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Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors

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Abstract A field study was conducted to evaluate the relative importance of factors affecting seedling establishment and survival on a mangrove-dominated island in Belize. An examination of spatial patterns of seedling relative densities in relation to reproductive adults and physico-chemical conditions provided correlative information on factors affecting mangrove regeneration patterns. Distance from reproductive adults explained 89–94% of the variation in relative density of *Rhizophora mangle* seedlings, whereas availability of resources (light and NH_4) explained 73–80% of variation in *Avicennia germinans* seedling relative density. Just after dispersal (December), 89% of the variation in *Laguncularia racemosa* seedling relative density was attributable to distance from reproductive adults, but 7 months later (July) 74% of the variation was explained by intensity of flooding- and salinity-related stresses. Survivorship (after 2.5 years) of propagules and seedlings of *R. mangle* and *A. germinans* transplanted to zones of contrasting physico-chemical conditions demonstrated that: (1) mortality was highest during the establishment phase and major causes were failure to strand before viability was lost, consumption by predators and desiccation; and (2) after establishment, differences in sensitivity to physico-chemical stress factors such as flooding (*A. germinans*) and initial orientation of the seedling axis (*R. mangle*) exerted a further influence on seedling survival. The results indicate that seedling recruitment in these neotropical forests is strongly influenced by dispersal patterns, differential establishment abilities and effects of physico-chemical factors that vary with elevation and distance from the shoreline.

Key words Mangrove zonation · Propagule
Seedling recruitment · Physico-chemical

Introduction

An understanding of the mechanisms that generate species distribution patterns has been a major goal of plant community ecologists. Zonation patterns in plant communities typically coincide with gradients in physico-chemical factors, although biotic effects may modify individual species' distributions (e.g., Grace and Wetzel 1981; Bertness 1991). Zonation of wetland vegetation is particularly striking and often results in monospecific bands of vegetation relative to the environmental gradient (Pielou and Routledge 1976; Nixon 1982; Vince and Snow 1984).

Mangrove forests, which develop in the intertidal zone along tropical and subtropical coastlines, are characterized by distinct, recurring patterns of species distribution. Mangrove zonation patterns are relatively simple in the Caribbean compared to other geographic regions (Chapman 1976; Tomlinson 1986) and thus represent an ideal system in which underlying mechanisms can be studied. The red mangrove, *Rhizophora mangle* L., typically forms monospecific stands along shorelines and creekbanks where inundation by the tides is frequent. At more interior sites, where tidal inundation is less frequent, the black mangrove, *Avicennia germinans* (L.) Stearn., is dominant. The white mangrove, *Laguncularia racemosa* (L.) Gaertn. f. forms extensive stands at the highest reaches of the tide, where flooding and salinity stresses are minimized, but occurs occasionally at lower elevations. Delineation of mechanisms underlying even simple zonation patterns may be difficult, however, since the mangrove habitat is characterized by spatial and temporal variation in several physico-chemical factors (Boto and Wellington 1984; McKee 1993a,b). Changes in soil surface elevation from low to high tidal positions causes variation in depth and duration of flooding. Variation in tidal inundation influences a number of edaphic factors including soil redox potential, salinity, pH, and concentrations of nutrients and phytotoxins such as sulfide that are known to influence growth and distribution of mangrove vegetation (Ball 1988; McKee 1993a,b). In addi-

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tion, biotic factors such as seed predation may vary across the intertidal zone and influence mangrove species distribution patterns (Smith 1987a; Smith et al. 1989; McKee 1994a).

Mangroves have little capacity for vegetative reproduction and are dependent on seedling recruitment for forest maintenance and spread (Tomlinson 1986). Consequently, establishment and survival of seedlings directly affect species distribution and abundance patterns. Some mangroves exhibit either vivipary (i.e., germination while attached to the parent tree: *R. mangle* and *A. germinans*) or precocious germination (i.e., during dispersal: *L. racemosa*) (Tomlinson 1986). Because there is no period of embryo dormancy or a buried seed bank in mangroves, mechanisms controlling seedling recruitment patterns are more easily studied than in other plant communities.

Clarke and Myerscough (1993) have shown that seedling distributions of an Australian mangrove (*Avicennia marina*) were attributable to dispersal patterns, but intertidal limits were controlled by physico-chemical factors. Clarke and Allaway (1993) further suggested that propagules of *A. marina* must establish in a suitable regeneration niche for recruitment to the sapling stage. Detailed studies relating seedling distribution patterns to specific physico-chemical conditions that vary with tidal elevation and influence recruitment have not been conducted in neotropical mangrove forests, however. Dispersal properties (Rabinowitz 1978a), seed predation (Smith et al. 1989; McKee 1994a) and seedling dynamics (Rabinowitz 1978b,c; Jimenez and Sauter 1991; Ellison and Farnsworth 1993) have been examined in relation to neotropical mangrove zonation, but information about the effects of establishment ability and physico-chemical conditions on seedling recruitment is lacking. In addition, most field studies have neglected to identify causes of seedling mortality, which would provide valuable information about biotic versus abiotic factors affecting mangrove regeneration patterns.

The work reported here is the first comparative study of establishment abilities and physico-chemical factors contributing to the spatial distribution of neotropical mangrove seedlings. I examined: (1) seedling distributions of *R. mangle*, *A. germinans* and *L. racemosa* in relation to adult zonation patterns and variation in environmental conditions, (2) relative abilities of two dominant species (*R. mangle* and *A. germinans*) to establish and survive in areas of contrasting physico-chemical conditions, and (3) major causes of seedling mortality during establishment. This evaluation of interspecific differences in seedling establishment and survivorship provides insight into the determinants of zonation patterns in mangrove forests.

Methods

Study site

The study site was a mangrove island range called Twin Cays (91.5 ha), 2.3 km west of the barrier reef crest and 17 km from the mainland in central Belize (16°50'N, 88°06'W). Mangrove islands in the Belizean coastal zone are predominately intertidal systems, unaffected by runoff of freshwater, sediment, and pollutants from terrestrial uplands, and also relatively isolated from anthropogenic activities. Examination of mechanisms underlying vegetation zonation patterns was thus greatly facilitated, since the total number of potential factors that might influence species distribution and abundance was minimized. The range consists primarily of two large islands bisected by a 0.5–2.0 m deep channel and is surrounded by a shallow (≤ 1 m deep) sand flat vegetated by turtle grass (*Thalassia testudinum*). The substrate of Twin Cays is composed of a dense, reddish peat formed from the fine roots of red mangrove and sand derived from calcareous algae (*Halimeda* spp.). A detailed description and map of Twin Cays is given in McKee (1993a).

Tidal amplitude at Twin Cays is 21 cm, and tidal exchange with the island interior occurs via deep, narrow creeks and over shallow, broad channels (Urish and Wright 1988). Tidal flow and velocity, which are maximal at the margins of the main channel, attenuate with distance from the shoreline. The elevational gradient is gradual and most of the island range lies within the intertidal zone.

The climate is tropical and temperatures recorded in the vicinity of Twin Cays vary from 21°C in February to 33°C in August–September (Ruetzler and Ferraris 1982). A rainy season occurs in Belize from June to December with an average annual rainfall of 218 cm reported for the mainland coastal district of Dangriga. Humidity varies between 58 and 96%. The last major hurricane (Hurricane Hattie) to affect the study area occurred in 1961.

The vegetation of Twin Cays is dominated by *R. mangle*, which occurs in monospecific stands along the island periphery and creekbanks. *Rhizophora mangle* tree size and vigor decreases with distance from the shoreline to interior ponds, where a dwarf growth form (i.e., <1.5 m in height) occurs. The black mangrove, *A. germinans* also forms monospecific stands, but primarily in the interior of Twin Cays, just landward of the *Rhizophora*-dominated shoreline. *Laguncularia racemosa* does not form extensive stands at Twin Cays, but individual trees up to 6 m tall can be found approximately 20–25 m from the shoreline and interspersed with the other two species. A common feature of the island interior is the occurrence of unvegetated flats, which resulted from *A. germinans* dieback. Herbaceous species at Twin Cays include *Batis maritima*, *Spartina spartinae*, *Sesuvium portulacastrum*, and *Distichlis spicata*. Zonation patterns and associated edaphic conditions at Twin Cays are described in detail in McKee (1993a).

Zonation patterns, physico-chemical conditions and seedling distributions

An area of Twin Cays characterized by a distinct spatial variation in dominant canopy species was selected for this study. Three replicate transects, 55 m in length and 10 m apart, were established perpendicular to the shoreline and traversed three distinct zones: a *Rhizophora*-dominant zone, a transition zone where *R. mangle* and *A. germinans* both occurred, and an *Avicennia*-dominant zone. The transects terminated at the margin of an unvegetated flat in the island interior.

Ten plots (15×3 m size, long axis oriented parallel to shoreline) were established at 5-m intervals along each transect for a total of 30 plots in the study area. Density of trees and height and diameter (at breast height in the case of *A. germinans* and *L. racemosa* and just above the highest prop root for *R. mangle*) of three individuals of the dominant species in each plot were measured with an extendible stadia rod and diameter tape, respectively. Individuals ≥ 4.0 m in height and 10 cm diameter at breast height (dbh) were

considered to be reproductive based on observations (over 7 years) that trees in this size class are the primary sources of seedlings at the study site.

Measurements of environmental conditions thought to influence mangrove establishment and growth were conducted twice (July and December) in each plot. Edaphic factors measured were: soil temperature, redox potential, and bulk density as well as interstitial water pH, salinity, and concentrations of sulfide, NH_4 , and P (see below for detailed methods). Quantum flux density was also determined in each plot at 10 cm above the ground.

Densities of *R. mangle*, *A. germinans*, and *L. racemosa* seedlings were determined in July and December in 5-m² plots established at 5-m intervals along the three transects described above. Seedlings were defined as rooted individuals characterized by a small stature and a lack of stem branching and belonged, therefore, to the same size class, but not necessarily the same cohort. No attempt was made to distinguish among cohorts, since these species can exist for several years as suppressed individuals in the understory.

Physical characteristics of propagules and seedlings

Size and buoyancy of mangrove propagules were determined to assess potential for dispersal by tidal action and potential ability to establish at different tidal elevations. Mature propagules of *R. mangle*, *A. germinans*, and *L. racemosa* were collected from trees at Twin Cays and nearby mangrove ranges during July, August, and December. Propagule length and fresh and dry masses were determined. Dispersing *R. mangle* and *A. germinans* propagules were collected at the study site and examined within 24 h of collection for propensity to sink or float. Flotation was assessed by placing each propagule into a tank of seawater and observing its flotation characteristics. *Rhizophora mangle* propagules, which are elongated, were additionally scored at to whether they floated in a horizontal or vertical position. Specific gravity of each propagule was determined by dividing the fresh weight of the propagule by its volume, which was measured by displacement of water in a graduated cylinder. Flotation characteristics of dispersing *L. racemosa* were not assessed due to an insufficient sample size.

The average stem height and basal diameter of newly-established seedlings (i.e., with embryonic structures present and with a single node above the cotyledonary scar; $n=30$) of each species were also determined by measurements of individuals occurring in the plots described above.

Seedling establishment and survival in contrasting zones

A manipulative experiment was conducted to assess the relative abilities of *R. mangle* and *A. germinans* to establish and survive in two contrasting forest zones, each exhibiting different physico-chemical characteristics and dominant canopy species. The design was completely randomized with a factorial treatment arrangement (2 species \times 3 growth stages \times 2 zones). Light gaps (10–15 m² in area) occurring in areas dominated by either *R. mangle* or *A. germinans* were selected and environmental conditions measured prior to initiation of the experiment. Three growth stages were collected from the study area: propagules, new seedlings (i. e., rooting initiated, but plumule unexpanded), and old seedlings (i. e., well-rooted with one node above the cotyledonary scar). Seedlings were carefully exhumed with a plug of soil to minimize disruption of the root systems. Six individuals representing all treatment combinations were randomly assigned to each of ten light gaps per forest zone and arranged in a circular pattern equidistant from the center of the gap and approximately 0.5 m apart. The propagules were laid on the soil surface, but tethered with nylon twine (c. 30 cm length) to restrict horizontal, but not vertical, movement by the tides. The seedlings (new and old) were similarly tethered, but also implanted in the soil in an upright position. The experiment was conducted in the area described above where vegetation and physico-chemical patterns had been previously characterized. A

duplicate site with the same zonation pattern was also established on the adjacent island. Survival was assessed at 6-months intervals for 2.5 years.

Analyses

Soil measurements

Soil redox potentials at 1 and 15 cm depths were measured with brightened platinum electrodes allowed to equilibrate for 15 min prior to each measurement. Each electrode was checked before use with quinhydrone in pH 4 and 7 buffers (mV reading for quinhydrone is 218 and 40.8, respectively, at 25°C). The redox potential (Eh) was calculated by adding the potential of the calomel reference electrode (+244 mV) to each value. Soil temperature at 5 cm depth was determined with a thermocouple probe and digital meter. Soil bulk density (oven-dry weight per volume) was determined with soil cores (50 cm³) collected with a coring device designed to minimize compaction.

Interstitial water measurements

Pore water was collected as described in McKee et al. (1988). An aliquot of the interstitial water was immediately added to an equal volume of an antioxidant buffer and later analyzed for sulfide with a sulfide micro-electrode according to instrument directions. Additional aliquots of interstitial water were collected in separate containers for the measurement of pH, salinity, and nutrient concentrations (after filtration through a 0.45 μm filter). Elemental concentrations of P were determined on filtered, acidified water samples with an inductively coupled plasma emission spectrometer (ICP) (Williams et al. 1986). Filtered, non-acidified samples for ammonium determination were frozen and later analyzed according to US EPA Method 350.1 (US EPA 1979).

Light levels

Photosynthetically active radiation (PAR) was measured with a quantum radiometer/photometer (LiCor Model LI-185A). A minimum of five measurements were taken at 10 cm above the soil and averaged to give a single reading for each sampling station.

Statistical analyses

Factor analysis was used to extract linear combinations from a correlation matrix of the environmental variables measured across the study area. The factor extraction method was principal components analysis (PCA) and varimax factor rotation was used to clarify the results (Gorsuch 1984). The factor scores were then used as dependent variables in a repeated-measures analysis of variance (ANOVA) to assess differences among zones and between sampling dates. Those environmental variables found to exhibit heterogeneous variance were log-transformed prior to multivariate analysis.

Relative seedling densities were observed to vary with distance from reproductive, conspecific adults and with factor scores derived from the environmental data. This relationship was examined by multiple regression analysis. The relative seedling densities of *L. racemosa* and *A. germinans* exhibited a linear relationship with the independent variables and no transformation was necessary. The relationship between *R. mangle* relative density and distance was non-linear, and the independent variable was transformed prior to analysis (Gomez and Gomez 1984). The observed nonlinear relationship was described by the equation:

$$Y = \alpha + \beta/X$$

The relationship was linearized by transforming the independent variable X to $1/X$. After transformation, a multiple regression anal-

ysis was performed using a stepwise procedure. Distance from reproductive, conspecific adults and the three factors extracted from the environmental data were the independent variables (X_1-X_4).

The 2.5-year survival data (after arcsine transformation of percent survival; Gomez and Gomez 1984) from the transplantation experiment were analyzed by a three-way ANOVA with site, species, and growth stage as the grouping factors. Differences in environmental variables measured at the transplantation sites were compared with unpaired *t*-tests. Flotation characteristics of propagules were assessed by a chi-square test of independence.

Results and discussion

The spatial distribution of plants reflects the outcome of a series of dynamic processes such as dispersal, predation, establishment, growth, and mortality. Dispersal patterns, predation rates, and establishment of diaspores are

processes that determine initial species distribution patterns. After establishment, differential tolerance of environmental stress factors can modify the initial pattern by eliminating some species from portions of an environmental gradient. The mangrove habitat is heterogeneous with spatial and temporal variation in light, salinity, redox potential, nutrients, phytotoxins and other factors (Boto and Wellington 1984; McKee 1993a,b), which, depending on species-specific attributes, may differentially influence establishment and subsequent survival of seedlings.

Zonation pattern and physico-chemical conditions

Although precise zonation patterns vary among geographic regions, mangrove forests are characterized by

Fig. 1 A Canopy height, B relative tree density (*Rhizophora mangle* □, *Avicennia germinans* ▨, *Laguncularia racemosa* ▩), and C relative elevation measured from the shoreline to 55 m in the island interior. Values are mean ± 1 SE

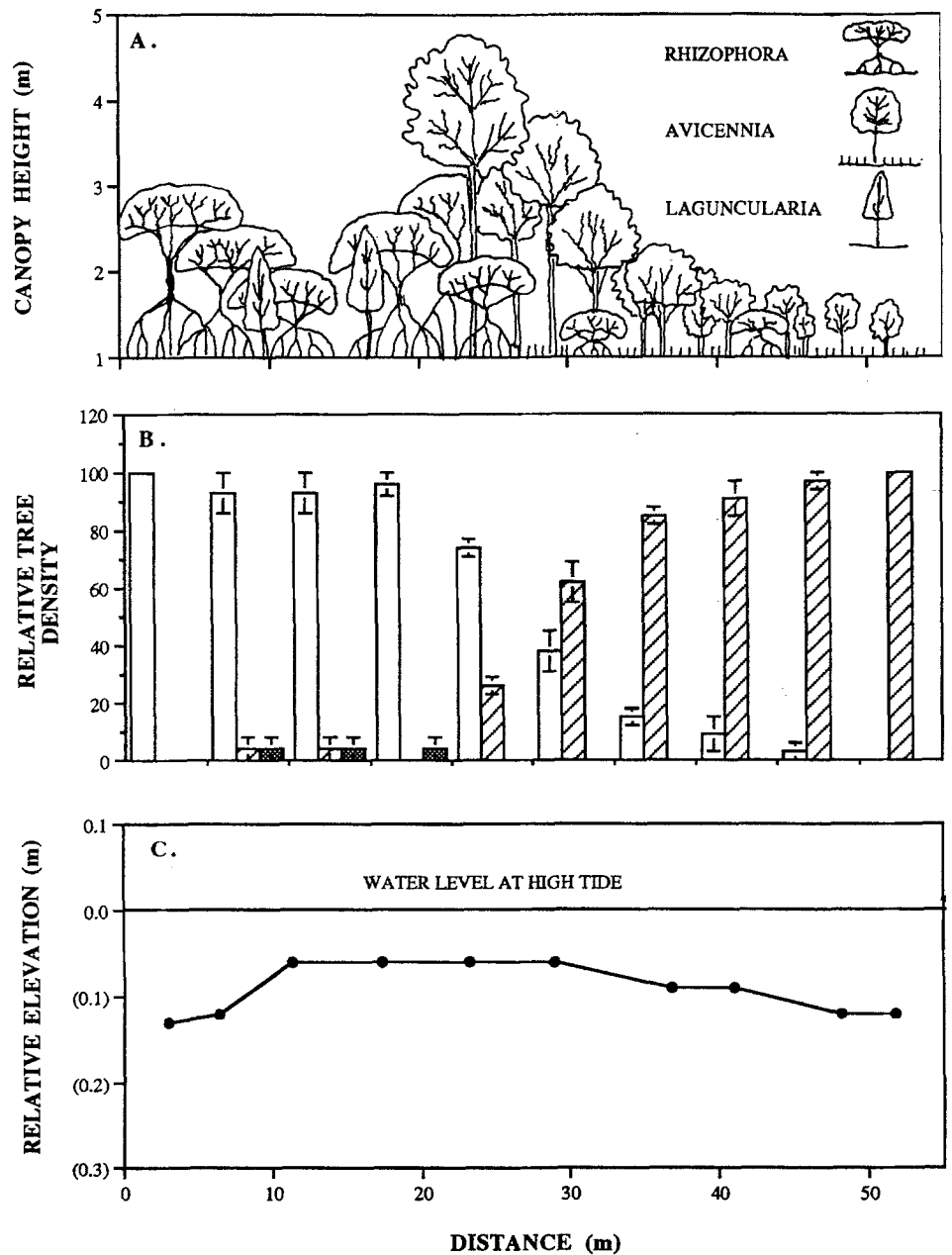


Table 1 Summary of physico-chemical data collected from the shoreline to 55 m in the island interior in December and July. The mean ($n=30$), 1 SE, minimum (*Min*) and maximum (*Max*) values measured across three replicate transects are given for two sampling dates

Variable	December				July			
	Mean	SE	Min	Max	Mean	SE	Min	Max
Soil:								
Relative elevation (m) ^a	-0.10	0.01	-0.06	-0.15	-	-	-	-
Bulk density (g cm ⁻³) ^a	0.194	0.007	0.126	0.276	-	-	-	-
Temperature (°C)	26.3	0.1	25.4	27.3	32.4	0.3	29.5	34.9
Eh at 1 cm (mV)	-135	12	-279	+166	+20	16	-147	+217
Eh at 15 cm (mV)	-136	9	-233	-14	-48	16	-247	+169
Interstitial water:								
Salinity (‰)	34	1	28	44	53	2	35	72
pH	7.4	0.1	6.8	7.8	6.1	0.1	5.3	7.3
Sulfide (mmol/l)	0.17	0.05	0.00	1.09	0.25	0.08	0.00	2.46
NH ₄ (μmol/l)	22.3	7.3	4.9	260.8	22.7	4.5	2.4	114.9
P (μmol/l)	38.7	0.7	30.2	48.1	42.3	0.6	34.8	50.3
PAR (%) ^b	57	6	1	100	55	6	2	100

^a Relative elevation (measured relative to water depth at high tide) and soil bulk density were determined once

^b Photosynthetically active radiation (PAR) expressed as a percent of full sunlight

distinct species distributions relative to tidal inundation and salinity (see Ball 1988; Smith 1992 for reviews). Detailed studies of edaphic factors have not been conducted extensively in neotropical mangrove forests, however, but are required for identification of factors controlling species distributions (e.g., McKee 1993a,b).

At Twin Cays, the transects intersected three zones: a shoreline zone dominated by *R. mangle*, a transition zone with a mixed canopy, and a landward zone dominated by *A. germinans*. This pattern is similar to that reported for other mangrove-dominated islands in the Caribbean and Florida (Cintron et al. 1978; Carlson et al. 1983). Canopy height, which was low in these island forests compared to mainland forests (personal observations), varied from 3 m near the creekbank to 4.6 m in the transition and 1.5 m at the most landward plots in the *Avicennia* zone (Fig. 1A). Relative density of *R. mangle* trees was highest in the plots located 0–25 m from the shoreline, whereas that of *A. germinans* trees was highest at 30–55 m (Fig. 1B). Relative density of *L. racemosa* trees was low in all three zones and reflected the infrequent occurrence of this species in the canopy (Fig. 1B). Relative elevation, which also varied with distance from the shoreline, was low next to the creekbank (0–10 m) and in the interior (45–55 m) (Fig. 1C). Elevations were highest in the landward portion of the *Rhizophora* zone and in the transition zone.

Qualitative observations over 7 years indicate that the higher-elevation sites were infrequently flooded over the soil surface, whereas the lower elevation sites near the shoreline were inundated twice daily. Tidal amplitude and water velocity decrease strongly with increasing distance from the shoreline and lead to restricted water movement and incomplete drainage of interior areas (Urish and Wright 1988; D. Urish personal communication). This hydrologic regime leads to spatial and temporal variation in physico-chemical conditions at Twin Cays (Table 1).

Table 2 Correlations of environmental variables with factors. (*Eh1* and *Eh15* soil redox potential at 1 and 15 cm depths, respectively, PAR percent of photosynthetically active radiation measured in full sunlight)

Variables	FACTOR		
	1	2	3
Relative elevation	0.213	-0.883	0.019
Bulk density	-0.015	0.496	0.676
Soil temperature	0.857	0.246	0.301
Eh1	0.864	-0.192	0.050
Eh15	0.833	-0.182	-0.017
Salinity	0.833	0.135	0.379
pH	-0.852	0.235	0.116
sulfide	0.007	0.834	0.033
NH ₄	0.246	0.005	0.825
P	0.565	0.428	0.392
PAR	0.018	-0.102	0.909
Percent variance explained by each factor			
	40.4	23.8	13.1

Because a number of the environmental variables were correlated, a factor analysis was conducted to simplify the data set. Three factors with eigenvalues greater than 1 were extracted and accounted for 77% of the variation in the data. The first factor was interpreted as a salinity factor with high positive loadings of interstitial salinity and soil temperature (Table 2). Soil redox potentials at 1 and 15 cm depths were also positively correlated with factor 1, while pH was negatively correlated. The second factor was interpreted as a flooding factor and had a high negative loading of relative elevation and a high positive loading of sulfide. Sulfide tends to accumulate in waterlogged soils, a process that is promoted in low elevation areas where water levels may not fall below the soil surface during a tidal cycle (McKee 1993a). The third factor was interpreted as a resource availability factor with high positive loadings of light

Table 3 Summary of ANOVA results for factor scores derived from physico-chemical measurements conducted across mangrove zones (see Table 2 and Fig. 1). *F* values are given in the table. Effect of transect (replicate) was not significant ($P>0.05$)

Source of variation	Factor 1 (salinity)	Factor 2 (flooding)	Factor 3 (resource)
Zone	5.04*	12.4***	36.2***
Date	433***	19.6***	9.8**
Zone×date	3.55*	7.17**	NS

* $P\leq 0.05$, ** $P\leq 0.01$, or *** $P\leq 0.001$

levels and NH_4 concentrations. Concentration of P was not strongly correlated with any factor.

When the factor scores were subjected to ANOVA, significant differences among zones (*Rhizophora*, transition, and *Avicennia*) were found for all three factors (Table 3). Overall, salinity and resource availability were low in the *Rhizophora* zone, but flooding intensity was high (Fig. 2). The *Avicennia* zone was characterized by high salinity and flooding as well as high resource availability (Fig. 2). Flooding intensity was low in the transition zone, whereas salinity and resource availability were relatively high (Fig. 2). Salinity and flooding were highest and resource availability was lowest during July (Table 3). Salinity, flooding, and resource availability factors differed significantly between July and December in the *Rhizophora* zone ($F_{1,27}=123.0$, 24.2, and 12.2, respectively; $P\leq 0.005$, 1 *df* contrasts). The transition zone differed between sampling dates in salinity and flooding factors ($F_{1,27}=104.5$ and 9.6, respectively; $P\leq 0.005$, 1 *df* contrasts), whereas the *Avicennia* zone differed only in terms of salinity-related factors ($F_{1,27}=212.2$; $P\leq 0.005$, 1 *df* contrast). Canopy structure also varied with increasing distance from the shoreline and as the dominant species changed from *R. mangle* to *A. germinans*. Consequently, PAR increased from less than 10% in the *Rhizophora* zone to near 100% full sunlight in the stunted portion of the *Avicennia* zone.

These results agree with other work in Australia (Boto and Wellington 1984; Clarke and Allaway 1993) and Florida (McKee 1993b) that demonstrated the heterogeneity of the mangrove habitat. The variation in physico-chemical factors observed across the intertidal zone in mangrove forests, thus, generates a continuum of contrasting conditions that may differentially influence seedling recruitment.

Seedling distributions across mangrove zones

Seedlings of *R. mangle*, *A. germinans*, and *L. racemosa* occurred throughout the three zones at the study site, but relative densities varied substantially with position along the transects (Fig. 3). The relative density of *R. mangle* seedlings was highest in the *Rhizophora*-dominated zone and decreased with distance from the shoreline. The pattern for *A. germinans* seedlings was different with highest relative densities 30–55 m inland and decreasing to

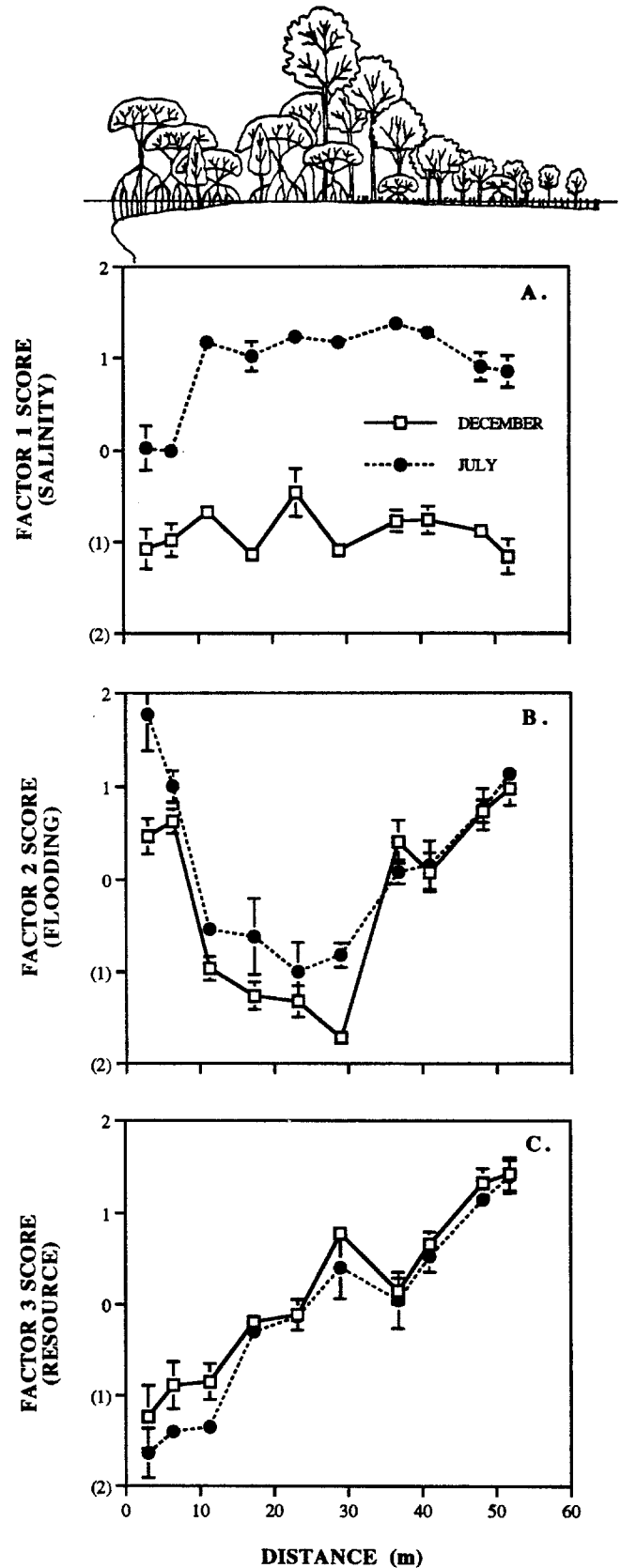


Fig. 2A–C Spatial and temporal variation in factor scores extracted from environmental data measured across the transects during July and December. Values are mean \pm 1 SE

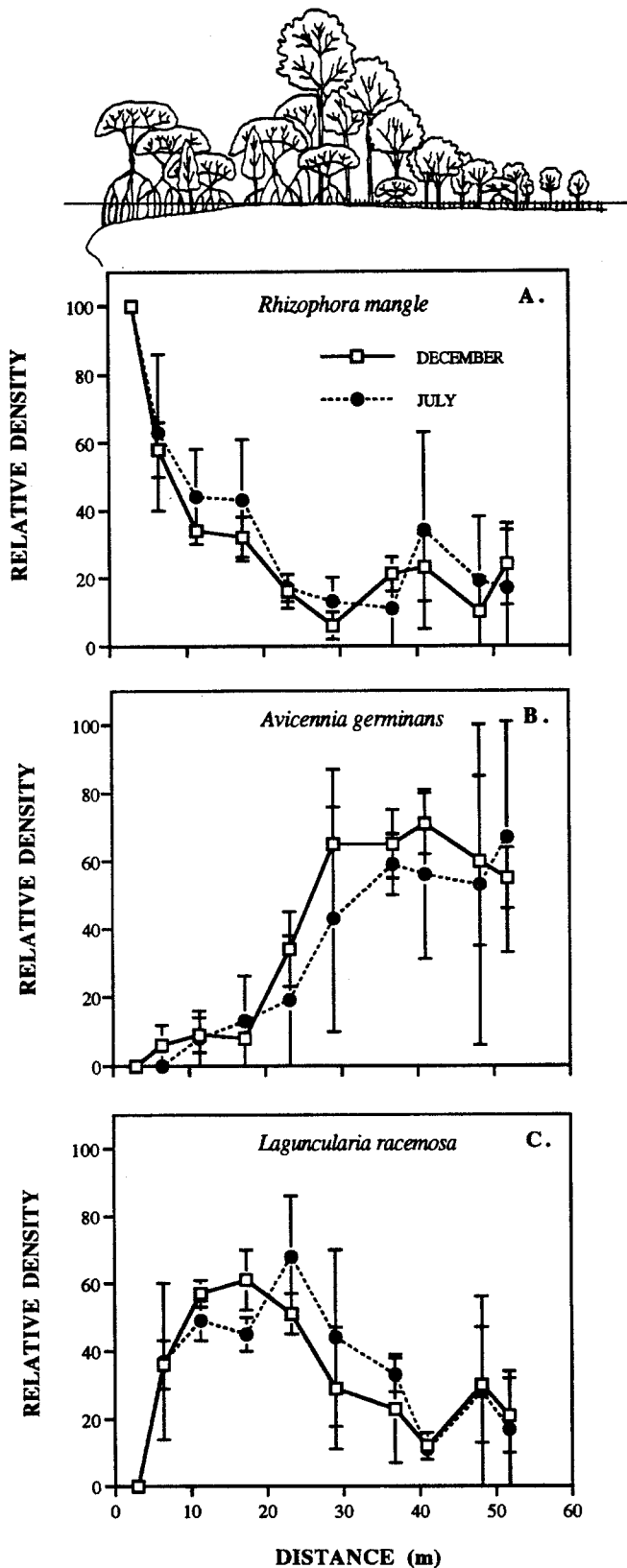


Fig. 3 Relative densities of A *Rhizophora mangle*, B *Avicennia germinans*, and C *Laguncularia racemosa* seedlings measured across the transects in December and July. Values are mean \pm 1 SE

ward the shoreline. Relative density of *L. racemosa* seedlings increased to a maximum 15–20 m from the shoreline and then declined thereafter. The peaks in relative seedling densities coincided with the region dominated by conspecific adults. The spatial pattern for each species in July was similar to that found in December, just after dispersal, but variances were higher in July.

Stepwise regression analysis was conducted with seedling relative density as the dependent variable and the average factor scores and distance from reproductive, conspecific adults as the independent variables (Table 4). In December, just after dispersal, distance from adults was the only independent variable to enter the equations and accounted for 94 and 63% of the variation in relative densities of *R. mangle* and *L. racemosa* seedlings, respectively. None of the factors extracted from the environmental data contributed significantly to the variation. Relative densities of *A. germinans* seedlings exhibited a different pattern with factor 3 (resource availability) explaining 73% of the variation in the dependent variable in December.

In July, distance from reproductive adults was still the only variable contributing significantly to the spatial variation in *R. mangle* relative seedling density ($R^2=0.89$). For *A. germinans* in July, factor 3 accounted for 80% of the variation in seedling relative density. Distance from reproductive adults was not important in explaining the variation in relative density of *L. racemosa* seedlings in July. At the 5% significance level, factor 2 (flooding) accounted for 54% of the variation in the dependent variable, and no other variable entered the equation. When the significance level was increased to 10%, factor 1 (salinity) also entered the equation and together with factor 2 accounted for 74% of the variation in relative density of *L. racemosa* seedlings.

Thus, distance from reproductive adults and environmental conditions were both important in explaining relative abundance of seedlings across zones. These results differ from those reported for the Pacific coast of Costa Rica where establishment rates of *Avicennia bicolor* and *Rhizophora racemosa* seedlings were not correlated with distance from reproductive adults (Jimenez and Sauter 1991). In Australia, however, Clarke (1993) found that the majority of *A. marina* propagules strand and establish close to the parent, but may be dispersed over greater distances by tidal action, similar to the results in Belize. Clarke and Allaway (1993) also found patterns of *A. marina* seedling and sapling survival that correlated with salinity, light and sediment factors.

The pattern of higher relative densities of seedlings near conspecific adults may have a number of explanations: (1) the propagules are not dispersed far from adults, (2) establishment rates of each species vary spatially, depending on buoyancy characteristics and tidal fluctuation relative to the soil surface, and/or (3) factors contributing to seedling mortality vary spatially and are less intense near conspecific adults. These alternatives are examined below.

Table 4 Results of a stepwise multiple regression analysis of seedling relative densities across Twin Cays. The values for the equation parameters (α , β_1 , β_2 , β_3 , β_4) and R^2 are given in the table. The independent variables (X_{1-4}) are distance from reproductive, conspecific adults and factors 1, 2, and 3 extracted from the

environmental data (see Table 2 and Fig. 2). Distance from *Rhizophora mangle* adults was transformed to $1/X$ prior to analysis to linearize the relationship with the dependent variable. Values in parentheses are the partial F -values for the regression coefficients ($P \leq 0.05$, except as indicated)

Dependent variable (Y) Relative seedling density (%)	Independent variables (X_{1-4})					R^2
	Distance	Factor 1 (Salinity)	Factor 2 (Flooding)	Factor 3 (Resource)		
Equation parameters:	α	β_1	β_2	β_3	β_4	
December						
<i>Rhizophora</i>	10.3	274 (118.7)	— ^a	—	—	0.937
<i>Avicennia</i>	34.5	—	—	—	26.37 (21.26)	0.727
<i>Laguncularia</i>	53.4	-0.925 (11.84)	—	—	—	0.628
July						
<i>Rhizophora</i>	14.35	270 (67.73)	—	—	—	0.894
<i>Avicennia</i>	34.2	—	—	—	22.21 (31.11)	0.795
<i>Laguncularia</i>	60.8	—	-23.57 (4.47 ^b)	-23.05 (16.44)	—	0.735

^a Partial F -value for the variable was not significant

^b Significant at $P \leq 0.10$

Physical characteristics of propagules and seedlings

Because of their unusual reproductive biology, recruitment of these mangrove species is not constrained by germination requirements, and the propagules begin to take root when they come into contact with the soil surface. Other factors such as size and buoyancy, however, may contribute to differential dispersal or establishment (Rabinowitz 1978a).

The propagules of *R. mangle*, *A. germinans*, and *L. racemosa* differed significantly in terms of size and shape. *Rhizophora mangle* propagules, which were composed of an elongated hypocotyl and unexpanded plumule, averaged 23.5 ± 0.6 cm in length and 20.2 ± 0.3 g fresh mass. The propagules of *A. germinans* were considerably smaller (1.05 ± 0.01 g fresh mass) with a flattened, elliptical shape comprised of two folded cotyledons. *Laguncularia racemosa* propagules were also small (0.30 ± 0.01 g fresh mass), obovoid in shape, and consisted of an embryo enclosed in a pericarp. These characteristics are the same as those described for Panamanian mangroves (Rabinowitz 1978a).

The dispersing propagules of *R. mangle* and *A. germinans* collected at Twin Cays also exhibited flotation characteristics similar to that reported in Panama (Rabinowitz 1978a). Of 117 *A. germinans* propagules examined, 92.3% floated and 7.7% sank in seawater (Table 5). Floaters were characterized by specific gravities lower than that of seawater ($\chi^2=9.18$, $P < 0.01$). Dispersing *R. mangle* propagules also showed a preponderance of floaters (86.6%) compared to sinkers (13.4%), but the orientation among floaters differed. Of the total propagules tested, 29.9% floated with the hypocotyl oriented in a horizontal position relative to water surface and 56.7% float-

Table 5 Flotation characteristics and specific gravity (SG) (g cm^{-3}) of dispersing *R. mangle* and *Avicennia germinans* propagules. Flotation response was determined by placing each propagule in a tank of seawater and observing if it sank or floated. Propagules of *R. mangle* were additionally scored as to flotation in a horizontal (FLH) or vertical (FLV) position. Values are the mean \pm 1 SE. SG of seawater = 1.025 g cm^{-3}

Flotation response	Species			
	<i>Rhizophora</i>		<i>Avicennia</i>	
	SG	n	SG	n
Sink	1.044 ± 0.006	13	1.068 ± 0.016	9
FLH	0.997 ± 0.005	29	1.003 ± 0.003	108
FLV	1.020 ± 0.003	55	—	—
Total	1.015 ± 0.003	97	1.012 ± 0.004	117

ed vertically. The flotation response of *R. mangle* also differed depending on the specific gravity of propagules ($\chi^2=12.91$, $P < 0.01$). The sinkers had an average specific gravity greater than that of seawater (Table 5). The specific gravity of propagules that floated in a horizontal position was lower than that of vertical floaters.

Rabinowitz (1978a) hypothesized that small, consistently buoyant propagules (e. g., *A. germinans*) could only become established at higher positions in the intertidal zone, whereas larger, heavier propagules (e. g., *R. mangle*) would be restricted to lower elevations. Propagule characteristics measured in Belize and Panama suggest that the establishment of *R. mangle*, *A. germinans*, and *L. racemosa* would be influenced by tidal action and the time required for rooting (15, 7 and 5 days, respectively; Rabinowitz 1978a). Other studies also support the role of propagule characteristics and tidal action in determining

differential establishment of mangroves across elevational gradients (Tamai and Iampa 1988; Jimenez and Sauter 1991).

In addition to differences in propagule size and buoyancy, seedling dimensions after establishment will also influence recruitment. Seedlings of the three species differed significantly in stature at an equivalent stage of development. At the two-leaf stage, *R. mangle* was substantially taller (27.3 ± 0.6 cm) than either *A. germinans* (11.0 ± 0.4 cm) or *L. racemosa* (7.0 ± 0.3 cm) ($F_{2,87}=420$, $P=0.0001$). These interspecific differences in seedling dimensions are comparable to that observed in the greenhouse at salinity and flooding intensities equal to field conditions (McKee 1993a). The elongated hypocotyl of *R. mangle* is primarily responsible for this species' height advantage at this stage of development. A comparison of average seedling heights with the water depths at high tide (Fig. 1C) illustrates these species' relative potential for submergence at Twin Cays. The average *R. mangle* seedling would be tall enough to maintain its leaves and upper stem above water at high tide across the entire elevational gradient, whereas *A. germinans* and *L. racemosa* seedlings would be substantially submerged at the lower elevation sites.

Because mangrove soils are usually anoxic with low redox potentials (Boto and Wellington 1984; McKee et al. 1988; McKee 1993a,b; Table 1), the roots of seedlings must receive oxygen from the atmosphere via diffusion through the stem. The average diameter of the seedling stem bases differed significantly among species, however, with *R. mangle* (1.01 ± 0.054 cm) > *A. germinans* (0.216 ± 0.002 cm) = *L. racemosa* (0.173 ± 0.002 cm) ($F_{2,87}=257.4$, $P=0.0001$). The smaller diameter of *A. germinans* and *L. racemosa* stem bases limits aeration of their root systems because of a lower cross-sectional area for oxygen diffusion (McKee 1993a). Thus, variation in depth and duration of submergence could differentially inhibit the oxygen supply to seedling root systems and contribute to mortality patterns.

Seedling establishment and survival in contrasting zones

Although mangrove dispersal properties and seedling morphologies and relative densities were suggestive of differential establishment abilities and tolerance of physico-chemical conditions (Fig. 3, Tables 4 and 5), they did not provide conclusive evidence that these factors were important in determining recruitment patterns across Twin Cays. Transplantation of propagules and seedlings allowed examination of relative establishment and survival in different physico-chemical regimes and identification of causes of mortality.

Measurement of environmental conditions in the two transplantation zones demonstrated significant differences in relative elevation, soil Eh, sulfide concentrations, salinity, and pH (Table 6). The sites dominated by *R. mangle* were characterized by a relatively lower elevation, more reducing soil conditions, and lower salinity than the sites dominated by *A. germinans*. Differences in

Eh at a 15 cm depth, soil temperature, and PAR were not significant ($P>0.05$). Although interstitial water pH was significantly higher at the *R. mangle* site, the difference with the *A. germinans* site was small (0.19 pH unit).

The survival patterns of *A. germinans* and *R. mangle* propagules and seedlings transplanted to these contrasting zones are presented in Fig. 4. Survival over 2.5 years was significantly influenced by species and growth stage at transplantation (Table 7). Overall survival of propagules (8%) was lower than for new seedlings (51%) ($F_{1,12}=120$, $P \leq 0.01$; 1 *df* contrast) or old seedlings (49%) ($F_{1,12}=106$, $P \leq 0.01$; 1 *df* contrast). Survival of *R. mangle* (averaged over growth stage and site) (47%) was greater than that of *A. germinans* (25%) (Table 6). Conditions at the sites where *A. germinans* dominated the canopy were more conducive overall to *A. germinans*' survival (42%) compared to sites dominated by *R. mangle* (8%) (Table 7). *Rhizophora mangle* survived equally well (averaged over growth stage) in areas dominated by conspecific adults (50%) or by *A. germinans* (43%).

Rabinowitz (1978 b) found greatest survival and growth of neotropical mangroves in areas not dominated by their conspecifics and concluded that this was evidence against physiological specialization as an explanation for zonation. Instead, she hypothesized that differential dispersal was the only explanation for the zonation patterns observed in Panama. Smith (1987b) similarly found that three of four Australian mangrove species performed best in the habitat where adult conspecifics were least abundant, and all four species appeared to prefer the same zone (high intertidal). Smith and coworkers proposed that differential predation on propagules was a major factor determining species' distribution patterns in mangrove forests (Smith 1987a; Smith et al. 1989). Ellison and Farnsworth (1993) examined survival of *R. mangle* and *A. germinans* in a Belizean mainland forest at three tidal heights and found that *R. mangle* survived well at the low and mid-tidal positions, *A. germinans* survived only at the mid-tidal position, and neither species survived at the high tidal position. Zonation patterns in that Belizean forest were attributed to differential spe-

Table 6 Physico-chemical conditions measured in contrasting zones characterized by different dominant species (*R. mangle* or *A. germinans*) and where survival of propagules and seedlings was determined (see Fig. 4). Values are the mean \pm 1 SE ($n=20$). Significant differences between zones were determined by unpaired *t*-tests

Variable	CANOPY DOMINANT		Probability of > <i>t</i>
	<i>Rhizophora</i>	<i>Avicennia</i>	
Relative elevation (cm) ^a	-15.1 \pm 0.2	-1.9 \pm 0.1	0.0001
Soil temperature (°C)	32.6 \pm 0.7	32.6 \pm 1.7	NS
Eh (1 cm depth) (mV)	-31 \pm 24	88 \pm 13	0.0001
Eh (15 cm depth) (mV)	-78 \pm 24	-41 \pm 30	NS ^b
Sulfide (mmol/l)	0.68 \pm 0.18	0.27 \pm 0.04	0.0335
Salinity (‰)	40 \pm 1	59 \pm 1	0.0001
pH	6.33 \pm 0.05	6.14 \pm 0.04	0.005
PAR (μ mol m ⁻² s ⁻¹)	1211 \pm 119	1120 \pm 170	NS

^a Elevation referenced to water depth at high tide

^b Non-significant difference

Fig. 4 Percent survival of *R. mangle* and *A. germinans* propagules, new seedlings (rooting initiated, but plumule unexpanded), and old seedlings (well rooted with one node above cotyledonary scar) transplanted simultaneously to two contrasting zones dominated by either *R. mangle* or *A. germinans*. Values are mean \pm 1 SE

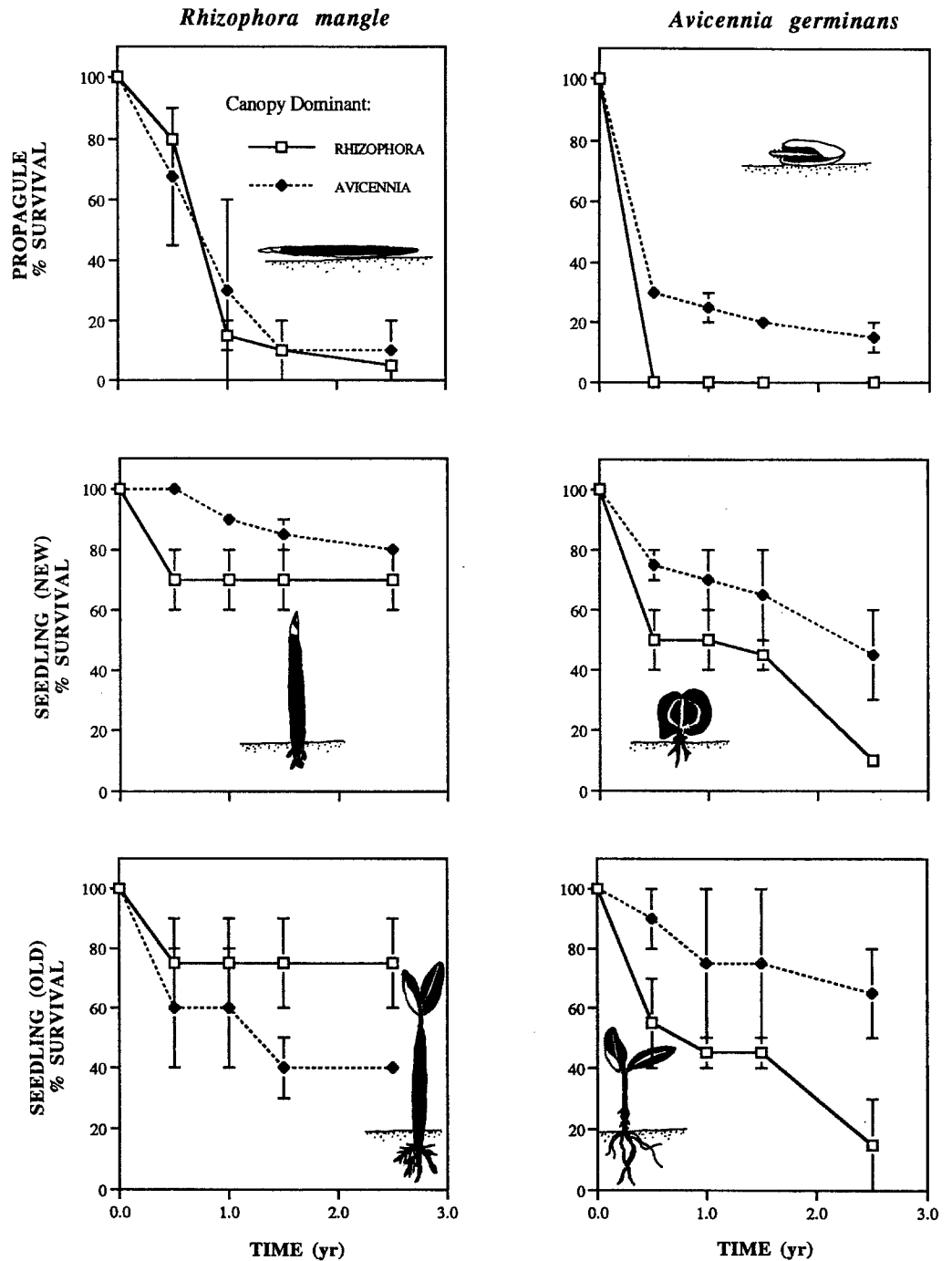


Table 7 Summary of ANOVA results for survival of *R. mangle* and *A. germinans* growth stages (propagules and new and old seedlings) transplanted to two contrasting zones

Source of variation	F value	Probability of > F
Species	12.3	0.0043
Zone	3.44	NS
Species \times zone	9.58	0.0093
Stage	19.0	0.0002
Zone \times stage	0.703	NS
Species \times stage	5.06	0.026
Species \times zone \times stage	3.96	0.0479

NS=not significant ($P>0.05$)

cies' responses to spatial variation in edaphic conditions, even though no environmental data were presented to support this conclusion. In all three cases, these experiments were initiated with planted propagules or seedlings, forcing establishment, and in two cases (Rabinowitz 1978b, Ellison and Farnsworth 1993) were of a shorter duration (c. 1 year) than the current study (2.5 years). Because these studies failed to account for species' differences in establishment ability, did not fully assess causes of mortality and/or were of short duration, they obtained an incomplete picture of the recruitment process in mangrove forests.

At Twin Cays, failure to strand before loss of viability, predation, and desiccation were major causes of mor-

Table 8 Proportion of propagule mortality (%) (all sites combined) attributable to various causes during the first year after transplantation to zones dominated by *R. mangle* or *A. germinans*

Source of mortality	Species	
	<i>Rhizophora</i>	<i>Avicennia</i>
Difficulty stranding	40	38
Predation	17	35
Desiccation	17	18
Unknown	26	9

tality of both species' propagules (Table 8). Propagules had difficulty becoming firmly rooted at the *Rhizophora*-dominated sites because of the relatively lower elevation and the fact that tidal action regularly buoyed them away from contact with the soil surface. Of propagule mortality at this site 68% was attributable to a failure to become rooted before viability was lost. Although the proportion of propagule mortality attributable to stranding difficulties was similar for the two species (Table 8), none of the *A. germinans* propagules was successful in establishing before viability was lost, whereas a few *R. mangle* propagules became firmly rooted and survived for 2.5 years (Fig. 4). Several *R. mangle* propagules remained viable for the first 6 months in an unrooted state, but finally died after 1 year.

Desiccation was the primary cause of mortality at the *Avicennia*-dominated sites (41% of deaths). Non-viable *R. mangle* propagules remaining after 6 months were shriveled and brown in color, but with no other signs of damage. Several *A. germinans* propagules became desiccated within 2 weeks of placement and ultimately succumbed to this factor.

Observations during the week after transplantation indicated that several propagules placed in the *Rhizophora* zone were eaten by mangrove crabs, whereas those placed in the *Avicennia* zone were damaged by snails. Combined losses to predators were similar at the *Rhizophora* and *Avicennia* sites (24 and 30%, respectively), although a larger proportion of propagule mortality of *A. germinans* at each site was assignable to consumption by predators (Table 8). Cause of mortality could not be confidently assigned for *R. mangle* and *A. germinans* in 26 and 9% of cases, respectively. These were all unrooted propagules that disappeared during the first 6 months. Other work at Twin Cays suggests that these individuals were completely consumed or buried in burrows by crabs (McKee 1994a). If so, then the proportion of mortality attributable to predators would increase to 43–44% for both mangrove species. Post-dispersal predation is a major factor affecting seedling recruitment patterns in Australian mangrove forests (Smith 1987a). Research in Belize and Panama, however, indicates that predation plays a less important role in the Caribbean compared to other geographic regions (Smith et al. 1989; McKee 1994a). *Rhizophora mangle*, in particular, fails to conform to the predictions of the dominance-predation hypothesis (*sen-*

su Smith 1987a) and is most abundant in the low intertidal zone where predation on its propagules is highest (McKee 1994a). Predation also could not account for the infrequent occurrence of *L. racemosa* trees at Twin Cays, since rates of propagule consumption were not different from that of *R. mangle* and significantly less than that of *A. germinans*. Only the predation pattern for *A. germinans* propagules was consistent with intertidal dominance of conspecific trees.

Mortality of *R. mangle* was additionally influenced by initial orientation of the seedling axis. All of the *R. mangle* propagules that established in the *Avicennia* zone took root with the hypocotyl in a prostrate position. Subsequent curvature of the hypocotyl allowed reorientation of the seedling axis into a vertical position. Even though these recurved seedlings produced leaves and appeared to grow well during the first year after establishment, most did not survive. Of *R. mangle* propagules that initially rooted in a horizontal position 90% died within 1.5 years. In contrast, more than 60% of the seedlings initially planted in a vertical position survived 2.5 years (Fig. 4). The cause of death of recurved seedlings could not be determined with certainty, but this growth response produced a deformed and presumably weakened seedling axis.

A number of early workers debated the significance of *R. mangle*'s potential ability to plant itself in the soil with the axis in a vertical position (Egler 1948; Lawrence 1949; La Rue and Muzik 1951). The propagules, which are elongated in shape and have pointed tips, were thought to drop from the parent tree and plunge into the soil substrate, effectively planting themselves in an upright position. Egler (1948) and Lawrence (1949) questioned the importance of this phenomenon because many seedlings appeared to establish in a prone position, but would subsequently develop a vertical axis through curvature of the hypocotyl, as observed at Twin Cays. The results of the current study, however, indicate that establishment in a vertical position, regardless of the mechanism, promotes survival of *R. mangle*. Thus, when *R. mangle* propagules are dispersed to areas where they strand and take root in a prone position (e.g., at higher elevations in the intertidal), long-term survivorship will be low. Seedling studies initiated by artificially planting propagules have not accounted for this response and, consequently, may have overestimated survivorship of *R. mangle* at some tidal elevations (e.g., Rabinowitz 1978b,c; Ellison and Farnsworth 1993).

Responses of transplanted *A. germinans* and *R. mangle* seedlings indicated differences in these species' physiological tolerance of conditions prevalent in the two zones (Fig. 4). The *Rhizophora*-dominated zone was characterized by greater flooding depths and more reducing soil conditions, whereas the *Avicennia*-dominated zone was less flooded but had higher salinities (Table 6). Seedlings of *A. germinans* transplanted to the *Rhizophora*-dominated zone had a lower survivorship compared to those transplanted to the *Avicennia*-dominated zone, but the difference was highly significant only for the old-

er seedlings ($F_{1,12}=9.95$, $P\leq 0.01$; 1 *df* contrast). Survival of *R. mangle* in the *Rhizophora*-dominated zone equaled (new seedlings) ($F_{1,12}=0.611$, $P>0.05$; 1 *df* contrast) or exceeded (old seedlings) ($F_{1,12}=6.64$, $P\leq 0.05$; 1 *df* contrast) that in the *Avicennia*-dominated zone. Comparison of species by zone showed that *R. mangle* seedlings (70–75%) had a higher survivorship than *A. germinans* seedlings (10–15%) transplanted to the *Rhizophora*-dominated zone ($F_{1,12}=15.1$, $P\leq 0.01$). Thus, when differences in establishment ability were excluded by planting the seedlings, *R. mangle* exhibited a higher survival rate than *A. germinans* in a more flooded situation. These results are consistent with work conducted in another Belizean mangrove forest (Ellison and Farnsworth 1993) and with greenhouse experiments showing that *A. germinans* seedlings are less tolerant of reducing soil conditions and sulfide than *R. mangle* seedlings (McKee 1993b).

The reverse, however, was not true in the *Avicennia*-dominated zone where flooding intensity was less, but salinity was higher (Table 6). Survival rates of both species' seedlings were high and indicated an equal tolerance of conditions in the *Avicennia*-dominated zone when establishment was not a factor ($F_{1,12}=0.153$, $P>0.05$). Ellison and Farnsworth (1993) also found that *R. mangle* and *A. germinans* both exhibited relatively high survivorships (69 and 47% after 1 year, respectively) when planted at a mid-tidal position in a mainland forest. Thus, the low relative densities of *R. mangle* seedlings in the *Avicennia*-dominated zone (Fig. 3A) appear to be primarily a function of limited dispersal and low survival of seedlings that establish in a prone position, rather than an intolerance of high salinity. This finding agrees with controlled experiments in which *R. mangle* seedlings survived salinity excursions exceeding those measured at Twin Cays (McKee 1993a).

Laguncularia racemosa readily establishes throughout the forest at Twin Cays, but the majority of seedlings do not survive. The variation in seedling density with flooding and salinity factors (Table 4) suggested that this species' distribution is strongly influenced by these physico-chemical factors. Laboratory experiments have shown that this species is even less flood tolerant than *A. germinans* and quickly succumbs to excessive inundation (McKee 1993a). Seedlings of *L. racemosa* also exhibit a lower lethal salinity level (80‰) than *R. mangle* (130‰) or *A. germinans* (100‰) in controlled experiments (McKee 1993a).

Conclusions

A complete understanding of the mechanisms causing zonation patterns in plant communities requires information about recruitment patterns since it is typically the seedling stage that experiences the highest mortality (Harper 1977). If all species in a community had similar dispersal properties, susceptibilities to seed predators, establishment abilities, and tolerances of edaphic conditions, their seedling distribution patterns across a gradi-

ent would initially coincide. In that case, zonation would have to be explained by some other mechanism such as competition during the juvenile or adult stages.

In Belize, spatial patterns of seedling relative densities indicated differential recruitment in relation to physico-chemical factors, but effect of proximity to reproductive adults demonstrated that dispersal patterns were also important. Evaluation of propagule and seedling characteristics suggested differences among species in ability to establish and initially survive conditions prevalent at different intertidal locations. Transplantation of propagules to contrasting zones confirmed that establishment rates vary spatially and in a pattern consistent with seedling distributions and conspecific dominance. After establishment, differential seedling tolerances of physico-chemical conditions further refined survivorship patterns in each zone.

The relative importance of factors determining seedling success differed among the three mangrove species and between high and low intertidal elevations. *A. germinans* propagules, which were small and consistently buoyant, could establish at higher elevations in the intertidal zone, but failed to take root in the low intertidal zone where tidal action limited contact with the soil surface. Even when establishment was forced, *A. germinans* seedling survival was significantly reduced by flooding-related stresses at lower elevations. In contrast, establishment of *R. mangle* seedlings was not differentially affected by site conditions, but long-term survivorship was low unless the seedlings initially established in a vertical position. Spatial and temporal variation in *L. racemosa* seedling densities in relation to distance from reproductive adults and physico-chemical factors suggested that this species' distribution was initially influenced by dispersal patterns, but was ultimately restricted by its lower tolerance of flooding and salinity. The conditions on mangrove islands such as Twin Cays are apparently too stressful for *L. racemosa* to achieve dominance in the community.

In addition to the factors discussed above, mangrove seedling recruitment may be influenced by availability of light and nutrients. Correlations between seedling densities and environmental factors suggested that *A. germinans*' survival patterns were modified by resource availability. Greenhouse experiments have shown that *R. mangle*, *A. germinans*, and *L. racemosa* seedlings differ significantly in their potential for growth and acquisition of resources (McKee 1994b). A nutrient enrichment and shading experiment conducted at Twin Cays has further demonstrated that growth of *A. germinans* and *L. racemosa* seedlings can be dramatically enhanced relative to that of *R. mangle* by increasing the availability of nutrients and decreasing the solar radiation load (McKee and Feller 1994). Seedling recruitment patterns across the intertidal zone in neotropical mangrove forests may, therefore, differ locally and regionally depending on nutrient input and canopy structure.

Biotic factors such as seed predation were not as important as physico-chemical factors in explaining differ-

ential recruitment of mangroves at Twin Cays. Although predators accounted for a large proportion of propagule mortality, there were no differences among species and combined losses due to stranding difficulties and desiccation were higher. Furthermore, an extensive investigation has demonstrated that spatial patterns of predation on *R. mangle* and *L. racemosa* propagules cannot explain variation in conspecific adult dominance at Twin Cays (McKee 1994a).

In summary, the results support the regeneration niche concept that seedlings require a specific combination of conditions for recruitment to the adult population. The patterns of recruitment observed at Twin Cays also indicate that seedling dynamics (i. e., change in species' distributions and relative abundances during establishment and early growth) is an important process contributing to the development of horizontal zonation patterns occurring on these mangrove-dominated islands.

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References

- Ball MC (1988) Ecophysiology of mangroves. *Trees* 2:129–142
- Bertness MD (1991) Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125–137
- Boto KG, Wellington JT (1984) Soil characteristics and nutrient status in a northern Australian mangrove forest. *Estuaries* 7:61–69
- Carlson PR, Yarbro LA, Zimmerman CF, Montgomery JR (1983) Pore water chemistry of an overwash mangrove island. *Fl Sci* 46:239–249
- Chapman VJ (1976) Coastal vegetation. Pergamon Press, Oxford
- Cintron G, Lugo AE, Pool DJ, Morris G (1978) Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10:110–121
- Clarke PJ (1993) Dispersal of grey mangrove (*Avicennia marina* var. *australasica*) propagules in south-eastern Australia. *Aquat Bot* 45:195–204
- Clarke PJ, Allaway WG (1993) The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia* 93:548–556
- Clarke PJ, Myerscough PJ (1993) The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia; the effects of physical conditions, interspecific competition, and predation on establishment and survival. *Aust J Ecol* 18:325–344
- Egler FA (1948) The dispersal and establishment of red mangrove in Florida. *Carib For* 9:299–310
- Ellison AM, Farnsworth EJ (1993) Seedling survivorship, growth, and response to disturbance in Belizean mangal. *Am J Bot* 80:1137–1145
- Grace JB, Wetzel R (1981) Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *Am Nat* 118:463–474
- Gomez KA, Gomez AA (1984) Statistical procedures for agricultural research. Wiley, New York
- Gorsuch RL (1984) Factor analysis. Lawrence Erlbaum, London
- Harper JL (1977) Population biology of plants. Academic Press, London
- Jimenez JA, Sauter KA (1991) Structure and dynamics of mangrove forests along a flooding gradient. *Estuaries* 14:49–56
- La Rue CD, Muzik TJ (1951) Does the mangrove really plant its seedlings? *Science* 114:661–662
- Lawrence DB (1949) Self-erecting habit of seedling red mangroves (*Rhizophora mangle* L.). *Am J Bot* 36:426–427
- McKee KL (1993a) Determinants of mangrove species distribution patterns in neotropical forests: biotic and abiotic factors affecting seedling survival and growth. Ph.D. Dissertation, Louisiana State University
- McKee KL (1993b) Soil physicochemical patterns and mangrove species distribution: reciprocal effects? *J Ecol* 81:477–487
- McKee KL (1994a) Mangrove species distribution and propagule predation in Belize: An exception to the dominance-predation hypothesis. *Biotropica* (in press)
- McKee KL (1994b) Interspecific variation in growth, biomass partitioning and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. *Am J Bot* (in press)
- McKee KL, Feller IC (1994) Effects of nutrients and shading on growth and architecture of mangroves in Belize (abstract only). *Ecol Soc Am Bull Suppl* 75:149
- McKee KL, Mendelssohn IA, Hester MW (1988) Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *Am J Bot* 75:1352–1359
- Nixon SW (1982) The ecology of New England high salt marshes: a community profile. United States Department of the Interior, Washington
- Pielou E, Roulledge R (1976) Salt marsh vegetation: latitudinal gradients in the zonation patterns. *Oecologia* 24:311–321
- Rabinowitz D (1978a) Dispersal properties of mangrove propagules. *Biotropica* 10:47–57
- Rabinowitz D (1978b) Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. *J Biogeogr* 5:113–133
- Rabinowitz D (1978c) Mortality and initial propagule size in mangrove seedlings in Panama. *J Ecol* 66:45–51
- Ruetzler K, Ferraris JD (1982) Terrestrial environment and climate, Carrie Bow Cay, Belize. In: Ruetzler K, Macintyre IG (eds) The atlantic barrier reef ecosystem at Carrie Bow Cay, Belize I: structure and communities. Smithsonian Institution Press, Washington, pp 77–91
- Smith TJ III (1987a) Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology* 68:266–273
- Smith III (1987b) Effects of light and intertidal position on seedling survival and growth in tropical, tidal forests. *J Exp Mar Biol Ecol* 110:133–146
- Smith III (1992) Forest structure. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. American Geophysical Union, Washington, DC, pp 101–136
- Smith TJ III, Chan HT, McIvor CC, Robblee MC (1989) Comparisons of seed predation in tropical tidal forests from three continents. *Ecology* 70:2146–151
- Tamai S, Iampa P (1988) Establishment and growth of mangrove seedlings in mangrove forests of south Thailand. *Ecol Res* 3:227–238
- Tomlinson PB (1986) The Botany of Mangroves. Cambridge University Press, Cambridge
- Urish D, Wright R (1988) Mangrove island hydrologic model development. In: Ruetzler K (ed) A mangrove ecosystem: Twin Cays, Belize. (Western Atlantic mangrove program workshop report). Solomons, Smithsonian Institution, Washington, DC, pp 7–8
- US EPA (1979) Methods for chemical analysis of water and wastes. Environmental Monitoring and Support Laboratory, Office of Research and Development, Cincinnati
- Vince SW, Snow A (1984) Plant zonation in an Alaskan salt marsh. I. Distribution, abundance, and environmental factors. *J Ecol* 72:651–667
- Williams TR, Van Doren JB, Smith BR, McElvany SW, Zink H (1986) ICP analysis of biological samples. *Am Lab* 18:52–57