

Influence of Propagule Flotation Longevity and Light Availability on Establishment of Introduced Mangrove Species in Hawai'i¹

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Abstract: Although no mangrove species are native to the Hawaiian Archipelago, both *Rhizophora mangle* and *Bruguiera sexangula* were introduced and have become naturalized. *Rhizophora mangle* has spread to almost every major Hawaiian island, but *B. sexangula* has established only on O'ahu, where it was intentionally introduced. To examine the possibility that differences in propagule characteristics maintain these patterns of distribution, we first reviewed the literature on surface currents around the Hawaiian Islands, which suggest that propagules ought to disperse frequently from one island to another within 60 days. We then tested the ability of propagules of the two species to float for periods of up to 63 days and to establish under two light intensities. On average, *R. mangle* propagules floated for longer periods than those of *B. sexangula*, but at least some propagules of both species floated for a full 60 days and then rooted and grew for 4 months under relatively dense shade. A large percentage (~83%) of *R. mangle* propagules would be expected to float beyond 60 days, and approximately 10% of *B. sexangula* propagules also would have remained afloat. Therefore, it seems likely that factors other than flotation ability are responsible for the failure of *B. sexangula* to become established on other Hawaiian islands.

THE HAWAIIAN ARCHIPELAGO, located in the central Pacific Ocean between 18 and 30° N and 155 and 180° W, has no native mangroves, despite having climatic conditions and geomorphic settings well suited to mangrove growth (Wester 1981, Allen 1998). Hawai'i's vast distance from other landmasses and its isolation relative to major ocean currents have most likely prevented natural mangrove colonization (Guppy 1906, Carlquist 1967, Wester 1981).

Mangrove species were first introduced to Hawai'i in 1902, when *Rhizophora mangle* L. propagules from Florida were planted on the island of Moloka'i to stabilize mudflats created by the erosion of cattle pastures and sugarcane fields (MacCaughy 1917). At least five other mangrove species have also been introduced, but of these only *Bruguiera sexangula* (Lour.) Poir. and *Conocarpus erectus* L. are naturalized (Wagner et al. 1999, Allen et al. 2000). *Rhizophora mangle* is by far the most widespread and common mangrove in Hawai'i. *Rhizophora mangle* is found on all the main islands with the possible exceptions of Kaho'olawe and Ni'ihau; *C. erectus* is naturalized on Kaua'i, Lāna'i, Maui, and O'ahu; and *B. sexangula* is naturalized only on O'ahu (Wagner et al. 1999).

Rhizophora mangle began to spread rapidly after its introduction. Fifteen years after the first planting on Moloka'i, seedlings had become established at least 8 km from the original planting site and propagules were found over 90 km away on the opposite side of the island (Cooke 1917). Although there is some documentation of deliberate plantings of *R. mangle* on O'ahu and Maui (Allen 1998), the

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capacity of this species to disperse by water is apparent from previous work (Davis 1940, Ellison 1996, Sengupta et al. 2005), and it may therefore have spread among the Islands primarily without further human assistance (Sauer 1988). It is reportedly continuing to spread, especially along the eastern shore of the island of Hawai'i (the "Big Island"), the western shore of Maui, and the southern shore of Kaua'i (Allen 1998; D. Lorence, National Tropical Botanical Garden, pers. comm.).

In contrast to *R. mangle*, *B. sexangula* and *C. erectus* have shown little tendency to spread beyond their original planting sites and may not have become established on islands other than those on which they were planted. *Conocarpus erectus* is widely used ornamentally, and planting stock is commercially available, so its movement from O'ahu to Kaua'i, Lāna'i, and Maui may well have been human-assisted. *Bruguiera sexangula*, on the other hand, is not known to have been deliberately planted other than during its introduction in 1922, and, of the four known locations where it is found on O'ahu, at least three are believed to be original planting sites (McEldowney 1922). Fosberg (1948:8), contrasting *B. sexangula* to *R. mangle* in Hawai'i, noted that "[*B. sexangula*] seems to be much less able to scatter its seedlings to a distance from the parent trees, though very well able to hold its own locally," and this still seems to be the case nearly 60 yr later.

The apparent inability of *B. sexangula* to spread much, if at all, beyond its original planting sites in Hawai'i is puzzling. This species has an extensive natural range that includes a number of South Pacific islands (Spalding et al. 1997), suggesting that it must have at least moderately effective dispersal capabilities. *Bruguiera sexangula* is distributed throughout Australasia (Duke et al. 1998) and has dispersed at least 100 km or more among locations in Sri Lanka (Jayatissa et al. 2002). Although it is one of the least salt tolerant of the true mangroves, *B. sexangula* is more shade tolerant than *R. mangle* (Smith 1992) and should be able to establish and compete effectively with *R. mangle* on less-saline sites or under reduced light levels (Krauss and Allen 2003).

The differential potential for dispersal and establishment of *B. sexangula* and *R. mangle* in Hawai'i, then, is the central issue addressed in this paper. First, we review the literature on ocean surface currents in Hawai'i as they might relate to the interisland dispersal of mangrove propagules. Second, we compare the flotation longevity of *B. sexangula* and *R. mangle* in an experiment designed to simulate oceanic dispersal. Third, we follow the growth of propagules after various periods of flotation and under two light regimes.

Ocean Surface Currents in Hawai'i

Although Hawai'i does not lie directly in the path of any of the major North Pacific Ocean currents, there is a general movement of water in a westerly direction through the Islands driven by the North Pacific Drift and the trade winds (Barkley et al. 1964, Hourigan and Reese 1987). The movement of water within the archipelago is greatly complicated by bottom features, tides, seasonal effects, and physical barriers that the Islands pose to the smooth flow of water and air. The results are that currents at some locations and times may run in directions directly opposite to the prevailing flow, mesoscale eddies are formed that may circulate downwind of the Islands for 2 months or more, and the prevailing surface flow may be in either a northwesterly or a southwesterly direction (Barkley et al. 1964, Wyrski et al. 1969, Lobel 1989).

Perhaps of most immediate relevance to the interisland movement of mangrove propagules are two studies that have made use of drift bottles or drift cards. Both drift bottles and cards are relatively small and float at the surface; thus, their drift patterns might resemble those of mangrove propagules (which are affected by both prevailing currents and surface winds) more closely than those of newer technologies used for studying currents, such as surface drifters with submerged drogues or subsurface floats.

A total of 16,285 drift bottles or cards was released in the central Pacific, most in the immediate vicinity of the Hawaiian Islands (Barkley et al. 1964). Many were released off the southern or eastern coasts of O'ahu or

southwestern Moloka'i (i.e., not far from some of the largest existing mangrove stands) and recovered on other islands (Figure 1). Estimated minimum velocities of the drift bottles and cards ranged from 1.6 to 24 km day⁻¹, with the objects most commonly floating in the range of 4.8 to 9.6 km day⁻¹ from July to December when many propagules are disseminating in Hawai'i (Cox and Allen 1999). A propagule originating from the windward coast of O'ahu therefore might reach the island of Kaua'i within about 20 to 40 days. Preliminary results from an ongoing National Oceanic and Atmospheric Administration (NOAA) study (<http://response.restoration.noaa.gov/drifter.html>, 27 June 2005) showed that drift cards released from O'ahu have reached the islands of Kaua'i, Moloka'i, and Maui in as little as 1 week.

Propagules caught up in mesoscale eddies, which seem to be particularly common downwind of the more southern islands, might circulate for a longer period before stranding, given a mean eddy life span of 65 days (Patzert 1969). In general, though, the prospects are good that propagules originating from any given Hawaiian island have the potential to reach one of the other islands in 7 to 60 days.

MATERIALS AND METHODS

Mature, freshly fallen propagules of *B. sexangula* were collected from a dry stream bank from a small stand on the Anahulu River in Hale'iwa (O'ahu) on 30 July 1999. Propagules were collected from the ground below at least six parent trees and were not exposed to seawater initially. Propagules were immediately transported to a greenhouse where they were placed in tap water for 7 days to ensure full hydration and to limit the need for osmotic adjustment among propagules initially. Floating propagules were individually numbered with a permanent marker on the outside of the cuticle, weighed, and the length measured. A total of 300 propagules was then placed in three floating wire-mesh cages ($n = 100$ per cage) tied to a dock at the Hawai'i Institute of Marine Biology, which is located on an island in Kāne'ohe Bay (O'ahu).

The dock is within a small inlet that provides shelter from wave action but has no notable source of freshwater input. Periodic measurements of salinity taken over the course of the experiment ranged from 34.6 to 35.1 ppt, and water temperature (generally measured between 0830 and 1200 hours) ranged from 26.4 to 28.2°C.

Because approximately 20% of *B. sexangula* propagules sank after only 2 weeks, we decided to remove approximately one-third of the propagules still floating after 14 days. Half of those propagules still floating were removed after 28 days (4 weeks), and all the remaining floating propagules were removed after 63 days (9 weeks). Actual sampling dates, hence, were determined by the flotation characteristics of *B. sexangula*. Immediately after removal, each group of propagules was transported to a greenhouse, where the propagules were planted in trays filled with a commercial potting mix (Sunshine 1 Mix, Sun Gro Horticulture, Bellevue, Washington). The greenhouse was covered with translucent plastic roofing material; maximum light levels were approximately 800 $\mu\text{mol m}^{-2} \text{sec}^{-1}$, and temperatures typically were in the range of 22–32°C during the day and 16–23°C at night. Approximately half of the propagules in each group were placed on an open bench (unshaded) and half were placed on a bench covered with 80% neutral-density shade cloth (shaded). Seedlings were watered regularly (with freshwater) but not fertilized. Height was measured and the number of leaves counted monthly for 4 months.

The same procedure was followed for *R. mangle*, except that the propagules were collected from approximately 30 parent trees on sites in Kāne'ohe Bay (O'ahu). Most of the propagules were collected directly from trees, and those few propagules collected from the ground were freshly fallen and unlikely to have floated in seawater for more than a few hours. The *R. mangle* propagules were collected on 19 October 1999 (closer to the period of peak propagule fall for this species [Cox and Allen 1999]), and flotation began on 22 October after 3 days of hydration in freshwater. Sampling dates of 2 weeks, 4 weeks, and 8 weeks were similar to those for

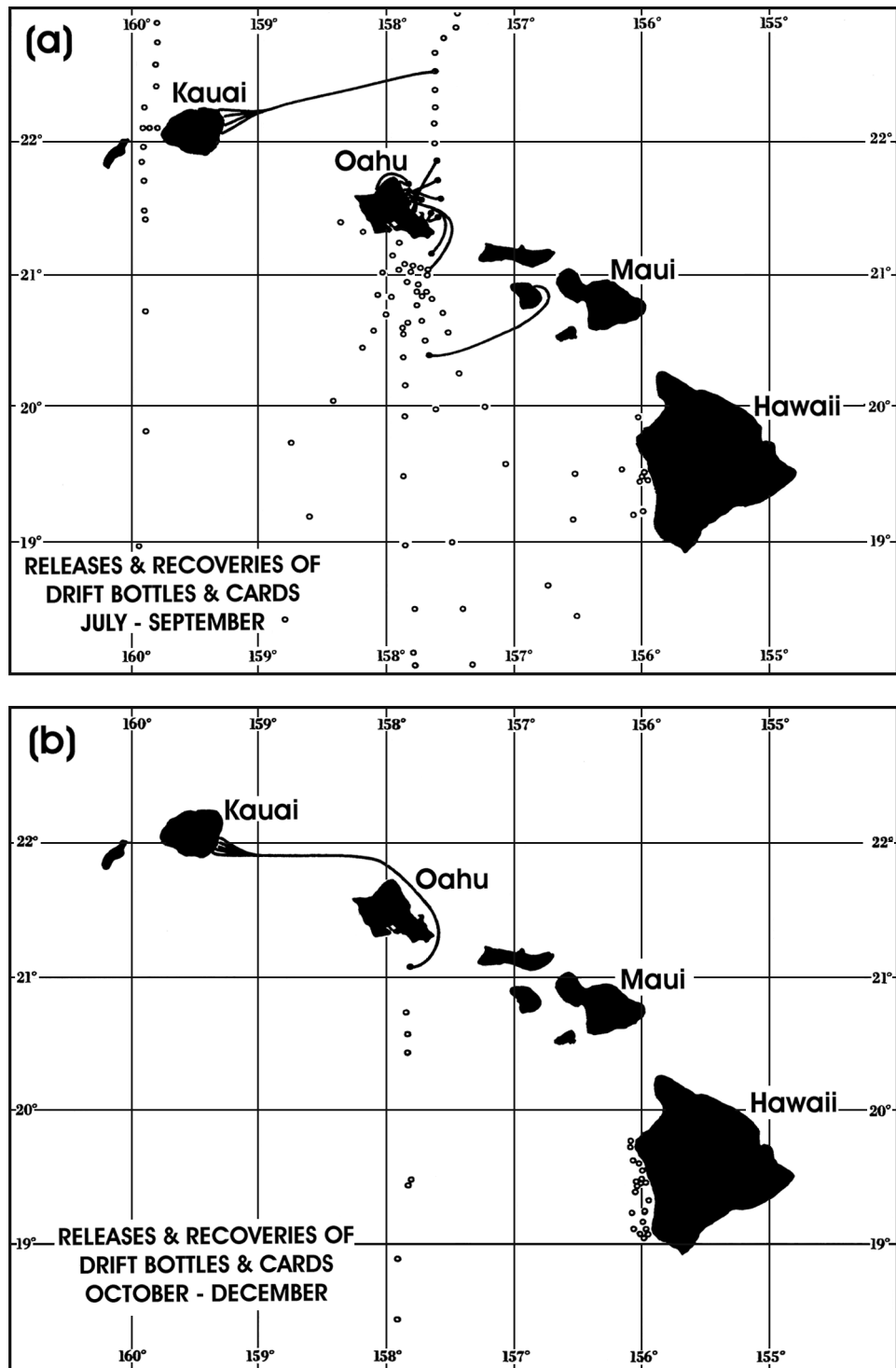


FIGURE 1. Accounts of drift bottle or card release and recovery experiments within the Hawaiian Archipelago over two time periods between 1961 and 1963 (*a*, July–September; *b*, October–December) depicting some of the mesoscale current patterns potentially affecting interisland mangrove propagule dispersal (after Barkley et al. 1964). Circles depict release points, line intercepts with islands depict recoveries, and lines predict dispersal trajectories.

B. sexangula. Mean salinity was also similar between the periods when *B. sexangula* and *R. mangle* were floating in the cages.

Flotation data were analyzed with linear regression to estimate propagule flotation longevities for either *B. sexangula* or *R. mangle*. Hence, we assumed a linear relationship between propagule flotation versus time; our data were not sufficient to use curvilinear regression for these estimates. After propagules floated for predetermined periods (0, 2, 4, or 8/9 weeks), propagules were placed under different light regimes (unshaded, shaded). Growth was analyzed as a split-plot design, with light treated as a random effect. Analysis of covariance (ANCOVA) was specified, with initial propagule weight as the covariate; propagules differed significantly in initial size. Growth data were square-root transformed to improve normality and homogeneity of residual variances. Leaf count data could not be normalized and were subjected to the Wilcoxon signed-rank test, pitting either week 0 against weeks 2, 4, or 8/9 to expose possible trends with flotation longevity or shaded versus unshaded to expose possible trends with light regime. All analyses were performed using SAS version 8.02 (SAS Institute, Cary, North Carolina).

RESULTS

The propagules of *R. mangle* had an average fresh weight of 22.0 g (range: 8.5–50.8 g; $n = 400$) and an average length of 22.5 cm (range: 11.7 to 36.6 cm). *Bruguiera sexangula* propagules were much smaller, with an average fresh weight of 10.7 g (range: 5.6–15.5 g; $n = 500$) and an average length of only 8.2 cm (range: 6.0–10.1 cm).

At least some propagules of both species floated for up to 63 days, but, by then, a much greater proportion of *B. sexangula* had sunk than *R. mangle* (Figure 2). The proportion of propagules still floating at each time period declined linearly. If the trends for each species were to continue in a linear fashion, all of the *B. sexangula* propagules ($r^2 = 0.914$; $P < .001$; $y = 93.49 - 1.39x \pm 10.68$ SEM) would have sunk by 67 days and all of the *R. mangle* propagules ($r^2 = 0.844$;

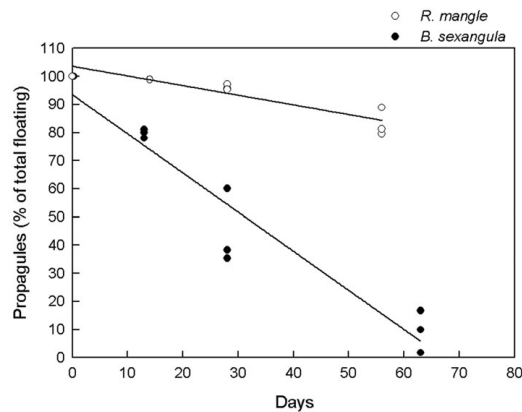


FIGURE 2. Percentage of propagules sinking after up to 63 days in flotation baskets located within a lagoon at Coconut Island, O'ahu, Hawai'i. Regressions were performed on all three replications combined for either *Bruguiera sexangula* or *Rhizophora mangle* propagules.

$P < .001$; $y = 103.55 - 0.34x \pm 3.18$ SEM) would have sunk by 302 days (Figure 2).

The duration of the flotation period had virtually no effect on subsequent survival of the propagules; every floating propagule that was removed from the cages and sown eventually developed viable shoots. No clear trend was evident for height growth of *B. sexangula* propagules exposed to differing periods of flotation in salt water (Table 1), but there was evidence of a stimulation in the height growth of *R. mangle* floating in salt water for 2 weeks or more (Table 1, Figure 3). The numbers of leaves declined slightly for *B. sexangula* floating for 4 weeks (Table 1); plants not floating in baskets produced 8.4 leaves compared with 7.5 and 7.25 leaves for propagules floating for 4 and 9 weeks, respectively. In contrast, flotation in salt water stimulated leaf production slightly for *R. mangle* (Table 1). Propagules produced 2.9 leaves without floating but between 3.4 and 3.6 leaves after floating for 2 to 8 weeks.

Over the 4-month period after flotation during which seedlings were sown and monitored, shading had no effect on survival, no effect on the numbers of leaves produced per seedling for *R. mangle*, and only minimal effects on the numbers of leaves produced per

TABLE 1

(A) Analysis of Covariance for 4-Month Height Growth and (B) Analysis of Nonparametric Distributions for Leaf Count from *Bruguiera sexangula* and *Rhizophora mangle* Propagules Planted in a Greenhouse after Floating for 0, 2, 4, or 8/9 Weeks in Experimental Baskets in a Lagoon at Coconut Island, O'ahu, Hawai'i

A (Height)	<i>B. sexangula</i>					<i>R. mangle</i>				
	df, df _{error}	MSE	F Value	P > F		df, df _{error}	MSE	F Value	P > F	
Light	1, 2	13.72	214.47	.0046		1, 2	2.25	14.93	.0609	
Replication	2, 2	0.01	0.23	.8146		2, 2	0.58	3.83	.2072	
Light × Replication – <i>er. a</i>	2, 285	0.06	0.69	—		2, 264	0.15	0.66	—	
Week	3, 285	0.03	0.31	.8160		3, 264	1.87	8.19	.0001	
Light × Week	3, 285	0.26	2.81	.0397		3, 264	0.12	0.51	.6755	
Initial propagule weight (covariate)	1	5.53	59.72	.0001		1	49.86	218.90	.0001	

B (Leaf Count)	<i>B. sexangula</i>			<i>R. mangle</i>		
	n	T Value	P > T	n	T Value	P > T
Light (sun versus shade)	152	25,068.5	.0126	142	20,147.0	.6185
Week (no flotation versus 2 weeks)	55	7,044.0	.9433	74	7,371.0	.0022
Week (no flotation versus 4 weeks)	40	3,100.5	.0001	48	4,325.0	.0007
Week (no flotation versus 8/9 weeks)	12	643.5	.0007	65	6,201.0	.0026

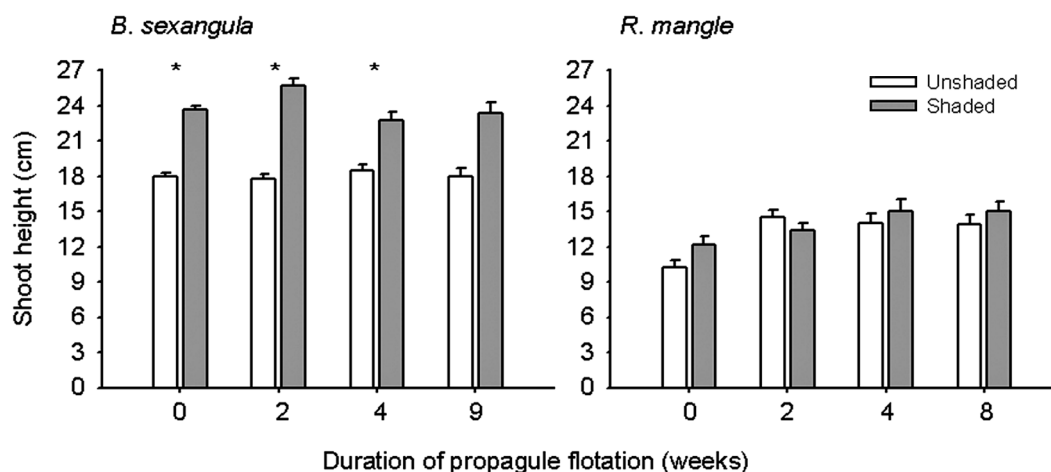


FIGURE 3. Height (± 1 SEM) after 4 months for propagules that floated for 0, 2, 4, or 8/9 weeks in experimental baskets in a lagoon at Coconut Island, O'ahu, Hawai'i. Growth comparisons in shaded versus unshaded environments depicted by an asterisk (*) were significantly different at $\alpha = .05$.

seedling for *B. sexangula* (Table 1). Shading did have a significant positive effect on height growth of *B. sexangula* but no effect on the growth of *R. mangle* over 4 months (Table 1, Figure 3).

DISCUSSION

Differential Flotation and Interisland Dispersal

Based on flotation longevity, *R. mangle* is likely to be more effective at interisland dis-

persal than *B. sexangula*, although both species should be capable of at least occasionally dispersing across the relatively short distances between most of the main Hawaiian Islands. This agrees with the wide distribution pattern of *B. sexangula* throughout most of Australasia (Duke et al. 1998). A much higher proportion of *R. mangle* propagules remained floating after 60 days, and their robust appearance suggested that many would have been capable of floating for much longer periods. This impression is supported by earlier experiments on flotation properties of *R. mangle*, which have found that some *R. mangle* propagules can float for 8–12 months and remain viable (Davis 1940; O. Steele, University of Hawai'i, pers. comm.).

Bruguiera sexangula and perhaps the entire genus may be generally less capable of long-distance dispersal by water than *Rhizophora*. Propagules of *R. harrisonii* (Rabinowitz 1978 [now known as *R. racemosa*]) and *R. apiculata* and *R. mucronata* (Drexler 2001) can float for 60 days or more and retain viability, whereas *B. gymnorhiza* propagules floated for only 1 month, compared with at least 8 months for *R. mangle* propagules (O. Steele, University of Hawai'i, pers. comm.). One possible reason for the lower capacity of *B. sexangula* to float for long periods is that a fouling community, consisting of unidentified polychaetes (possibly *Spirobis* spp. or *Hydroides* spp. [M. Hadfield, University of Hawai'i, pers. comm.]), developed somewhat more extensively on the *B. sexangula* propagules. Although differential colonization of the fouling community was not dramatic, nor were the populations generally large on either type of propagule, almost all of the *B. sexangula* propagules were colonized. Some *B. sexangula* propagules floating for 63 days did have as much as 50% of the surface area covered by a fouling community, but that level of coverage was not common. The differential susceptibility of the two mangrove species to fouling community development during open-ocean dispersal may merit further investigation. Propagule colonization by invertebrates, for example, may be more common in the experimental inlet than in the ocean.

Other Factors Limiting Dispersal or Establishment of Bruguiera sexangula

Factors other than those directly related to the effects of flotation in salt water may be limiting the interisland dispersal or establishment of *B. sexangula* in Hawai'i. One possibility is that a much greater proportion of *B. sexangula* propagules may be stranded in the vicinity of their parent trees, due to their higher intertidal location. With the notable exception of the small population of *B. sexangula* on the banks of the Anahulu River in Hale'iwa, it is uncommon to find *B. sexangula* trees in a position to disperse propagules directly into water bodies with a direct connection to the ocean under usual water-level conditions (pers. obs. [see Krauss and Allen 2003]). Much more often, the mature *B. sexangula* trees are located near the landward edges of swamps where the tides may be least effective as an agent of dispersal. A possible further complication affecting *B. sexangula* propagule dispersal is the abnormally high overall seedling density in Hawaiian mangrove swamps, which may exceed 50 seedlings m⁻² (Allen 1998, Cox and Allen 1999, Steele et al. 1999). The dense cover of seedlings (mainly *R. mangle*) present in Hawaiian mangrove stands may effectively trap many propagules, especially in the upper intertidal areas where tides may not be high enough to lift propagules above the seedling layer. High seedling densities of *R. mangle* are the result of very high levels of monospecific propagule production (Cox and Allen 1999). The limited number of *B. sexangula* trees capable of producing propagules relative to *R. mangle* indicates another limitation to dispersal for *B. sexangula*.

Although it seems unlikely, *B. sexangula* propagules may have reached other islands but failed to establish due to either a lack of suitable sites or excessive competition. In the former case, we believe that there are at least some suitable sites on most islands, including a small number that appear quite highly suited for *B. sexangula*, such as along the Hulē'ia River on Kaua'i. In the latter case, we believe that the high degree of shade tolerance exhibited by *B. sexangula* should allow it to

compete effectively with possible competitors such as *R. mangle*, *Hibiscus tileaceus*, or *Thespesia populnea*. Accordingly, interspecific differences in dispersal were less important as predictors for mangrove species distribution in Australia than were inherent constraints to root and shoot growth initiation during or shortly after dispersal (Clarke et al. 2001). Growth was good for *B. sexangula* relative to that of *R. mangle* under both light levels, however (Figure 3).

Two other possibilities that cannot be entirely dismissed are that *B. sexangula* has indeed succeeded in establishing on other islands and the trees have not yet been located, or that it was established at one time and then either died out naturally or was eradicated. Many mangrove stands in Hawai'i are very dense (Cox and Allen 1999) and difficult to walk through and, hence, have not been fully explored. Also, we have received one intriguing report that *B. sexangula* may have occurred at the Menhune Fishpond, on the Hulē'ia River, Kaua'i, 20 or more years ago, and was subsequently eradicated during an operation to clear mangroves from the fishpond wall (T. Goo, local resident, pers. comm.). The Hulē'ia River basin, with its substantial area of low-salinity intertidal habitat, seems particularly well suited for *B. sexangula*, but an extensive search of the mangroves in the basin by J.A.A. failed to locate any *B. sexangula* trees, seedlings, or propagules.

Prospects for Mangrove Dispersal beyond Hawai'i

Although *R. mangle* and possibly *B. sexangula* seem to have the inherent capacity to disperse within the main Hawaiian Islands, the prospect of these introduced mangroves dispersing beyond Hawai'i to other Pacific islands seems much more remote. The prevailing direction of surface water movement during the period of peak propagule dispersal was shown by Barkley et al. (1964) to be first slightly to the southwest (Figure 1a) and later to the northwest (Figure 1b). Currents moving in those directions would carry propagules either into virtually island-free waters or

through the Northwestern Hawaiian Island chain, which contains few or no sites suitable for mangroves. *Rhizophora mangle* propagules have been found on the Northwestern Hawaiian Islands at least 640 km from Kaua'i (e.g., in the French Frigate Shoals area), but no established trees are known to exist there (B. Flint, U.S. Fish and Wildlife Service, pers. comm.). Climatic events such as El Niño also change current patterns in the Pacific Ocean (Ramage 1986, Johnson and O'Brien 1990); this effect may influence dispersal more among the main Hawaiian Islands than beyond.

There is some evidence of plant material and aquatic organisms drifting from Hawai'i to Johnston Atoll, located approximately 1,200 km southwest of O'ahu (Lobel 1989). Johnston Atoll is likely to contain few, if any, sites suitable for *R. mangle* and especially for *B. sexangula*, and none is known to exist there currently (B. Flint, U.S. Fish and Wildlife Service, pers. comm.). If even a few trees were to establish, the island might serve as a stepping-stone for eventual dispersal farther to the west (e.g., to the Marshall Islands), a possibility that might be aided by Johnston Atoll's somewhat closer proximity to the strong, westward-moving North Pacific Equatorial Current.

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