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Stand Structure and Productivity of the *Rhizophora mangle* in Hawaii

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Stand Structure and Productivity of the Introduced *Rhizophora mangle* in Hawaii

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ABSTRACT: Since its introduction in the early part of this century, *Rhizophora mangle* L. has spread extensively through most of the main islands of the Hawaiian Archipelago. We investigated the structural properties and estimated productivity of a *R. mangle* population at Nuupia Ponds Wildlife Management Area (NPWMA), on windward Oahu, where the mangroves were being controlled due to their propensity to overgrow archaeological sites and the habitat of endangered Hawaiian waterbirds. Mangroves within NPWMA were very dense (> 24,000 trees ha^{-1}) and most were relatively small (only 3.3% of the trees were ≥ 10 cm DBH). Mean basal area, aboveground biomass, and number of seedlings were all high, at 37.2 m^2 ha^{-1}, 279 t (dry wt) ha^{-1}, and 121 m^{-2}, respectively. The seedling density may be particularly unusual and appears to be due to extremely high rates of propagule production coupled with low rates of propagule predation. Stand productivity was estimated by stem growth (allometry), litterfall, and a light attenuation approach to determining net canopy photosynthetic production. All three methods yielded estimates that are higher than previously reported for *R. mangle* and comparable with estimates of highly productive *Rhizophora* spp.-dominated stands in Australia and Asia. The high density, biomass, and productivity of this stand relative to stands within the species' native range may be due to a combination of favorable site conditions, lack of competition from other woody plants, and very low rates of herbivory and propagule predation.

Introduction

Mangroves have been highly successful in colonizing sheltered coastlines throughout the tropics (Tomlinson 1986; Duke 1992). Indeed, the Hawaiian Archipelago is one of the relatively few locations in the tropics suited to their growth that has no native mangroves. Hawaii's sheer distance from other land masses, combined with its isolation relative to major ocean currents, apparently has prevented mangrove colonization (Guppy 1906; Wester 1981).

In 1902, *Rhizophora mangle* L. propagules from Florida were planted on the island of Molokai, primarily to help stabilize coastal mudflats created by erosion from pastures and sugarcane fields (MacCaughey 1917). At least five other mangrove species have since been introduced, but only *Bruguiera sexangula* (Lour.) Poir. and *Conocarpus erectus* L. are known still to be present in Hawaii, and nei-

ther has thrived as much as *R. mangle* (Wester 1981; Allen 1998). In contrast to the other introduced mangroves, *R. mangle* spread rapidly and presently occurs on all the main islands with the possible exceptions of Kahoolawe and Niihau (Wagner et al. 1990; Allen 1998).

Mangroves are valued throughout the tropics for the ecological services they provide. In Hawaii, however, they are known to have several important negative impacts, especially the occupation of prime foraging and nesting habitat for four endangered waterbird species and the tendency to overgrow native Hawaiian archaeological sites (Allen 1998). Concern about these impacts has resulted in efforts to control mangroves at a national park, several wildlife refuges, and a number of other sites.

Mangrove control efforts in Hawaii have been frustrated to some degree by the need to remove the seedlings that constantly recolonize cleared sites. This problem is compounded by the pattern of mangrove distribution within the state, which includes many small, scattered, and relatively line-

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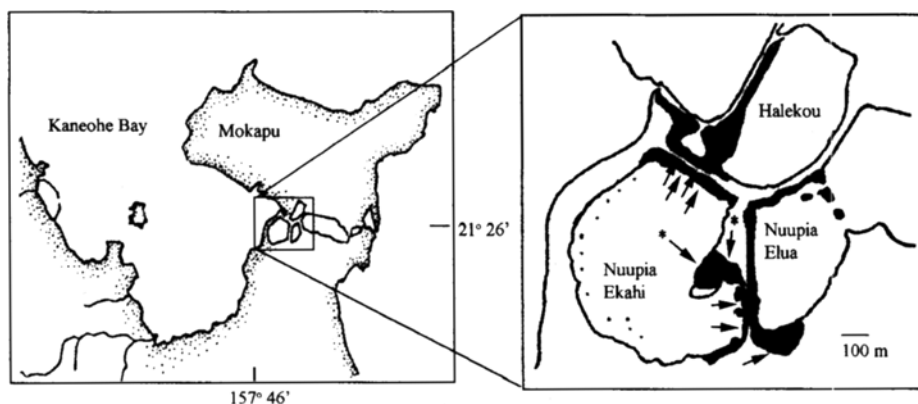
Fig. 1. Map of the study area, depicting (a) the location of the Nuupia Ponds on Mokapu Peninsula, and (b) the western Nuupia Ponds, with the locations of the mangroves indicated by the dark shading and the approximate locations of the nine plots indicated by the arrows. The two plots remeasured in 1996 are indicated by asterisks.

ar stands with high amounts of edge. Such stands appear to be generally productive and in particular to be generating very large amounts of propagules. A relatively small stand in the vicinity of a mangrove control project may therefore have a disproportionate ability to contribute to mangrove recolonization.

This study documents the overall productivity and propagule production of a small stand of the alien *R. mangle* in Hawaii. A major goal of the study was to determine the potential of such stands to affect the success of mangrove control programs by acting as propagule sources. The study also contributes to our overall understanding of mangrove productivity, because there are apparently no similar studies conducted in any location where mangroves are not native and where they may be substantially free of natural pests.

Methods

STUDY SITE

The Nuupia Ponds Wildlife Management Area (NPWMA) is located within the Kaneohe Bay Marine Corps Base, on the windward side of the island of Oahu, Hawaii (Fig. 1). The NPWMA is approximately 195 ha in size. It includes eight historic Hawaiian fishponds (areas of shallow water impounded by rock walls and natural shorelines) with a combined surface area of 96 ha and about 99 ha of wetlands, consisting largely of mudflats, *Batis maritima* L. meadows and monospecific stands of *R. mangle*. The NPWMA is located in one of the drier areas of windward Oahu, with an average annual rainfall of 950 mm. There is a slight seasonal variation in rainfall, with the driest period being from May through October. Temperatures typically are between 21 and 30°C. Soils in the area are saline sands, which, in depressions, are overlain by silty alluvial material flocculated by the high con-

centration of soluble salts. Salinity of the fishponds is variable, ranging from 15 to 55‰, with highest salinities typically occurring in August and September (Cox and Jokiel 1996).

In 1995, there were approximately 7.5 ha of mangroves in and around the NPWMA fishponds, mostly in the form of narrow bands along the pond margins or small, roughly circular stands on dredge spoil islands (Fig. 1). Aerial photos of the site indicate that the mangroves began invading the NPWMA in the mid-1960s to early 1970s (S. Henderson and D. Drigot personal communications). There apparently was minimal competition from other plant species on the site, and the mangroves expanded rapidly within the refuge. Because the NPWMA is one of three core breeding areas for the endangered Hawaiian stilt (*Himantopus mexicanus knudseni*), which require open mud flats and marshes, the refuge managers became concerned about the effects of the mangroves on the stilts' habitat.

With funding from the Marine Corps, NPWMA managers implemented a control program to clear 95% of the mangroves (D. Drigot personal communication). Mangrove clearing occurred in two phases. The first phase commenced in March 1995, the second in December 1996. This study began prior to phase one. Initially, research was conducted throughout the whole mangrove area except the dredge spoil islands, but became concentrated in a smaller area along the eastern shore of Nuupia Ekahi Pond (where most of the remaining mangroves were located) after the initial phase of clearing.

STAND STRUCTURE

In February and March 1995, nine 25-m² plots were randomly located within the NPWMA mangroves (Fig. 1). Diameter at breast height (DBH,

1.3 m) was measured for all trees of sufficient height within the plots. Seedling density (trees < 1.0 m) was estimated by counting all seedlings in 13 randomly located 1-m² plots.

To estimate total aboveground biomass, a relationship between DBH and dry weight was established from 18 trees harvested in March 1995. The trees were between 2 and 12 cm DBH. Eleven of the trees were whole-tree chipped, and estimates of wet weight were made by collecting the chipped material. Subsamples of chipped material were oven dried at 60°C to a constant weight. The other 8 trees were cut into sections, and each piece was weighed in the field. Because the relationship was based on a logarithmic transformation, the technique described by Baskerville (1972) was applied to correct for bias during back transformation.

PRODUCTIVITY

Seven of the 9 plots used to characterize stand structure were cut during the first phase of mangrove removal. The two remaining plots (Plots 8 and 9) were remeasured in November 1996, prior to the second phase of mangrove removal, during which they, too, were cut. The DBH-dry weight relationship developed to estimate aboveground biomass was used to estimate total aboveground production.

Litterfall was monitored over a 23-mo period from January 1995 to November 1996. Traps were constructed of 2-mm mesh shade cloth stapled to a 0.5 × 0.5 m wooden frame and held 1 m above the ground with wooden legs. Fourteen traps were initially deployed in the stand. Some trap locations were shifted following the cutting in March of 1995, and the number of traps was reduced to 10 at this time. The number and location of the traps remained the same for the remainder of the study. Litterfall was collected monthly, separated into leaves, reproductive material, and wood (including material such as loose bark), dried at 60°C, and weighed. The number of propagules was also recorded.

Net canopy primary productivity was estimated using the methods of Bunt et al. (1979) and Boto et al. (1984), with the modifications for leaf area index estimation and the higher light extinction coefficient recommended by English et al. (1994) and Clough et al. (1997). This method measures the reduction of photosynthetically active radiation (PAR) through the canopy, approximates leaf area index by measuring light attentuation through the canopy, and uses assumptions for the relationship between PAR absorption and carbon fixation to estimate the net primary productivity of the canopy. Net canopy primary productivity is estimated as PN = A*d*L, where d is the daylength, A is the aver-
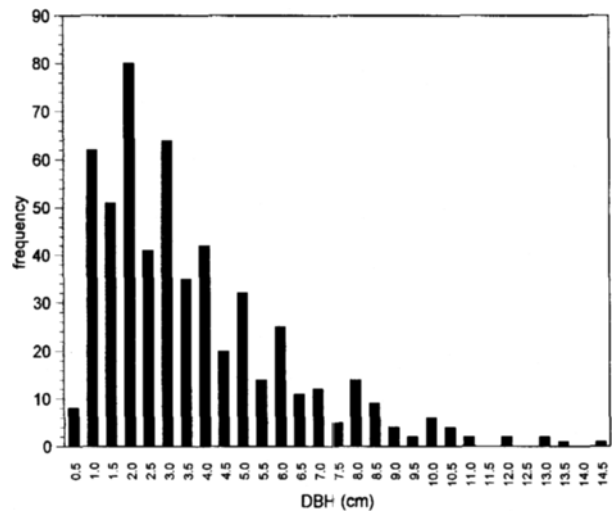

Fig. 2. Diameter distribution for all trees ≥ 1.3 m in height. Data are based on the nine plots prior to the first phase of mangrove removal.

age rate of photosynthesis for all leaves in the canopy, and L is leaf area (m² leaf area m⁻² ground area). A has been measured for *Rhizophora* species in Australia and Southeast Asia and varies from poor (i.e., hot, dry, high salinity) conditions where $A = 0.216$ gC m⁻² hour⁻¹ to $A = 0.648$ gC m⁻² hour⁻¹ under optimal conditions (English et al. 1994).

Measurements of PAR through the canopy were recorded with a Li-Cor integrating quantum meter (Model LI188B, Li-Cor, Lincoln, Nebraska) with a cosine sensor on October 3, 1996, between 11:00 and 12:30. Three sets of 100 measurements each were made within the forest stand, interspersed with measurements in adjacent open areas. Data were processed using the methods of English et al. (1994).

LEAF DAMAGE

Fifty tree branches were collected from around Nuupia Ekahi Pond on February 22, 1995. Branches were collected from shaded portions of tree crowns and portions exposed to full sunlight, in roughly equal proportions. Five hundred leaves (about 10 per branch) were inspected for tissue damage or loss. Damage was classified into three categories: interior holes, leaf margin loss, and visible tissue damage without loss of leaf material.

Results

STAND STRUCTURE AND BIOMASS

The NPWMA mangroves were characterized by a high density of small trees (Fig. 2 and Table 1). Mean DBH of all trees 1.3 m or greater in height was 3.9 cm (SE = 0.3). The bulk of the trees and

TABLE 1. Structural characteristics of NPWMA stand. Means (±1 SE) are expressed on a per hectare basis.

Tree Size Class (cm)	Number of Trees	Basal Area (m²)	Aboveground Biomass (t)
≥0.5–<2.5	8,930 (209)	1.74 (0.38)	12.24 (2.68)
≥2.5–<10	14,700 (488)	27.39 (2.55)	204.67 (19.12)
≥10	800 (231)	8.03 (2.30)	62.22 (17.79)
Total	24,430 (3,160)	37.16 (3.48)	279.13 (26.42)

basal area is accounted for by trees in the ≥ 2.5–< 10 cm DBH size class; only 3.3% of the trees had a DBH ≥ 10.0 cm (Table 1). The density of seedlings was also high, at 121 m^{-2} (s. e. = 13.6).

Biomass of harvested trees was estimated with the equation: ln biomass (kg dry wt.) = −0.668 + 2.05 ln DBH (r^2 = 0.93; Fig. 3). Using this relationship, mean stand aboveground biomass in March 1995 was estimated to be 279 dry t ha^{-1}. Trees in the intermediate size class accounted for the bulk (73.3%) of the total aboveground biomass (Table 1).

PRODUCTIVITY

Aboveground Biomass Production

The two resurveyed plots on the margin of Nuupia Ekahi Pond increased from a mean of 80 trees in 1995 to 118 trees in 1996, while the mean DBH declined by 0.4 cm. The net result for these two plots was an increase in mean aboveground stand biomass from 231.2 t ha^{-1} (s. e. = 33.6) in March 1995 to 284 t ha^{-1} (s. e. = 16.0) in November 1996. The estimated annual rate of aboveground biomass increase for the two plots was 29.1 t ha^{-1} yr^{-1}.

Litterfall

Mean litterfall in 1995 was 6.8 g m^{-2} d^{-1} and 7.0 g m^{-2} d^{-1} in 1996, for an average of 25.2 t ha^{-1} yr^{-1} over the period of measurement. The bulk of this material consisted of leaves and reproductive material (Fig. 4). Litterfall showed a distinct seasonal pattern, with an increase during the late summer and fall that was clearly driven by the fall of propagules (Fig. 4). Reproductive material ranged from 7% of the total during May 1995 to 73% of the total during October 1995 and November 1996. An average of 46 propagules per year was collected from each trap, for an overall production rate of 1,840,000 ha^{-1} yr^{-1}.

Net Canopy Primary Productivity

Estimates of net daytime canopy primary productivity, primarily from the area of mangroves to the east of Nuupia Ekahi, ranged from 5 (A = 0.215) to 16 (A = 0.648) gC m^{-2} d^{-1}. If 10.5 gC m^{-2} d^{-1} is taken as an average rate of net canopy
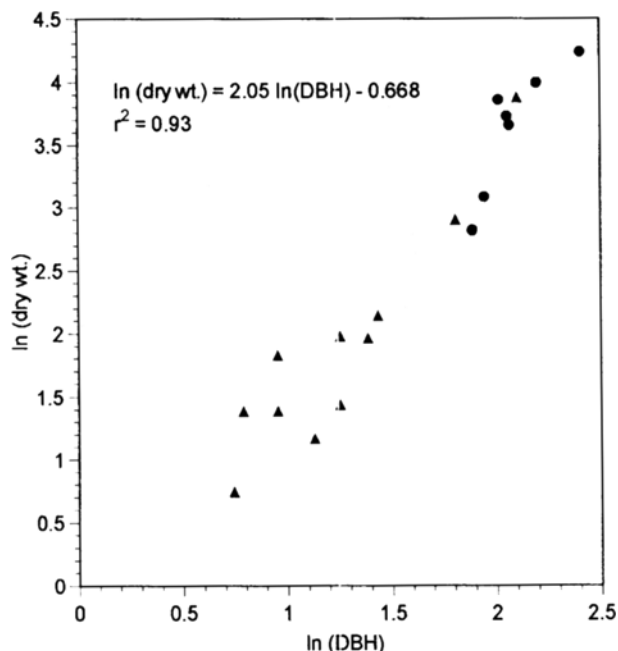

Fig. 3. The relationship of DBH to aboveground biomass. Triangles indicate trees that were chipped; circles indicate trees that were cut and weighed in the field (n = 18).
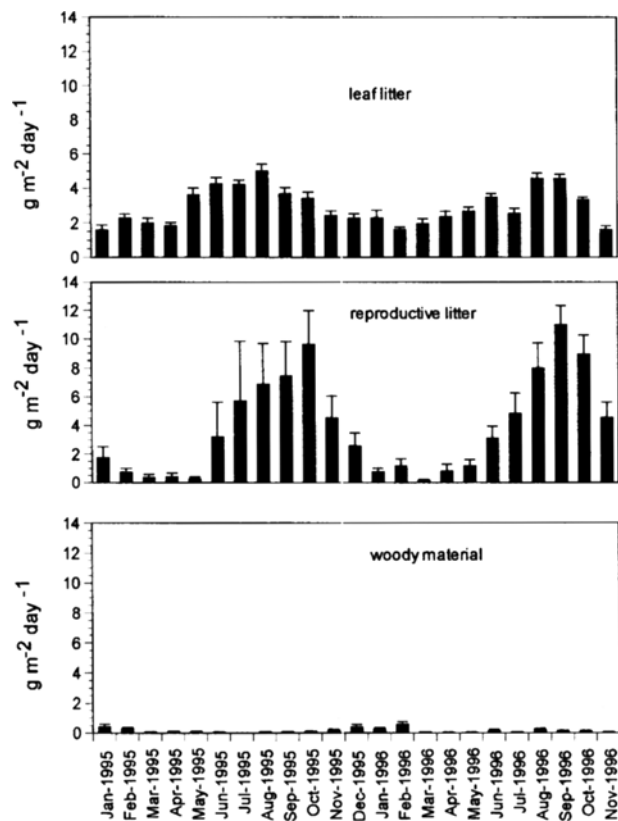

Fig. 4. Mean and standard errors for litterfall by category. Data are for a 23-mo period from January 1995 to November 1996.

primary productivity, this represents an annual production of 76.7 t ha^{-1} yr^{-1} of dry matter.

LEAF DAMAGE

Of 500 leaves examined, only 31 (6%) had tissue loss. Tissue loss was generally in the form of small interior holes or small portions of the leaf margin. An additional 71 leaves (14%) had marks on the surface that were attributed to damage by insects or pathogens. Overall, 20% of the leaves had some loss or damage, but damaged areas were generally substantially less than 10% of the total surface area. Thus, less than 2% of the total stand leaf area was damaged or lost (excluding an unknown proportion of leaves that may have been totally consumed or prematurely abscised).

Discussion

STAND STRUCTURE

The structure of NPWMA stand is similar in some ways to a number of sites within the species' native range, including restored sites, stands developing on altered sites not formerly occupied by *R. mangle,* and sites that had been clearcut (Ball 1980; Snedaker et al. 1992; Blanchard and Prado 1995; Proffitt unpublished data). Ball (1980), for example, described a roughly 40-year-old mixed stand of *R. mangle* and *Laguncularia racemosa* along Biscayne Bay, Florida, that developed in a freshwater marsh affected by saltwater intrusion (the lower part of "Induced Forest A"). The forest had a similar overall density (approx. 25,500 trees ha^{-1}) and distribution of tree size classes. Data from clearcut stands in Ecuador (Blanchard and Prado 1995) suggest that stand structure on some sites where mangroves occur naturally may resemble the NPWMA stand. One of the 3-year-old clearcut stands had a density of > 40,000 trees ha^{-1} and a mean height > 2 m. Such a stand may increasingly resemble the NPWMA stand as it grows and self-thins.

The total stand biomass of the NPWMA stand (279 t ha^{-1}), however, is higher than reported for most other *R. mangle* stands (Lugo and Snedaker 1974; Odum et al. 1982; Saenger and Snedaker 1993; Wiebe et al. 1997), though well below the level of 500–700 t ha^{-1} reported for some relatively undisturbed stands in Asia and the Pacific (Clough 1992). Few biomass estimates are available for *R. mangle* stands of densities as high as the NPWMA stand. Neither Ball (1980) nor Snedaker et al. (1992) reported biomass estimates for the stands they investigated. Chen and Twilley (In press) recently investigated mangrove forest recovery from a large hurricane (Donna) in southern Florida and found some of the highest amounts of aboveground biomass reported for stands with a signifi-

cant *R. mangle* component. Two of the stands had basal areas (40.4 and 39.7 m^2 ha^{-1}) and aboveground biomass (245.7 and 250.8 t ha^{-1}) similar to NPWMA, but they were comprised of fewer, larger trees.

The most significant difference in stand structure between the NPWMA stand and *R. mangle* stands elsewhere may be seedling density. Seedling density in "Induced Stand A" in Florida ranged from 0–2.4 m^{-2} for *R. mangle* and 0–3.6 m^{-2} for *L. racemosa* (Ball 1980). Most other studies of *R. mangle*-dominated stands have reported less than 20 seedlings m^{-2} (Golley et al. 1962; Lugo and Snedaker 1975; Rabinowitz 1978). Seedling densities of less than 20 m^{-2}, often much less, also appear to be the norm in stands of other mangrove species (Rabinowitz 1978; Jimenez and Sauter 1991; Saifullah et al. 1994; O'Grady et al. 1996). The mean density of 121 seedlings m^{-2} in the NPWMA stand therefore may be quite exceptional.

One reason for the extraordinarily high seedling density may be the proximity of the plots to the forest edge. Since seedling density was measured in February and March, the number of seedlings might be near an annual high. *R. mangle* propagules can persist for a year or more below forest canopies, however, and do not vary in number seasonally as dramatically as do mangrove species with smaller propagules (Rabinowitz 1978; Ellison and Farnsworth 1993).

Unusually high densities of seedlings have also been found in other Hawaiian *R. mangle* stands, including at least one older stand with a much greater area of forest interior. Lee (1971) reported a mean seedling density of 69 m^{-2} for Heeia Swamp, a 14 ha mixed stand of *R. mangle* and *B. sexangula* less than 10 km from NPWMA that was approximately 50 years old at the time. Steele (1998), working only in the lower intertidal portion of Heeia Swamp, reported a mean of 59 seedlings m^{-2}.

We believe that high seedling densities are common in Hawaiian mangroves and that they are attributable primarily to a lack of pre- and post-dispersal propagule predation as well as a low amount of seedling herbivory. There is a small but growing amount of evidence to support this conclusion. Farnsworth and Ellison (1997), for example, reported that only 2.9 and 2.1% of propagules were attacked prior to dispersal at two sites in Hawaii, compared to amounts ranging from 10 to 93% for *R. mangle* propagules at sites in Ecuador and Venezuela investigated at the same time of year (Oct.–Nov.). Onuf et al. (1977) found that 43 to 100% of pre-dispersal *R. mangle* propagules at two sites in Florida had been infested by the scolytid beetle *Coccotrypes* (syn. *Poecilips*) *rhizophorae* by mid-Octo-

TABLE 2. Contribution of major components to total litterfall for predominantly monospecific mangrove stands. Stands are arranged in ascending order of percent contribution of reproductive material.

Predominant Species	Location	Total Litterfall (t ha⁻¹ yr⁻¹)	Leaves[1]	Reproductive Material	Other	Source
Avicennia spp.	Australia	8.05	74.9	1.6	23.5	Duke et al. 1981
R. stylosa	Tuvalu	7.77	83.3	1.9	14.8	Woodroffe and Moss 1984
R. mucronata	Sri Lanka	6.24	83.5	2.2	14.3	Amarasinghe and Balasubramaniam 1992
A. germinans	Mexico	6.14	83	8	9	López-Portillo and Ezcurra 1985
A. marina var. *resinifera*	New Zealand	8.10	69.4	12.3	18.3	Woodroffe 1982
R. stylosa[2]	Australia	9.3	62.1	12.9	25.0	Duke et al. 1981
Ceriops tagal	Australia	7.52	71.0	18.0	11.0	Woodroffe et al. 1988
B. gymnorrhiza	Australia	8.61	54.3	19.2	26.5	Bunt 1982
Sonneratia alba[2]	Australia	7.9	48.8	21.2	30.0	Duke et al. 1981
R. apiculata	Australia	11.15	53.9	22.5	23.6	Bunt 1982
B. parviflora[2]	Australia	10.0	40.3	30.0	29.7	Duke et al. 1981
R. mangle	Oahu, HI	25.2	51.9	44.8	3.3	this study

[1] Excludes stipules, when listed separately.
[2] The mean of several stands.

ber. Some damage by scolytid beetles, possibly *C. rhizophorae*, was noted on rooted seedlings during a survey of Heeia Swamp in 1979 (D. Simberloff personal communication), but such damage appears to be uncommon.

Post-dispersal attacks on propagules are less frequent than for some Asian and Pacific species of *Rhizophora* and for *R. mangle* in Belize, and roughly similar to estimates for *R. mangle* from Florida and Panama (Smith et al. 1989; McKee 1995). Steele (1998) reported that in Heeia Swamp a mean of 28.3% of tethered (i.e., post-dispersal) propagules were damaged to some degree (mostly by rats), but overall mortality was only 6.7%.

PRODUCTIVITY

Net primary productivity of the NPWMA was assessed using three different methods, all of which resulted in higher estimates of NPP than for most other *R. mangle* stands. The estimated total aboveground biomass increase of 29.1 t ha⁻¹ yr⁻¹ (based on allometry) is higher than even productive riverine *R. mangle* stands and considerably higher than estimates for basin, fringe, or scrub mangroves (Golley et al. 1962; Twilley et al. 1986; Day et al. 1987).

The rate of biomass increase estimated for the NPWMA stand is comparable to *R. apiculata/R. stylosa* forests in Queensland, Australia, comprised of much larger trees (Clough 1992), which have among the highest rates of biomass increase yet recorded for mangroves. In general, the relationship between stand structure and productivity is poorly understood for mangroves (Clough 1992), and our results suggest it merits further investigation.

We are aware of only one report of a higher rate of litterfall than the 25.2 t ha⁻¹ yr⁻¹ estimate for the NPWMA stand: 28.1 t ha⁻¹ yr⁻¹ for an *R. apiculata* stand on Hinchinbrook Island, Australia (Bunt 1982). Litterfall rates greater than 20, or even 15, t ha⁻¹ yr⁻¹ have been reported for very few other stands (Bunt 1982; Saenger and Snedaker 1993; Wiebe et al. 1997). The highest litterfall rate previously reported for *R. mangle* that we are aware of is 16.3 t ha⁻¹ yr⁻¹ for a stand in southwest Florida (Lahmann 1988 in Saenger and Snedaker 1993), but a new report, describing preliminary results for various locations in the Caribbean, lists one site in Venezuela as producing 21 t ha⁻¹ yr⁻¹ (Wiebe et al. 1997).

The main factor responsible for the high litterfall rate of the NPWMA stand is the reproductive component. In contrast to other studies, which have generally found the reproductive component to be less than 20% of total litterfall (Table 2), it accounted for 43–46% of the total for the NPWMA stand. The low rate of pre-dispersal propagule predation referred to above (Farnsworth and Ellison 1997) may be one important reason for the exceptional rate of propagule production. There also may be little damage to buds and flowers from insects or disease, although to our knowledge this has not been investigated in Hawaii.

Another factor that may contribute to the high litterfall (and the high overall productivity) is the small amount of leaf material lost to herbivory. Leaf fall alone at the NWPMA site averaged 10.6 t ha⁻¹ yr⁻¹—higher than total litterfall for many *R. mangle*-dominated stands (Pool et al. 1975; Twilley et al. 1986). At NPWMA, insect herbivory or other damage was noted on only 20% of 500 leaves in-

spected and generally affected less than 10% of the area of damaged leaves. This contrasts with studies reporting herbivore damage on close to 100% of leaves for the same species in Belize (Farnsworth and Ellison 1991, 1993) and 34–63% of *Rhizophora* spp. leaves in Australia (Robertson and Duke 1987). In Belize, normal levels of insect herbivory on *R. mangle* generally resulted in less than 20% loss of total leaf area, although leaf area loss of up to 50% occurred in some sets of new leaves (Ellison and Farnsworth 1996). In other regions up to 35% of the total leaf area may be consumed prior to leaf fall (Johnstone 1981; Robertson and Duke 1987).

Although we do not know what proportion of leaves may have been totally consumed or prematurely abscised due to insect damage, we suspect it is very low. In a 1979 survey of insects at Heeia Swamp, no *Ecdytolopha* or similar species, which damage leaf buds and young leaves in Florida (Onuf et al. 1977) were found (D. Simberloff personal communication). Also, we have seen little evidence, such as the partial remains of new leaves on branches or in litter traps, to suggest that this type of damage occurred at our study site to any significant degree.

The rate of net canopy photosynthesis as estimated by the light attenuation method (5 to 16 gC m^{-2} d^{-1}, depending on the choice of A) is higher than NPP estimates for Florida mangroves based on gas exchange; these estimates ranged up to 7.5 gC m^{-2} d^{-1} but were generally much lower (Lugo and Snedaker 1974). Using the midpoint of 10.5 gC m^{-2} d^{-1}, net canopy photosynthesis is substantially lower than that of a 20-year-old stand of *R. apiculata* in Malaysia (15.5 gC m^{-2} d^{-1}; Clough et al. 1997). Based on a tentative carbon budget derived from the estimates of aboveground biomass accumulation and litterfall, however, we suspect that it may be more appropriate to use the higher estimate of A (0.648; English et al. 1994) for the NPWMA stand. Aboveground biomass accumulation and litterfall alone account for an estimated 54.3 t of dry matter production ha^{-1} yr^{-1}, so the estimate of 77.7 t yr^{-1} net canopy production (based on the midpoint of 10.5 gC m^{-2} d^{-1}) is probably insufficient to account for belowground processes, aboveground woody tissue respiration, and night-time foliar respiration.

We believe the higher A, which reflects near optimal conditions (English et al. 1994), is appropriate for the site, given the reasonably favorable physical environment, the lack of competition from other plant species, and the apparently low level of leaf herbivory and other damaging agents. Use of the higher A would result in an estimate of 116.8 t ha^{-1} yr^{-1} for net canopy production, a value

very similar to that recently reported by Clough et al. (1997), and one much more likely to account for the other, unmeasured, components of the carbon budget. Although no longer possible for our site, the development of site-specific values for the average rate of net canopy photosynthesis (A) would greatly improve the accuracy of productivity estimates using this method.

IMPLICATIONS FOR MANGROVE MANAGEMENT IN HAWAII

Managers of coastal wetlands in Hawaii face a significant challenge in their attempts to control the nonindigenous *R. mangle*. The species is widely distributed in the state (Wester 1981; Allen 1998) and occurs on property controlled by many private landowners and a variety of federal, state and county government agencies. Even though the total acreage is not large compared with some nonnative species infestations (Stone et al. 1992; Schmitz et al. 1997), the high costs of mangrove control in Hawaii (Allen 1998), their wide distribution, and the high production rate of propagules suggest that eradication is a difficult prospect.

In the absence of a commitment to eradication, a program of maintenance control on sensitive sites (e.g., waterbird breeding areas and ancient Hawaiian fishponds) will most likely be the approach for the foreseeable future. Our data on propagule production, combined with the apparent lack of propagule/seedling predators (Farnsworth and Ellison 1997; Steele 1997) and *R. mangle*'s propensity for dispersal (Tomlinson 1986), indicate that maintenance control will be needed on a regular basis even if only small stands are in the vicinity.

It may be possible to improve the efficiency of a maintenance control program by using a biocontrol approach to lower the production of viable propagules and/or increase post-dispersal mortality. One possibility is to determine whether the scolytid beetle *C. rhizophorae*, which destroys many mangrove propagules and seedlings in Florida (Onuf et al. 1977; Devlin unpublished data) is currently present in Hawaii and, if not, to introduce it. Such introductions must be made very cautiously, of course. Useful first steps would be to document more completely the current level of herbivory and predation on leaves, flowers, propagules, and seedlings of *R. mangle* in Hawaii and to begin to determine the degree of host-specificity for promising biocontrol agents.

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