SUPPLY-SIDE ECOLOGY IN MANGROVES: DO PROPAGULE DISPERSAL AND SEEDLING ESTABLISHMENT EXPLAIN FOREST STRUCTURE?

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Abstract. Theory and empirical evidence suggest that spatial and temporal variation in propagule availability can have as great or greater an influence on community structure as post-recruitment biotic interactions, a phenomenon known as supply-side ecology. One of the first theories to invoke supply-side dynamics, D. Rabinowitz's Tidal Sorting Hypothesis (TSH), attributed the tidal zonation of mangrove tree species to the interacting effects of water depth and propagule size on dispersal and establishment. According to the TSH, smaller propagules are carried farther inland by flood tides than larger ones, stranding and establishing in greater numbers at upper tidal elevations. In contrast, larger propagules are better able to establish in deeper, more seaward areas because their size affords greater access to the soil surface and resistance to buffeting by moving water. Here we present results of the first comprehensive investigation of the TSH. In a series of experiments conducted at Punta Galeta on the Caribbean coast of Panama, we quantified patterns of propagule dispersal and establishment of the three dominant species: *Avicennia germinans, Laguncularia racemosa,* and *Rhizophora mangle.*

To measure dispersal patterns, we monitored movements (directions and distances) of marked propagules released at three elevations along each of three transects. On all transects, regardless of species or elevation, propagules moved seaward rather than being carried inland by tides, as predicted by the TSH. Rates of seedling establishment were monitored in experiments conducted at different tidal elevations. Contrary to the TSH, all three species established best in the lower intertidal, where they were in prolonged contact with the soil surface during low tides, and established more poorly in the upper intertidal basin, where standing water made rooting difficult. Seedling establishment was lowest in the wave-exposed, back reef habitat, but in accordance with the TSH, the large propagules of *Rhizophora* rooted and persisted better in this turbulent habitat than did the smaller propagules of the other species.

We conclude that the TSH does not explain the vertical distributions of mangrove species on Punta Galeta. Rather, a different form of supply-side dynamics imposed by the strong seaward movement of dispersing propagules is important in structuring our study forests.

Key words: Avicennia germinans; dispersal limitation; hydrochory; Laguncularia racemosa; *mangrove; propagule dispersal;* Rhizophora mangle; *seedling establishment; supply-side ecology; tidal sorting hypothesis; tropical forests; zonation.*

Introduction

It has long been recognized that dispersal can strongly affect population dynamics and community structure (e.g., Hutchinson 1951, Skellam 1951, Andrewartha and Birch 1954, Huffaker 1958, MacArthur and Wilson 1967, Krebs et al. 1969). Detailed studies of juvenile recruitment in populations of marine fishes and benthic invertebrates conducted during the early to mid 1900s provide some of the earliest empirical support for the importance of larval production, dispersal, and successful metamorphosis/settlement to population dynamics (Young 1987, Underwood and Fairweather 1989). Later, during the 1960s and 1970s, the focus of research

in marine benthic ecology shifted to the role of post-recruitment biotic interactions in determining community structure. These biotic interactions could be rigorously investigated with the then-novel technique of manipulative field experimentation. The 1980s saw a renewed interest by marine ecologists in the influence of a variable propagule supply, but with greater emphasis on its consequences for the structure and dynamics of multispecies assemblages, as opposed to populations of individual species (Underwood and Denley 1984, Connell 1985, Mapstone and Fowler 1988, Underwood and Fairweather 1989, Grosberg and Levitan 1992, Booth and Brosnan 1995, Morgan 2001, Underwood and Keough 2001). The term "supply-side ecology" (credited to J. Roughgarden by Lewin [1986]) was coined for the hypothesis that, in ecological systems comprised of local assemblages linked by dispersal, community structure can be more strongly influenced by the supply of new

individuals arriving and recruiting to a site (i.e., dispersing larvae or diaspores) than by post-recruitment biotic interactions. This idea was formalized in a number of mathematical models (e.g., Gaines and Roughgarden 1985, Roughgarden et al. 1985, 1988, Dial and Roughgarden 1998).

While this supply-side paradigm was developing in marine ecology, terrestrial-plant ecologists independently began to focus their attention on the role of a spatially and temporally variable seed supply in structuring terrestrial plant assemblages (Schupp and Fuentes 1995, Tilman and Kareiva 1997, Nathan and Muller-Landau 2000, Hubbell 2001, Levin et al. 2003, Levine and Murrell 2003). Much of this work has focused on the role of dispersal limitation, and its interplay with competition, in determining the membership and coexistence of species in plant assemblages. While the terminology is somewhat different, this concept is directly analogous to the concept of supply-side dynamics on sessile marine assemblages. Work in this area has given rise to a rich body of mathematical theory that, as discussed by Levine and Murrell (2003), has largely outpaced empirical evidence concerning the role of seed limitation in structuring plant assemblages. These authors call for more empirical studies that (1) measure seed dispersal patterns, (2) correlate these patterns with spatial or temporal variation in the species composition and structure of vegetation, and (3) experimentally manipulate seed shadows to confirm a causal relationship between seed dispersal patterns and the distribution and structure of plant assemblages.

One of the earliest supply-side theories of community structure, Rabinowitz's (1978a) Tidal Sorting Hypothesis (hereafter TSH), predates the coining of the term and has been largely overlooked in discussions of the phenomenon (excepting Levine and Murrell [2003]). The TSH attributes the differential distribution of mangrove tree species with tidal elevation (i.e., zonation) to the interacting effects of water depth and propagule size on propagule dispersal and seedling establishment. Mangrove forests, like the biota of rocky seashores, lakeshores, salt marshes, and mountainsides, have often been cited as a classic example of the zonation of species along environmental gradients (but see Ellison et al. [2000]). Rabinowitz (1978a) proposed the TSH as an alternative to prevailing hypotheses that invoked species-specific physiological specialization to, or preference for, differing edaphic conditions as explanations for mangrove zonation (e.g., Watson 1928, Macnae 1968, Lind and Morrison 1974, Chapman 1976; see Smith [1992] for a comprehensive discussion of alternative models of mangrove zonation). Rabinowitz developed the TSH after reciprocally transplanting different species of mangrove seedlings along the tidal gradient and observing that they grew and survived as well or better in zones dominated by adults of other species than they did in zones dominated by adults of their own species. This finding did not support the idea that the species were physiologically adapted to survive and grow best under distinct regimes of tidal inundation and soil salinity.

Mature mangrove propagules are buoyant when first released from the parent plant; the length of time that they remain buoyant varies among species, populations of the same species in some cases, and with water conditions (e.g., Rabinowitz 1978b, Steinke 1986, Clarke and Myerscough 1991, Clarke et al. 2001). While afloat, propagules may be dispersed by tidal currents or runoff following rain storms. According to the TSH (Fig. 1), mangrove zonation results from a combination of (1) the directional dispersal of floating propagules that passively sorts them spatially according to species-specific differences in size and (2) the differential size-related ability of propagules to establish as rooted seedlings as a function of water depth. More specifically, it was hypothesized that incoming tidal currents, especially during higher spring tides, carry smaller propagules farther inland than larger propagules and that, due to their size, the latter are physically restricted from dispersing into these shallower areas. Thus, smaller propagules strand and establish as seedlings farther inland than larger propagules. Conversely, larger propagules are better able to establish in deeper, more seaward portions of the swamp because their large size affords both greater access to the soil surface and more resistance to buffeting by moving water, and therefore they have a better chance of taking root. The TSH was consistent with Rabinowitz's (1978a) observation that, in her study areas on both coasts of Panama, the species that dominates near the water's edge where water depth is greater, has larger, heavier propagules than species that dominate more landward areas of the swamps where the water is generally shallower. She argued that this pattern was characteristic of mangrove distributions along tidal gradients in many parts of the world.

While Rabinowitz's original findings have been criticized and observations at some sites do not fit its predictions (see Discussion), a complete test of the TSH has yet to be conducted at a single site. We present here the results of what we believe to be the first comprehensive investigation of the TSH. Our study was designed to specifically evaluate both the dispersal and establishment components of the hypothesis, and it was conducted in the forests of Punta Galeta on the Caribbean coast of Panama, one of Rabinowitz's primary study sites. Thus, our results provide a highly relevant test of her model. In addition, our study is one of very few that has directly quantified the propagule dispersal patterns of several co-occurring, forest tree species (Levine and Murrell 2003).

METHODS

Study area and species

Our study was conducted in mainland mangrove forests near the Smithsonian Tropical Research Institute's Galeta Marine Laboratory (9°24′18″ N,
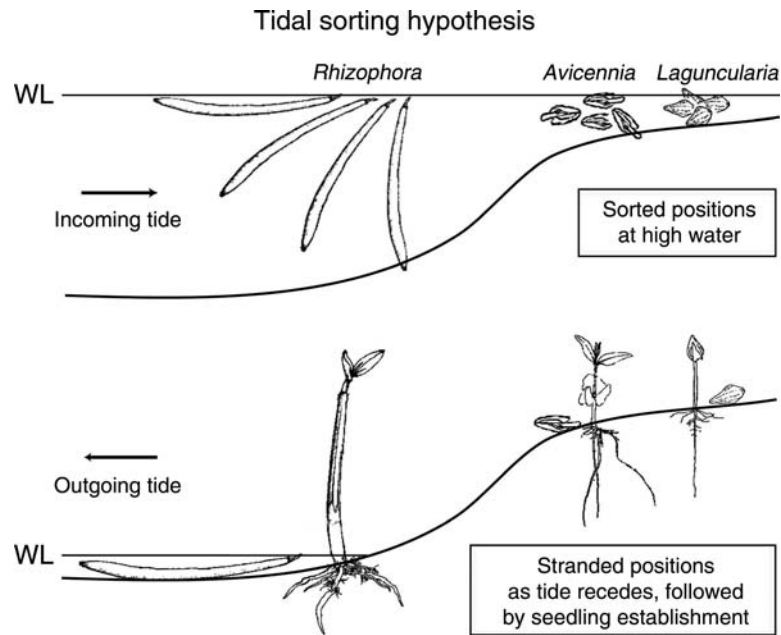
Tidal sorting hypothesis

Fig. 1. Schematic of the Tidal Sorting Hypothesis (Rabinowitz 1978a). The top panel shows the expected differential movement of propagules by incoming tidal flow: species with smaller propagules are dispersed farther inland and to higher elevations than species with larger propagules. Water levels (WL) at these higher elevations are shallower, and flow is less strong and turbulent than at lower tidal heights. The bottom panel shows that the differential dispersal of propagules results in smaller propagules being stranded farther inland as the tide recedes. This passive sorting process, combined with the expectation that larger propagules are better able to establish a root hold in deeper, more turbulent, nearshore locations, results in species with larger propagules dominating at lower elevations and those with smaller propagules dominating at upper elevations. Illustrated propagules represent the three common canopy species in mangrove forests on the Caribbean coast of Panama (see *Methods: Study area and species*); images are adapted from Rabinowitz (1978b).

79°51′48.5″ W) at Punta Galeta on the Caribbean coast of Panama, approximately 8 km northeast of the city of Colón (see Fig. 2). Three tree species (hereafter referred to by their generic names) comprise the canopy of the study forests: *Avicennia germinans* (Avicenniaceae), *Laguncularia racemosa* (Combretaceae), and *Rhizophora mangle* (Rhizophoraceae). In these forests, as elsewhere (Davis 1940, Schaeffer-Novelli et al. 1990, McKee 1995, Imbert and Menard 1997, Sherman et al. 2000), these species are distributed differentially with distance from the water's edge, forming several zones of differing canopy composition along the tidal gradient.

The typical pattern of species distributions in our study area is illustrated in Fig. 3A with data from one of the three transects used in this study (*Methods: Propagule dispersal: Direction and distance*). *Rhizophora* grows in a pure stand at the seaward forest edge. About 10–20 m from the water's edge, *Laguncularia* joins the canopy, forming a nearly even mixture with *Rhizophora* in the low intertidal. *Avicennia* enters the canopy in the mid-intertidal, creating a mixed canopy of the three species, and it then gradually monopolizes most upper intertidal stands. *Laguncularia* often reappears in the canopy near the upland edge, growing as scattered individuals or small monospecific stands along the mangrove–rain forest ecotone.

The topographic profile of the intertidal zone (Fig. 3B) is more complex than the monotonic rise in surface elevation assumed by the TSH (Fig. 1). Moving inland from the water's edge, surface elevation increases over the first ~50 m, remains roughly constant for another 50 m, then declines again to form a shallow (5–15 cm deep) upper intertidal basin that holds standing water throughout the wet season. Such inland basins are a common geomorphic feature of many mainland Caribbean mangrove forests (Lugo and Snedaker 1974, Cintrón et al. 1985, McKee 1993, Ewel et al. 1998).

All three species disperse their propagules during the rainy season, which runs roughly from May to late December. More than 90% of the 200–400 cm of rainfall Punta Galeta receives annually occurs during these months (Cubit et al. 1988, 1989, Duke et al. 1997). Within the rainy season, the dispersal periods of the species overlap to differing degrees (Rabinowitz 1978b, Duke and Pinzón 1993; W. Sousa, *personal observation*). Mature *Rhizophora* propagules are dispersed primarily between April and October, with a peak from May to July. *Avicennia* propagules are released only between June and early August, although unrooted, dispersing seedlings of this species can be found on the forest floor into September or October (W. Sousa, *personal observation*). *Laguncularia* propagules are dispersed from late August to late November. The propagules of all three
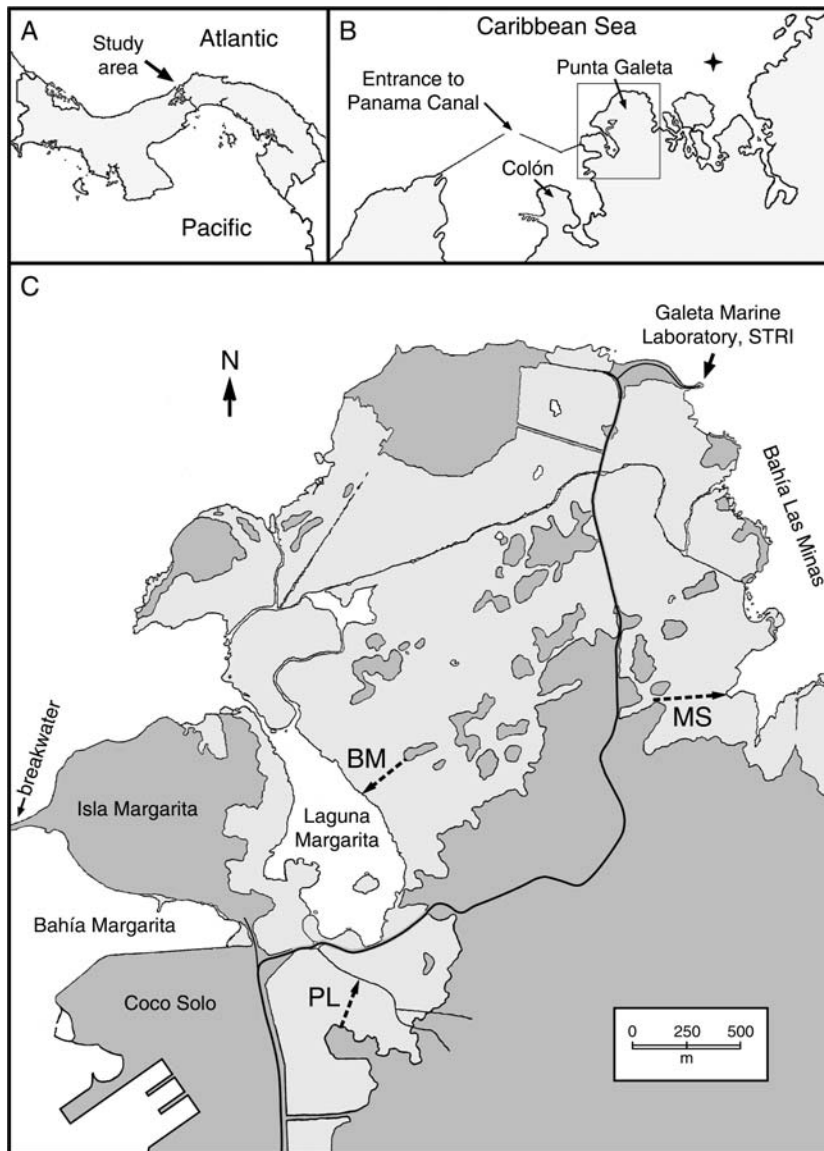
Fig. 2. (A) Location of study area within Panama; (B) Punta Galeta, Panama and environs (the four-pointed star in the upper right panel is at 9°25′ N, 79°50′ W); and (C) enlargement of the Punta Galeta study area showing the three study transects: Minas South (MS), Bahía Margarita (BM), and Pipeline (PL). In the study area, light gray shading indicates mangrove forest, and dark gray shading indicates upland forest and developed areas.

species are buoyant and dispersed by water (hydrochory) but differ in the duration and pattern of floating and time to establishment as rooted seedlings (Rabinowitz 1978b). Dispersing propagules are transported across the forest floor by runoff following rainfall and by tidal action.

The size and shape of the three species' propagules differ markedly (see Plate 1; Sousa et al. 2003a; also see drawings in Rabinowitz [1978b] and Tomlinson [1986]). *Rhizophora* has the largest propagules, averaging 223 mm in length and 17.5-g fresh mass. The species is viviparous; the hypocotyl is rod-like in shape with pointed ends, one being the plumule (embryonic shoot)

and the other the radicle. *Avicennia* propagules have a flattened, ovoid shape with a short stylar beak; they average 19 mm in length and 1.0-g fresh mass. When released from the parent tree, *Avicennia* propagules are covered by a thin pericarp, which separates from the propagule soon after it falls into water on the forest floor. The fleshy cotyledons of *Avicennia germinans* are positively buoyant; buoyancy of the propagule does not depend on the presence of the pericarp, as seems to be the case for its Indo-Pacific congener *Avicennia marina* (Steinke 1986, Clarke and Myerscough 1991). *Laguncularia* propagules have a flattened, obovoid shape and are the smallest of the three species' propagules, averaging
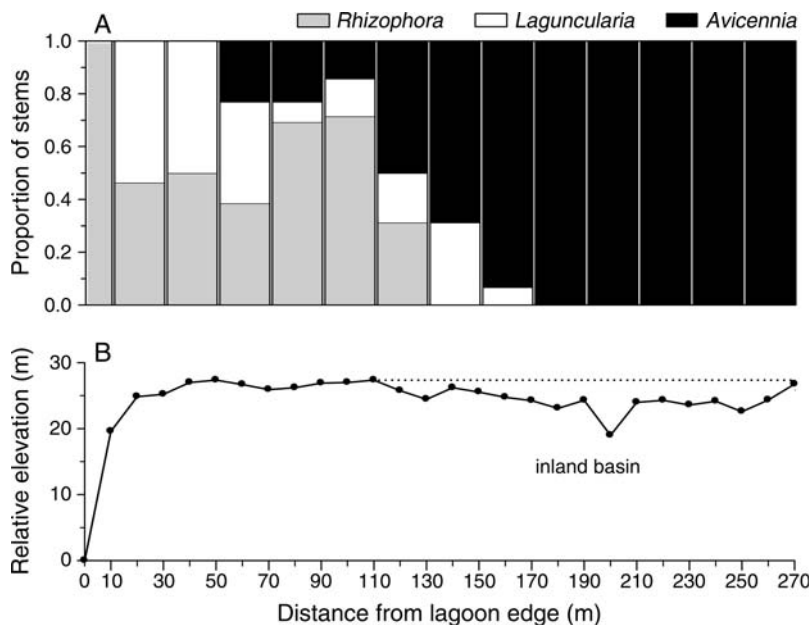
Fig. 3. Plots of the relative (A) abundances of three mangrove species and (B) soil surface elevations along the BM transect. The transect was sampled on 2 December 1994. Tree data are proportions of living individuals ≥4 cm diameter at breast height (1.3 m) within the indicated sections of a 10 m wide belt transect running from a lagoon edge to the lower edge of upland rain forest (Fig. 2). Relative elevation was measured with an auto level every 10 m along the transect; plotted points are means of three replicate stadia-rod positions at each distance. The dotted line on the elevational profile (B) demarcates the inland basin habitat.

20 mm in length and 0.6-g fresh mass. *Laguncularia* propagules have a thick, cork-like, and very buoyant seed coat, which remains attached until the propagule develops into a rooted, upright seedling.

Based on these differences in propagule size, we would expect, under the TSH, that (1) the rank order of propagule dispersal distances would be *Laguncularia* > *Avicennia* > *Rhizophora* and (2) the expected relative tidal elevations at which the species would strand and establish at maximum density would be from highest to lowest elevation: *Laguncularia* > *Avicennia* > *Rhizophora*.

Propagule dispersal: direction and distance

To evaluate whether patterns of propagule dispersal matched the predictions of the TSH, we released marked propagules at three elevations/distances along each of three permanent transects (Fig. 2C) and monitored the directions and distances of their movement. The three transects were established as part of an earlier descriptive study of mangrove species distributions and ran from the water's edge to the lower edge of upland rain forest; BM (Bahía Margarita; 270 m long) originated on the edge of a brackish lagoon; PL (Pipeline; 210 m long), on a small, tidal river; and MS (Minas South; 310 m long), on a large bay. These transects were intentionally established in areas where relatively undisturbed, closed canopy forest was distributed along uninterrupted, intertidal gradients. For logistical reasons, we selected sites that were accessible by foot, rather than choosing a strictly random sample of sites with similar physiogno-

my. The chosen transect locations were widely dispersed across the study area (Fig. 2) and incidentally in three somewhat distinct environmental settings (i.e., one each originating on a lagoon, river, and bay). We did not intend to compare propagule dispersal and establishment among these specific habitats; rather, we considered these three transects to be samples drawn from a larger population of undisturbed sites. Consequently, "transect" was treated as a random factor in our statistical analyses.

The elevations/distances at which propagules were released along each transect were selected to represent the major forest types along the tidal gradient (Table 1). At each elevation/distance, replicate groups of propagules of each species were released during low tide at three different points along a 60–70 m line running perpendicular to the main transect. The locations of these release points were determined in a stratified random manner, such that adjacent release points for a given species were separated by at least 25 m. The number of marked propagules released at each replicate release location was 30 for *Avicennia* and *Laguncularia*, and 20 for *Rhizophora*. For each species, the size distributions of the released propagules were held constant across all release points (ranges of propagule lengths: *Avicennia,* 23–33 mm; *Laguncularia,* 20–28 mm; *Rhizophora,* 150–280 mm).

Propagules used in this dispersal study and the following experiment on propagule establishment were drawn from large pooled collections of propagules that had recently dropped from canopy trees in several forest

TABLE 1. Composition of the forest canopy at different tidal elevations and distances along three transects (BM, PL, and MS) where propagules were released in dispersal trials (PD) and/or where seedling establishment pens (SEP) were located.

Transect	Forest type or tidal elevation	Distance (m) from transect origin at water's edge	Experiment type	Relative abundance (%)		
				Rhizophora	Laguncularia	Avicennia
BM	Fringe	1.5–4.0	SEP	100.0	0.0	0.0
	Low	25	PD, SEP	47.2	52.8	0.0
	Mid	100	PD, SEP	39.3	21.4	39.3
	High	235	PD, SEP	0.0	0.0	100.0
PL	Low	35	PD, SEP	40.0	60.0	0.0
	Mid	95	PD, SEP	30.0	28.3	41.7
	High	185	PD, SEP	0.0	7.1	92.9
MS	Low	70	PD, SEP	52.6	47.4	0.0
	Mid	220	PD, SEP	30.8	44.2	25.0
	High	255	PD, SEP	0.0	11.5	88.5

Note: Data are percentages of canopy trees along 60–70 m long, 10 m wide belt transects running perpendicular to the main transects along the linear array of release points and/or establishment pens.

stands of each type within the study area. This ensured that the source of propagules did not vary among treatments and that the propagules were in an early stage of development, not yet having developed roots or an expanded shoot with leaves. As described earlier, the pericarp had fallen off the *Avicennia* propagules before they were collected and marked, but their cotyledons remained tightly closed. The rolled cotyledons and other embryonic tissues of *Laguncularia* propagules were fully enclosed within the seed coat when the propagules were released. *Rhizophora* propagules had a tightly closed stipule. All propagules were inspected for predispersal insect damage; only undamaged ones were used in the study. Minchinton (2006) found that insect-damaged propagules of *Avicennia marina* were initially more buoyant than undamaged ones. This enhanced buoyancy did not, however, increase the effective dispersal distance of the propagules, as had been predicted, because their viability declined over time due to continuing damage from insect feeding and tissue decay.

Avicennia and *Rhizophora* propagules were released in mid-July 1995, during the peak annual period of natural propagule release for both species. Because a full day was required to monitor both species at each site, releases on the three transects were staggered by one day (19, 20, 21 July) to allow intertransect comparisons of movement after equal time intervals. A consistent search protocol was followed each time a transect was monitored: over a period of about four hours, four or five people searched for marked propagules within a ~100 m wide strip that extended from the uppermost release points to the water's edge, a distance that ranged from 185 to 255 m. We measured the compass direction and distance from the point of release of each relocated propagule at 1, 5, 14, 19, and 28 d following release. We also recorded whether the propagule was still floating or had sunk, what object or barrier, if any, it was in contact with, and whether it had firmly rooted into the soil. *Laguncularia* propagules were released on 8 (BM and PL transects) or 9 (MS transect) September 1995, during the peak period of natural propagule release by this species.

Using the same procedure as for *Avicennia* and *Rhizophora,* we mapped the position of each relocated *Laguncularia* propagule at 1, 6, and 14 d after release, collecting the same ancillary information on propagule condition. Because *Laguncularia* propagules dispersed much more rapidly than those of *Rhizophora* and *Avicennia* (see *Results*) and began to lose their buoyancy more quickly, searches conducted 21 d following release failed to relocate a sufficient number of marked *Laguncularia* to meaningfully characterize their directional and spatial distributions. Therefore, our analysis examined movements of this species' propagules over 14 d.

At each release point, the propagules were deposited within 25 cm of a PVC pipe that marked the location. On subsequent visits, propagules that remained within this radius of the pipe were scored as not having moved. To aid in the relocation of released propagules, they were marked with a thin coat of fluorescent paint (red [ServiStar, Cary, Illinois, USA] or pink [Plasti-Kote, Medina, Ohio, USA]) sprayed on the exterior of the propagule. To ensure that propagules of the same species released at different distances along a transect could be distinguished, propagules released at the three distances were painted with different color schemes (all red, all pink, or half pink/half red). We tested for the potentially confounding effect of paint marks on propagule buoyancy with a laboratory experiment (Appendix A). We did not detect a significant effect of the fluorescent paint marks on flotation patterns of any of the three mangrove species' propagules. Therefore, it is unlikely that paint marks had any significant effect on patterns of propagule dispersal in the field.

Mean proportions of marked propagules relocated two and four weeks following their release were compared among transects, elevations, and species using mixed-model ANOVA. There were three levels of each factor: transect (BM, PL, or MS), tidal elevation (high, mid, or low), and species of propagule (*Avicennia*, *Laguncularia*, or *Rhizophora*). Transect was considered a random factor; elevation and species were fixed factors.

We compared propagule recovery rates over the different periods of time with two analyses. The first analysis compared rates for the three species' propagules over equal two-week time intervals (starting 19–21 July for *Avicennia* and *Rhizophora* and 8–9 September for *Laguncularia*). The second analysis compared recovery rates of *Avicennia* and *Rhizophora* over the full four-week duration of our monitoring effort. For both analyses, proportions were arcsine transformed to ensure homogeneity of variance (Cochran's $C = 0.234$ and 0.189, respectively; $P > 0.05$).

The directions of propagule movement were summarized and compared with circular statistics (Batschelet 1981, Fisher 1993, Anderson and Wu 1996, Zar 1999). These analyses examined angular data collected at 28 d for *Avicennia* and *Rhizophora* and 14 d for *Laguncularia*. We restricted the analyses to the 66 release points (out of 81) for which angular measurements could be made on at least four propagules. At the remaining 15 release points fewer than four of the released propagules moved out of the 25 cm radius circle in which they had been deposited; in these cases, small sample sizes precluded accurate estimates of the mean direction of propagule dispersal. We analyzed data from the longest available sampling intervals because this maximized the number of release points meeting our minimum sample size criterion and because mean directions of propagule movement at two vs. four weeks were very similar. To determine if the direction of movement differed among species, transects, or elevations, we calculated the mean angle of propagule dispersal and its circular variance ($V = 1 - \overline{R}$, where $\overline{R}$ is the length of the mean resultant vector), which varies from 0 to 1. A value of 0 indicates no variation in the direction of movement, while a value of 1 indicates maximal dispersion of the directions, i.e., a mean angle cannot be described. While a uniform distribution has a $V = 1$, so will some symmetrical multimodal distributions (e.g., diametrically bimodal distributions that are centrally symmetrical; Fisher 1993, Zar 1999). We used Rayleigh's test to evaluate whether the distribution of directions measured at each release point differed significantly from uniform. Since the orientations of the three transects with respect to the water's edge–upland gradient were different (Fig. 2), we conducted separate statistical comparisons of mean directions of dispersal within transects. Treating the mean vectors of dispersal from each release point as replicate measures of angular movement, we used separate Watson-Williams F tests to compare the grand mean directions of movement among species and elevations along each transect. Ideally, we would have employed the equivalent of a multi-way ANOVA to examine the effects of these two main factors (species and elevation), the nested factor (release point), and their interactions. However, the application of such techniques to circular data is at an early stage of development (Anderson and Wu 1995). Since summary statistics indicated no evidence of interaction among the

factors, we chose to conduct more conventional univariate tests of the two main factors within each transect. The angular distributions were unimodal in form (approximating von Mises distributions) with very similar variances, meeting the assumptions of the parametric Watson-Williams F tests. All circular statistics were calculated with Oriana software (Kovach 2003).

We compared the mean distances moved by marked and released propagules among transects, elevations, species, and points of release using mixed-model ANOVA. There were three levels of each factor: transect (BM, PL, or MS), tidal elevation (high, mid, or low), species of propagule (*Avicennia*, *Laguncularia*, or *Rhizophora*), and release point (each species was released at three points per elevation on a transect). Transect and release point were considered random factors, and elevation and species fixed factors. Release point was nested within transect, elevation, and species. We compared the mean distances moved over different periods of time with two different analyses. The first analysis compared movements of the three species' propagules over equal two-week time intervals (starting 19–21 July for *Avicennia* and *Rhizophora*, and 8–9 September for *Laguncularia*). The second analysis compared movement over the full duration of our monitoring effort: four weeks for *Avicennia* and *Rhizophora* vs. two weeks for *Laguncularia*. The latter analysis determined whether interspecific differences seen at two weeks would persist or disappear if slower dispersing species (*Avicennia* and *Rhizophora*) were allowed more time for movement. For both analyses, distances were $\log_{10}(X + 1)$ transformed to improve homogeneity of variances (Cochran's $C = 0.104$ and 0.087, respectively; $P > 0.05$ in both cases).

Seedling establishment at different distances from the water's edge

To evaluate the hypothesis that the establishment success of seedlings of the three species of mangroves differs with elevation/distance from the water's edge in the size-dependent manner predicted by the TSH, we conducted a series of three experiments, each in a different year. These experiments measured propagule establishment rates in a landward to seaward sequence of habitats: three elevations within interior forests (1994), fringing stands (1999), and the back reef (2004). In each experiment, we stocked open-topped, plastic-mesh (6 mm wide opening) pens with propagules of each of the mangrove species and monitored their rates of establishment as seedlings. A propagule/seedling was considered to be established when it became firmly rooted in the soil.

The 1994 experiment was conducted along the three transects used for the propagule dispersal study. On each transect, at the same three elevations/distances employed in the dispersal study (Table 1), we installed and stocked four replicate pens for each species. The replicate pens at a particular distance were located, like the release points

in the propagule dispersal study, along a 60–70 m line running perpendicular to the transect; they were positioned in a stratified random manner with adjacent replicate pens of a particular species no closer than 5 m apart. Because the prediction of the TSH with regard to seedling establishment specifically concerns the effects of water depth on propagule establishment, the positions of several of the pens were slightly displaced (<1 m) to avoid spots that had particularly high densities of herbivorous crab burrows. At our sites, crabs consume a considerable number of dispersing propagules, particularly in the lower intertidal zone (Sousa and Mitchell 1999). Even with the repositioning of the pens, crabs consumed a modest number of propagules (≤3) in some pens during the two-week interval between the first and second censuses. In these cases, the propagules lost to crabs were excluded when calculating the proportion of propagules that established.

The pens were circular and 60 cm tall; those used for *Rhizophora* propagules were 80 cm in diameter, while the pens used for *Avicennia* and *Laguncularia* were 40 cm in diameter. These pen sizes afforded each propagule roughly equal soil surface area relative to its projected size (i.e., length × width). Each pen was stocked with 20 propagules of the target species; the resulting densities were moderate relative to natural ranges of propagule and seedling density (W. Sousa, *unpublished data*). Replicate groups of each species' propagules had a common size distribution (ranges of propagule lengths: *Avicennia,* 24–34 mm; *Laguncularia,* 23–30 mm; *Rhizophora,* 150–300 mm). All propagules were visually screened for predispersal insect infestations; only insect-free propagules were used. After stocking each pen, a roof of fiberglass insect screening was secured over the top opening to prevent propagules released from overhanging trees from falling in.

The establishment rates of *Avicennia* and *Rhizophora* propagules were monitored concurrently over 12 weeks, beginning 23 August 1994. At the end of this period, *Avicennia* seedlings and propagules were removed from their pens, which were then stocked with *Laguncularia* propagules on 16 November 1994. At the time of their removal, *Avicennia* seedlings were only 10–15 cm tall with modest root development. They were easily pulled from the firm, peat-dominated soil with little or no disturbance of the surface sediments. We continued to monitor the establishment of both these *Laguncularia* propagules and the original *Rhizophora* propagules for another seven weeks. At each census, we recorded the numbers of propagules that had firmly rooted in the soil and those that had not.

Because the timing and durations of the trials differed among the three species, patterns of propagule establishment were examined with two separate analyses. For the 12 weeks of concurrent monitoring of *Avicennia* and *Rhizophora* propagules, the mean proportions of propagules that established were compared among transects (BM, PL, or MS), elevations (low, mid, or high), and

species using a mixed-model, three-factor ANOVA. Transect was treated as a random factor, and elevation and species treated as fixed factors. Establishment rates of *Laguncularia* propagules after seven weeks were examined with a separate mixed-model, two-factor ANOVA testing the independent and interactive effects of transect (random factor) and elevation (fixed factor). The same analysis was applied to *Rhizophora* propagules after a total of 19 weeks. For all three analyses, proportions were arcsine transformed to improve homogeneity of variances (Cochran's $C = 0.164$, 0.256, and 0.342, respectively; $P > 0.05$ in all cases).

While the 1995 propagule dispersal study was designed to measure the distance and direction of propagule dispersal, it also yielded information on patterns of seedling establishment at different elevations in the forest interior; in essence, it provided temporal replication of the 1994 seedling establishment experiment. For *Rhizophora* and *Avicennia*, we used a mixed-model, two-factor ANOVA to test for the independent and interactive effects of transect (random factor) and elevation (fixed factor) on the mean proportion of marked propagules dispersing from a release point that were found to be firmly rooted in the soil at the final census dates (i.e., after four weeks for *Rhizophora* and *Avicennia*). Proportions were arcsine transformed to ensure homogeneity of variance (Cochran's $C = 0.353$ and 0.241, respectively, $P > 0.05$). Too few *Laguncularia* propagules established on the BM and PL transects for meaningful statistical analysis, so for this species we simply compared the two-week seedling establishment rates among the three different elevations on the MS transect. An arcsine transformation homogenized the variances (Cochran's $C = 0.541$; $P > 0.05$).

The other two establishment experiments (1999 and 2004) were designed to compare establishment rates of the three species at even lower tidal levels, where the influence of water depth on seedling establishment might be stronger. The 1999 experiment was conducted within the 10–20 m wide pure *Rhizophora* stands that fringe the lagoon at the BM site (Table 1). At each of three haphazardly chosen sites along the lagoon edge, separated by 75–100 m, we established four pens for each species 1.5–4 m landward of the water's edge at low tide. These pens were identical in design to those employed in the 1994 trials, and each was stocked with 20 propagules of the target species on 4 September 1999. The length distributions of the three species matched those used in the 1994 trials, and all were free of insect damage. Unlike the 1994 trials, this experiment tested all three species simultaneously and over the same length of time. Overlapping fruiting times in this particular year allowed a concurrent test of the three species. The condition of these propagules was monitored at 21, 29, 38, and 130 d (the last data set gathered on 12 January 2000, after almost 19 weeks). We used a mixed-model, two-factor ANOVA to test the independent and interactive effects of site (random factor with three

levels) and species of propagule (fixed factor with three levels) on the proportion of propagules establishing over the 130-d period. These proportions were arcsine transformed to homogenize variances (Cochran's $C =$ 0.242; $P > 0.05$) prior to analysis.

The 2004 experiment was conducted at the lower edge of the fringing *Rhizophora* stands at the back of the Galeta reef, about 75 m southwest of the main laboratory building (Fig. 2). Ten small and ten large pens were installed in pairs (one of each size) along a 30 m length of fringing forest, among or just beyond the prop roots of the most seaward trees. They were constructed of the same materials and had the same diameters as used in the first two experiments, but the height of their walls was increased from 60 to 90 cm so that waves would not break over them at high tide and displace floating propagules. The pens were placed in locations where there was adequate sediment for seedling establishment and where reinforcing bars could be driven into the underlying dead coral pavement to support the pens. Water depth was spatially variable in this back reef area; blocking the pens as pairs ensured that water depths were matched between cages containing propagules of different species. Measurements of water height at low tide indicated that the tidal height of the enclosed areas ranged from 0.05 to 0.15 m below Mean Lower Low Water.

The temporal sequence of trials for the different species was similar to the 1994 experiment in that *Rhizophora* and *Avicennia* propagules were stocked first (on 13 July 2004) in the large and small pens, respectively. Each pen was stocked with 20 propagules of the appropriate species; replicate groups of each species' propagules had a common size distribution (ranges of propagule lengths: *Avicennia,* 20–35 mm; *Rhizophora,* 150–270 mm). All propagules were pre-screened for insect infestations, as in the earlier trials. The fates of these propagules were monitored weekly until 2 December 2004, by which time all the *Avicennia* propagules had either established as seedlings or died. At that time, established *Avicennia* seedlings were removed from the 10 small pens, which were then stocked with 20 insect-free *Laguncularia* propagules, with a common distribution of lengths in each pen (range 25–30 mm). As in the 1994 experiment, removal of the small *Avicennia* seedlings caused little disturbance to surface sediments. The condition of the *Laguncularia* and remaining *Rhizophora* propagules was monitored weekly until 5 January 2005. The *Rhizophora* pens were censused a final time on 29 July 2005. Mean proportions of propagules that rooted firmly in the substrate were compared between species with paired t tests on arcsine-transformed data.

RESULTS

Rates of marked propagule recovery

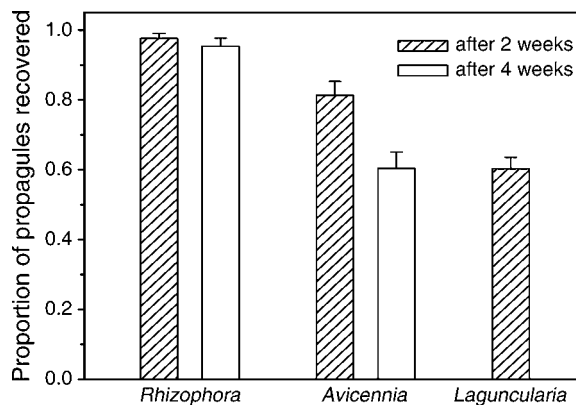Mean rates of marked propagule recovery varied among species (two weeks, $F_{2,4} = 168.78$, $P = 0.0001$;

FIG. 4. Species-specific rates of marked propagule relocation two and four weeks after release. Bars show grand mean proportions (+SE) of the propagules deposited at individual release points that were relocated during the indicated census (data from replicate release points were averaged over transect and elevation, neither of which significantly affected relocation rates; Appendix B). There were no data for *Laguncularia* at four weeks.

four weeks, $F_{1,2} = 93.47$, $P = 0.011$) and through time (Fig. 4) but did not differ among transects (two weeks, $F_{2,54} = 0.36$, $P = 0.701$; four weeks, $F_{2,36} = 0.44$, $P = 0.649$) or elevations (two weeks, $F_{2,4} = 1.43$, $P = 0.340$; four weeks, $F_{2,4} = 0.96$, $P = 0.457$), and there was no evidence that the influence of any of these factors interacted ($P > 0.05$ in all cases; Appendix B). The mean recovery rate for *Rhizophora* propagules exceeded 95% at each monitoring date (release point median = 100%). On average, more than 80% of *Avicennia* propagules released at a particular point were recovered after two weeks (release point median = 90%), and over 60% were recovered after four weeks (release point median = 67%). *Laguncularia* propagules were followed for two weeks, with a mean recovery rate of 60% (release point median = 60%). As discussed in *Results: Propagule dispersal distance,* some of the propagules that were not relocated, particularly those of *Laguncularia,* may have dispersed out of the monitored areas. There are, however, good reasons to believe that most of the propagule disappearances were the result of predation or sinking. During our searches, we found a number of marked *Avicennia* and *Laguncularia* propagules that had been torn apart by herbivorous crabs. In an earlier study (Sousa and Mitchell 1999), we found that crabs consumed 30–40% of tethered propagules in the lower intertidal over a period of four weeks. Therefore, marked propagules dispersing into or through this zone probably experienced high rates of predation, accounting for many, if not most, of the disappearances. Sinking was probably another important cause of propagule disappearance, particularly for *Laguncularia.* When tested in the laboratory under the low salinity conditions typical of the rainy season (the period of natural dispersal, also when our study was conducted), more than half of *Laguncularia* propagules had lost their
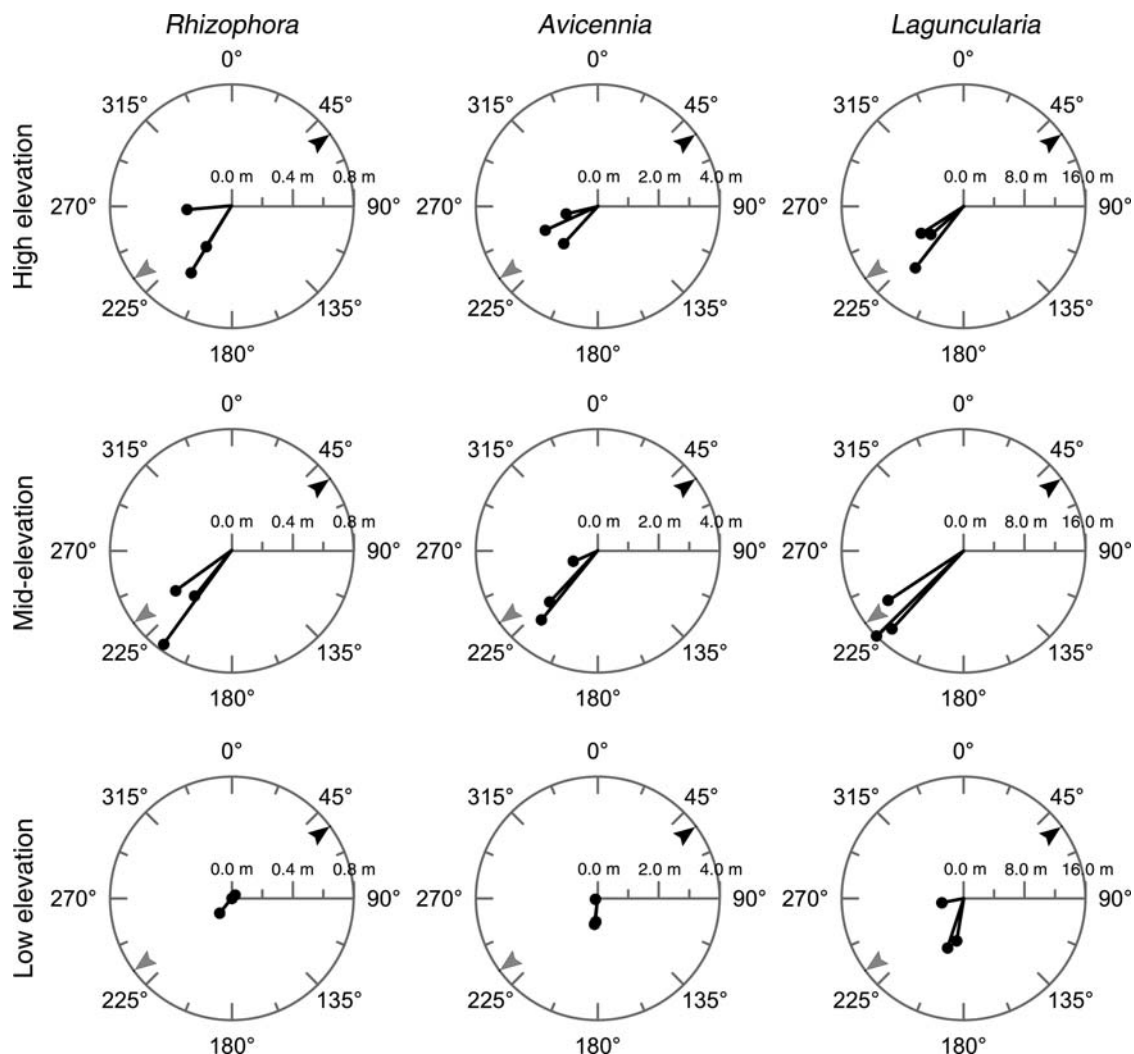
FIG. 5. Circular plots of the mean directions and distances moved by propagules of the three species along the BM transect. Each plot displays values for the three replicate release points at each elevation. The black and gray arrowheads on the periphery of each plot point toward the upland and low intertidal, respectively (see Fig. 2 for a large-scale view of transect orientations).

buoyancy by 16 d (Appendix A), the length of time that their movements were monitored in the field. When these small propagules sink to the bottom among dense stands of pneumatophores and leaf litter, they become difficult to find.

Direction of propagule dispersal

The movement of propagules away from release points was highly directional and practically linear in many cases. Of the 66 releases for which the direction of movement was measured for four or more propagules, 63 (95.5%) had $V < 0.20$ and 54 (81.8%) had $V < 0.10$, indicating very little variation in the direction of propagule dispersal from individual release points. Rayleigh's tests showed that the distributions of propagule dispersal directions were significantly different ($P \leq 0.05$) from random in 64 of the 66 releases (97.0%). The two cases that could not be distinguished

from random (one *Avicennia* and one *Rhizophora* release) were characterized by small numbers of dispersing propagules (fewer than seven in both cases) that moved short distances, resulting in greater variance ($V = 0.392$ and 0.348, respectively) and therefore less power to reject the null hypotheses of random movement.

On each transect, the propagules moved downward, towards lower elevations and the water, be it a bay (MS), lagoon (BM), or river (PL): exactly opposite the direction predicted by the TSH (Fig. 1). The 27 propagule releases on the BM transect illustrate this consistency of dispersal direction (Fig. 5). The propagules were moved by sheet-flow runoff across the forest floor following rain storms (W. P. Sousa, *personal observation*). The range of mean dispersal directions from the release points on each of the transects was less than 90° (Fig. 6). The grand mean directions of
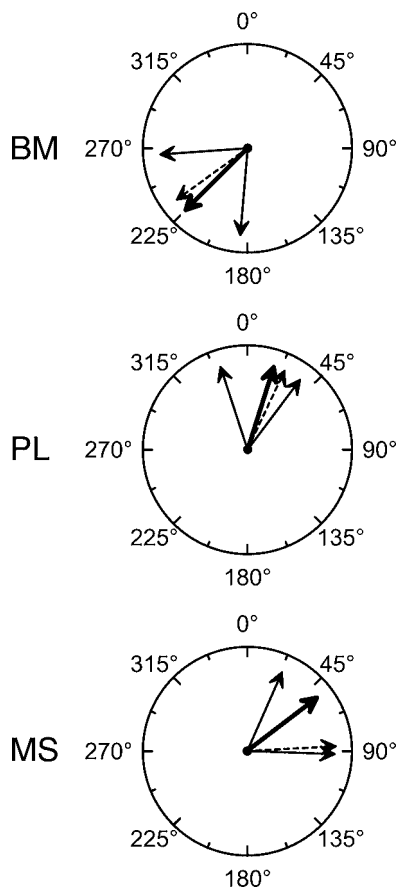
FIG. 6. Circular plots of the grand mean directions of propagule dispersal of the three study species pooled (thick solid vector) on each of the three study transects (BM, PL, and MS; see *Methods: Propagule dispersal: Direction and distance* for computational details). In each plot, extremes of mean dispersal directions from individual release points (thin solid vectors) and transect direction toward the low intertidal (thin dashed vectors) are also shown.

to the transect. The transects had been established to cut across visually apparent forest zones, running roughly perpendicular to the water's edge, without attention to patterns of surface water flow. The contours of the watershed that contributes surface flow to the MS region are more heterogeneous than those of the other sites, making the relationship between flow and zonation more complex. Nonetheless, the direction of the MS transect fell within the range of mean dispersal angles measured at the site (Fig. 6).

Propagule dispersal distance

Propagules of the three species exhibited very different rates of dispersal (Fig. 7). On average, over a two-week period *Laguncularia* propagules moved more than 10 times farther than *Avicennia* propagules and more than 200 times farther than *Rhizophora* propagules. Even after an additional two weeks of dispersal by *Avicennia* and *Rhizophora* propagules, large differences persisted. *Laguncularia* propagules moved much farther over a two-week period than propagules of *Avicennia* or *Rhizophora* did over a four-week period (5 and 25 times, respectively). While there was a significant transect × species interaction at both two ($F_{4,54} = 5.47$, $P < 0.001$) and four weeks ($F_{4,54} = 3.49$, $P = 0.013$; Appendix C), Tukey's hsd tests comparing species differences within transects (Fig. 7) confirmed that *Laguncularia* propagules consistently dispersed greater distances than those of *Avicennia*, which in turn moved farther than propagules of *Rhizophora*.

The transect × species interactions resulted from differences in the influence of transect on species dispersal rates (Fig. 7). There was little variation in the dispersal of *Rhizophora* propagules among the transects; they moved very short distances regardless of where they were released. On the other hand, the more vagile propagules of *Avicennia* and *Laguncularia* moved greater distances on some transects than others. There was no significant effect of elevation on dispersal distance at either two or four weeks, and this factor exhibited no significant interactions with transect or species ($P > 0.05$ in all cases; Appendix C). Maximum dispersal distances showed very similar patterns of variation among transects and species (Fig. 7).

propagule movement on each of the transects did not differ among species or elevations (Table 2). On the BM and PL transects, the grand mean direction of movement corresponded quite closely (within 10°) to the landward to seaward direction of the transects, while on the MS transect the propagules moved at a 35.8° angle

TABLE 2. Results of Watson-Williams *F* tests comparing grand mean angles (directions of propagule dispersal, in degrees) (A) among species within a transect and (B) among elevations within a transect.

Transect	A) Angle for species within transect						B) Angle for elevations within transect					
	Rhizophora	*Laguncularia*	*Avicennia*	*F*	df	*P*	Low	Mid	High	*F*	df	*P*
BM	225.8° (7)	223.7° (9)	226.4° (9)	0.032	2, 22	0.968	209.5° (7)	227.4° (9)	233.3° (9)	2.021	2, 22	0.156
PL	1.0° (3)	22.2° (9)	17.1° (8)	2.796	2, 17	0.089	25.8° (7)	16.2° (7)	8.8° (6)	2.275	2, 17	0.133
MS	52.2° (4)	52.9° (9)	50.3° (8)	0.052	2, 18	0.950	55.0° (5)	54.2° (9)	46.2° (7)	0.679	2, 18	0.520

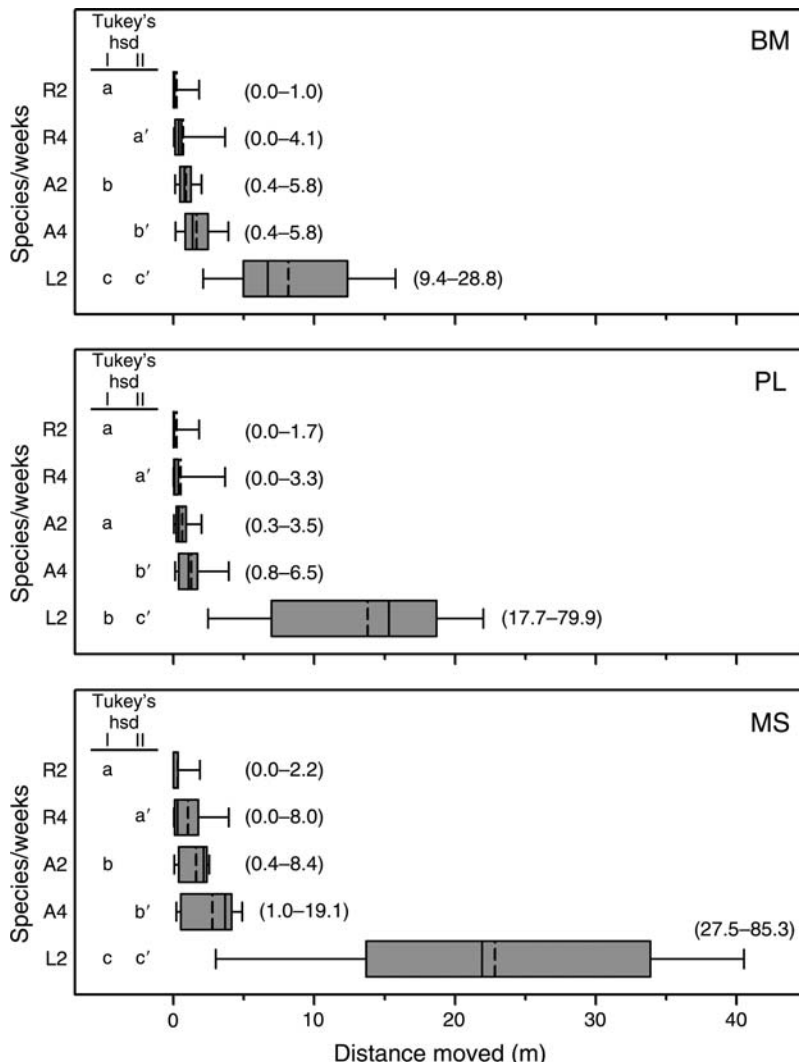*Note:* The number of release points is given in parentheses.

FIG. 7. Box plots of the distributions of mean distances moved by propagules from individual release points along each of the three study transects. Propagules of each species were released at nine points on each transect; see *Methods: Propagule dispersal: Direction and distance* for details. Mean distances moved did not differ with elevation along a transect, nor did this factor interact significantly with either transect or species (Appendix C). In each plot, upper and lower hinges represent the 75th and 25th percentiles, upper and lower whiskers represent the 95th and 5th percentiles, and the median and mean are shown, respectively, as solid and dashed lines across the box. The range of the maximum distances moved by a species' propagules from each of the nine release points is enclosed in parentheses to the right of the respective box plot. Two-week values are presented for *Laguncularia* (L2), and two-week and four-week values are presented for *Avicennia* (A2, A4) and *Rhizophora* (R2, R4).

The results of Tukey's hsd tests comparing mean distances moved by propagules of the three species on each study transect are reported on the left of each panel. Separate results are presented for analyses of movement over two-week periods (Analysis I) and over the entire periods of monitoring (Analysis II; four weeks for *Avicennia* and *Rhizophora* and two weeks for *Laguncularia*). Lowercase letters summarize test results: within the column for a given analysis, species marked with different unprimed or primed letters exhibited significantly different ($P < 0.05$) rates of propagule dispersal.

Consistent with these differences in dispersal rate, the average percentages of propagules that failed to move out of the 25 cm radius circle surrounding a release point differed markedly among the three species: 76.7% after four weeks for *Rhizophora*, 29.2% after four weeks for *Avicennia*, and 4.3% after two weeks for *Laguncularia* ($F_{2,4} = 192.01$, $P < 0.001$). These proportions did not vary significantly among transects ($F_{2,54} = 2.98$, $P = 0.059$) or elevations ($F_{2,4} = 3.53$, $P = 0.131$), nor were

there any significant interactions among the three factors (range of $P = 0.107–0.905$; Appendix D).

Groups of propagules released at different points within an elevation exhibited significant differences in mean dispersal distance at both two and four weeks (Fig. 8; Appendix C). Some of this variation was due to small scale spatial variation in sheet flow across the forest floor. In other cases, propagules dispersing from particular release points were blocked by physical barriers such as
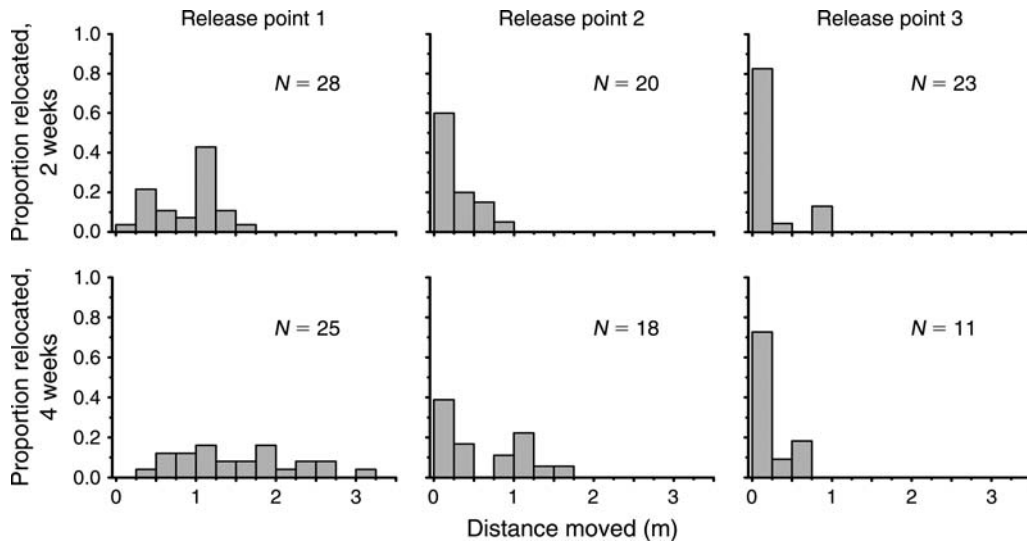
FIG. 8. Example of variation in the dispersal of marked propagules from three release points within a single elevation and site. Data are the proportions of *Avicennia* propagules relocated at the indicated distances two and four weeks following their release on 21 July 1995 at mid-elevation on the PL transect.
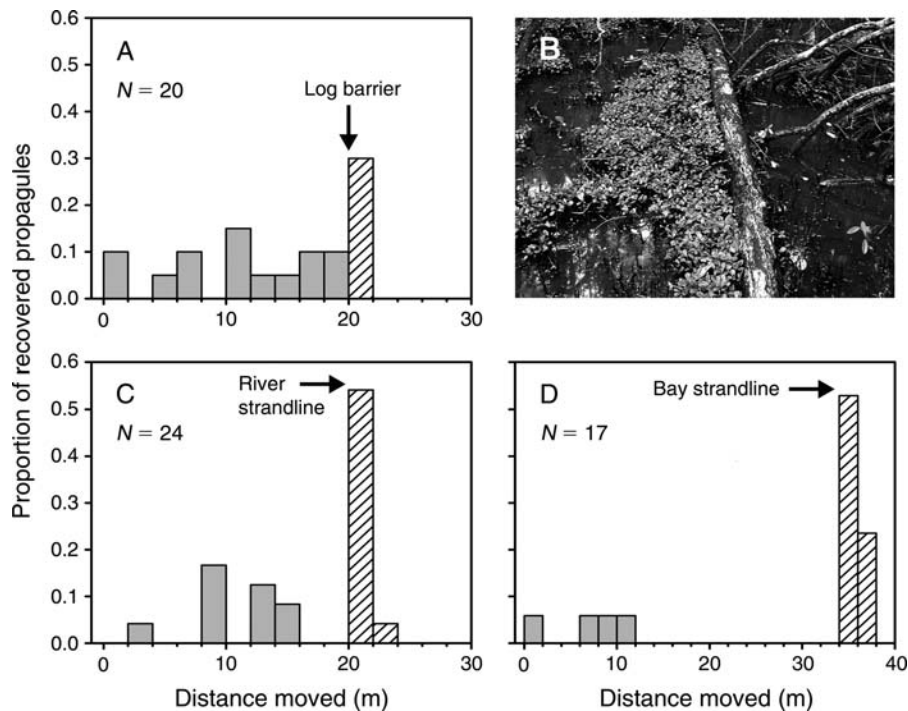

FIG. 9. Proportions of recovered propagules found at different distances from the release point, with hatched bars showing marked propagules accumulating against forest floor obstacles or at the edges of water bodies. (A) *Laguncularia* propagules trapped behind a fallen log lying perpendicular to their path of movement. Data are from a census conducted 14 d after the propagules were released on 8 September 1995 at a mid-elevation point on the BM transect. (B) Photo of *Laguncularia* seedlings established in dense aggregations on the landward side of a log after propagules accumulated there. Note the prop roots of low intertidal *Rhizophora* on the seaward side of the log. (C) *Laguncularia* propagules accumulating in the strand line of the small, tidal river, Rio Coco Solo. Data are from a census conducted 14 d after the propagules were released on 8 September 1995 at a low-elevation point on the PL transect. (D) *Laguncularia* propagules accumulating in the strand line of a small embayment within Bahía Las Minas. Data are from a census conducted 6 d after the propagules were released on 9 September 1995 at a low-elevation release point on the MS transect.
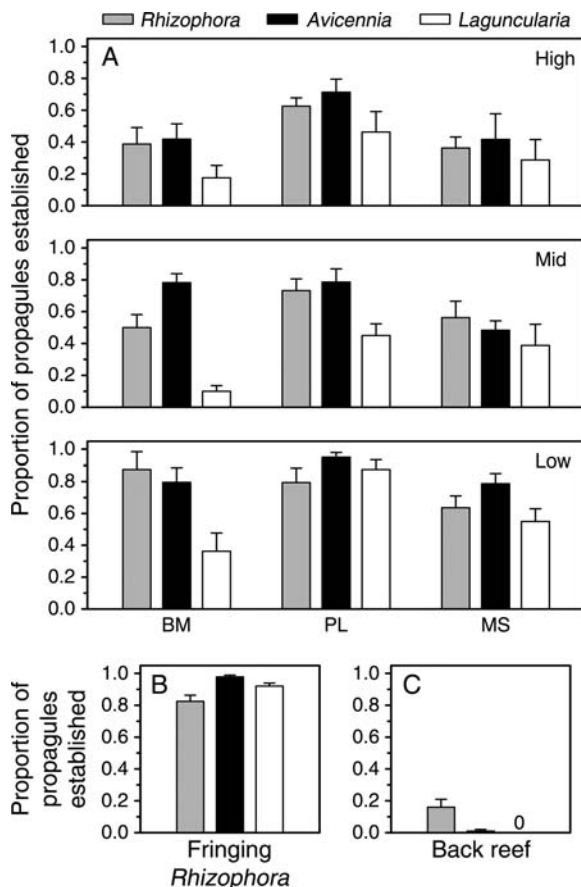
FIG. 10. Rates of propagule establishment in three experiments conducted in (A) 1994 at different tidal elevations along the three study transects (BM, PL, MS) in the forest interior, (B) 1999 within a fringing *Rhizophora* stand, and (C) 2004 in a back reef area, along the seaward edge of a fringing *Rhizophora* stand. Bars show grand mean proportions (+SE) of stocked propagules establishing as rooted seedlings in replicate pens.

logs (Fig. 9A, B), or they accumulated along strandlines of rivers (Fig. 9C) or bays (Fig. 9D).

We believe that the four-week dispersal distances measured for *Rhizophora* and *Avicennia* propagules and the two-week dispersal distances measured for *Laguncularia* propagules represent nearly the full extents of their movements. This conclusion is supported by the observation that the average and maximum distances that *Rhizophora* and *Avicennia* propagules dispersed changed little between the second and fourth week (Fig. 7). By four weeks, an average of 64.3% of viable *Avicennia* propagules associated with individual release points had firmly rooted into the soil, and 74.0% of these had developed into erect seedlings and flushed their first pair of leaves. *Rhizophora* was slower to become rooted; by four weeks, an average of 14.1% of viable *Rhizophora* propagules associated with individual release points had become firmly rooted and none had flushed leaves. A small proportion of *Laguncularia* propagules had

become rooted within two weeks of being released (an average of 6.7% of those associated with individual release points). By this time, however, most *Laguncularia* propagules were no longer buoyant and had either sunk to the soil surface within dense stands of pneumatophores or become trapped in leaf litter and were therefore unlikely to be moved much farther by currents.

Due to their high vagility, *Laguncularia* propagules, particularly those released at lower tidal elevations, were the most likely to be carried to a tidal river, bay, or lagoon and be transported greater distances. We relocated 14 marked *Laguncularia* propagules in the strandline of the Rio Coco Solo at the bottom of the PL transect and 13 at the edge of Bahía Las Minas at the bottom of the MS transect (see Fig. 2). Therefore, some *Laguncularia* propagules may have been carried greater distances, but these represented a modest proportion of those relocated after two weeks.

Propagule establishment

In the 1994 experiment, the three species exhibited very similar patterns of seedling establishment (Fig. 10A). In the first trial of this experiment, which involved *Rhizophora* and *Avicennia* propagules, the species did not differ in mean rates of establishment ($F_{1,2} = 5.33$, $P = 0.147$), but rates of propagule establishment differed among transects ($F_{2,54} = 10.08$, $P < 0.001$) and elevations ($F_{2,4} = 25.96$, $P = 0.005$), with no significant interactions among the factors (range of $P = 0.095$–0.977; Appendix E). Propagules of both species established better at the lower elevation, in mixed *Rhizophora–Laguncularia* stands (Fig. 10A), than at mid- or high elevations (Tukey's hsd test: $P < 0.05$); rates did not differ between the latter two elevations. These patterns persisted for *Rhizophora* propagules over the additional seven weeks that they were monitored. In early January 1995, 19 weeks after being stocked in the pens, the proportion of *Rhizophora* that had established as rooted seedlings differed among transects ($F_{2,27} = 8.30$, $P = 0.002$) and elevations ($F_{2,4} = 9.49$, $P = 0.03$), with no transect × elevation interaction ($F_{4,27} = 1.98$, $P = 0.126$). The proportion of *Rhizophora* that had established as rooted seedlings was higher at low ($\bar{x} = 0.921$) than mid- (0.716) or high (0.617) elevations (Tukey's hsd test: $P < 0.05$), which did not differ.

In the second 1994 trial, *Laguncularia* propagules exhibited the same patterns of establishment as *Rhizophora* and *Avicennia* in the first trial (Fig. 10A): significant differences among transects ($F_{2,27} = 9.69$, $P = 0.001$) and elevations ($F_{2,4} = 16.74$, $P = 0.011$), with no transect × elevation interaction ($F_{4,27} = 0.46$; $P = 0.767$). Rates of *Laguncularia* establishment were higher at low tidal elevation than mid- or high elevations (Tukey's hsd test: $P < 0.05$), which did not differ. The *Laguncularia* trial ran for only seven weeks compared to 12 weeks for the *Rhizophora/Avicennia* trial; however, by seven weeks, no viable, unrooted *Laguncularia* remained in the pens.
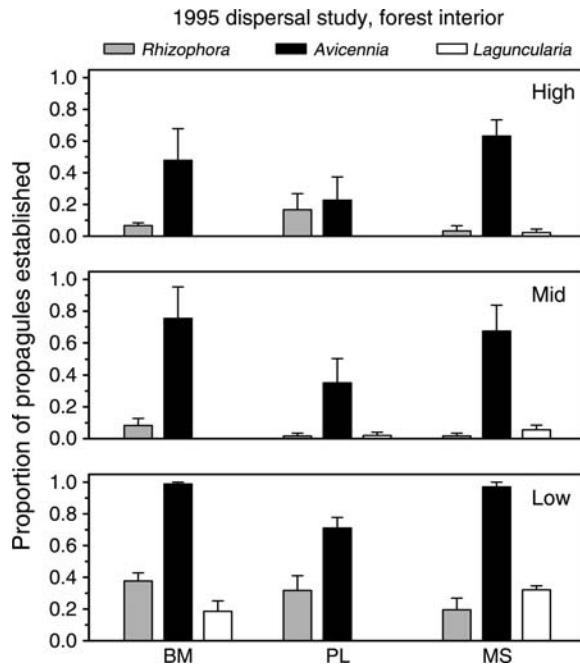
FIG. 11. Patterns of establishment by freely dispersing marked propagules in 1995. Bars show grand mean proportions (+SE) of propagules establishing as rooted seedlings after being released at replicate points at each of three different elevations along the three study transects (BM, PL, MS).

Thus, the overall rate of establishment of *Laguncularia* propagules was lower than for the other two species (Fig. 10A).

The patterns of establishment of marked, freely dispersing propagules in the 1995 dispersal study with respect to tidal elevation were quite similar to those observed in the pens. When released at the low elevation points, propagules of all three species exhibited significantly higher rates of establishment than those released at mid- or high elevation points (Fig. 11, Table 3). *Avicennia*, but not *Rhizophora*, propagules varied in their establishment rates among the three transects.

In the 1999 experiment, we assayed seedling establishment rates at an even lower tidal elevation, within fringing stands of pure *Rhizophora* on the edge of the BM lagoon trial. Propagules of the three species established equally well ($F_{2,4} = 5.01$, $P = 0.081$) and at high rates (Fig. 10B), with no difference between sites ($F_{2,27} = 1.68$, $P = 0.205$) or interaction between site and species ($F_{2,27} = 2.07$, $P = 0.113$).

In 2004, we compared seedling establishment rates in the back reef area, at or just below the lower edge of the fringing *Rhizophora* stands, where tidal influence is strong and propagules can float more than 50 cm off the substrate at high tide. At this elevation, overall rates of seedling establishment were much lower than those measured in the 1994 and 1999 experiments conducted at higher elevations inside the forest (Fig. 10). Also, in marked contrast to those experiments, there was a striking difference in the establishment rates of the three species in the back reef environment. Over the first 20-week phase of the experiment, the mean proportion of *Rhizophora* propagules that established as rooted seedlings was significantly higher than the proportion of *Avicennia* propagules (Fig. 10C; $t = 4.39$, df = 9, $P = 0.002$). In fact, only 2 out of 200 *Avicennia* propagules secured a roothold; both of these established in the shallowest of the 10 pens stocked with *Avicennia*, consistent with the hypothesis that deep water interferes with the establishment of species with smaller propagules. These two individuals had rooted by 21 July 2004 and subsequently developed into leafed, upright seedlings, but they both disappeared from the pen by 23 September 2004. In the second phase of the experiment, none of the 200 *Laguncularia* propagules successfully rooted in the sediment during the 34 d of monitoring; many of the propagules had developed roots while floating, but all had died and rotted. Thus, with the exception of the two *Avicennia* seedlings that became established in the shallowest pen in the experiment, *Rhizophora* was the only species whose seedlings were able to establish in the deeper water characteristic of back reef areas. When the *Rhizophora* pens were rechecked on 5 January 2005 (~25 weeks after stocking) and 29 July 2005 (~54 weeks after stocking), 90.6% and 87.5%, respectively, of the established propagules remained alive and growing.

TABLE 3. ANOVAs examining the independent and interactive effects of transect (BM, PL, or MS; a random factor) and tidal elevation (low [L], mid [M], or high [H]; a fixed factor) on the mean proportion of propagules of three species dispersing from a release point that established as rooted seedlings.

	Rhizophora			*Avicennia*			*Laguncularia*		
Source of variation	F	df	hsd	F	df	hsd	F	df	hsd
Transect	2.39	2, 18		6.557**	2, 18		NA		
Elevation	28.78**	2, 4	L > <u>M H</u>	56.24***	2, 4	L > M > H	12.25**	2, 6	L > <u>M H</u>
Transect × Elevation	0.49	4, 18		0.16	4, 18		NA		

Notes: Separate analyses were conducted for the three mangrove species: *Rhizophora*, *Laguncularia*, and *Avicennia*. *Laguncularia* establishment was too low on transects BM and PL (see Fig. 10) for meaningful comparisons (NA stands for not analyzed); instead, a one-way ANOVA was conducted to examine the effects of elevation on the MS transect. The results of Tukey's hsd multiple comparisons are also shown; underlines connect elevations for which the means did not differ significantly. Propagule releases were conducted in 1995 (see *Methods: Propagule dispersal: Direction and distance*). Asterisks indicate significance levels of F tests: **$P <$ 0.01; *** $P <$ 0.001; F values without asterisks were not significant ($P >$ 0.05).

DISCUSSION

What specifically do our results say about the applicability of the TSH to the mangrove forests of Punta Galeta, and more generally, about the role of propagule dispersal/limitation in maintaining patterns of mangrove zonation? In general, our findings show that the TSH sensu stricto does not explain the distribution of mangrove species on Punta Galeta, in large part because several of its central assumptions about patterns of propagule dispersal and establishment do not apply to our study forests.

Direction of propagule dispersal

Contrary to the assumption of the TSH that dispersing propagules are carried inland to higher tidal elevations by tidal flow, all the marked propagules that we released were moved by sheet-flow runoff from higher to lower elevations, toward the edges of a lagoon (BM), river (PL), or bay (MS). This highly directional pattern of dispersal was the same for all three mangrove species and for all elevations on each of the three study transects. Such strong directionality of diaspore dispersal is typical of hydrochorous (water-dispersed) species, be it in rain-washed deserts (Friedman and Stein 1980), streams and rivers (Waser et al. 1982, Willson 1993, Honnay et al. 2001, Levine 2001, 2003), or freshwater swamps (Schneider and Sharitz 1988). While we monitored the movements of released, marked propagules only once, during July–September 1995, we believe the results are generally representative of propagule dispersal patterns in our study area. We have worked at the site in each of the past 10 rainy seasons when propagules were dispersing, and regularly observed seaward transport of floating propagules by sheet flow, as well as piles of propagules trapped on the landward side of fallen logs, tree trunks, and against lines of dense pneumatophores radiating out from the bases of trees (Fig. 9A, B). Apparently, the strongly directional flow of runoff following rain storms overwhelms any tendency for incoming tidal flow to carry propagules inland.

This pattern of propagule dispersal may be typical for the Caribbean, where the tidal range is quite small and seasonal rainfall is high. For example, at the regional tidal reference station at Cristóbal, immediately adjacent to Colón, the mean range of spring tides is only 33.5 cm (NOAA National Ocean Service; *available online*).[4] This station is located behind breakwaters at the mouth of Bahía Limón, the Atlantic entrance to the Panama Canal, where it is protected from oceanic waves. The sheltered conditions at this station are very similar to those found at the lower ends of our study transects. This very modest tidal range contrasts markedly with the large tidal ranges characteristic of the Pacific coast of Panama. For example, the mean range of spring tides at Balboa, located at the Pacific entrance to the Panama Canal, is 5.0 m (NOAA National Ocean Service,

available online [see footnote 4]). With such large tidal ranges, combined with the generally lower rainfall on the Pacific coast, it is conceivable that the pattern of propagule dispersal assumed by the TSH might occur. To our knowledge, however, no study of mangrove propagule dispersal comparable to ours has been conducted along the Pacific coast of Central America. Nonetheless, Jiménez and Sauter (1991) inferred from natural patterns of seedling recruitment that tidal sorting is a key process controlling the vertical distributions of *Rhizophora* and *Avicennia* along a tidal flooding gradient in the Tivives mangrove forest on the Pacific coast of Costa Rica. The TSH may also apply in other regions where flood tides carry freshly fallen mangrove propagules to higher elevations where they strand as the tide ebbs (e.g., southeastern Australia; Clarke 1993, Clarke and Myerscough 1993; T. Minchinton, *personal communication*).

Propagule dispersal distance

While their direction of movement was exactly opposite that predicted by the TSH, the average distances that propagules of the three species moved from their release points were, as predicted, inversely related to the sizes of the species' propagules. *Laguncularia* propagules, which are the smallest and lightest of the three, dispersed farther than intermediately sized *Avicennia* propagules, which in turn dispersed farther than *Rhizophora* propagules, by far the largest and heaviest of the three types. There was considerable small-scale variation in the distances that propagules traveled from points of release, due in large part to physical barriers such as fallen logs and other emergent substrates that blocked propagule movement, especially in shallow areas. Propagules often accumulated along the landward sides of these objects, as well as in strandlines at the edge of water bodies. This contributes to the patchy distribution of annual seedling cohorts across the forest floor (W. Sousa, *personal observation*).

The accumulation of plant propagules against barriers is commonly observed in habitats where propagules are dispersed by water. Jiménez (1990) describes the stranding and establishment of *Avicennia bicolor* propagules against fallen branches and tree trunks in mangrove forests on the Pacific coast of Costa Rica. Schneider and Sharitz (1988) documented a very similar pattern of accumulation adjacent to emergent substrates by the water dispersed seeds of bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) in a temperate floodplain forest. As in our system, this small-scale heterogeneity in seed density affected the distribution of seedlings across the forest floor (Huenneke and Sharitz 1986). Moegenburg (2002) showed that leaf litter (e.g., fallen palm fronds) on the forest floor or aboveground tree roots acted as barriers to the dispersal of hydrochorous seeds in a tidally flooded Amazonian forest. The topography of the substrate itself can also influence spatial patterns of propagule supply. Minchin-

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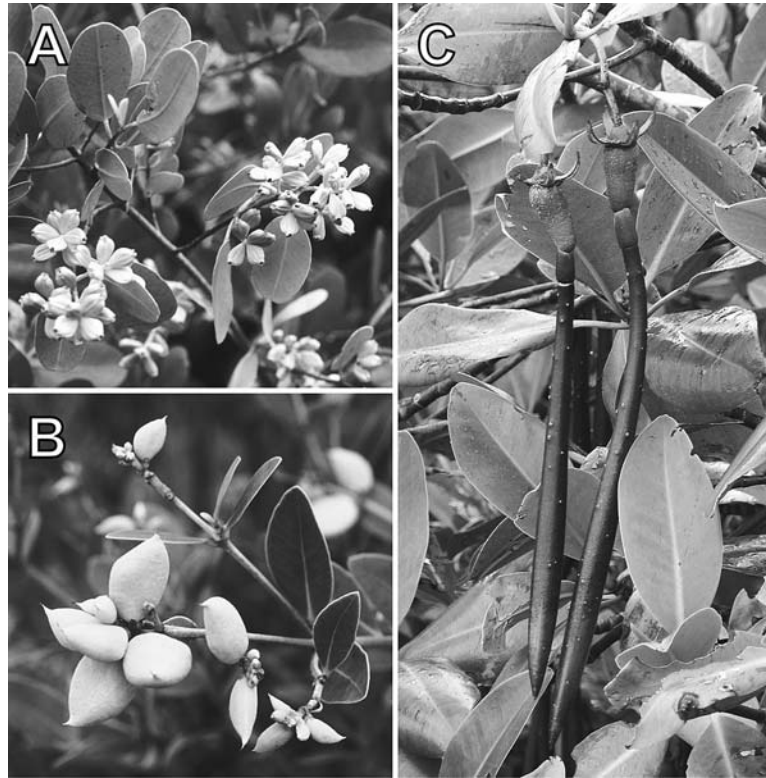[4] ⟨http://co-ops.nos.noaa.gov/tide_pred.html⟩

PLATE 1. Propagules of the three species that comprise the mangrove forest canopy at Punta Galeta, Panama: (A) *Laguncularia racemosa*, (B) *Avicennia germinans*, and (C) *Rhizophora mangle*. Photo credit: W. P. Sousa.

ton (2001) found that mounds of sediment created during the excavation of burrows by crabs had a marked influence on the spatial distribution of dispersing propagules of *Avicennia marina* in an Australian mangrove forest. Propagules accumulated disproportionately in the flat areas between mounds. When experimentally placed on mounds, most propagules dispersed off them, onto the surrounding flats. Though the few propagules that remained on mounds exhibited higher rates of establishment as rooted seedlings than those that dispersed to the flats, the strongly disproportionate numbers that accumulated in flat areas resulted in a higher density of seedlings in these areas than on mounds.

While some *Laguncularia* propagules moved considerable distances (85 m or more) from their points of release during the two weeks that their dispersal was monitored, propagules of *Avicennia* and *Rhizophora* were seldom found more than 10 m from their release points, and most moved less than a couple of meters during the four weeks of observation. Such limited movement would seem surprising for hydrochorous species that are generally assumed to be dispersed long distances by tidal and oceanic currents. Observations of viable plant diaspores adrift in the sea or stranded at sites far from potential source areas suggest they are

dispersed greater distances than those that are wind- or animal-dispersed (Cain et al. 2000; also see Kinlan and Gaines 2003). In his classic treatise on plant dispersal, Ridley (1930:242) declared, "We know … that the distances seeds travel in the sea unharmed and in a fit stage for germination are the longest of any method of transport, certainly over 1000 miles." Such statements are probably true with respect to maximum dispersal distances, but they may not be correct for the modal or average distances that propagules are moved, particularly inside mature forest stands.

While dispersal of mangrove propagules has seldom been quantified in any setting, the few studies that have documented their movements within established forests report patterns very similar to those we observed. For example, at the mid-tidal level of a northern Australia mangrove forest, McGuinness (1997) found that 94% of *Ceriops tagal* propagules moved ≤ 3 m over a 70-d observation period, and none moved more than 8 m. Similarly, in a Malaysian mangrove forest, Chan and Husin (1985) observed that on average 86.2% of *Rhizophora mucronata* propagules dispersed less than 5 m from the parent tree and 92.3% less than 20 m; only 7.7% moved more than 35 m, and none farther than 56 m. Clarke and Myerscough (1991) concluded from their study of buoyancy properties of *Avicennia marina*

propagules in south-eastern Australia that in more saline parts of their study estuary, "most propagules strand close to the parent...." Yamashiro (1961) monitored the fates of paint-marked, dispersing propagules of *Kandelia candel* over a 30-d period at three different tidal elevations in a mangrove forest in southern Japan. Of the 227 marked propagules that were recovered (all of them found within 50 m of the parent trees), 70.5% (160/227) had remained within 10 m of the parent tree. Interpretation of these data is clouded by the fact that 88% of the marked propagules (1627/1854) were never found again. Yamashiro inferred that the missing propagules had been carried away by tidal currents, but predation by herbivorous crabs (as suggested by McGuinness 1997) or loss of the paint marks are equally viable alternative explanations that were not considered. Crabs consume a considerable proportion of dispersing propagules in our study area (Sousa and Mitchell 1999) and other mangrove forests (e.g., Smith et al. 1989, Allen et al. 2003).

Although McKee (1995) did not directly measure the movements of mangrove propagules at her study site on a barrier reef island off the coast of Belize, she found that distance from reproductive adult trees explained 94% and 63% of the variation in the relative density of recently recruited seedlings of *Rhizophora* and *Laguncularia*, respectively, on the forest floor. This pattern strongly suggested that the propagules of these species dispersed only short distances, especially those of *Rhizophora*. Blanchard and Prado (1995) observed a similar spatial pattern of *Rhizophora* recruitment during recolonization of strip clearcuts in northwest Ecuador: the density of *Rhizophora* seedlings was highest within 5 m of large reproductive trees growing along the edge of the clearcut. In contrast, McKee (1995) found that variation in the relative density of newly recruited *Avicennia* seedlings was best explained (73%) by resource availability (light and soil NH_4); distance from reproductive adults did not contribute significantly to this variation.

On the other hand, when mangrove propagules are dispersed to, or dropped directly into, tidal creeks or open coastal waters, they may be carried much longer distances by currents. Clarke (1993) found that *Avicennia marina* propagules were moved during a single flood tide as far as 500 m from their point of release along tidal creeks that enter Jervis Bay, New South Wales, Australia. He assessed patterns of more distant dispersal by surveying beaches along the southeast coast of Australia for the occurrence of stranded *A. marina* propagules. Clarke conservatively estimated the distances the stranded propagules had to have dispersed to reach the beach on which they stranded as the distance to the nearest estuary containing the species. These observations indicated that while *A. marina* propagules that reach open water can be dispersed up to 50 km from their source population, most such propagules strand within 1 km of their origin. Using an approach similar to

Clarke's, Sengupta et al. (2005) found that the density of *Rhizophora mangle* propagules stranded on beaches along the coast of southwestern Florida declined with distance from likely source areas, and most were deposited within 2 km of potential source locations. Davis (1940) cast sets of marked *Rhizophora mangle* propagules over the side of a boat at four locations while en route from Key West to the Tortugas Keys off south Florida and then searched for them on beaches of the islands of the Tortugas. Those he found had traveled 13–37 km from their point of release. Similarly, Gunn and Dennis (1973) found viable *Avicennia germinans* and *Rhizophora mangle* propagules stranded on beaches along the Gulf coast of Texas many kilometers from possible source areas. Stieglitz and Ridd (2001) estimated from a drift-drogue experiment that, during flood tides, mangrove propagules were transported upstream at an average speed of 3.2 km per day (maximum of 14.6 km per day) in the Normanby River estuary in northeastern Australia.

The observation that most mangrove propagules do not disperse far from the parent tree, establishing as seedlings nearby, while a smaller number may move large distances, is typical of most plant species. Such seed shadows are usually modeled with a unimodal, leptokurtic distribution that peaks close to the parent's position, rapidly declines with distance, and ends with a long tail of varying thickness (Harper 1977, Portnoy and Willson 1993, Willson 1993, Nathan and Muller-Landau 2000, Levin et al. 2003). Both the preponderance of local establishment and the potential for long-distance dispersal have important implications for the ecology and evolution of mangroves. The fact that most dispersing propagules establish as rooted seedlings close to the parent tree means that local forest composition can strongly affect patterns and rates of light gap regeneration, the primary mode of canopy tree replacement in our study sites (Sousa et al. 2003b). Since most recruits to gaps, either in the form of new seedlings or advance regeneration, will come from the immediate area, dispersal limitation can strongly affect the density and species composition of regenerating vegetation and therefore, the strength and outcomes of interspecific interactions, such as competition or facilitation, that will determine which species fill the gap.

Such local dispersal, which limits the exchange of propagules between adjacent sites, may also account for the considerable genetic variation that has been observed among local populations of *Avicennia germinans* (Dodd et al. 2002, Dodd and Rafii 2002, Cerón-Souza et al. 2005), *Avicennia marina* (Duke et al. 1998a, Maguire et al. 2000), and *Rhizophora mangle* (D. Devlin, E. Proffitt, and S. Travis, *personal communication*). On the other hand, variation in patterns of longer distance dispersal among species, and barriers thereto, have been important in shaping biogeographic patterns of mangrove distribution, species diversity, and evolution (Ricklefs and Latham 1993, Duke 1995, Duke et al.

1998*b*, 2002, Ellison et al. 1999, Cain et al. 2000, Ellison 2002, Renner 2004). Even if the rates of effective migration resulting from long-distance propagule dispersal are low, they can maintain genetic similarity among widely separated populations, as appears to be the case for eastern and western Atlantic populations of *Avicennia germinans* (Dodd et al. 2002). Exploration of the link between propagule dispersal patterns and the genetic structure of mangrove populations is at a very early stage but appears to be a promising area for future research.

A variety of life history features and environmental factors besides propagule size, water depth, and current speed and direction can affect patterns of mangrove propagule dispersal. Irrespective of size/mass, propagules vary, both inter- and intraspecifically, in their buoyancy and duration of floating (Steinke 1986, Clarke and Myerscough 1991, Clarke et al. 2001). For example, in laboratory floating trials we found that *Laguncularia* and *Rhizophora* propagules floated longer in higher salinity water; *Avicennia* propagules floated throughout the test period, regardless of salinity (Appendix A). Rabinowitz (1978*b*) documented the same pattern in her earlier study of these species, as did Davis (1940) for *Rhizophora*. Increased propagule buoyancy in denser, higher salinity water has also been observed for a wide variety of other mangrove species, although not all (Clarke and Myerscough 1991, Clarke 1995, Clarke et al. 2001). This interaction between propagule buoyancy and salinity can potentially affect dispersal distance and direction, particularly in estuarine river systems where marked gradients in salinity and tidal eddies are common.

Propagule establishment

The assumption of the TSH, that species with larger propagules would be better able to establish in deeper water, was generally supported by our findings. At the lowest tidal height tested, in the back reef at or just below the lower edge of fringing *Rhizophora* stands, *Rhizophora* propagules established as rooted seedlings with much higher frequency than either *Avicennia* or *Laguncularia*. Additional evidence that *Rhizophora* propagules are able to establish as rooted seedlings in deeper water than those of *Avicennia* and *Laguncularia* comes from a census we conducted in July 2003 of mangrove seedlings that had naturally recruited to the Galeta reef flat. All of the 121 seedlings we observed were *Rhizophora*. In fact, rooted and leafed *Rhizophora* seedlings have been photographed at 2 m depth in a channel that drains the Galeta reef flat (E. Bravo, *personal communication*).

McKee (1995) documented a similar pattern of propagule establishment in the regularly inundated low intertidal zone of Twin Cays, off the coast of Belize, where a modest number of tethered *Rhizophora* propagules were able to firmly root in the soil and survive for the 2.5 years of the study, while none of the tethered

Avicennia propagules were able to establish. McMillan (1971) also observed that *Avicennia* propagules rarely established as rooted seedlings when the water depth exceeded 5 cm. However, rates of seedling establishment did not increase monotonically with distance from the water's edge for smaller propagules as predicted by the TSH. Instead, peak establishment rates for all three species were observed in the low intertidal zone where propagules were in regular and prolonged contact with the exposed soil surface during low tides. At mid- and upper intertidal zones, the soil surface was covered by 5–15 cm of standing water that accumulated during the wet season within the shallow basin that is characteristic of inland areas of the swamp. This lens of standing water was sufficiently deep to limit access of buoyant propagules to the soil surface; thereby reducing rates of establishment. Propagules that failed to establish a roothold eventually rotted and died. While seedlings established more poorly in this upper basin, the standing water was not an absolute barrier to establishment; seedlings of all three species were able to recruit there, and vigorous stands of mature *Avicennia* typically dominate in these areas.

Criticisms of the Tidal Sorting Hypothesis (TSH)

Observational and experimental evidence collected since the TSH was first published (Rabinowitz 1978*a*) more than 25 years ago has provided little support for the mechanism of mangrove zonation it proposed. Criticisms have been wide-ranging but fall into three categories. First, physiologists have challenged Rabinowitz's premise that differences in tolerance of edaphic conditions do not explain zonation, pointing out that Rabinowitz's reciprocal transplant experiments did not run long enough to rigorously confirm this. During the one year period that she monitored her experiments, seedlings could have been surviving and growing on stored embryonic reserves, thereby buffered from the stresses of their new habitats (A. Smith, *personal communication*). Not until such reserves are exhausted and the plants are coping independently of maternal investment, physiologists argue, can one determine whether differential tolerance of, and performance in, the new locations will generate differences in distribution along the tidal gradient. While this argument has merit, a growing number of studies, conducted with different species of mangroves in various parts of the world, have obtained results similar to Rabinowitz's. When seedlings are reciprocally transplanted among zones of differing species composition and tidal elevation, no strong differences in survival or growth are observed (Smith 1987, Delgado et al. 2001, Clarke 2004) or the performance of seedlings actually improves when moved to a different zone (Jiménez and Sauter 1991). We have also conducted long-term reciprocal transplant experiments in our study forests, planting seedlings of the three canopy species at different positions along the tidal gradient. These experiments have run for 10 years

and yielded the same general result found by Rabinowitz (1978a). Each of the species survives and grows as well, or better, in zones dominated by other species than in the zone where their own species is most abundant (W. Sousa, *unpublished data*). Consistent with this finding, we have observed that many of the *Rhizophora* seedlings that established as seedlings in pens located within *Avicennia* stands during the present study have survived, albeit in a suppressed state, for more than 10 years. Thus, the majority of field experiments have tended to confirm Rabinowitz's (1978a) conclusion that species-specific differences in physiological tolerance of, or specialization to, varying edaphic conditions is not a sufficient explanation for the differential distribution of species along the tidal gradient.

A second criticism of the TSH concerns its prediction that seaward stands should be dominated by species that produce relatively large propagules while more inland stands should be comprised of species that produce smaller propagules. Smith (1987, 1992) and Delgado et al. (2001) describe sites in which the opposite pattern holds, and the Clarke et al. (2001) study of the relationship between early life history traits and dispersal potential of 14 mangroves species of northern Australia found little or no correlation between features such as diaspore mass, shape, orientation or buoyancy, and patterns of species zonation with distance from the shoreline. In our study forests, *Rhizophora*, which has the largest propagule, is, as predicted, the most successful species at establishing in deeper water at the seaward edge of the forest, which likely explains its dominance of fringing stands. However, the relationship between propagule size and tidal distribution is less clear for the other two species. *Avicennia* propagules are nearly twice as large as those of *Laguncularia* (Rabinowitz 1978b, Sousa et al. 2003a); so according to the TSH, *Avicennia* should be most abundant just landward of *Rhizophora*, with *Laguncularia* dominating the most inland areas of the forest. This is not the distributional pattern we see on Punta Galeta. *Avicennia* typically dominates the upper intertidal basin habitat, while in many areas *Laguncularia* exhibits a bimodal distribution along the tidal gradient. It is abundant below basin stands of *Avicennia*, growing in nearly even mixtures with *Rhizophora* in the low intertidal, but also grows in small, nearly pure stands along the ecotone between the mangrove forest and upland rain forest, often immediately landward of *Avicennia*.

Thirdly, the TSH has been criticized for its assumption that shallow waters characteristic of higher tidal elevations restrict the landward movement of larger propagules carried by rising tides; in effect, sorting the upper distributional limits of species by propagule size. In other words, species with smaller propagules are dispersed farther inland than species with larger propagules. While this phenomenon might occur in locations with substantial tidal ranges, we observed a very different scenario in our study areas. The upper limit of *Rhizophora*, the species with the largest propagule in our system, is set by a different sort of dispersal limitation imposed by the strongly directional movement of propagules from upper to lower tidal levels by runoff following storms.

Our observation that mangrove propagules consistently disperse in a seaward direction within our study area raises the question of how the species characteristic of mid- and upper intertidal stands (i.e., *Avicennia* and *Laguncularia*) were originally able to recruit to those elevations. We cannot know for certain, but a variety of contemporary and historical processes could account for it. One possible explanation is that infrequent large storm surges, possibly coincident with extreme high tides, occasionally transport the relatively small propagules of these species inland to higher elevations. In essence, the TSH would operate during these periods of unusually high tidal flow. Alternatively, the answer may simply lie in the historical patterns of mangrove biogeography and sea level fluctuations. The three principal canopy mangrove species first appeared in the Caribbean domain at distinctly different times. *Rhizophora* first appeared in the late Eocene ~38.6–35.4 million years ago, increased markedly in abundance during the Oligocene, and has been a dominant species along the Caribbean coast since the early Miocene (Germeraad et al. 1968, Graham 1985, 1995, Muller et al. 1987, Rull 1998a, b). *Avicennia* established in the Caribbean region by the late Miocene ~10 million years ago (Muller et al. 1987). *Laguncularia*, the last to arrive, first appeared in the middle Pliocene ~3–4 million years ago (Graham 1976, Graham and Dilcher 1998). Thus, *Rhizophora* and *Avicennia* were already abundant in the region at the time the Isthmus of Panama closed ~3.5–2.5 million years ago (Coates et al. 1992, Coates and Obando 1996, Cronin and Dowsett 1996), while *Laguncularia* established roughly coincident with its emergence.

All three species colonized the Caribbean region during periods when sea level was 60–150 m higher than it is presently (Haq et al. 1987) and must have established populations at higher elevations and farther inland than they presently occupy. While there has been a general declining trend in sea level since these species established in the Caribbean, cycles of glaciation have driven marked fluctuations in sea level. Since *Laguncularia*, the last of the three species to arrive in the region, established along the Caribbean coast, sea level has exceeded the current level by as much as 20 m during several interglacial periods (Haq et al. 1987). As recently as the last interglacial period ~128–116 thousand years ago, sea level was ~2–8 m above present levels (Ku et al. 1974, Chen et al. 1991, Gallup et al. 1994, Szabo et al. 1994, Stirling et al. 1998, Hearty and Neumann 2001, Potter and Lambeck 2003, Schellmann and Radtke 2004, Siddall et al. 2006). Therefore, since establishing in the Caribbean, all three species have lived at substantially higher shore levels than they presently do, and

their distributions have presumably shifted up and down with changes in sea level. Populations of *Avicennia* and *Laguncularia* may simply have persisted better at upper elevations than those of *Rhizophora* during periods when sea level was dropping. Even if propagules of these mid- and upper intertidal species tend to be moved seaward by sheet-flow runoff, physical barriers to their movement (e.g., dense beds of pneumatophores or woody debris) ensure that a substantial number of them establish as seedlings immediately below the adult canopy, thereby maintaining the vertical distributions of these species.

Supply-side dynamics in mangroves

What do our results say about the contemporary role of propagule supply in structuring our study forests? We have documented (1) that seedlings are able to survive and grow well when transplanted above their species' current upper distributional limits and (2) that dispersing propagules are consistently transported downward toward lower tidal heights. This strongly suggests that dispersal limitation plays an important role in structuring higher elevation, inland forest stands. In contrast, at the lower, seaward boundary of the forest, deeper water and associated agitation by waves, rather than a limited propagule supply, prevent all but the species with the largest propagules from establishing. Between these upper and lower boundaries, neither propagule supply nor water depth is limiting, and a variety of interacting biotic and abiotic processes determine forest composition, species distributions, and patterns of regeneration following canopy disturbance. Our ongoing experimental and observational studies are examining the independent and interacting effects of competition, insect herbivory, and edaphic conditions on spatial and temporal variation in mangrove forest structure.

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APPENDIX A

Methods and results of an experiment testing the effects of paint marking and salinity on buoyancy of mangrove propagules (*Ecological Archives* M077-003-A1).

APPENDIX B

ANOVAs testing the effects of transect, tidal elevation, and species of propagule on the mean proportion of marked propagules that were relocated after two or four weeks (*Ecological Archives* M077-003-A2).

APPENDIX C

ANOVAs testing the effects of transect, tidal elevation, species of propagule, and release point on the mean distance moved by marked and released propagules (*Ecological Archives* M077-003-A3).

APPENDIX D

ANOVA testing the effects of transect, tidal elevation, and species of propagule on the mean proportion of marked propagules that failed to disperse from a release point (*Ecological Archives* M077-003-A4).

APPENDIX E

ANOVA testing the effects of transect, tidal elevation, and species of propagule on the mean proportion of propagules that established as rooted seedlings in the first trial of the 1994 propagule establishment experiment (*Ecological Archives* M077-003-A5).