WETLANDS, Vol. 19, No. 3, September 1999, pp. 705–708

NOTE

THE IMPORTANCE OF PROPAGULE PREDATION IN A FOREST OF NON-INDIGENOUS MANGROVE TREES

Orlo C. Steele[1,2], Katherine C. Ewel[3], and Guillermo Goldstein[1]
[1] *Department of Botany*
University of Hawai'i at Manoa
Honolulu, Hawai'i, USA 96822

[2] *Present Address:*
American Samoa Community College Land Grant Program
PO Box 6242
Pago Pago, American Samoa, USA 96799
email: orlo@samoatelco.com

[3] *USDA Forest Service*
Pacific Southwest Research Station
1151 Punchbowl St., Rm. 323
Honolulu, Hawai'i, USA 96813

Abstract: Predation on propagules of *Rhizophora mangle* was compared in forests where this species is non-indigenous (Hawai'i, USA) and where it is native (American Samoa). Tree density and basal area of the non-indigenous stand were intermediate when compared to natural stands in other places where *Rhizophora* is common. Propagules were tethered on the forest floor at both sites for 14 days, predation was recorded, and survival rates of both attacked and control individuals were determined by placing them in a mist room. Mortality was significantly greater in American Samoa ($\bar{x}$ = 25%) than in Hawai'i $\bar{x}$ = 8%). The lower effectiveness of the non-indigenous predators in Hawai'i may help explain the unusually high rate at which *R. mangle* propagules become established there.

Key Words: *Rhizophora, Bruguiera,* seed predation, Hawai'i, American Samoa, basal area, tree density

INTRODUCTION

Since mangroves were introduced to the Hawaiian islands in the early part of the 20th century, primarily to prevent shoreline erosion and stabilize newly accreting mudflats, they have invaded much of the protected shoreline. They were estimated to cover 72% of all estuarine intertidal habitats along Hawaiian coastlines in 1977 (U.S. Fish and Wildlife Service 1985). *Rhizophora mangle* L., first introduced in 1902 to the island of Moloka'i, has spread to all the main Hawaiian islands except Kaho'olawe and Ni'ihau and now dominates existing mangrove forests (Allen 1998). Another non-indigenous species, originally identified as *Bruguiera gymnorrhiza* (L.) Lamk. but referred to in this paper as *Bruguiera* sp. because it is more likely to be *B. sexangula* (Lour.) Poir (J. Allen, K. Krauss, N. Duke, and D. Herbst, ms. in prep.), was introduced in 1922 from the Philippines and is now known from four locations on O'ahu (Wagner et al. 1990, Allen 1998).

Rhizophora mangle, like many other mangrove species, is viviparous (i.e., its seeds germinate while still on the tree and therefore are called propagules when they fall). These propagules are dispersed by ocean currents until they become stranded in a suitable habitat where, provided predation is not excessive, they become established as what are commonly recognized as seedlings (McKee 1995). The purpose of this paper is to examine more closely one of the apparent causes of this species' success by describing predation on propagules in a Hawaiian mangrove forest and comparing it to predation on propagules in a native mangrove forest in American Samoa that also contains both New World and Old World species: *R. mangle* and *B. gymnorrhiza,* respectively.

MATERIALS AND METHODS

Study Sites

The mangrove forest at He'eia State Park, on the northeast coast of the island of O'ahu, is currently the only mangrove stand in the Hawaiian islands where both *R. mangle* and *Bruguiera* sp. are common. The site is on the windward side of the island and is fed by He'eia stream, which is approximately 25 m wide and 30–130 cm deep, depending on the tide, where it discharges into Kaneohe Bay (Walsh 1967). Average rainfall is 1500 mm/yr, mean annual temperature range is 22.2°–25.5°C, and the average tidal range is 68 cm. This forest occupies approximately 14.2 ha and is dominated by *R. mangle*. *Bruguiera* sp. occurs throughout the forest but is more common further upstream.

The study site in American Samoa was a 54-ha mangrove forest surrounding the Nu'uuli Pala lagoon on the south central side of the island of Tutuila. Average rainfall is 3,200 mm/yr, mean annual temperature range is 23.6°–29.7°C, and average daily tidal range is 76 cm. *Bruguiera gymnorrhiza* dominates the middle and inland portion of the intertidal zone, whereas *R. mangle* is usually found only in the low intertidal zone and along the edges of small brackish streams.

Experimental Design

Six 10 × 10 m plots were established in the middle to high intertidal zone of the He'eia mangrove forest in Hawai'i, and eight similar plots were established in the Nu'uuli mangrove forest in American Samoa. In each plot, the diameters of all tree trunks were measured: at 30 cm above the highest prop root for *R. mangle* and at breast height (1.5 m) for *Bruguiera* sp. Numbers of saplings (≥ 1 m in height and < 3 cm dbh) and propagules were also counted in each plot. Density of seedlings (propagules that had rooted and were < 1 m tall) was estimated from 20 randomly located 1-m^2 quadrats per plot.

Freshly fallen, intact *R. mangle* propagules were collected from the forest floor at each site, from 27 May to 1 June 1996 in Hawai'i and 29 August to 9 September 1996 in American Samoa. Twenty propagules were assigned to each plot and tethered to prop roots with 1-m lengths of nylon string (Smith 1987). The propagules were evenly distributed within the plots to avoid entanglement and were inspected every 2 days for 14 days. Propagules are produced continuously at both sites. They are most abundant from June to January in American Samoa (Steele, pers. obs.); in 1996 at a nearby site in Hawai'i, production was lowest in March and highest in September (Cox and Allen 1999). In both areas, predation dropped off rapidly after 14 days. Most propagules in an Australian mangrove forest had either been eaten or become established by 18 days (Smith 1987). A propagule was declared non-viable if more than 50% of its volume had been removed (Robertson et al. 1990). After 14 days, an equal number of propagules that had been attacked but were still viable and propagules that had not been attacked were placed in a greenhouse mist room. Seedlings were scored as having survived if growth was observed in both the root and shoot ends after two months in the mist room.

Statistical Analysis

Because of the limited amount of area available for sampling in this ecologically unique pair of sites, sample sizes were unequal and small, and variances were unequal. In order to establish trends, a two-sample Mann-Whitney test was used to compare the median level of propagule attack and mortality between Hawai'i and American Samoan mangrove forests. Means and standard deviations are reported to facilitate comparison with other studies.

RESULTS AND DISCUSSION

The American Samoan mangrove forest was dominated by *B. gymnorrhiza* and had more basal area and greater density of trees but many fewer propagules and seedlings than the Hawaiian forest (Table 1). *R. mangle* dominated the Hawaiian forest, which contained more saplings, including *Bruguiera* sp., and had two orders of magnitude more propagules, almost all of them *R. mangle*. Some of the differences in propagule density may be due to different rates of predispersal predation, which is usually attributed to crabs and insects. This was estimated at 2.5% for *R. mangle* at two sites in Hawaii, compared to an average of 28.3% at 42 sites around the world (Farnsworth and Ellison 1997).

Fewer trees, lower basal area, and a greater density of saplings of both species than in the American Samoan forest suggest that the Hawaiian mangrove forest was still growing (it was no more than 75 years old at the time of this study). All size classes were dominated by *R. mangle*. In Hawai'i, *Bruguiera* trees are regularly cut down to get at their flowers, which are used to make leis. *Bruguiera gymnorrhiza* was more common than *Rhizophora* spp. in the middle and high intertidal zones, not only in American Samoa but also in the Federated States of Micronesia (FSM; Devoe and Cole 1998), and it was reported to be replacing *Rhizophora* spp. in other Asian stands (e.g., Malaysia: Putz and Chan 1986).

Table 1. Structural characteristics of mangrove forests at He'eia State Park, Hawaii, and Nu'uuli Pala Lagoon, American Samoa. Values are means (± 1 SE).

Location and Species	Basal Area (m^2/ha)	Density (number/100 m^2)			
		Trees	Saplings	Seedlings	Propagules
Hawaii					
Rhizophora mangle	27.2 ± 1.7	13.2 ± 1.35	8.3 ± 6.3	5840 ± 5.7	211.7 ± 53.8
Bruguiera sp.	1.0 ± 0.1	1.0 ± 0.82	4.5 ± 4.5	0.15 ± 0.01	0
Total	27.3 ± 1.7	14.2 ± 1.4	12.8 ± 7.0	5855 ± 5.7	211.7 ± 53.8
American Samoa					
Rhizophora mangle	8.6 ± 0.3	2.1 ± 1.2	1.13 ± 0.4	3.8 ± 2.9	3.0 ± 0.8
Bruguiera gymnorrhiza	33.8 ± 6.1	21.3 ± 6.3	1.62 ± 0.4	47.5 ± 18.5	95.9 ± 23.2
Total	34.4 ± 6.1	23.4 ± 6.7	1.75 ± 0.4	51.3 ± 18.4	98.9 ± 23.1

The two mangrove stands had fewer trees but more basal area than were recorded for five plots in a stand dominated by *R. mangle* and *Avicennia germinans* (L.) Stearn at Rookery Bay, Florida (59 trees/100m^2, 19.4 m^2/ha; Lugo and Snedaker 1975). They had substantially more trees and only slightly more basal area than were recorded for 13 plots throughout FSM, representing six species (including *B. gymnorrhiza, R. apiculata* BL., and *R. mucronata* Lamk.), (3.6 trees/100m^2, 23.3 m^2/ha; Devoe and Cole 1978).

Of the propagules in the mangrove forest at He'eia State Park in Hawai'i, 28.3% (SE = 9.9) were attacked by what were probably rats or mongooses. Characteristic broad scrapings (1–2 mm wide) were generally made at the middle portion of the propagules, and in some cases, the propagule was completely severed. Polynesian rats (*Rattus exulans* Peale) and black rats (*Rattus rattus* L.) occur in Hawaiian mangrove forests (Shallenberger 1977), and Indian mongooses (*Herpestes auropunctatus* Hodgson) were trapped at He'eia State Park during this study (V. Yap, unpublished data). None of these mammals have been previously reported to consume mangrove propagules; herbivorous or frugivorous crabs, which are usually implicated in propagule mortality elsewhere, have not been reported in Hawai'i. Mortality of both attacked (but presumably still viable) and control *R. mangle* propagules was 6.7% (SE = 2.1).

At the Nu'uuli mangrove forest in American Samoa, 58.0% (SE = 10.0) of the *R. mangle* propagules were attacked. Characteristic scrape marks and the fact that propagules were sometimes found pulled into burrows suggested that the herbivorous crab *Sesarma erythrodactyla* Hess (Grapsidae), which inhabits this forest, was responsible for predation there. This rate was higher than those measured in a comparative study of consumption of *Rhizophora* spp. propagules by crabs: 24% of *R. apiculata* propagules were consumed in tropical Australia, 9% of *R. mangle* in Panama, and none of *R. mangle* in Florida (Smith et al. 1989). Nevertheless, the median attack rate in American Samoa was not significantly different than in Hawai'i ($T = 17$, $p > 0.05$). Mortality of all propagules at this test site was 25.0% (SE = 2.9). Median mortality rate was significantly higher ($T = 24$, $p < 0.01$) in this mangrove forest than in Hawai'i.

The success of *R. mangle* in Hawai'i may therefore be due not only to an abundant supply of propagules and low predispersal predation rates but also to lower effectiveness of the predation that does occur. We did not measure predation of *Bruguiera* propagules and so cannot explain why it does not dominate more stands in Hawai'i. Differential harvesting may play a role, but habitat suitability is likely to be more important, as both *B. gymnorrhiza* and *B. sexangula* have lower salinity tolerances than *R. mangle* (Smith 1992), and *Bruguiera* sp. in Hawai'i is more common further upstream from the coast.

ACKNOWLEDGMENTS

We thank the Village Council of Nu'uuli for granting permission to use their mangrove forest as a study site, the American Samoa Community College Land Grant Forestry Program for providing greenhouse space, and Carole McLean, Executive Director of Friends of He'eia State Park, for logistic support in Hawai'i. Clifford Smith assisted with advice on experimental design and techniques, as well as manuscript review; Andrew Taylor and James Baldwin provided statistical advice; and James. A. Allen and Kenneth W. Krauss provided constructive comments on the manuscript. This study was sponsored in part by the American Samoan Environmental Protection Agency.

LITERATURE CITED

Allen, J. A. 1998. Mangroves as alien species: the case of Hawaii. Global Ecology and Biogeography Letters 7:83–94.
Cox, E. F. and J. A. Allen. 1999. Stand structure and productivity

of the introduced *Rhizophora mangle* in Hawaii. Estuaries 22: 276–284.

Devoe, N. N. and T. G. Cole. 1998. Growth and yield in mangrove forests of the Federated States of Micronesia. Forest Ecology and Management 103:33–48.

Farnsworth, E. J. and A. M. Ellison. 1997. Global patterns of pre-dispersal propagule predation in mangrove forests. Biotropica 29: 318–330.

Lugo, A. E. and S. C. Snedaker. 1975. Properties of a mangrove forest in south Florida. p. 170–237. *In* G. Walsh, S. Snedaker, and H. Teas (eds.) Proceedings of International Symposium on Biology and Management of Mangroves. University of Florida, Gainesville, FL, USA.

Putz, F. E. and H. T. Chan. 1986. Tree growth, dynamics and productivity in a mature mangrove forest in Malaysia. Forest Ecology and Management 17:211–230.

Robertson, A. I., R. Giddens, and T. J. Smith III. 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. Oecologia 83:213–219.

Shallenberger, R. J. 1977. An ornithological survey of Hawaiian wetlands. Vol. 1. Ahuimanu Productions for U. S. Army, Engineer District, Honolulu, HI, USA.

Smith, T. J. III. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68:266–273.

Smith, T. J. III. 1992. Forest structure. p. 101–136. *In* A. I. Robertson and D. M. Alongi (eds.) Tropical Mangrove Ecosystems. Coastal and Estuarine Studies, 41. American Geophysical Union, Washington, DC, USA.

Smith, T. J. III, H. T. Chan, C. C. McIvor, and M. B. Robblee. 1989. Comparisons of seed predation in tropical, tidal forests from three continents. Ecology 70:146–151.

U.S. Fish and Wildlile Service. 1985. Recovery plan for Hawaiian waterbirds. Portland, OR, USA.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1990. Manual of the Flowering Plants of Hawai'i. Vol. 2. Bishop Museum Special Publication 83, Honolulu, HI, USA.

Walsh, G. E. 1967. An ecological study of a Hawaiian mangrove swamp. p. 420–431. *In* G. H. Lauff (ed.) Estuaries. American Association for the Advancement of Science, Publication No. 83.

Manuscript received 3 September 1998; revision received 3 May 1999; accepted 1 June 1999.