johansson et al., 1996; Duke et al., 1998). *Laguncularia* propagules showed a floating period between 2 and 7 days, and the ability to establish and grow under water. *Avicennia*, however, floated during the 25-day experiment. In contrast to our studies, Rabinowitz (1978a) reported for *Laguncularia* in Panama an average floating period of 23 days in freshwater and 31 days in salt water, while *Avicennia* floated during an 82-day period. *A. germinans* propagules from Twin Cays, Belize showed a similar floating behavior as reported by Rabinowitz (McKee, 1995b). Being a “floater”, *Avicennia* has an increased chance of long distance dispersal and deposition in the upper intertidal (spring high tide), but also of being carried out of the system by tidal action.

On mud banks *Avicennia* propagules would require a longer stranding period to establish (Rabinowitz, 1978a). This process may occur during low tides, and if sediment becomes trapped within the cotyledons the propagules may lose their effective buoyancy and are more likely to remain sunken during succeeding tides (personal observation, Rabinowitz, 1978a). Under natural conditions, however, we did not find *A. germinans* or *A. bicolor* colonizing mud banks influenced by regular tidal action. This suggests that being a “floater” may ensure *Avicennia* dispersal to higher elevation zones where seedlings can better survive and grow once rooted (Rabinowitz, 1978a; Jiménez and Soto, 1985; Duke et al., 1998). Similarly, in a forested floodplain in South Carolina, bald cypress and water tupelo seeds, which remained buoyant up to 3 months, were dispersed during high water levels to elevated, less frequently flooded substrates where conditions were more favorable for seed germination (Schneider and Sharitz, 1988). Propagules that sink rapidly, such as *Laguncularia*, may result in restricted dispersal away from parent trees. In a Belizean mangrove forest, relative densities of *Laguncularia* seedlings just after dispersal coincided with the region dominated by conspecific adults (McKee, 1995b). Being a “sinker”, however, appears also to be an advantageous characteristic for a pioneer species colonizing frequently flooded environments such as mud banks. Similar to *Laguncularia*, propagules of *A. marina*, sometimes found in the seaward edge of mangroves (Semeniuk, 1985; Fujimoto and Miyagi, 1993; Osunkoya and Creese, 1997), sink within 1–3-day period (Steinke, 1975; Clarke and Myerscough, 1991; Clarke, 1993). This process of propagule dispersal, which relies on water level and buoyancy capacities seems to agree with the hypothesis of “directed dispersal” proposed by Howe and Smallwood (1982), which assumes that adaptations for dispersal increase the probability of seeds to reach suitable sites for germination.

If propagules of *Laguncularia* and *Avicennia* reach a mud bank and become stranded, differential tolerance of physico-chemical characteristics of the environment might become important in seedling survival. Results from this study have shown, however, that artificially-retained propagules of both species established and grew similarly on the mud
bank, and Avicennia even survived better than Laguncularia during early establishment. Even though significant interspecific differences in establishment success were not found due to high variability, 23% more Laguncularia propagules established in mud banks compared to Avicennia, and approximately 28% more Avicennia propagules remained non-established by the end of the 40-day experiment.

Establishment of Avicennia appeared to be more influenced by tidal water movements than Laguncularia. Under the action of relatively strong water currents buoyant Avicennia propagules tended to remain above the soil surface, making stranding more difficult. Those propagules that were able to stay on the bottom had to spend more energy and time reorienting their anchoring roots each time they were moved from their original position (personal observation). Similarly, A. germinans and R. mangle propagules had difficulty becoming established at a lower intertidal Rhizophora dominated zone, where tidal action regularly buoyed them away from the soil surface (McKee, 1995b). McMillan (1971) demonstrated a negative relationship between water turbulence and A. germinans root development under laboratory experiments. Under field conditions mortality of A. germinans of clipped plots in a Spartina low marsh was attributed to the physical effects of the tides (Patterson et al., 1993, 1997). The effect of water movement has also been shown on the establishment of other mangrove and wetland species (Foote and Kadlec, 1988; Clarke and Allaway, 1993; Clarke and Myerscough, 1993).

In our study, calculated half-life values for Laguncularia and Avicennia seedlings were 45 and 117 days, respectively; this compares well to values reported by Rabinowitz (1978b): 45 days for Laguncularia and 85 days for Avicennia. Much higher half-life values were calculated for A. bicolor in a monospecific stand (242 days), and in a mixed stand (732 days) in a mangrove forest in the Pacific coast of Costa Rica (Jiménez and Sauter, 1991). However, these experiments were conducted under different environmental conditions. Primary causes of early propagule mortality in mud banks were loss of viability and decay. Waves and water currents also washed a number of propagules out of the system. Herbivory and burial were not important sources of mortality. Crab activity in mud banks was very low or absent, and when present, corresponded to members of the genus Uca spp. (personal observation), which are not known for predating in mangrove propagules (Jiménez, 1994; Sousa and Mitchell, 1999). The percentage of buried propagules as a result of reworking and/or sediment deposition was lower than expected, especially since mud banks in this region are very active sedimentary environments. It appears that the same tidal action causing burial also lead to propagule uncovering. In Thailand, mortality of R. apiculata seedlings in an expanding mud flat increased linearly with increasing sediment accretion (accretion ranging from 0 to 32 cm; Terrados et al., 1997). Under mesocosm conditions, both Laguncularia and A. germinans were, however, very sensitive to only 2–3 cm of permanent burial, similar to other coastal plants (Jurik et al., 1994; Wang et al., 1994).

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

4.3. Lower intertidal mangrove distribution

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

Establishment of retained *Avicennia* propagules in the lower intertidal zone was significantly higher than in mud banks. Lower intertidal zones offer more consolidated soils and reduced water scour due to the presence of tree trunks, roots and debris on the forest floor, increasing the probability of propagule establishment. The growth of *Avicennia* (4.8 mm per day) and *Laguncularia* seedlings (5.2 mm per day) under simulated flooding according to tidal cycle (FT in mesocosm experiment) was high and did not differ between species. These values, probably an overestimation of growth under natural conditions, are higher than those obtained for *A. bicolor* in a reciprocal field planting experiment in a mangrove forest in the Pacific coast of Costa Rica. In that experiment, *A. bicolor* grew 1.8 and 1.4 mm per day when growing in monospecific *R. racemosa* and *A. bicolor* forests, respectively (Jiménez and Sauter, 1991). Additionally, *A. germinans* seedlings growing under three different zones (*Avicennia*, high-elevation *Spartina* and low-elevation *Spartina*), exhibited growth rates of 1.1, 0.9, and 0.9 mm per day, respectively (Patterson et al., 1993).

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

4.4. Upper intertidal mangrove distribution

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

Several factors are related to differential crab-induced propagule predation. Crab preference among different mangrove species has been related to propagule characteristics such as size and chemical composition (Smith, 1987b; McKee, 1995a,c). Differential predation has also been related to depth and frequency of flooding, which can affect crab forage time (Osborne and Smith, 1990) and crab community structure, favoring some species over others or affecting size or age distributions (Warner, 1969; McKee, 1995a). In this study, higher zones were flooded less regularly, and had significantly larger crab burrows than lower intertidal zones, which may partially explain the higher crab predation on these upper zones. Contrary to our observations, Sousa and Mitchell (1999) reported, higher crab propagule predation in the lower intertidal zones of a mangrove forest on the Caribbean coast of Panama. This zone was dominated by larger crab species such as *Ucides cordatus* and *Goniopsis cruentata*, while the upper intertidal zone was dominated by small species (*Uca* spp.). Even though crabs were not directly observed feeding on propagules in this study, a high abundance of the grapsidae *S. sulcatum* (personal observation) suggests that this might be one of the main species predating *Laguncularia* and *Avicennia* propagules in this upper intertidal zone. Crabs of the same family and genus have also being reported responsible for propagule predation in other mangrove ecosystems (Smith et al., 1989; McGuinness, 1997b; Dahdouh-Guebas et al., 1998).

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

In summary, limited propagule dispersal and selective crab predation of *Laguncularia* propagules are important factors limiting *Laguncularia* distribution in higher intertidal zones, favoring *Avicennia* development in this environment. Similarly, the effect of crab predation on the distribution and zonation of mangrove species has been shown for other mangrove ecosystems around the world (Smith, 1987b; Robertson, 1991; McKee, 1995a).

5. Conclusions

A characteristic distribution of mangrove species is observed across the intertidal gradient of point bars and islands in the Tempisque–Bebedero estuarine system. *Laguncularia*, a species with small propagule size, colonizes rapidly emergent mud banks and lower intertidal zones. *R. racemosa*, *A. germinans*, *A. bicolor*, *P. rhizophorae*, and associated mangrove vegetation are observed colonizing middle and upper intertidal zones. The
results of this study suggest that both physical and biological factors affecting early stages of mangrove establishment are important in determining mangrove species’ distribution in this environmental setting. These factors include propagule abundance, dispersal, buoyancy and sensitivity to flooding and mechanical stress. For *Laguncularia*, high propagule production, effective dispersal, short propagule floating period, and low propagule sensitivity to moderate tidal action and hydrologic regimes, are important factors explaining its successful colonization of emergent mud banks and lower intertidal zones. *Laguncularia*’s limited distribution in upper intertidal zones, on the other hand, is closely related to restricted propagule dispersal and an intensive and selective crab propagule predation, which greatly increases its mortality in this zone. Restricted dispersal and stranding requirements (buoyancy) are important factors limiting *Avicennia* establishment in lower intertidal areas, giving an advantage to *Laguncularia* in this environment.

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References


