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Author(s): Zuleika S. Pinzón, Katherine C. Ewel, Francis E. Putz

Source: *Journal of Tropical Ecology*, Vol. 19, No. 2 (Mar., 2003), pp. 143-153

Published by: Cambridge University Press

Stable URL: <http://www.jstor.org/stable/4092152>

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Gap formation and forest regeneration in a Micronesian mangrove forest

Zuleika S. Pinzón*¹, Katherine C. Ewel^{†2} and Francis E. Putz*

*Department of Botany, University of Florida, Gainesville FL 32611, USA

†USDA Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, 1151 Punchbowl St., Rm. 323, Honolulu HI 96813, USA

(Accepted 27 January 2002)

Abstract: Gaps created by the death of one or more contiguous trees are common in mangrove forests but are poorly understood. In Kosrae, Federated States of Micronesia, where mangrove wood is harvested for local use, most natural gaps were < 50 m², whereas most logging gaps were > 100 m². Interior zones, where access is facilitated by roads, were the most heavily exploited. Although the forests contained 11 species, two species were primarily responsible for gap formation. Natural gaps were caused mainly by broken stems and large branches of *Sonneratia alba* trees, whereas logging gaps were created primarily by harvesting *Rhizophora apiculata* trees. Most natural gaps were formed by the fall of more than one tree or branch. Seedling densities were higher in logging gaps than in natural gaps and higher in gaps than under intact canopy. *Bruguiera gymnorhiza* was the most common seedling species in gaps and under intact canopy. Relative rates of growth in height were faster in gaps than under intact canopy for *R. apiculata* and *B. gymnorhiza* seedlings. Current harvesting practices on the island do not seem to be altering species richness, although *R. apiculata* may become less common as gaps are increasingly captured by *B. gymnorhiza*.

Key Words: *Bruguiera gymnorhiza*, firewood harvesting, Kosrae, *Rhizophora apiculata*, *Sonneratia alba*

INTRODUCTION

Mangrove forests are subject to a wide range of natural and anthropogenic disturbances. Although much attention has been paid to the cataclysmic disturbances of hurricanes and cyclones (Bardsley 1985, Craighead 1964, Lugo & Snedaker 1974, Roth 1992, Smith *et al.* 1994) and frost damage (Everitt *et al.* 1996, West 1977), mangrove forests in many parts of the tropics are principally affected by small-scale disturbances such as lightning strikes (Craighead 1971, Pajmans & Rollet 1977, Sherman *et al.* 2000, Smith 1992), insect damage (Feller & McKee 1999, Putz & Chan 1986), and tree and branch breakage during wind storms (Putz *et al.* 1984). Because mangrove forests provide many ecological services (e.g. protection of coasts from storm surges, sediment trapping, production of wood, fish and shellfish; Ewel *et al.* 1998b, Hamilton & Snedaker 1984, Watson 1928), it is important to understand natural forest dynamics well enough to predict how a forest will respond to both natural and anthropogenic disturbances (Boot & Gullison 1995, Lorimer & Frelich 1994). The effects of silvicultural management,

such as for production of building materials and charcoal, on diversity and ecosystem processes are expected to be minimal if they resemble natural forest dynamics; management techniques appropriate for local ecosystems and individual stands are now being recommended in lieu of general silvicultural prescriptions (Pfister 1993, Putz 1996, Rogers 1996).

Mangrove forest regeneration processes are unique, because both viviparity and cryptoviviparity are common, as is dispersal by water. Recruitment in this forest is therefore likely to be affected by propagule dispersal properties (Rabinowitz 1978), hydro-edaphic factors (Jiménez & Sauter 1991), propagule predation (Robertson *et al.* 1990, Smith 1987a), and interspecific variation in response to resource availability (McKee 1995). Seedling recruitment in logging gaps in mangrove forests may also be affected by distance from the forest edge. In Ecuadorian mangrove forests, for example, most seedlings in clearcut strips were within 5 m of seed trees, especially in plots with low inundation frequency (Blanchard & Prado 1995).

A better understanding of differences in regeneration between natural and logging gaps in mangrove forests is required if silvicultural treatments are to mimic natural disturbances as closely as possible. On oceanic islands, making good silvicultural decisions is particularly critical, because limited natural resources are threatened by

¹ Current address: Fundacion Natura, Apartado 2190, Panama 1, Republic of Panama.

² Corresponding author.

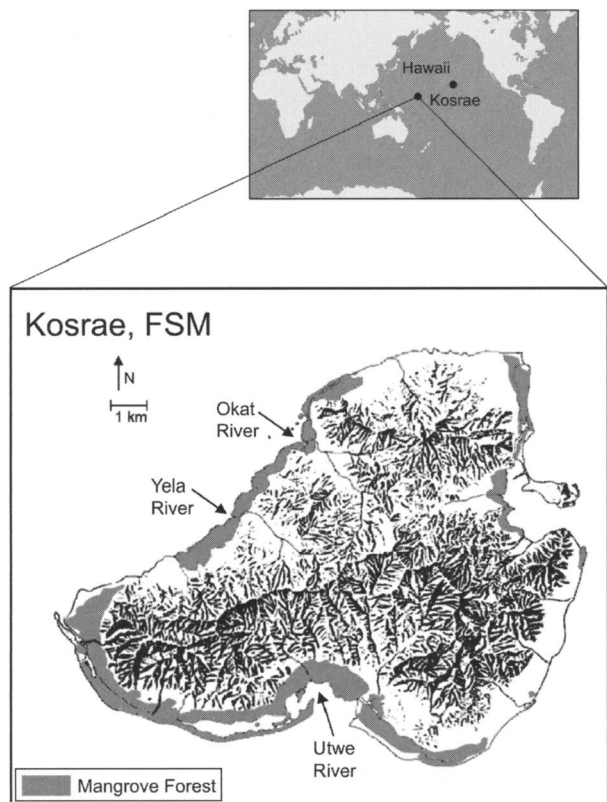


Figure 1. Location of Kosrae, Federated States of Micronesia (FSM), and the study sites.

increasing human populations. The island of Kosrae in the Federated States of Micronesia ($5^{\circ}19'N$, $163^{\circ}00'E$), at the extreme eastern end of the Caroline Islands (Figure 1), offers a good opportunity to study mangrove forest dynamics and the effects of anthropogenic disturbances in a part of the world where patterns and rates of natural and anthropogenic disturbances, as well as vegetation recovery mechanisms, are poorly understood. Kosrae has a relatively large and intact expanse of mangrove forests, local people exploit mangrove resources on a regular basis, and the variety of disturbances that have apparently affected the forests is low.

The objectives of this study of mangrove forests on Kosrae were to investigate the characteristics of gaps, the types of disturbance causing their formation, and differences among patterns of recruitment in intact forest, in natural gaps and in gaps created by people.

Study area

Kosrae, a 112-km² high-volcanic island, has a mountainous interior and a narrow, flat coastal plain dominated by mangrove and freshwater swamp forests. The climate of Kosrae is humid tropical, with a mean annual temperature of 27 °C on the coastal plain (Merlin *et al.* 1993). Rainfall is generally non-seasonal, with an annual mean of 5000

mm (Karolle 1992). Major typhoons tend to travel mostly north and west of Kosrae, and none has hit the island since 1905 (Segal 1995). Tidal variation is about 1 m.

In 1994, the population of Kosrae was 7317, with a net annual population growth of 1.3% (Kosrae State Government 1996). Most people in this young and rapidly growing population live on the coastal lowlands, and most are involved in subsistence activities, such as fishing, agriculture and firewood extraction.

Mangrove forests on Kosrae

Mangrove forests occupy 1562 ha on Kosrae: about 22% of the native forest area and 14% of the total land area (Whitesell *et al.* 1986). They surround most of the island, either along the coast or behind narrow sand bars that support coastal strand vegetation, and they have been continuously present for at least 4200 y (Kawana *et al.* 1995). Net stand volume for mangrove forests (total inside-bark volume, based on trees with diameter at breast height ≥ 12.5 cm) is 215 m³ ha⁻¹ (Cole *et al.* 1999). All mangroves are under the jurisdiction of the state government, and there were no restrictions on harvesting at the time of this study.

Of the 11 mangrove tree species found on Kosrae, *Bruquiara gymnorrhiza*, *Sonneratia alba* and *Rhizophora apiculata* are the most common, with importance values ranging from 137 for *B. gymnorrhiza* to 102 for *Rhizophora apiculata* (Ewel, in press). They grow in mixed stands, although *S. alba* is most common in the fringe zone, *B. gymnorrhiza* in the riverine zone, and *R. apiculata* in the interior zone. *Nypa fruticans*, *Xylocarpus granatum*, *Barringtonia racemosa*, and *Heritiera littoralis* also occur throughout the forest but are more common toward the landward edge and along some rivers. *Rhizophora mucronata*, *R. stylosa*, and *R. × lamarckii* generally grow at the mouths of estuaries, where there is frequent tidal flushing; in this study, no distinction was made among these last three taxa, and all are referred to as *R. mucronata*. *Lumnitzera littorea*, the least common species, grows in the middle and landward portions of the mangroves and sometimes forms small stands behind sandy protective barriers.

Mangroves on Kosrae are harvested mainly for firewood; *R. apiculata* is the preferred species, and *B. gymnorrhiza* is also commonly used. During major social events such as funerals, when the family of the deceased feeds mourners, mangrove wood consumption increases dramatically. There is also a moderate amount of commercial exploitation, mostly for firewood but also for carving (especially *X. granatum*) and occasionally for saw timber (Lal 1989, Metz 1994).

Threats to mangrove forests on Kosrae are also associated with the proposed construction of a road around the island (Scott 1993), which will involve filling some man-

grove areas, possibly changing hydrologic patterns, and, most importantly, increasing access to the forest. In the past, clearcutting of mangroves has often occurred adjacent to roads.

METHODS

This study was conducted adjacent to the estuaries of three rivers: Okat, Utwe and Yela (Figure 1). These forests were divided into three hydrogeomorphic zones: the fringe zone, which is tide-dominated with nearly constant salinity and bi-directional fluxes of water; the riverine zone, which is dominated by the influence of the adjacent river and experiences lower salinities; and the interior zone, which is flooded less frequently but has prolonged periods of soil saturation (Woodroffe 1992).

Gap sizes and causes of gap formation

A canopy gap was defined as the vertical projection of a hole that was $\geq 10 \text{ m}^2$ in area and $\geq 2 \text{ m}$ wide in the forest canopy, extending down to a height of $\leq 2 \text{ m}$ above ground (after Brokaw 1982). To estimate individual gap size and overall gap densities in the interior zone of each of the three mangrove stands, a 2-ha plot ($100 \times 200 \text{ m}$) was established. The starting point was randomly located, and the longest axis of the plot was established parallel to either the shore or the nearest road, whichever was nearer. Large cleared patches destined to be filled for house sites or roads were avoided. In the fringe and riverine zones of each estuary, two 20-m-wide transects were randomly located perpendicular to the coastline and to riverbanks, respectively, so that they included the entire tidal gradient in each zone. Minimum distance between transects was 100 m, and transect lengths varied from 100 to 200 m depending on the extent of the respective mangrove zone. We sampled 0.8% of the total mangrove forest area on Kosrae.

To estimate gap size, we measured distances and angles from the centre to the edge of each gap in at least eight directions (usually every 45°) and then summed the area of all triangles so formed. We measured canopy openness at the centre of each gap with a spherical densiometer (Lemmon 1956) held 1.2 m above the ground.

We classified canopy gaps as either natural (i.e. showing no evidence of having been caused by human activity) or logging-induced, depending on the fates of the principal gap-making trees. We used a diameter tape to measure the diameter at the base of each tree, and we recorded the species of all fallen and felled trees and large fallen branches ($\geq 10 \text{ cm}$ basal diameter), as well as the type of damage (felled, snapped-off, uprooted, branchfall or dead standing tree). We also measured the dbh (diameter at breast height, 1.3 m or above the highest prop root) and

identified to species all trees $\geq 10 \text{ cm}$ dbh with crowns bordering each gap.

We estimated the age of each gap based on stages of decomposition of the gap-making trees. Visits to gaps of known age helped us to assign gaps as < 3 and > 3 y according to the age of the disturbance event(s) that contributed most substantially to gap creation.

The fraction of the forest under gaps (gap fraction) was calculated for each zone and gap type (natural and logging). In cases where gaps overlapped the borders of the transects or plots, the portion of the gap that fell outside of the sampled area was disregarded.

A split-plot ANOVA for unbalanced data using the General Linear Model (GLM) procedure with the RANDOM statement of the Statistical Analysis System Institute Inc. (SAS 6.12; Littell *et al.* 1991) was used to compare size, gap fraction and gap density of natural and logging gaps. Estuary was treated as a random factor, whereas zone and gap type were treated as fixed factors. Data for gap size were log-transformed for the analysis to homogenize variances. Comparisons within zones used the Tukey–Kramer method.

Seedling density

Mangrove seedling densities in gaps and under the adjacent canopy were estimated by species using a stratified random sampling procedure. To sample within gaps, a baseline was located along the longest axis of each gap, and perpendicular transects of contiguous 1-m^2 quadrats were extended at stratified random intervals to the border of the gap. The total number of 1-m^2 quadrats that was sampled in each gap ranged from 6 to 118, depending on gap size. Seedling densities were estimated as a weighted average based on the length of the transects containing the quadrats. All seedlings in these quadrats were recorded by species and height class: $< 50 \text{ cm}$; 50–100 cm; 100–150 cm; and 150–200 cm.

To estimate seedling densities outside gaps, 1-m^2 plots were located in a stratified random fashion along the transects used to estimate gap densities. An additional transect was established in the interior zone of Utwe to estimate seedling densities under the intact canopy in the interior zone. A plot was not sampled when it fell directly in a gap or $< 3 \text{ m}$ from the border of a gap. Per cent canopy cover was estimated at the centre of each plot with a spherical densiometer (Lemmon 1956) held 1.2 m above the ground.

Differences in total seedling densities between types of gaps (natural and logging) and between gaps and intact canopy sites were tested with a split-plot ANOVA for unbalanced data using the GLM procedure of SAS 6.12. Gap size was tested as a covariate but was not significant and was removed from the model. Comparisons within gaps and between gaps and in adjacent plots under a

closed canopy were based on Tukey's Honestly Significant Difference (HSD) method. The Tukey-Kramer method was used to compare total seedling densities in gaps within each zone in the estuaries. Data were log-transformed to homogenize variances.

Differences among seedling densities for the three major species (*B. gymnorrhiza*, *R. apiculata* and *S. alba*) were tested using a split-split ANOVA for unbalanced data and empty cells (SAS 6.12; Littell *et al.* 1991). The Tukey-Kramer method was used for comparisons within zone and within canopy condition (i.e. natural gap, logging gap and intact canopy).

Seedling growth

We compared seedling growth of *R. apiculata* and *B. gymnorrhiza* under the intact canopy and in gaps in the Yela River interior zone. There were too few seedlings of other species to be included in this study. In June 1995, we randomly selected and marked seedlings ≤ 1 m tall of *R. apiculata* and *B. gymnorrhiza* growing in gaps ($n = 56$ and 89 , respectively) and under the intact canopy ($n = 28$ and 29 , respectively). Total height was measured from the ground to the base of the apical leaf pair. Total leaf production was estimated by counting the number of leaf scars and leaves. Seven mo later, we re-measured these seedlings to estimate rates of relative height growth and leaf production. Height growth increment was measured from the last node counted during the first sampling to avoid errors due to changes in the soil level. Relative height growth rates were estimated using the formula:

$$\text{RGR} = [\ln(ht_2) - \ln(ht_1)] \times (t_2 - t_1)^{-1},$$

where ht_1 and ht_2 were the seedling heights (mm) at the first and second sampling measurements during the time interval $t_2 - t_1$ (mo). A similar formula was applied to estimate relative stem diameter growth rate. Leaf production rates were estimated by subtracting the combined number of leaf scars and leaves at the first sampling from that present at the second sampling and dividing it by the time interval. Differences in seedling growth rates between gap and intact canopy plots were tested with a Mann-Whitney U test.

Nomenclature follows Tomlinson (1986).

RESULTS

Gap size distribution

Logging gaps were significantly larger (mean = 114 ± 160 (SD) m^2 , $n = 72$) than natural gaps (mean = 64.4 ± 79.5 (SD) m^2 , $n = 78$; $P < 0.05$). Minimum and maximum sizes were 10 and 498 m^2 for natural gaps, and 13 and 943 m^2 for logging gaps. Most natural gaps were $< 50 \text{ m}^2$, and very few were $> 200 \text{ m}^2$ (Figure 2). In contrast, logging

gaps were significantly over-represented among gaps $> 100 \text{ m}^2$ (Kolmogorov-Smirnov test, $KD = -0.21$, $P < 0.05$). Even though large gaps of both types were rare, they represented a substantial proportion of the total area in gaps. Logging gaps contributed more to the total gap area than natural gaps. Of the 150 gaps measured, the 23 logging gaps $> 100 \text{ m}^2$ accounted for almost 50% of total gap area (Figure 2). Neither logging nor natural gaps differed significantly in size among the three zones or three estuaries.

There was no overall difference in gap densities of natural and logging gaps (Figure 2), but the gap-zone interaction was significant for both gap fraction ($P = 0.002$) and gap abundance ($P = 0.033$). The interior and riverine zones had more logging gaps (mean = 6 and 8 gaps ha^{-1} , $n = 5$ and 6 , respectively) than the fringe zone (mean = 3 gaps ha^{-1} , $n = 7$; Figure 3), but only in the interior zone was the density of logging gaps higher (mean = 6 gaps ha^{-1} , $n = 5$) than the density of natural gaps (mean = 4 gaps ha^{-1} , $n = 5$; Figure 3). Utwe had the most harvesting activity in all three zones.

Overall, the gap fraction of logging gaps was significantly higher (mean = 4.2%) than the gap fraction of natural gaps (mean = 2.3%; $P = 0.006$; Figure 3). The highest overall harvesting intensity was in the interior zone (mean gap fraction = 9.2%, Figure 3). The Yela estuary differed from this trend, with most logging activity in the riverine zone.

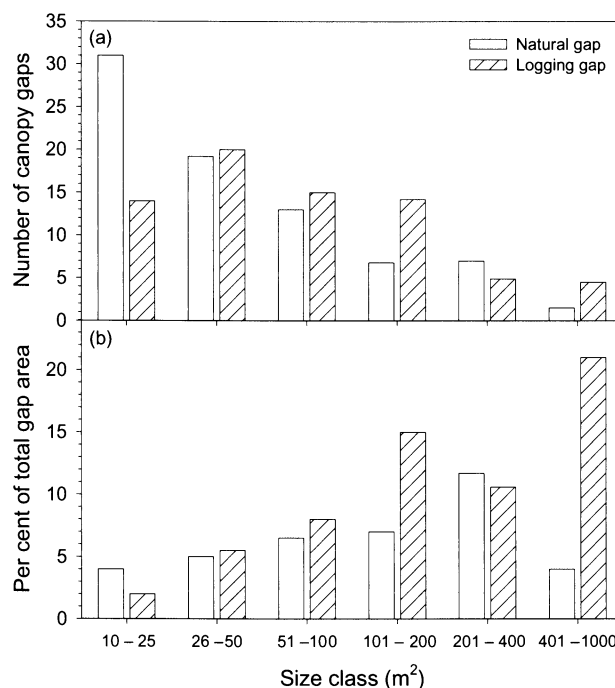


Figure 2. Gap size distribution (a) for all gaps sampled in the mangrove forests of Kosrae and (b) according to the proportion of each category in total gap area ($n = 78$ and 72 for natural and logging gaps, respectively).

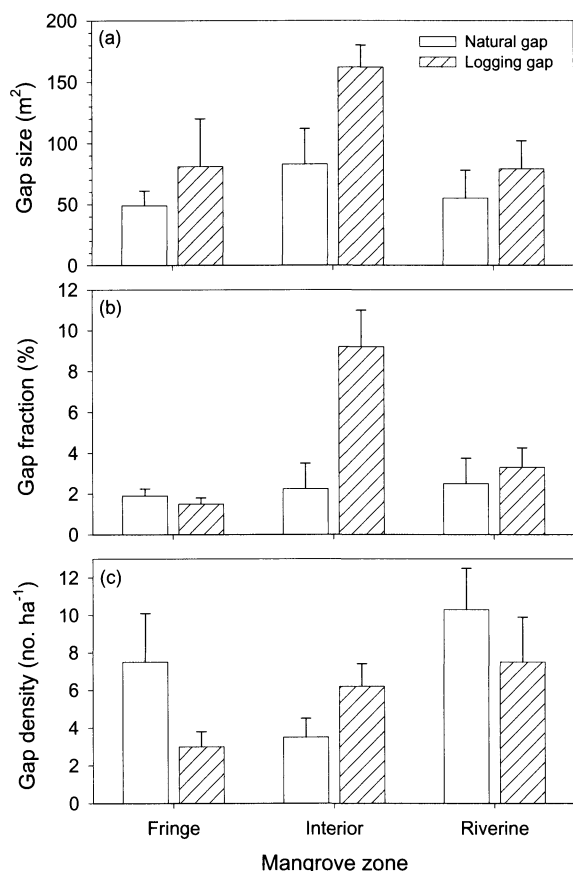


Figure 3. For both natural and logging gaps, mean (SE) (a) gap size, (b) per cent of area in gaps and (c) density of gaps in each mangrove zone for three estuaries combined.

Modes of gap formation

Rhizophora apiculata was the preferred species for harvesting, representing 53% of the trees logged. Trees as small as 5.4 cm dbh were harvested (Table 1). Most of the largest trees that were logged were *B. gymnorrhiza* (31% of the trees harvested) and *S. alba* (16% of the trees harvested).

Snapping-off of tree stems was a common cause of nat-

ural gap formation for *S. alba* especially but for *B. gymnorrhiza* as well (Table 1). Uprooted trees and dead standing trees were less frequent. *Sonneratia alba* often created large gaps when branches fell that were 20–80 cm in diameter, larger than many of the *B. gymnorrhiza* and *R. apiculata* gap-making trees.

Large *S. alba* trees caused 65% of the natural gaps in the mangrove forests on Kosrae, primarily from branch-falls and stem breakage (Table 1). *Rhizophora apiculata* caused the fewest natural gaps (9%), whereas gaps created by *B. gymnorrhiza* were fairly abundant (26%).

Most gaps were formed by the fall of more than one tree or branch. Only 18 of 65 (28%) natural gaps were created by a single gap-making tree or branch (eight by the death of single trees and ten by *S. alba* branchfalls). Among logging gaps, only two of 55 gaps (4%) were created by extraction of a single tree. In many cases (36%), gap-making events occurred on the borders of existing gaps, often after a delay of more than a year, and many of these (36%) were created by a combination of natural and anthropogenic forces. Among these gaps, about the same proportion was enlarged by logging on the perimeter of natural gaps (8%) as by natural treefalls on the perimeter of logging gaps (9%).

Seedling density

Total seedling densities (all species combined) were nearly twice as high in logging gaps (mean = 1.76 ± 1.71 (SD) seedlings m^{-2} , $n = 63$) than in natural gaps (mean = 0.90 ± 0.85 seedlings m^{-2} , $n = 62$; Tukey HSD, $P < 0.0001$). Under intact canopy, total seedling density was lower (mean = 0.54 ± 0.78 seedlings m^{-2} , $n = 38$) than in either type of gap (Tukey HSD, $P < 0.0001$). A separate split-plot ANOVA showed that neither the difference between natural and logging gaps < 3 y old nor the difference between gaps and forest canopy was significant. Among older gaps (> 3 y old), however, seedling densities were higher in logging gaps (mean = 1.96 ± 1.97 seedlings m^{-2} , $n = 41$) than in natural ones (mean = 0.88 ± 0.88

Table 1. Basal diameter (cm) of all gap-making trees measured in this study.

Species	Logged	Mode of natural gap formation			
		Snapped off	Branchfall	Uprooted	Standing dead
<i>Rhizophora apiculata</i>					
Mean \pm SD	21.5 \pm 7.6	17.9 \pm 7.7		27.9 \pm 13.1	17.9 \pm 7.7
n	308	6	0	6	6
Range	5.4–45	10–30		11–40.4	10–30
<i>Bruguiera gymnorrhiza</i>					
Mean \pm SD	24.8 \pm 15.4	27.8 \pm 12.2		31.6 \pm 6.9	22.0 \pm 8.2
n	180	39	0	11	3
Range	5–99.4	10–55		22–44.5	14.9–31
<i>Sonneratia alba</i>					
Mean \pm SD	54.9 \pm 24.9	90.2 \pm 42.3	42.6 \pm 19.6	103 \pm 27.6	
n	32	43	32	8	0
Range	19.6–100	18–180	10–90	70–150	

seedlings m^{-2} , $n = 48$; Tukey HSD, $P = 0.001$). Seedling densities were also significantly higher in logging gaps than under the intact canopy for gaps > 3 y old ($P < 0.01$), but there was not a significant difference between seedling densities in natural gaps and under the intact canopy ($P = 0.075$).

Overall seedling densities were higher in the riverine (mean = 1.88 ± 1.86 seedlings m^{-2} , $n = 33$) and interior (mean = 1.31 ± 1.18 seedlings m^{-2} , $n = 65$) zones than in the fringe zone (mean = 0.71 ± 1.01 seedlings m^{-2} , $n = 27$; $P = 0.033$). The interaction between canopy condition and zone was not significant. In the riverine zone, however, total seedling densities were significantly higher in gaps (mean = 1.37 ± 1.04 seedlings m^{-2} , and 2.56 ± 7.47 seedlings m^{-2} , for natural and logging gaps, respectively; $n = 19$ and 14) than under the intact canopy (mean = 0.57 ± 0.76 seedlings m^{-2} , $n = 17$; $P < 0.005$, Tukey–Kramer). In the other two zones, the differences were not significant. Under the intact canopy, seedling densities in the fringe zone were not significantly different from those in the riverine and interior zones (overall mean = 0.54).

Seedlings of six species were found in our plots (Figure 4). Four species (*B. gymnorrhiza*, *R. apiculata*, *S. alba* and *X. granatum*) were found in all three zones. Of the other two species, *N. fruticans* was never found in the fringe zone, and *R. mucronata* was never found in the interior zone.

Seedlings of all six species were found in gaps, and *R.*

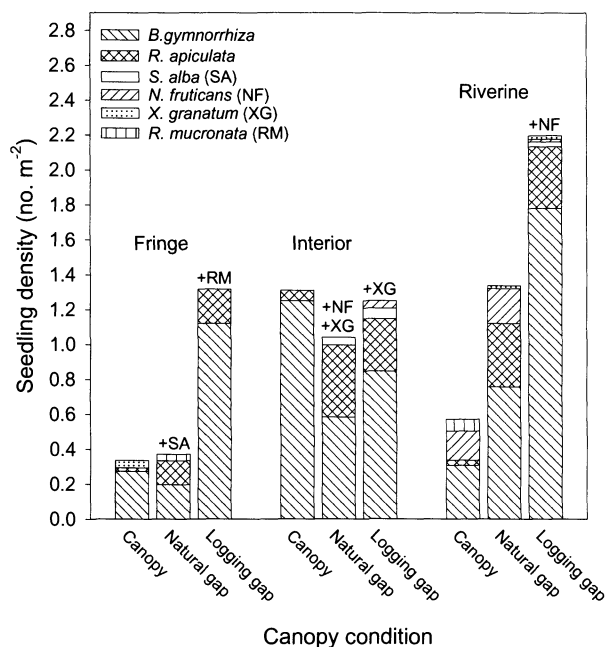


Figure 4. Mean density of each species of seedling in natural gaps, logging gaps and under intact canopy, for three estuaries combined. Initials above a bar indicate that the corresponding species was present but rare at that type of location.

apiculata, *B. gymnorrhiza* and *S. alba* seedlings were found in gaps in all zones. *Rhizophora mucronata* was the rarest seedling among the species that occurred in gaps (overall mean = 0.004 seedlings m^{-2} , $n = 126$). Seedlings of *N. fruticans* and *X. granatum* were absent from gaps in the fringe zone (Figure 4).

Distribution of seedlings by species under the intact canopy was different from their distribution within gaps. Under the intact canopy, *R. mucronata* and *N. fruticans* seedlings were found only in the riverine zone, whereas *X. granatum* seedlings were found only in the fringe zone (Figure 4).

Bruguiera gymnorrhiza seedlings (all zones combined) were significantly more abundant in logging gaps (mean = 1.34 ± 1.61 seedlings m^{-2}) than in natural gaps (mean = 0.57 ± 0.69 seedlings m^{-2} ; Tukey–Kramer, $P = 0.0001$), but the difference was not significant in the interior zone. They were also more abundant in logging gaps than under the intact canopy (Tukey–Kramer, $P = 0.004$), but the difference was again not significant in the interior zone. There was no difference in seedling abundance between natural gaps and the intact canopy for this species in any zone. Seedling densities of *R. apiculata* and *S. alba* were not significantly different between gap types nor between gaps and under intact canopy in all zones.

In natural gaps, *B. gymnorrhiza* seedlings were more dense (mean = 0.57 ± 0.69 (SD) seedlings m^{-2}) than *S. alba* seedlings (mean = 0.02 ± 0.07 seedlings m^{-2}), but no different in density from *R. apiculata* seedlings (mean = 0.34 ± 0.33). In logging gaps, *B. gymnorrhiza* seedlings were more dense (mean = 1.35 ± 1.61 seedlings m^{-2}) than *R. apiculata* and *S. alba* seedlings (mean = 0.34 ± 0.35 seedlings m^{-2} , and mean = 0.04 ± 0.09 seedlings m^{-2} , respectively). *Rhizophora apiculata* seedlings were more dense than *S. alba* seedlings in both natural and logging gaps ($P < 0.01$, Tukey–Kramer). Under intact canopy, *B. gymnorrhiza* seedlings were more dense than the other species (mean = 0.26 seedlings m^{-2} , $n = 38$, $P < 0.001$, Tukey–Kramer), being particularly abundant in the interior zone (Figure 4). *Rhizophora apiculata* seedling densities did not differ significantly from those of *S. alba* under intact canopy.

Bruguiera gymnorrhiza represented more than 50% of the total number of seedlings under all conditions. *Rhizophora apiculata* varied from 12% under the forest canopy to a maximum of 37% in natural gaps. *Sonneratia alba* seedlings were rare under intact canopy and represented only about 10% of all seedlings in both natural and logging gaps (Figure 5).

Seedling growth and mortality

Growth of *R. apiculata* and *B. gymnorrhiza* seedlings was higher in gaps than under intact canopy, but survival did

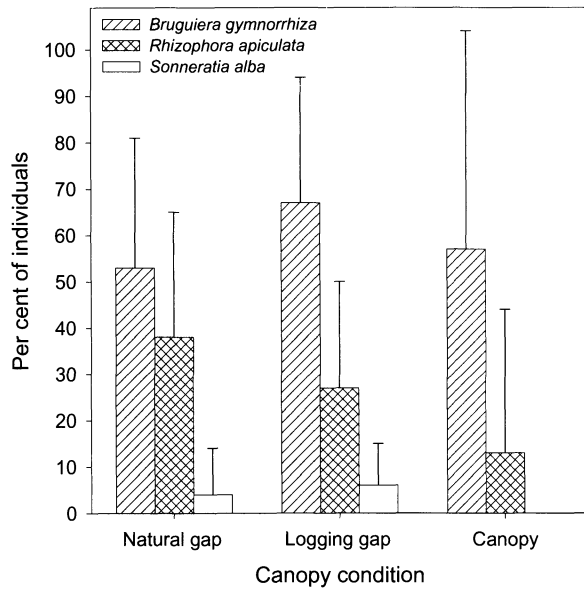


Figure 5. Mean relative abundance (SD) of the three most common species of mangrove tree seedlings in natural gaps, logging gaps and under the intact canopy for all estuaries and zones combined.

not follow the same trend. Over the 7-mo monitoring period, *B. gymnorrhiza* seedling survival was significantly higher in gaps (62%) than under intact canopy (36%; $\chi^2 = 5.9$, $P = 0.02$). There was no difference in survival between *R. apiculata* seedlings growing under intact canopy (75%) and in gaps (68%). Per cent canopy cover was significantly higher under the intact canopy (mean = $91\% \pm 5\%$, $n = 38$) than in gaps (mean = $69\% \pm 11\%$, $n = 108$; $t = 15.8$, $P < 0.001$).

Relative height growth rates were significantly larger in gaps than under intact canopy for both *B. gymnorrhiza* (Mann–Whitney U test, $U = 58$, $P = 0.0002$) and *R. apiculata* (Mann–Whitney U test, $U = 106$, $P = 0.0002$; see Table 2). Seedlings of both species growing in gaps also produced more leaves than seedlings in the shade, more than twice as many in the case of *B. gymnorrhiza* (Table 2).

DISCUSSION

Canopy gap dynamics

Although the importance of cataclysmic typhoons that occur at long intervals cannot be discounted (Cole *et al.* 1999), the most common disturbances in the mangrove forests on Kosrae are small canopy gaps created by fuel-wood harvesting and by natural tree and branch falls. This pattern probably has a long history, at least since first contact with Western cultures in the 19th century. During the Japanese occupation (1914–45), mangrove wood was intensively harvested for charcoal that was exported to other Pacific islands (B. Sigrah, pers. comm.).

Natural gaps in mangrove forests around the world are often characterized by the presence of dead standing trees killed by lightning, termites and fungal pathogens (Smith 1992). In contrast, dead standing trees in Kosrae were rare, and snapped-off and uprooted trees or the fall of large *S. alba* branches created most natural gaps. In several cases, enormous uprooted trees (e.g. *S. alba* > 1 m dbh) caused a ‘domino’ effect by knocking over other trees, similar to what has been observed in other tropical forests (van der Meer & Bongers 1996). On Kosrae very few gaps were caused by the fall of a single tree, and sometimes the fall of one tree did not create a canopy gap.

Canopy gaps in mangrove forests on Kosrae, as in many other tropical forests (Hartshorn 1978, Lawton & Putz 1988, van der Meer 1995), were spatially aggregated. About the same proportion (9%) of natural and logging gaps expanded after initial creation. Loggers tend to select trees on the margins of canopy gaps to facilitate felling. Also, trees and branches that develop in closed-canopy areas may be particularly susceptible to breakage when exposed to the high wind speeds and turbulence on the margins of gaps (Young & Hubbell 1991). Increased light availability to *S. alba* branches that are newly exposed to gap edges may stimulate eccentric branch growth and proliferation of epiphytes, both of which decrease branch stability.

Table 2. Seedling growth rates in canopy gaps and under the intact canopy.

Species and setting	n	Initial total height (cm)		Height increment (cm)		Relative height growth rate ($\text{mm m}^{-1} \text{mo}^{-1}$)		Leaf production (number mo^{-1})	
		Mean \pm SE	Range	Mean \pm SE	Range	Mean \pm SE	Range	Mean \pm SE	Range
<i>Bruguiera gymnorrhiza</i>									
Gap	50	53.2 ± 1.8	18.5–93.0	5.5 ± 0.7	1.5–30.0	13.9 ± 2.5	2.9–114	1.1 ± 0.04	0.8–1.8
Canopy	10	66.3 ± 5.0	43.5–90.0	2.1 ± 0.5	1.0–6.5	4.5 ± 1.5	1.5–17.7	0.6 ± 0.06	0.3–0.8
<i>Rhizophora apiculata</i>									
Gap	36	53.0 ± 1.8	38.5–92.5	3.8 ± 0.3	1.0–7.0	8.9 ± 0.6	2.1–14.4	0.9 ± 0.13	0.5–1.5
Canopy	15	57.1 ± 3.6	39.5–82.0	2.2 ± 0.3	1.5–9.3	5.0 ± 0.6	1.5–9.3	0.7 ± 0.04	0.5

Regeneration

Seedling densities were higher in logging gaps than in natural gaps, but there was no correlation between seedling density and canopy gap size, probably because differences in gap orientation and hence light availability were not taken into account. Seedling densities were higher in both gap types than under the intact canopy, but there was large variation among species. Characteristics of the soil environment may help to explain some of the differences. Soil temperature and redox potential were significantly higher in gaps in fringe (soil temperature only) and interior zones (both soil temperature and redox potential) in Kosraean mangrove forests (Ewel *et al.* 1998a). Seedling densities in that study were higher in gaps than under the intact canopy in the fringe zone but not in the interior zone. Similarly, in the present study, seedling densities for the three major species (*B. gymnorrhiza*, *R. apiculata* and *S. alba*) did not differ between gaps and intact canopy in the interior zone. In the other two zones, differences were significant for *B. gymnorrhiza* but not for *R. apiculata* and *S. alba*. These results suggest that the difference in pattern of regeneration between gaps and intact canopy is due mainly to the contribution of one species, *B. gymnorrhiza*.

Apparently, initial seedling establishment in mangroves is not affected by canopy condition, but survival is higher in gaps (Clarke & Allaway 1993). Light availability was positively correlated with seedling growth and survival of both *R. apiculata* and *B. gymnorrhiza* seedlings (and with higher densities for *B. gymnorrhiza* as well). Canopy removal in a mangrove forest in Panama resulted in a positive growth response of previously suppressed seedlings of *R. mangle* (Ellison & Farnsworth 1993). *Bruguiera parviflora* grew more rapidly in canopy gaps than under intact canopy in a Malaysian mangrove forest (Putz & Chan 1986). *Rhizophora stylosa* saplings were significantly more abundant in gaps than under the canopy in mangroves in Australia, and survival of *B. gymnorrhiza* there was higher in gaps than under the canopy in the high intertidal zone (Smith 1987b). In the same study, relative growth rates were significantly higher in light gaps than under the canopy for *R. stylosa* but not for *B. gymnorrhiza*.

Classifications of mangrove species as shade tolerant or intolerant do not agree (Macnae 1968, Putz & Chan 1986, Sukardjo 1987). For example, *R. apiculata* is reported to be light-demanding (Smith 1992), but on Kosrae seedling survival did not differ between the gap and canopy plots. *Bruguiera gymnorrhiza* provides another contrast; it has been classified as both shade tolerant (Putz & Chan 1986, Smith 1992) and 'highly intolerant of shade' (Sukardjo 1987).

Regeneration processes for *S. alba* differ substantially from the other species we studied. Despite the abundance

of parent trees, we encountered no *S. alba* seedlings under intact canopy and found very low densities in gaps. Similarly, no seedlings were found in the fringe zone (despite being the zone where the species is dominant in basal area), and no saplings were found in any zone in these estuaries in a previous study (Ewel *et al.* 1998c). This species might be regenerating mainly by branch layering, as described by Holbrook & Putz (1982) for the same species in Malaysia. *Sonneratia alba* produces small seeds that are not viviparous and thus may be at a disadvantage in gaps or under intact canopy compared to the other common trees in Kosraean mangrove forests. The three Rhizophoraceae (*B. gymnorrhiza*, *R. apiculata* and *R. mucronata*), the palm *N. fruticans*, and *X. granatum* (Meliaceae) all have large propagules that allow the seedlings to achieve heights of up to 70 cm rapidly and to colonize canopy gaps readily. We observed abundant seedling regeneration of *S. alba* only on some newly emerged mud banks outside the forest. Vegetative regeneration may be the only effective regeneration strategy for this small-seeded species within closed-canopy forests.

In Malaysian mangroves, advance regeneration (seedlings that survived logging damage) were the major components in the seedling layer; new recruits (seedlings < 30 cm tall) were still absent from stands 1 y after clear felling, although their density increased thereafter with time (Jawa & Srivastava 1989). In Kosrae, advance regeneration seemed also to be the major contributor to forest recovery in both natural and logging gaps. The higher seedling densities in older gaps, however, suggest seedling recruitment after gap creation. In the neotropics, *R. mangle* seems to have a 'seedling bank' growing under intact canopy, essentially waiting for a canopy opening; if such an event does not occur within about 3 y from establishment, those seedlings generally die (Duke *et al.* 1999). Seedling densities found in the present study (range: 0–3.25 seedlings m⁻² under the canopy and 0–9.82 seedlings m⁻² in gaps) are similar to those in other forests in the Asia Pacific region that have the same species. A range from 0.25–1.5 seedlings m⁻² under the canopy has been reported for Malaysia (Liew *et al.* 1975, Putz & Chan 1986, Sukardjo 1987). The continuous production of numerous propagules that are widely dispersed by water and that permit such a rapid response to gap formation is a characteristic that most mangrove trees share with pioneer species, even though other characteristics, such as long life spans, medium leaf sizes, low leaf palatability and hard, heavy wood, are more common in mature-phase species (Tomlinson 1986). Such a mix of characteristics in this interesting group of trees might be related to the unusual demands posed by their life history (Farnsworth & Ellison 1996).

Forest management implications

Residual forest damage is a major concern in selective logging operations using heavy equipment (Pinard & Putz

1996). Mangrove tree felling in Kosrae is done with axes and chainsaws, and logs are carried by hand to small boats or nearby roads, with no logging damage to advanced regeneration due to heavy machinery. The lack of difference in seedling densities between natural and logging gaps < 3 y old supports our observation that there was little evidence of logging damage in even the most recently harvested stands. Intensity of harvesting in Kosraean mangrove forests is low compared with systems such as the patch clearcuts used in Malaysia, and extraction of small diameter poles may simulate light thinning operations. Similarly, thinning promotes regeneration in the Matang mangroves in Malaysia (Chan & Ujang 1982).

Distance from gap edges and seed sources is another concern in mangrove logging that may not represent a problem on Kosrae. There were few seedlings at distances > 5 m from forest edges in Ecuadorian mangrove forests (Blanchard & Prado 1995). On Kosrae, even though there were occasionally large logging gaps (e.g. 1006 m²: Ewel *et al.* 1998a), gaps tended to be long and thin, so distance from the nearest forest edge rarely exceeded 10 m (pers. obs.), a small enough distance that recruitment is not affected adversely. The current intensity of logging activities on the island does not appear to be resulting in regeneration failures.

Logging activities on Kosrae were concentrated in the interior and riverine zones, where there were suitable densities of the desired tree species and sizes (Ewel *et al.* 1998a). Road access to mangroves also seemed to concentrate harvesting activities away from the fringe zone. In the two estuaries with high gap fractions (Okat and Utwe), roads provided easy access to forest interiors. In the Yela estuary, access was only by boat, and timber harvesting was concentrated in the riverine zone. These observations suggest that the indirect effects of road construction on mangrove forests on Kosrae should be of concern.

Rhizophora apiculata was the species most commonly harvested, but regeneration of *B. gymnorrhiza* was favoured by higher density in the seedling layer and high relative height growth rates in gaps. The fringe zone in these forests was dominated by *S. alba* in terms of basal area and by *R. apiculata* in terms of density (Ewel *et al.* 1998c). Nevertheless, our results indicate that *B. gymnorrhiza* also dominated the seedling layer in this zone. At the same time, *S. alba* may have been gradually decreasing its abundance, as evidenced by the rarity of seedlings both in gaps and under intact canopy and its high rate of branchfall.

Despite the difference in size of logging and natural gaps and the greater contribution of the logging gaps to total gap area in the forest, the current harvesting rate does not seem to affect the natural disturbance regime on Kosrae dramatically. Greater density of seedlings in logging gaps than in natural gaps suggests that, in general, regeneration processes have not been adversely affected

by wood-harvesting activities. This study underscores the importance of advance regeneration in mangrove forests. It also highlights the importance of post-logging seedling recruitment, which is facilitated in this case by the relatively small gaps that are formed.

Gradual removal of *R. apiculata*, as both individuals and seed sources, may be pushing forest composition slowly toward smaller stem size and dominance by *B. gymnorrhiza*. Interspecific differences in seedling densities in canopy gaps need to be elucidated, and post-logging regeneration processes should be examined more closely as Kosrae grows in population size and increases its dependence on its natural resources.

ACKNOWLEDGEMENTS

We thank the Compton Foundation, the Fulbright Foundation, the Britannica Foundation and the USDA Forest Service for financial support. Kimberlyn Williams and Susan Vince assisted with experimental design and data interpretation, and Jay Harrison with statistical analysis. In the Kosrae Department of Agriculture and Land, Erick Waguk was of inestimable assistance in many ways; we are also grateful to Nena Nena (Director), and Glasstine Cornelius for valuable logistic support. Idosi Jesse, Rock Niwac and Dais Aloka shared useful information. John Bourgeois, Zheng Songfa, Paliksru Brooks and, especially, Martha Prada assisted in the field.

LITERATURE CITED

- BARDSLEY, K. N. 1985. The effects of cyclone Kathy on mangrove vegetation. Pp. 167–186 in Bardsley, K. N., Davie, J. D. S. & Woodroffe, C. D. (eds). *Coasts and tidal wetlands of the Australian monsoon region*. Australian National University, Darwin.
- BLANCHARD, J. & PRADO, G. 1995. Natural regeneration of *Rhizophora mangle* in strip clearcuts in northwest Ecuador. *Biotropica* 27:160–167.
- BOOT, R. G. A. & GULLISON, R. E. 1995. Approaches to developing sustainable extraction systems for tropical forest products. *Ecological Applications* 5:896–903.
- BROKAW, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160.
- CHAN, H. T. & UJANG, R. 1982. Growth and natural regeneration of stand of *Rhizophora apiculata* trees at the Matang mangroves (Malaysia), following thinning. Pp. 67–73 in Kostermans, A. Y. & Sastroutomo, S. S. (eds). *Proceedings of the symposium on mangrove forest ecosystem productivity in Southeast Asia, April 20–22, Bogor, Indonesia*. BIOTROP Special Publication 17, Bogor.
- CLARKE, P. J. & ALLAWAY, W. G. 1993. The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia* 93:548–556.
- COLE, T. G., EWEL, K. C. & DEVOE, N. N. 1999. Structure of man-

- grove trees and forests in Micronesia. *Forest Ecology and Management* 117:95–109.
- CRAIGHEAD, F. C. 1964. Land, mangroves and hurricanes. *Fairchild Tropical Garden Bulletin* 19:5–33.
- CRAIGHEAD, F. C. 1971. *The trees of South Florida, vol. 1. The natural environments and their succession*. University of Miami Press, Coral Gables. 212 pp.
- DUKE, N. C., PINZÓN, Z. S. & PRADA, M. C. 1999. Recovery of tropical mangrove forests following a major oil spill: a study of recruitment, growth, and the benefits of planting. Pp. 231–254 in Yáñez-Arancibia, A. & Lara-Domínguez, A. L. (eds). *Mangrove ecosystems in tropical America [Ecosistemas de manglar en América tropical]*. Instituto de Ecología A. C. Mexico, UICN/ORMA Costa Rica, and NOAA/NMFS.
- ELLISON, A. M. & FARNSWORTH, E. J. 1993. Seedling survivorship, growth, and response to disturbance in Belizean mangal. *American Journal of Botany* 80:1137–1145.
- EVERITT, J. H., JUDD, F. W., ESCOBAR, D. E. & DAVIS, M. R. 1996. Integration of remote sensing and spatial information technologies for mapping black mangrove on the Texas Gulf Coast. *Journal of Coastal Research* 12:64–69.
- EWEL, K. C., BOURGEOIS, J. A., COLE, T. G. & ZHENG, S. 1998a. Variation in environmental characteristics and vegetation in high-rainfall mangrove forests. *Global Ecology and Biogeography Letters* 7:49–56.
- EWEL, K. C., TWILLEY, R. R. & ONG, J. E. 1998b. Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters* 7:83–94.
- EWEL, K. C., ZHENG, S., PINZÓN, Z. S. & BOURGEOIS, J. A. 1998c. Environmental effects of canopy gap formation in high-rainfall mangrove swamps. *Biotropica* 30:510–518.
- EWEL, K. C., HAUFF, R. D. & COLE, T. G. Analyzing mangrove forest structure and species distribution on a Pacific Island. *Phytocologia*, press.
- FARNSWORTH, E. J. & ELLISON, A. M. 1996. Sun-shade adaptability of the red mangrove, *Rhizophora mangle* (Rhizophoraceae): changes through ontogeny at several levels of biological organization. *American Journal of Botany* 83:1131–1143.
- FELLER, I. C. & MCKEE, K. L. 1999. Small gap creation in Belizean mangrove forests by a wood-boring insect. *Biotropica* 31:607–617.
- HAMILTON, L. S. & SNEDAKER, S. C. (eds). 1984. *Handbook for mangrove area management*. IUCN-UNESCO-UNEP, East-West Center, Honolulu. 123 pp.
- HARTSHORN, G. S. 1978. Tree falls and tropical forest dynamics. Pp. 617–638 in Tomlinson, P. B. & Zimmermann, M. H. (eds). *Tropical trees as living systems*. Cambridge University Press, Cambridge.
- HOLBROOK, N. M. & PUTZ, F. E. 1982. Vegetative seaward expansion of *Sonneratia alba* trees in a Malaysian mangrove forest. *The Malaysian Forester* 45:278–281.
- JAWA, R. R. & SRIVASTAVA, P. B. L. 1989. Dispersal of natural regeneration in some Piai-invaded areas of mangrove forests in Sarawak. *Forest Ecology and Management* 26:155–177.
- JIMÉNEZ, J. A. & SAUTER, K. 1991. Structure and dynamics of mangrove forests along a flooding gradient. *Estuaries* 14:49–56.
- KAROLLE, B. G. 1992. *Atlas of Micronesia*. Bess Press, Honolulu. 122 pp.
- KAWANA, T., MIYAGI, T., FUJIMOTO, K. & KIKUCHI, T. 1995. Late Holocene sea-level changes and mangrove development in Kosrae Island, the Carolines, Micronesia. Pp. 1–7 in Kikuchi, T. (ed.). *Rapid sea level rise and mangrove habitat*. Gifu University, Yanagido.
- KOSRAE STATE GOVERNMENT. 1996. *Kosrae State census report. 1994 FSM census of population and housing*. Division of Planning and Statistics, Department of Administration, Kosrae State. 208 pp.
- LAL, P. N. 1989. *Utilization and management of coastal wetland resources in Kosrae*. Working paper for the University of Hawaii Sea Grant Program, Honolulu. 40 pp.
- LAWTON, R. O. & PUTZ, F. E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69:764–777.
- LEMMON, P. E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2:314–320.
- LIEW, T. C., DIAH, M. N. & CHUN, W. Y. 1975. Mangrove exploitation and regeneration in Sabah. *The Malaysian Forester* 38:260–270.
- LITTELL, R. C., FREUND, R. J. & SPECTOR, P. C. 1991. *SAS system for linear models* (Third edition). SAS Institute Inc., Cary. 329 pp.
- LORIMER, C. G. & FRELICH, L. E. 1994. Natural disturbance regimes in old-growth northern hardwoods. *Journal of Forestry* 92:33–38.
- LUGO, A. E. & SNEDAKER, S. C. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* 5:39–64.
- MACNAE, W. 1968. A general account of the flora and fauna of mangrove swamps in the Indo-Pacific region. *Advances in Marine Biology* 6:73–270.
- MCKEE, K. L. 1995. Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. *American Journal of Botany* 82:299–307.
- MERLIN, M., TAULUNG, R. & JUVIK, J. 1993. *Sahk kap ac kain in acn Kosrae: Plants and environments of Kosrae*. East-West Center, Honolulu. 113 pp.
- METZ, W. D. 1994. *Mangrove management component of the Forest Management Strategy*. Volumes I & II. USDA Forest Service, Honolulu. 135 pp.
- PAIJMANS, K. & ROLLET, B. 1977. The mangroves of Galley Reach, Papua New Guinea. *Forest Ecology and Management* 1:119–140.
- PFISTER, R. D. 1993. The need and potential for ecosystem management in forests of the inland West. Pp. 217–239 in Aplet, G. H., Johnson, N., Olson, J. T. & Sample, V. A. (eds). *Defining sustainable forestry*. Island Press, Washington, DC.
- PINARD, M. A. & PUTZ, F. E. 1996. Retaining forest biomass by reduced impact logging. *Biotropica* 28:278–295.
- PUTZ, F. E. 1996. Research needs and information gaps. Pp. 164–178 in Viana, V. M., Ervin, J., Donovan, R. & Gholz, H. L. (eds). *Certification of forest products: issues and perspectives*. Island Press, Covelo.
- PUTZ, F. E. & CHAN, H. T. 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. *Forest Ecology and Management* 17:211–230.
- PUTZ, F. E., PARKER, G. G. & ARCHIBOLD, R. M. 1984. Mechanical

- abrasion and intercrown spacing. *American Midland Naturalist* 112:24–28.
- RABINOWITZ, D. 1978. Dispersal properties of mangrove propagules. *Biotropica* 10:47–57.
- ROBERTSON, A. I., GIDDENS, R. & SMITH, T. J. 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. *Oecologia* 83:213–219.
- ROGERS, P. 1996. *Disturbance ecology and forest management: a review of the literature*. General Technical Report INT-GTR-336. USDA Forest Service, Intermountain Research Station, Ogden. 16 pp.
- ROTH, L. L. 1992. Hurricanes and mangrove regeneration—effects of hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. *Biotropica* 24:375–384.
- SCOTT, D. (ed.) 1993. *A directory of wetlands in Oceania*. The International Waterfowl and Wetlands Research Bureau (IRWB), Slimbridge, and Asian Wetland Bureau (AWB), Kuala Lumpur. 444 pp.
- SEGAL, H. G. 1995. *Kosrae: the sleeping lady awakens*. Kosrae Print Shop, Kosrae. 17 pp.
- SHERMAN, R. E., FAHEY, T. J. & BATTLES, J. L. 2000. Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. *Journal of Ecology* 88:165–178.
- SMITH, T. J. 1987a. Effects of seed predator and tide level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests. *Estuarine, Coastal and Shelf Science* 25:43–51.
- SMITH, T. J. 1987b. Effects of light and intertidal position on seedling survival and growth in tropical tidal forests. *Journal of Experimental Marine Biology and Ecology* 110:133–146.
- SMITH, T. J. 1992. Forest structure. Pp. 101–136 in Robertson, A. I. & Alongi, D. M. (eds). *Tropical mangrove ecosystems*. Coastal and Estuarine Studies 41. American Geophysical Union, Washington, DC.
- SMITH, T. J., ROBBLEE, M. B., WANLESS, H. R. & DOYLE, T. W. 1994. Mangroves, hurricanes, and lightning strikes. *BioScience* 44:256–262.
- SUKARDJO, S. 1987. Natural regeneration status of commercial mangrove species (*Rhizophora apiculata* and *Bruguiera gymnorrhiza*) in the mangrove forest of Tanjung Bungin, Banyuasin district, South Sumatra. *Forest Ecology and Management* 20:233–252.
- TOMLINSON, P. B. 1986. *The botany of mangroves*. Cambridge University Press, Cambridge. 413 pp.
- VAN DER MEER, P. J. 1995. *Canopy dynamics of a tropical rain forest in French Guiana*. Ph.D. thesis, Wageningen Agricultural University, The Netherlands. 149 pp.
- VAN DER MEER, P. J. & BONGERS, F. 1996. Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. *Journal of Ecology* 84:19–26.
- WATSON, J. G. 1928. Mangrove forests of the Malay Peninsula. *Malayan Forest Records* 6:1–275.
- WEST, R. C. 1977. Tidal salt-marsh and mangal formations of middle and South America. Pp. 193–213 in Chapman, V. J. (ed.). *Wet coastal ecosystems*. Ecosystems of the World, Vol. 1. Elsevier, Amsterdam.
- WHITESSELL, C. D., MACLEAN, C. D., FALANRUW, M. C., COLE, T. G. & AMBACHER, A. H. 1986. *Vegetation survey of Kosrae, Federated States of Micronesia*. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station Resource Bulletin PSW-17. 8 pp.
- WOODROFFE, C. D. 1992. Mangrove sediments and geomorphology. Pp. 7–41 in Robertson, A. I. & Alongi, D. M. (eds). *Tropical mangrove ecosystems*. Coastal and Estuarine Studies 41 American Geophysical Union, Washington, DC.
- YOUNG, T. P. & HUBBELL, S. P. 1991. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. *Ecology* 72:1464–1471.