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Structure of mangrove trees and forests in Micronesia

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Abstract

Volume equations were constructed for five species of mangrove trees on volcanic high islands of Micronesia in the north Pacific Ocean, where islands that span a distance of more than 3000 km from east to west are characterized by a gradient of rainfall from 3080 to 5250 mm/year and a range of typhoon frequency from less than one per century to several per decade. We also calculated mean annual increments for a subset of the trees. The inclusion of very large trees in the data set makes these volume equations unique. For the five most common species, separate volume equations were calculated for each of the two easternmost islands (Kosrae and Pohnpei), the remaining islands ('Western Islands', including Chuuk, Yap, and Palau), and all the islands together (Micronesia). Tree structure differed significantly among the three island groupings and for two species, between Kosrae and Pohnpei, which are only 560 km apart. Mean annual diameter increments for *Sonneratia alba* and *Bruguiera gymnorrhiza* indicated significantly faster growth on Kosrae (0.96 and 0.44 cm/year, respectively) than on Pohnpei (0.33 and 0.26 cm/year, respectively). Frequency distributions of diameter size classes on these two islands demonstrated a more even distribution of sizes and more large trees on Kosrae (e.g., up to 3.2 m in diameter for *S. alba*). Differences in diameter distributions may be attributed to a typhoon that devastated Pohnpei, but not Kosrae, in 1905, but differences in growth rates cannot yet be explained.

Keywords: Regression equations; Volume equations; Federated States of Micronesia; Republic of Palau; *Sonneratia alba*; *Bruguiera gymnorrhiza*; *Rhizophora apiculata*; *Xylocarpus granatum*; *Rhizophora mucronata*; *Lumnitzera littorea*

1. Introduction

Mangrove forests around the world are harvested for a variety of wood products, including charcoal, firewood, and structural timber (Watson, 1928; Walsh, 1977). Increasing rates of harvesting in many of these stands mandate that management plans be established to keep harvesting within sustainable levels. An important component of a forest management plan is an estimate of standing wood volume, but few volume equations for mangroves exist, especially for species that are not extensively harvested for commercial purposes.

Some of the world's most intact mangrove forests are in Micronesia, one of the three major island groups, along with Melanesia and Polynesia, in the

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Table 1
Distribution of mangrove forests and inventory plots in the Federated States of Micronesia (FSM) and Palau

Geographic unit	Total land area (ha)	Total area surveyed (ha)	Mangrove area (ha)	Percent of surveyed land in mangroves	Number of plots
FSM					
Kosrae	10 956	10 956	1562	14	16
Pohnpei	34 551	33 670	5525	16	39
Chuuk	12 743	4170	306	2	2
Yap	11 810	9779	1171	10	3
FSM Total	70 060	58 575	8564	12	60
Palau	44 134	36 733	4025	9	5
Total	114 194	95 308	12 589	11	65

Pacific. Within these islands, the Federated States of Micronesia (FSM) and the Republic of Palau have extensive mangrove resources, representing ≈11% of inventoried land area (Table 1) and 13% of total standing timber volume (MacLean et al., 1986, 1988a, b; Whitesell et al., 1986; Cole et al., 1987; Falanruw et al., 1987a, b). Nine species of mangrove trees, including the palm *Nypa fruticans* (Thunb.) Wurmb., occur in Palau and Yap; seven occur in Chuuk, Pohnpei, and Kosrae (Stemmermann and Proby, 1978). Mangroves are particularly important to subsistence economies in these countries, providing firewood, building supplies, and other wood products, as well as ecosystem services such as water quality maintenance, storm wave protection, fish habitat, and ecotourism activities (Ewel et al., 1998a). With increasing population pressure, these forests are now extensively exploited (Devoe, 1994).

This paper characterizes Micronesian mangrove forests and presents volume equations for six species that are common throughout Micronesia, Southeast Asia, and Oceania. Equations were developed for the following species: *Sonneratia alba* J.E. Sm., *Bruguiera gymnorrhiza* (L.) Lam., *Rhizophora apiculata* (Jack) Voigt., *Xylocarpus granatum* Koenig., *Rhizophora mucronata* Lam., and *Lumnitzera littorea* (Jack) Voigt. The volume equations can be used to estimate inside-bark total and inside-bark stem-only tree volume from measurements of DBH alone (DBH-only), as well as from diameter and height measurements (DBH-height). These equations should assist resource managers throughout the Pacific Rim in estimating the volume of local mangrove resources. Volume measurements are also useful for comparing characteristics of a species in different parts of its range and in different ecological settings.

1.1. Study area

The FSM includes four states: Yap (9°33′N, 138°09′E), Chuuk (7°45′N, 151°42′E), Pohnpei (6°54′N, 158°14′E), and Kosrae (5°19′N, 163°00′E) (Fig. 1). Yap, the westernmost state, has four metamorphic volcanic high islands and about 15 coral atolls. Chuuk is composed of a group of partially submerged volcanic high islands inside a barrier reef with numerous coral atolls and other small islands beyond the reef. Pohnpei has one high volcanic island and nine coral atolls. Kosrae, the easternmost state, is a single high volcanic island. Data for this study were collected only from mangroves on those high islands for which aerial photography was available: one island, Moen, of the five within the barrier reef in Chuuk, and all the high islands in the other states.

The Republic of Palau (7°35′N, 134°28′E) lies 900 km east of the Philippines on the western edge of the Caroline Islands. It is composed of four volcanic high islands and numerous coral limestone islands. Data for this study were collected from Babelthuap, the largest and most extensively forested of the volcanic islands.

The distance from Palau to Kosrae is 3140 km, and there are substantial differences in geology among the islands. Kosrae and Pohnpei are the tallest of the islands (629 and 760 m, respectively). The more western islands are older and lower; the highest points

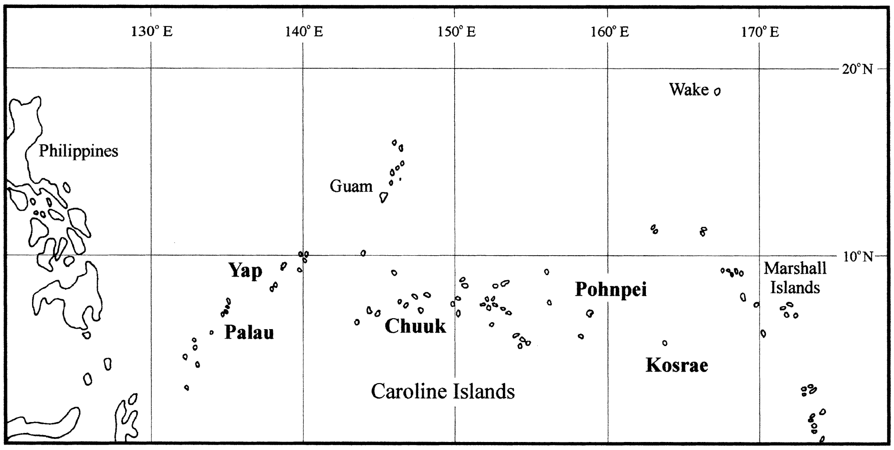

Fig. 1. Location of the Republic of Palau and the four island-states in the Federated States of Micronesia.

are 240 m on the island of Babelthuap in Palau and 174 m in Yap. The highest elevation surveyed in Chuuk is 370 m on Moen Island.

Kosrae and Pohnpei are also the wettest of the islands. In the lowlands, precipitation averages 5250 mm/year on Kosrae and 4840 mm/year on Pohnpei with no severe dry season (NOAA, 1997a, b). Rainfall in the uplands of Kosrae and Pohnpei is thought to be much higher, from 6000 to 7000 mm annually. Palau and Yap, while still very wet (3765 and 3086 mm/year, respectively (NOAA, 1997c, d)), have more noticeable dry seasons in late winter and early spring (February, March, and April) and wet seasons in the summer (July, August, and September). Although Chuuk is closer to Pohnpei than to Yap, its relatively low topography, moderately high rainfall (3525 mm/year [NOAA, 1997e]), and distinct winter dry season (February and March) make conditions more similar to the more western islands of Palau and Yap.

Typhoons are more common in the Western Carolines, particularly Yap, than in the eastern islands. A total of 10 typhoons passed within 50 km of Yap (and 14 within 50 km of Guam) from 1945 to 1995 (Ray, 1997). No typhoons were tracked within 50 km of either Kosrae or Pohnpei during the same period. The closest any typhoon came to Kosrae during that time was 100 km; one came within 89 km of Pohnpei; and Palau, which is southwest of Yap, experienced one close (10 km) typhoon during the same period.

2. Methods

Tree volume data were collected over an 11-year period (1985–1996) as part of four forest inventories conducted by the USDA Forest Service, FSM state forestry units, and the Palauan Division of Forestry. The inventories established 65 permanent plots that were randomly located in >12 500 ha of mangrove forest (Table 1). Thirteen of the plots were established in the FSM in 1983: four each on Kosrae and Pohnpei, three on Yap, and two on Chuuk (MacLean et al., 1988b). These plots were remeasured in 1991–1992 (Devoe and Cole, 1998); the more recent data were used for calculating volume equations. Another 35 plots were established on Pohnpei in 1990–1992 by Devoe, and 12 additional plots were established in Kosrae in 1995 (Ewel et al., 1998b). Five mangrove plots were established in Palau as part of the timber inventory of Babelthaup Island in 1985 (MacLean et al., 1988a). Because so few plots are on Chuuk, Yap, and Palau, which are also more similar to one another than to Kosrae and Pohnpei, these data (86 trees) are aggregated under the heading Western Islands.

During the forest inventories, all trees $\geq$2.5 cm DBH were surveyed, but volume was only calculated for trees having a DBH$\geq$12.5 cm. Several trees were excluded from the data set because of extremely poor form, such as broken tops. A total of 1085 trees were used to develop the volume equations.

Tree volume was estimated by visually dividing a tree into discrete segments (stems, upper stems, crotches, craftwood bolts, branches, etc.) following an established protocol (USDA Forest Service, 1983). The lower diameters were measured with a diameter tape, and upper stem diameters were estimated with a relaskop. All heights and segment lengths were estimated with a relaskop. The volume of each segment was calculated using the formula for the frustum of a cone:

$$\text{volume} = h/3(a_1 + a_2 + \sqrt{a_1 a_2}) \tag{1}$$

where a_1 and a_2 are the areas (m^2) of the bottom and top of the frustum, and h is the length of the segment (m). The volume of each segment was calculated separately, and all segments were summed to determine the total volume of the tree. Inside-bark volume was calculated by reducing diameter measurements by bark thickness, which was measured with a bark gauge at DBH (diameter at breast height: 1.3 m or 0.5 m above stilt roots or buttresses). Bark thickness of upper segments was not measured, but was assumed to be proportional to the ratio of the segment diameter to DBH. There was no compensation in the sawtimber portion of the tree for rotten wood (cull), poor form, or buttresses. The volume of wood in stilt roots or buttresses was not measured in the field. Branch volume was estimated by counting the number of branches and visually estimating their average lower diameter and length. Distal branch diameter was assumed to be 0.1 cm.

Stem volume included all wood in the main stem from the base of the tree (0.5 m) to an upper diameter limit of 10 cm. Stem segments were classified as one of the following: poletimber (12.5 cm$\leq$DBH<27.5 cm), sawtimber (DBH$\geq$27.5 cm and length$\geq$2.5 m), crotchwood (portion of stem $\approx$0.5 m below large tree limbs), craftwood bolts (length=2 m and mid-diameter$\geq$25 cm), and roughwood (non-sawtimber quality portions of the main stem, based on form). Total volume included stem volume, upper stem volume (from upper diameter=10 cm to tree tip), and branch volume.

2.1. Data analysis

The data were log-transformed to reduce heterogeneity of variance. During detransformation of the equations, a correction factor was calculated for each equation to correct for bias inherent in logarithmic transformations (Meyer, 1944; Baskerville, 1972; Crow and Schlaegel, 1988):

$$\text{correction factor} = e^{\text{variance}/2} \tag{2}$$

Three linear equations were fit to the data:

$$\ln v = x + y \ln(d) \tag{3}$$

$$\ln v = x + y \ln(dh) \tag{4}$$

$$\ln v = x + y \ln(d^2 h) \tag{5}$$

where ln is the natural log, v the actual inside-bark total or stem volume (m^3), d the DBH (cm), and h the total height (m) for total volume or height to a 10 cm top for stem volume equations. Detransformed forms of the equations are as follows:

$$v = x_1(d)^y \tag{6}$$

$$v = x_1(dh)^y \tag{7}$$

$$v = x_1(d^2 h)^y \tag{8}$$

where x_1 is the antilog of x in Eqs. (3)–(5) multiplied by the correction factor, and y is from Eqs. (3)–(5). For each species, precision of the equation was assessed by comparing the inside-bark total or stem volume of each tree calculated from field measurements (actual) with volume predicted by the equation:

$$\text{precision} = 100\left(\sum_{j}^{i=1} v_{ij} - \sum_{j}^{i=1} \hat{v}_{ij}\right) \Big/ \sum_{j}^{i=1} v_{ij} \tag{9}$$

where v is the actual inside-bark total or stem volume, and $\hat{v}$ the predicted inside-bark total or stem volume.

The percent bark volume was determined as follows:

$$\text{bark volume} = 100\left(\sum_{j}^{i=1} \text{ov}_{ij} - \sum_{j}^{i=1} v_{ij}\right) \Big/ \sum_{j}^{i=1} v_{ij} \tag{10}$$

where v is inside-bark total volume and ov the outside-bark total volume. Bark volume was based on a percentage of inside-bark volume in our calculations. Total outside-bark volume can be calculated for a tree by multiplying inside-bark volume by the species' bark volume percentage.

Volume equations for Kosrae, Pohnpei, the Western Islands (Chuuk, Yap, and Palau), and Micronesia as a whole were developed for each species if there were at least 10 trees in the data set. Mean annual inside-bark diameter increments (MAI) for 162 trees, including *S. alba*, *B. gymnorrhiza*, and *R. apiculata*, had previously been calculated for 13 plots by subtracting diameter measurements taken during the 1991–1992 remeasurement of the permanent FSM plots from the initial 1983 diameter measurement and dividing by the number of years since the first survey (Devoe and Cole, 1998). In this paper, data for 102 trees in Kosrae and Pohnpei from permanent FSM plots were used for estimating growth rates.

Analysis of variance was used to determine significance of differences in size among populations of trees on different islands and relationship between diameter size class or crown position and growth rate (MAI). Tree crown positions were defined as follows:

- dominant – trees with crowns emerging from the general canopy and receiving full sunlight from above and partly from the sides;
- co-dominant – trees with crowns that form the general canopy, receiving full sunlight from above but comparatively little from the sides;
- intermediate – trees with crowns that are below or barely reaching the general canopy and receiving little direct sunlight from above and none from the sides;
- overtopped – trees with crowns entirely below the general canopy, receiving no direct sunlight from above or the sides

For diameter, height, and bark thickness measurements, observations were weighted by density (number of trees/ha) in all analyses. Weighting was necessary because the original surveys were variable-radius plot inventories (using a BAF seven metric wedge prism), so the density of each counted tree varied with the size of the tree (Dilworth and Bell, 1985). Weighting therefore adjusted for unequal sample sizes by species and island (Steel and Torrie, 1980). All statistical analyses were performed with SAS Release 6.12 (SAS Institute, Cary, NC). Tukey's Studentized range test ($p \leq 0.05$) was used to identify differences among means for all analyses.

Black-and-white, vertical aerial photographs (scale 1 : 10 000) taken in 1944–1945 of Kosrae and Pohnpei mangroves were examined at the Bishop Museum Archives in Honolulu to search for size and density differences in the islands' mangrove forests 50 years ago, and for possible explanations for differences if found.

3. Results

3.1. Characteristics of volume equations

The six mangrove species surveyed in this study, ranked in order of abundance, were the following: *S. alba* (most abundant), *B. gymnorrhiza*, *R. apiculata*, *X. granatum*, *R. mucronata*, and *L. littorea* (least abundant). Volume equations were calculated for all species, but not for all islands. Eqs. (3) and (5) provided the best fit for both inside-bark stem volume (Table 2) and inside-bark total volume (Table 3) of mangrove trees in Micronesia, based on coefficients of determination (R^2). Coefficients of determination for Eq. (4) (dh) were generally 3–4 percentage points lower than for Eq. (5) (d^2h). Each of the 68 volume equations, based on Eqs. (3) and (5), was highly significant ($p \leq 0.0001$).

DBH-only equations tended to overestimate volume by an average of 2.7–3.2% for most species and islands; this was especially true for *S. alba*. Several of the DBH-height equations consistently predicted total volume within 1.0% of the actual volume. Overall, precision of the equations was greater in predicting inside-bark stem volume (1.6%) than inside-bark total volume (2.2%).

Slopes for DBH-height equations developed for *S. alba* on Pohnpei were significantly greater than those developed for Kosrae (Tables 2 and 3). Slopes of DBH-only equations for *S. alba* were also significantly different among Kosrae, Pohnpei, and the Western Islands. The Kosrae and Pohnpei equations were more precise than the Western Island equations. *S. alba* in Pohnpei had greater volume at larger diameters than in Kosrae or the Western Islands (Fig. 2(a)). Slopes for the equations that calculated inside-bark total volume (DBH-only) for *B. gymnorrhiza* differed significantly between Pohnpei and Kosrae (Table 3), although the Kosraean and Pohnpeian trees appeared to be more similar to each other than to either the Western Island or Australian trees (Clough and Scott, 1989) of the same species (Fig. 2(b)). Slopes for equations that calculated inside-bark total volume for *R. apiculata* were significantly different between Kosrae and Pohnpei (Table 3). Estimated volumes for these trees were intermediate among the Australian and Malaysian data (Fig. 2(c) (Clough and Scott, 1989; Ong et al., 1984; Putz and Chan, 1986)).

Table 2
Constants for equations calculating inside-bark stem volume (m^3/tree) from DBH (d) and height (h) of Micronesian mangrove trees and precision of the equation for predicting actual volume for each species [a]

Species and geographic unit	Volume=$x_1 d^y$			Precision (%)	Volume=$x_1(d^2 h)^y$			Precision (%)
	x_1	y	R^2		x_1	y	R^2	
Sonneratia alba								
Micronesia	1.97×10^{-4}	2.221	0.91	+13.5	3.80×10^{-5}	0.952	0.94	+6.0
Kosrae	1.41×10^{-3}	1.804 a	0.81	+3.9	1.72×10^{-4}	0.834 a	0.87	+1.2
Pohnpei	7.51×10^{-5}	2.458 b	0.91	+5.9	2.40×10^{-5}	0.993 b	0.94	+3.3
Western Islands [b]	3.57×10^{-4}	2.005 c	0.84	+4.4	6.28×10^{-5}	0.894 ab	0.83	+5.2
Bruguiera gymnorrhiza								
Micronesia	4.83×10^{-5}	2.542	0.87	+2.9	3.08×10^{-5}	0.954	0.92	−2.9
Kosrae	7.46×10^{-5}	2.439 ab	0.84	−2.6	2.19×10^{-5}	0.985 a	0.85	−3.4
Pohnpei	4.73×10^{-5}	2.539 a	0.83	+3.3	2.46×10^{-5}	0.978 a	0.92	−0.4
Western Islands	2.07×10^{-4}	2.084 b	0.89	−7.4	1.47×10^{-4}	0.797 b	0.88	−18.4
Rhizophora apiculata								
Micronesia	8.92×10^{-5}	2.521	0.87	+2.0	4.27×10^{-5}	0.948	0.92	+2.1
Kosrae	2.07×10^{-4}	2.308 a	0.90	0.0	7.44×10^{-5}	0.896 a	0.93	+0.3
Pohnpei	7.92×10^{-5}	2.546 a	0.84	+4.0	3.74×10^{-5}	0.960 a	0.90	+2.5
Xylocarpus granatum								
Micronesia	1.43×10^{-4}	2.259	0.88	+6.1	6.25×10^{-5}	0.903	0.93	−0.2
Pohnpei	1.49×10^{-4}	2.249	0.88	+5.8	5.69×10^{-5}	0.912	0.93	+0.6
Rhizophora mucronata								
Micronesia	1.34×10^{-4}	2.249	0.82	+0.4	3.08×10^{-5}	0.976	0.91	+1.2
Pohnpei	1.56×10^{-4}	2.191 a	0.86	+2.7	3.52×10^{-5}	0.958 a	0.91	+1.7
Western Islands	1.32×10^{-4}	2.192 a	0.75	+8.2	2.74×10^{-5}	0.989 a	0.81	+5.9
Lumnitzera littorea								
Micronesia	8.83×10^{-5}	2.351	0.88	−7.4	3.00×10^{-5}	0.996	0.78	−12.5

[a] Different lower-case letters indicate significantly different ($p\leq0.05$) slopes for equations within the same species among islands.
[b] Western Islands=Chuuk, Yap, and Palau.

3.2. Characteristics of trees among islands

Among the six species, *S. alba* was the most abundant and largest, *R. mucronata* had the least volume, and *L. littorea* was represented by the fewest trees in the data set although it was the most common tree in the Palau plots (Table 4). Inferences about *R. mucronata* beyond Micronesia must be treated cautiously, as recent preliminary observations suggest that these may have been misidentified in both Kosrae and Yap and may actually be *R. stylosa* Griff. (N. Duke, Australian Institute of Marine Sciences, pers. comm.).

S. alba trees on Kosrae were significantly larger in diameter, height, and volume, and had significantly thicker bark than trees on Pohnpei or the Western Islands (Table 4). The largest tree on Kosrae was 3.2 m in diameter, twice the size of any other tree measured during the survey. The Western Islands had the smallest and shortest *S. alba* trees in Micronesia. *S. alba* trees on Pohnpei tended to be smaller than in Kosrae, where no trees were measured that had diameters smaller than 40 cm, and 60% of the trees were larger than 100 cm in diameter (Fig. 3(a)).

B. gymnorrhiza trees growing on Kosrae were significantly larger in diameter, height, and volume than those found on Pohnpei or the Western Islands (Table 4). There was no difference in bark thickness between trees on Kosrae or Pohnpei, but *B. gymnorrhiza* trees on both islands had significantly thicker bark than those on the Western Islands. Kosrae had

Table 3
Constants for equations calculating inside-bark total volume (m^3/tree) from DBH (d) and height (h) of Micronesian mangrove trees and precision of the equation for predicting actual volume for each species [a]

Species and geographic unit	Volume=$x_1 d^y$			Precision (%)	Volume=$x_1(d^2h)^y$			Precision (%)
	x_1	y	R^2		x_1	y	R^2	
Sonneratia alba								
Micronesia	3.53×10^{-4}	2.108	0.91	+10.9	7.48×10^{-5}	0.903	0.94	+4.6
Kosrae	2.05×10^{-3}	1.733 a	0.81	+2.6	2.69×10^{-4}	0.802 a	0.86	+0.2
Pohnpei	1.28×10^{-4}	2.359 b	0.92	+5.0	4.49×10^{-5}	0.949 b	0.94	+2.4
Western Islands [b]	5.13×10^{-4}	1.967 c	0.88	+7.3	8.49×10^{-5}	0.884 ab	0.88	+6.3
Bruguiera gymnorrhiza								
Micronesia	5.91×10^{-5}	2.540	0.90	+6.4	3.69×10^{-5}	0.955	0.95	+0.2
Kosrae	1.64×10^{-4}	2.280 a	0.89	−0.9	4.58×10^{-5}	0.932 a	0.92	−2.2
Pohnpei	4.83×10^{-5}	2.589 b	0.86	+4.0	2.64×10^{-5}	0.992 a	0.94	+0.9
Western Islands	2.44×10^{-5}	2.101 a	0.95	−8.6	1.46×10^{-4}	0.820 b	0.97	+4.1
Rhizophora apiculata								
Micronesia	7.93×10^{-5}	2.604	0.91	+0.6	3.94×10^{-5}	0.972	0.95	+0.9
Kosrae	1.93×10^{-4}	2.365 a	0.94	+0.6	6.94×10^{-5}	0.916 a	0.96	+1.2
Pohnpei	5.79×10^{-5}	2.692 b	0.90	+2.5	2.81×10^{-5}	1.007 b	0.95	−0.1
×ylocarpus granatum								
Micronesia	1.74×10^{-4}	2.266	0.89	+7.4	7.54×10^{-5}	0.906	0.94	+0.6
Pohnpei	1.87×10^{-4}	2.249	0.89	+7.3	7.13×10^{-5}	0.911	0.94	+0.7
Rhizophora mucronata								
Micronesia	1.15×10^{-4}	2.357	0.84	−0.4	2.36×10^{-5}	1.027	0.94	+0.1
Pohnpei	1.32×10^{-4}	2.297 a	0.89	+1.5	2.81×10^{-5}	1.003 a	0.95	+0.7
Western Islands	2.19×10^{-4}	2.097 a	0.67	+7.4	2.41×10^{-5}	1.028 a	0.85	+5.8
Lumnitzera littorea								
Micronesia	7.96×10^{-5}	2.456	0.94	+0.1	1.86×10^{-5}	1.074	0.88	−6.1

[a] Different lower-case letters indicate significantly different ($p\leq0.05$) slopes for equations within the same species among islands.
[b] Western Islands=Chuuk, Yap, and Palau.

more large *B. gymnorrhiza* trees than Pohnpei, as well as a bimodal distribution, with the two most populous diameter classes being 2.5–7.4 cm (5 cm class) and 37.5–42.4 cm (40 cm class) (Fig. 3(b)). The largest *B. gymnorrhiza* tree, however, occurred in the Western Islands on Yap (Table 4).

R. apiculata trees on Kosrae were significantly taller and had significantly greater volume than those on Pohnpei and the Western Islands (Table 4). Kosrae trees also had significantly thinner bark than those on Pohnpei. This species tended to be larger on Kosrae than on Pohnpei, but differences were not so pronounced as for *S. alba* and *B. gymnorrhiza* (Fig. 3(c)).

Fewer *X. granatum*, *R. mucronata*, and *L. littorea* trees were measured in our survey compared to the other species. Of these species, *R. mucronata* was the most widely distributed, and *L. littorea* was the least (Table 4). *X. granatum* had the thinnest bark of any species, averaging 0.3–0.4 cm in thickness.

When all species in the database were combined by size class and analyzed, Kosrae's stands were significantly larger in diameter and height than Pohnpei's in the larger size class (Table 5). Kosrae mangrove stands also had significantly fewer trees/ha and greater inside-bark volume for trees ≥12.5 cm DBH. The basal areas of the stands on the two islands were similar, however. In the smaller size class, there was no difference in average diameter between Kosrae and Pohnpei. Kosrae's stands did have significantly less basal area and fewer trees/ha in the smaller size

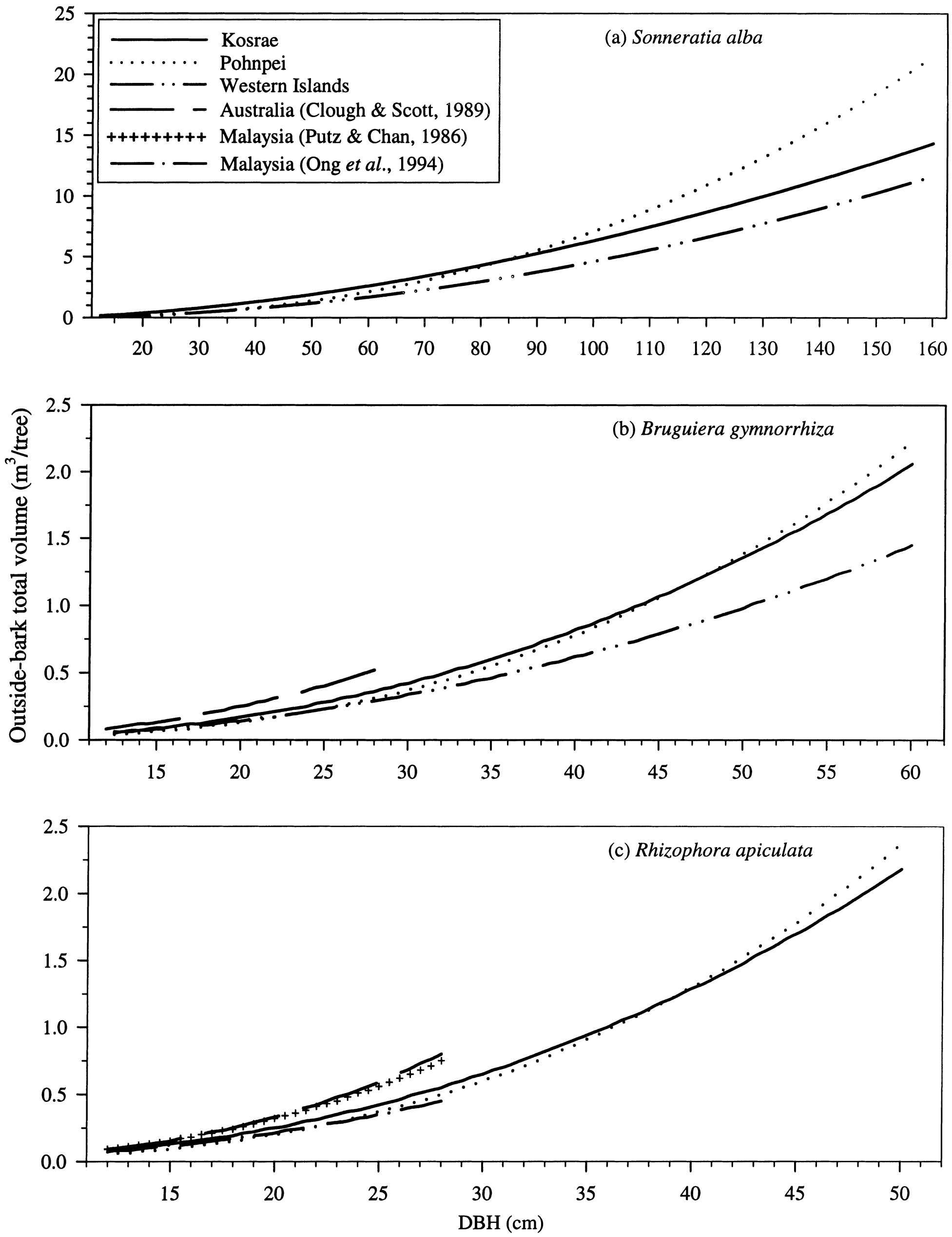

Fig. 2. Comparison of tree volumes based on equations relating outside-bark total volume and DBH-only. Equations for Australia and Malaysia were derived from data sets that included trees with diameters <28 cm. All curves, except those developed for Micronesia, were calculated by dividing biomass by wood density (*R. apiculata*: Malaysia – 980 kg dry weight m^{-3} fresh volume; Australia – 810 kg dry weight m^{-3} fresh volume; *B. gymnorrhiza*: 665 kg dry weight m^{-3} fresh volume).

class and when the two size classes were combined (Table 5). There were fewer large trees (>50 cm DBH) on Pohnpei and a more uneven diameter distribution of trees on Kosrae (Fig. 4).

3.3. Growth rates of trees on Kosrae and Pohnpei

Inside-bark diameter growth for *S. alba* and *R. apiculata* was significantly faster for trees on Kosrae

Table 4
Characteristics of six mangrove species common in Micronesia [a]

Species and geographic unit	Number of trees	Weighted [b] DBH (cm)	Weighted [b] height (m)	Weighted [b] bark thickness (cm)	Maximum DBH (cm)	Maximum height (m)	Total inside-bark volume (m^3/tree)	Stem inside-bark volume (m^3/tree)	Bark volume (% of total inside-bark volume)
Sonneratia alba									
Micronesia	351	40.6 (1.49)	17.7 (0.33)	1.2 (0.03)	323.0	42.0	1.36 (0.14)	1.24 (0.14)	5.7
Kosrae	156	75.9 (2.95) a	23.7 (0.41) a	1.9 (0.04) a	323.0	42.0	4.23 (0.37) a	4.01 (0.36) a	5.6
Pohnpei	159	38.3 (1.77) b	17.1 (0.51) b	1.3 (0.04) b	161.6	37.0	1.08 (0.16) b	0.96 (0.15) b	6.0
Western Islands	36	26.4 (2.38) c	15.7 (0.67) b	0.7 (0.05) c	117.8	24.0	0.40 (0.09) b	0.32 (0.07) b	4.7
Bruguiera gymnorrhiza									
Micronesia	329	23.2 (0.60)	12.8 (0.30)	1.5 (0.03)	132.0	34.0	0.25 (0.02)	0.21 (0.02)	12.7
Kosrae	128	33.0 (1.16) a	18.3 (0.43) a	1.5 (0.06) a	89.5	34.0	0.58 (0.05) a	0.48 (0.05) a	10.7
Pohnpei	183	20.7 (0.61) b	11.5 (0.34) b	1.6 (0.04) a	87.2	29.0	0.17 (0.02) b	0.14 (0.02) b	14.7
Western Islands	18	21.1 (2.77) b	10.4 (1.15) b	0.7 (0.05) b	132.0	22.0	0.20 (0.11) b	0.16 (0.10) b	6.5
Rhizophora apiculata									
Micronesia	193	20.9 (0.51)	16.1 (0.36)	1.1 (0.02)	60.0	35.0	0.27 (0.02)	0.23 (0.02)	9.1
Kosrae	47	22.4 (1.37) a	18.2 (0.71) a	0.9 (0.07) a	60.0	35.0	0.38 (0.06) a	0.34 (0.06) a	8.4
Pohnpei	140	20.7 (0.53) a	15.8 (0.42) b	1.1 (0.03) b	59.8	33.0	0.25 (0.02) b	0.21 (0.02) b	9.2
Western Islands	6	16.8 (2.51) a	12.0 (1.19) b	1.0 (0.08) ab	29.5	16.0	0.16 (0.06) ab	0.12 (0.05) b	11.5
Xylocarpus granatum									
Micronesia	117	25.7 (1.37)	12.4 (0.49)	0.4 (0.01)	128.5	31.0	0.41 (0.07)	0.32 (0.05)	2.3
Pohnpei	114	25.9 (1.41) a	12.7 (0.49) a	0.4 (0.01) a	128.5	31.0	0.42 (0.07) a	0.33 (0.06) a	2.3
Western Islands	3	21.4 (3.65) a	6.5 (1.64) b	0.3 (0.00) a	34.3	9.0	0.12 (0.05) a	0.11 (0.04) a	1.5
Rhizophora mucronata									
Micronesia	74	17.6 (0.68)	10.7 (0.32)	1.1 (0.06)	39.5	21.0	0.12 (0.01)	0.10 (0.01)	11.3
Kosrae	4	20.2 (5.36) a	16.8 (0.97) a	0.5 (0.41) a	38.0	21.0	0.36 (0.20) a	0.28 (0.15) a	10.0 ab
Pohnpei	59	17.3 (0.75) a	10.7 (0.32) b	1.3 (0.06) b	39.5	16.0	0.11 (0.01) b	0.09 (0.01) b	12.4 a
Western Islands	11	18.0 (1.60) a	9.3 (0.70) b	0.6 (0.14) a	32.2	14.0	0.10 (0.02) b	0.08 (0.02) b	6.1 b
Lumnitzera littorea									
Micronesia	21	18.5 (1.58)	9.6 (0.48)	1.1 (0.09)	70.6	19.0	0.13 (0.05)	0.10 (0.04)	9.6
Pohnpei	9	16.5 (1.76) a	9.4 (0.75) a	1.3 (0.07) a	44.9	19.0	0.09 (0.03) a	0.07 (0.02) a	14.6 a
Palau	12	23.6 (2.64) b	9.9 (0.68) a	0.6 (0.10) b	70.6	14.0	0.24 (0.11) a	0.19 (0.10) a	5.9 b

[a] Standard errors are in parentheses. Different lower-case letters indicate significant differences ($p \leq 0.05$) within the same species among islands.
[b] Weighted by trees/ha (only trees>12.5 cm in DBH).

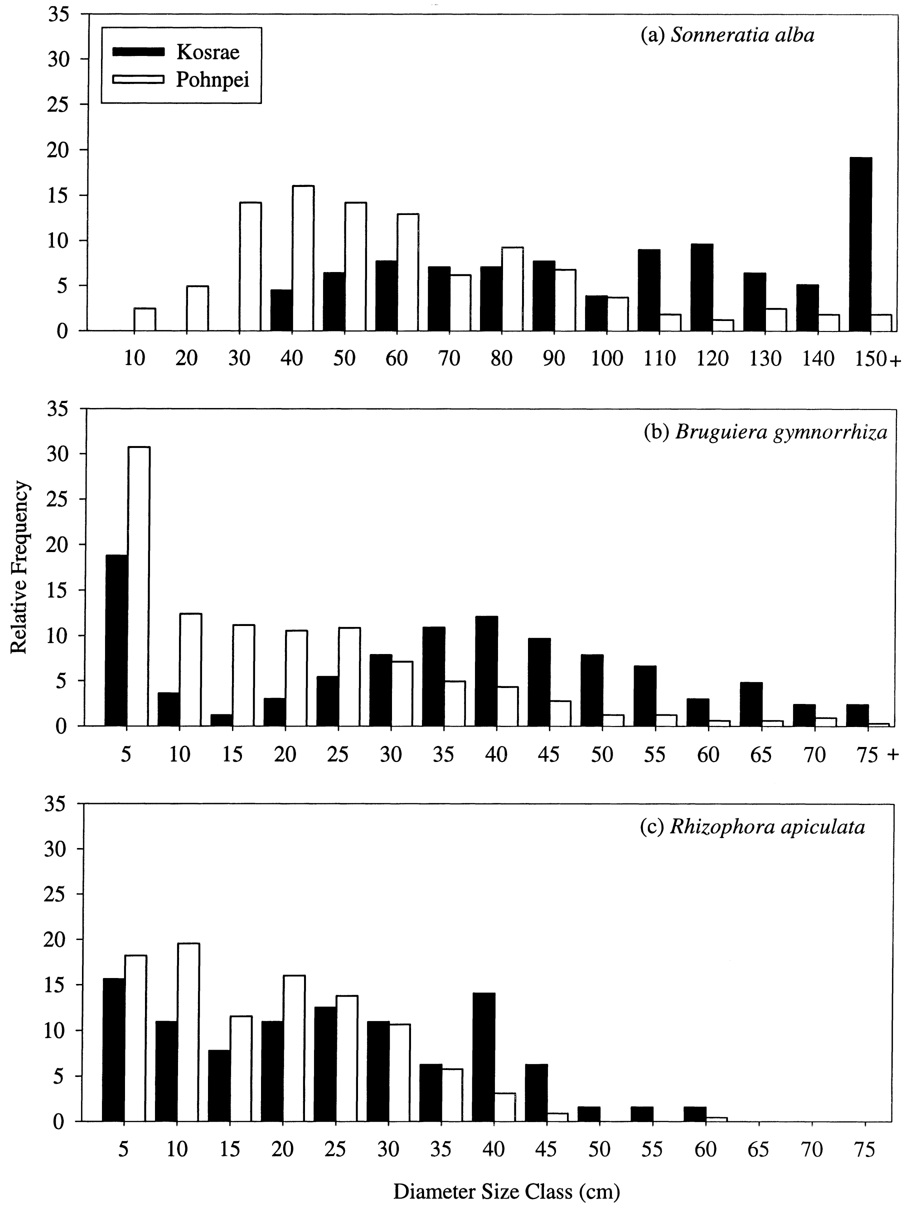

Fig. 3. Frequency distribution of diameter size classes for three mangrove species on Kosrae and Pohnpei, Federated States of Micronesia.

than on Pohnpei (Table 6). The growth rate of *R. apiculata* was significantly correlated with diameter size class on Pohnpei (R^2=0.44, $p\leq0.0021$), but not on Kosrae (R^2=0.08, $p\leq0.5144$). Neither *B. gymnorrhiza* nor *S. alba* showed any correlation between diameter size class and MAI on either island. In addition, none of the three species showed any relationship between tree crown position and MAI. On both islands, *S. alba* had the largest MAI, followed by *B. gymnorrhiza* and then *R. apiculata*.

Aerial photography of Pohnpei and Kosrae taken in 1944–1945 by the US military shows clear differences in mangrove stand structure and stature between the two islands during that time. In most Kosraean mangrove stands, crowns of large trees emerged from the general canopy, and the overall texture of the forest

Table 5
Structure of mangrove stands on Kosrae and Pohnpei, Federated States of Micronesia, by DBH size class [a]

Size class and island	Number of trees	Weighted [b] DBH (cm)	Weighted [b] height (m)	Basal area (m^2/ha)	Trees per hectare	Total inside-bark volume (m^3/ha)
2.5≥DBH<12.5 cm						
Kosrae	59	6.1 (0.7) a		1.6 (0.3) a	521 (137) a	
Pohnpei	381	7.0 (0.3) a		5.4 (0.7) b	1317 (174) b	
DBH≥12.5 cm						
Kosrae	335	37.9 (2.5) a	20.1 (0.8) a	30.4 (1.9) a	248 (49) a	215 (15) a
Pohnpei	664	23.8 (1.1) b	13.6 (0.6) b	25.1 (2.1) a	514 (48) b	144 (18) b
All trees						
Kosrae	394	19.6 (2.0) a		31.7 (1.8) a	671 (113) a	
Pohnpei	1045	15.1 (1.4) a		29.9 (1.8) a	1696 (173) b	

[a] Different lower-case letters indicate significant differences between islands ($p \leq 0.05$), standard errors are in parentheses.
[b] Weighted by trees/ha.

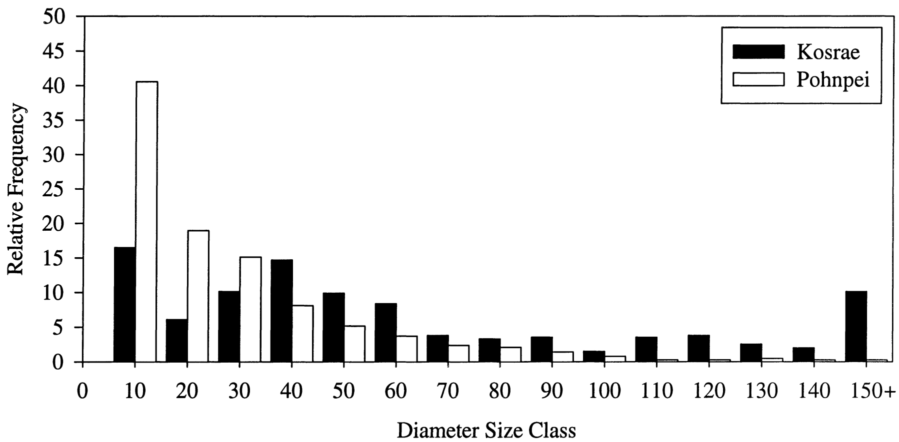

Fig. 4. Frequency distribution of diameter size classes for all mangrove species on Kosrae and Pohnpei, Federated States of Micronesia.

canopy was uneven. In contrast, the Pohnpeian stands were generally very smooth-textured, and the crowns of individual trees were rarely distinguishable, except in a few protected areas and along some of the major rivers. These observations suggest that Pohnpei had even-aged mangrove stands and Kosrae had uneven-aged mangrove stands that were perhaps older.

4. Discussion

The volume equations reported here are unique in the mangrove literature because of the range of tree diameters we measured (12.5–323 cm DBH). A search of the literature found no volume equations that were suitable for trees larger than 30 cm DBH. The Micronesia-wide equations therefore provide a basis of comparison for inventories elsewhere. The wide distribution of islands across a distance of more than 3000 km, with only subtle changes in topography and rainfall, helps to focus on the causes of differences in growth and form.

Although the volume equations reported here are heavily weighted to data collected in Pohnpei and Kosrae, where 55 of the 65 permanent plots and 999 of the 1085 measured trees were located, there were still important island-to-island differences, especially in the slopes of many of the volume equations for the two

Table 6
Mean diameters and mean annual diameter increments (MAI) of mangrove species on Kosrae and Pohnpei, Federated States of Micronesia, after 7–9 years of growth [a]

Species and geographic unit	Number of trees	Diameter in 1983 (cm)	Diameter in 1992 (cm)	MAI (cm/year)
Sonneratia alba				
Kosrae	23	71.2 (4.69) a	79.7 (4.98) a	0.96 (0.13) a
Pohnpei	10	32.5 (4.21) b	35.3 (4.33) b	0.33 (0.10) b
Bruguiera gymnorrhiza				
Kosrae	10	27.6 (3.59) a	31.5 (3.88) a	0.44 (0.09) a
Pohnpei	6	17.5 (4.06) b	19.4 (4.31) b	0.26 (0.05) a
Rhizophora apiculata				
Kosrae	29	21.7 (1.64) a	24.9 (1.84) a	0.38 (0.07) a
Pohnpei	24	11.7 (1.35) b	12.3 (1.46) b	0.12 (0.02) b

[a] Standard errors are in parentheses. Different lower-case letters indicate significant differences between islands ($p \leq 0.05$).

most abundant species, *S. alba* and *B. gymnorrhiza*. These differences suggest that only the generalized Micronesia equations should be used for comparison elsewhere, where conditions specific to Kosrae and Pohnpei are less likely to apply.

Rotten wood or poor stem form accounted for as much as 40% of the gross stem volume in many of the trees in our database (Devoe and Cole, 1998). Among *S. alba*, *R. mucronata*, and *X. granatum* trees with diameters >30 cm, 88% had signs of stem rot or had poor form. Consequently, depending on the goals of the inventory, when using these equations it may be important to estimate cull for each tree and to report net volume.

Sizes and frequency distributions of *B. gymnorrhiza*, *R. apiculata*, and *S. alba* on Pohnpei and Kosrae were strikingly different (Fig. 3). Tree structure also differed significantly between the Kosraean and Pohnpeian populations, although differences seemed subtle in comparison with trees from Malaysia and Australia (Fig. 2).

When the diameter distributions of all species on Kosrae and Pohnpei were combined (Fig. 4), a relative lack of large trees on Pohnpei was apparent. The exponential or 'J' shape of the Pohnpei curve is characteristic of uneven-aged forests (Gingrich, 1978; Oliver and Larson, 1990), but has also been found in even-aged forests (Harper, 1977). In Puerto Rico, the diameter/frequency distribution of the hurricane-damaged colorado forests (cloud forests) of the Luquillo Mountains also displays this classic exponential shape (Weaver, 1995).

Two factors that may explain the differences in mangrove stand structure on Kosrae and Pohnpei are the ages of the forests and the growth rates of the trees. Determining the age of mangrove trees or stands is difficult, as it is with most tropical forests (Harper, 1977; Lieberman et al., 1985; Worbes and Junk, 1989). The assumption that tree size relates to tree age ignores climate and site factors and their relationship to forest productivity (Harper, 1977). Nevertheless, the characteristics of the stands in the 1944–1945 aerial imagery suggest that the relationship of tree size to age may indeed be valid on these islands.

In South Florida and Puerto Rico, hurricanes limit the long-term development of mangroves, resulting in forests that are often characterized by short canopies and high densities of trees in the smaller size classes (Pool et al., 1977). The Pohnpei mangroves also had significantly shorter canopies and significantly more trees/ha than those on Kosrae (Table 5), suggesting that they had experienced large-scale disturbances in the past. Pohnpei and Kosrae lie outside the North Pacific typhoon belt and rarely receive major storms. Nevertheless, according to an unpublished report on the history of Kosrae, several typhoons and one tidal wave struck Kosrae between 1837 and 1905, but no indication of damage to the island was reported (Wilson, 1967). The only major typhoon in modern history to hit Pohnpei directly occurred in April 1905 and reportedly "...leveled the island so completely that people found it far easier to describe what survived...than what was destroyed (Berg, 1905a, b; cited by Hezel, 1995, p. 101).'' The German reports also mentioned that the typhoon did not cause extensive damage on Kosrae, although the two islands are only 560 km apart.

Although damage to the mangroves was not explicitly mentioned in German accounts of the 1905 typhoon, the mangrove trees on Pohnpei were probably defoliated and severely damaged by the high winds. Legends and songs still common in Pohnpei indicate that the ''mangroves and upland forests were totally destroyed, except for one mangrove tree in the Enipein area, and only taro was left standing (W. Raynor, The Nature Conservancy, Pohnpei, pers. comm.).'' The recovery period needed by the Pohnpei mangroves could therefore account for the differences we found in stand structure between the two islands (Table 5 and Fig. 4).

Mangrove forests on both islands have been subjected to sporadic, occasionally extensive harvesting (Devoe, 1994), as suggested by the abundance of *B. gymnorrhiza* and *R. apiculata* in the smaller size classes as well as the existence of bimodal distributions for the two species at one site on Pohnpei (Fujimoto et al., 1995). Nevertheless, mangroves in Kosrae were still more uneven-aged and had trees of larger stature than in Pohnpei, more than 75 years after the typhoon. The presence of very large, spreading *S. alba* trees in Kosrae suggests that large gaps at some earlier date had existed, perhaps themselves caused by typhoons, extensive harvesting, or natural gap-phase dynamics.

In spite of their putative older age, *S. alba* and *R. apiculata* were growing at a rate three times faster in Kosrae than in Pohnpei (Table 6). Because Pohnpei and Kosrae are so close to one another and have similar rainfall patterns and topography, differences in the major climate variables (e.g., daylength, solar radiation, temperature, potential evapotranspiration, and humidity) are unlikely. How site conditions (e.g., soils, hydrologic features) might differ between the islands is unclear. In Australia and Papua New Guinea, mangrove growth was positively correlated with levels of soil phosphorus and soil ammonium (Boto et al., 1984), but no soil chemistry data are available for Kosrae or Pohnpei.

Different substrate types (e.g., coral reef, estuary, or backmarsh, sensu Fujimoto and Miyagi, 1993) may account for differences in growth rate between the two islands. Trees on a 1 ha coral-reef-type plot were smaller than on a 1 ha estuarine-type plot (Fujimoto et al., 1995). The four Kosrae plots for which growth rates were determined included two in a backmarsh location and one in each of the others. Substrates for the four Pohnpei plots are not known, but most of the mangrove forests in Pohnpei are believed to be coral reef types (Fujimoto et al., 1995).

Porewater salinity levels on both islands reflect high rainfall and frequent tidal inundation. Average salinity ranged from 20‰ in interior mangroves near land to 37‰ near the ocean on Kosrae (Ewel et al., 1998b) and 14‰ near land and 28‰ near the ocean at one site on Pohnpei (Fujimoto et al., 1995). These values are not considered growth-limiting to any of the three major species (Smith, 1992). Tide tables for the region indicate that Kosrae has higher mean tides (0.97 vs. 0.70 m) and spring tides (1.40 vs. 1.04 m) than Pohnpei (NOAA, 1997f). The mangrove interiors of both islands, however, are frequently inundated by seawater (Pohnpei: Fujimoto et al., 1995; Kosrae: K. Ewel, pers. observ.).

Sixty years of mangrove growth data from Malaysia indicated that the MAI of neither *B. gymnorrhiza* nor *R. apiculata* was related to tree diameter (Putz and Chan, 1986). Growth, however, was related to crown position, with sub-dominant (intermediate) and suppressed trees growing more slowly than dominant and co-dominant trees. The MAI of *R. apiculata* in Pohnpei was slightly correlated with size class, but not with crown position. Tree density on Pohnpei was more than twice that of stands on Kosrae and may influence growth rates. The 1905 typhoon that struck Pohnpei is therefore likely to have caused the stand structure that we see today in its mangrove forests, but the differences in growth rates of the major species on Kosrae and Pohnpei cannot yet be explained.

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