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MANGROVE SPECIAL ISSUE

Variation in environmental characteristics and vegetation in high-rainfall mangrove forests, Kosrae, Micronesia

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Abstract. Understanding differences among fringe, riverine, and basin zones in mangrove forests may assist mangrove scientists in clarifying the relationships between tree distributions and environmental characteristics, and may assist resource managers in designing appropriate management policies for these important wetlands. This study examined differences in soil redox potential and porewater salinity as well as in characteristics and distribution of hardwood mangrove trees among these zones on the island of Kosrae in the Federated States of Micronesia. Neither porewater salinity nor soil redox potential differed significantly among the three types of forests. High annual rainfall (5000–6000 mm/year) and, perhaps, high rates of groundwater flow and surface runoff, may buffer these forests from extremes in salinity. Zonation of trees was not readily apparent, with *Sonneratia alba* J. Smith, *Bruguiera gymnorrhiza* (L.) Lamk., and *Rhizophora apiculata* Bl. dominant in volume and/or density in all three zones. Tree heights were significantly shorter in fringe forests than in basin forests. Growing conditions appear to vary among the three zones, but other environmental characteristics may be responsible. Data on regeneration patterns suggest that resource managers should restrict harvesting in fringe and riverine zones and attempt to increase regeneration of *S. alba* in basin zones where large gaps are formed.

Key words. Soil redox potential, porewater salinity, Micronesia, *Sonneratia alba*, *Bruguiera gymnorrhiza*, *Rhizophora apiculata*, mangrove.

INTRODUCTION

Much of the work devoted to studying mangrove forests around the world has been directed towards describing and interpreting the zonation patterns of mangrove trees. Early attempts to understand what generates the major plant communities in mangrove swamps concentrated on frequency of inundation (Watson, 1928) and salinity (de Haan, 1931). More recently, attention has focused on establishment, including the effects of tidal action on propagule dispersal (Rabinowitz, 1978) and crab predation on propagules (Smith, 1987). There is still no clear understanding of what factor, or combination of factors, controls species distributions in mangrove forests (Smith, 1992). With increasing population pressures on these important wetlands, however, attaining such an understanding has become necessary in order to formulate meaningful management policies that allow maintenance and restoration of characteristic patterns of biodiversity.

The purpose of this study was to determine whether mangrove forests can be divided into distinct zones, based on physical and biological differences. Two questions were addressed: (1) Can major hydrogeomorphic zones be differentiated by basic environmental characteristics? (2) Is there a tendency for a tree species to be found in a particular hydrogeomorphic zone? We also considered the usefulness of such an approach for dealing with management issues.

Understanding the differences among hydro-

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geomorphic zones has been a major organizing theme in mangrove forest ecology in recent years. Six such zones were proposed by Lugo & Snedaker (1974) and later aggregated to three by Cintrón *et al.* (1978): fringe, riverine, and basin. Woodroffe (1992) considered these three types to be specific to geomorphic settings in the Neotropics and constructed a broader framework that differentiated tide-dominated, river-dominated, and interior mangrove swamps. In this paper, we adopt Woodroffe's framework but continue to use the terms that have become familiar through work in the Neotropics. Fringe, or tide-dominated, mangrove swamps experience diurnal tides at nearly constant salinity. Riverine, or river-dominated, mangrove swamps also experience diurnal tides but at somewhat lower salinity levels. Basin, or interior, mangrove swamps experience flooding less regularly but are often subjected both to longer soil saturation because of slower drainage and to higher levels of salinity because of the greater influence of evapotranspiration on water flux. Working with a small number of readily identifiable zones in mangrove forests could assist in understanding how vegetation distribution patterns are related to environmental characteristics without trying to ascribe a set of environmental factors for each species of mangrove. Such an approach could also assist wetland managers in formulating appropriate management policies, particularly in regulating activities that are likely to lead to changes in hydrology or species composition.

Porewater salinity and soil redox potential were selected as the environmental characteristics most likely to reflect important differences in growing conditions for mangrove trees. Some species of mangrove are more tolerant of high salinity than others. Salinity levels are affected by inputs of both seawater and freshwater, as well as by evapotranspiration in less frequently flooded areas. Soil redox potential is an index of the availability of oxygen in flooded soils and therefore of length of inundation. It may also affect nutrient availability, can vary with soil physical characteristics, and can exhibit interactions with burrowing organisms such as crabs. Aboveground mangrove biomass in northern Australia was found to be negatively correlated with soil salinity and positively correlated with redox potential (Boto & Wellington, 1984). Growth and survival of seedlings of two species of mangroves in the Neotropics have different sensitivities to soil redox potential (McKee, 1993). The likelihood of low salinity and rapid water turnover in the riverine zone, high salinity and rapid turnover in the fringe zone, and high salinity and slow turnover in the basin zone, should assist in distinguishing these three basic zones in most mangrove forests.

METHODS

Study sites

This study was conducted in March–November 1995 on the island of Kosrae, a small (112 km^2), high volcanic island in the Federated States of Micronesia (5°19′N, 163°E), where mangroves are abundant (1562 ha, occupying approximately two-thirds of the shoreline; Whitesell *et al.*, 1986). Six species of hardwood trees are found in Kosraean mangrove swamps: *Bruguiera gymnorrhiza* (L.) Lamk., *Lumnitzera littorea* (Jack) Voigt., *Rhizophora apiculata* Bl., *R. mucronata* Lamk., *Sonneratia alba* J. Smith, and *Xylocarpus granatum* König. Annual rainfall is very high, approximately 5000–6000 mm, and is evenly distributed throughout the year (Merlin, Taulung & Juvik, 1993). Common gap-forming processes such as tropical storms and lightning strikes are rare in Kosrae.

Study plots were located near four rivers, each of which traverses a mangrove swamp that extends at least 400 m from upland to shoreline: the Utwe and Finkol Rivers on the south side of the island, and the Okat and Yela Rivers on the west side of the island. Tides regularly (but not always daily) inundate the entire forest. Each of these rivers passes through a freshwater, forested wetland before entering the mangrove swamp.

At each river, a five-point cluster plot covering approximately 1.9 ha (USDA Forest Service, unpubl. ms) was randomly located within each of the three swamp types. Two points were located 50 m north and 43 m south of a central point; two other points were located 50 m east and 50 m west of the same central point. At the fringe plots, at least one point was 20–25 m from the shoreline. At the riverine plots, at least one point was 20–25 m from the edge of the channel. At the basin plot, at least one point was 20–25 m from the uplands, and no point was closer than 200–m to the channel or the shoreline. Because a companion project was being conducted to identify the impacts of harvesting (Ewel *et al.*, in press), points that fell where more than two stumps were present were relocated, according to a systematic protocol, to an area with no more than two stumps. Points that fell in tidal channels or on upland soil were also relocated.

After the study was completed, a more careful consideration of geomorphologic positions of the various plots indicated that the fringe plot at the Finkol River was actually at a riverine site, as it is several hundred meters upstream from the coast. Consequently, our analyses were based on five riverine plots, four basin plots, and three fringe plots.

Measurements and data analysis

A 1-m^2 plot for determination of redox potential was randomly located within 10 m of each point. Platinum electrodes were constructed by welding 1.5 cm of 1-mm-diameter platinum wire to one end of a 60-cm length of 3-mm-diameter insulated, solid copper wire and sealing with epoxy resin so that only bare platinum wire was in contact with the soil. Ten of these electrodes were placed 5 cm into the soil with approximately 10 cm between each electrode, and they were allowed to equilibrate for at least 30 min. Redox values were read with an Orion model 250A pH/ISE meter, using a calomel reference electrode. Redox values for each probe were calculated by adding to each reading the potential for the reference electrode, corrected for soil temperature. Readings were not corrected for pH, which ranged only between 6.5 and 7.5. Readings of individual electrodes were pooled at each point. A perforated plastic tube was used to sample porewater at 5 cm depth for determination of porewater salinity with a handheld salinity refractometer.

At each point, all hardwood trees ≥12.5 cm dbh were tallied if they fell within the limiting distance of a prism with a basal area factor of 7 m^2/ha (Grosenbaugh, 1958). Total height and upper stem diameters of each tree were measured with a Spiegel relaskop, and bark thickness was measured with a bark gauge. The presence of stumps within 20 m of the point centre was noted. Dbh and height of each sapling (>2.5 cm and <12.5 cm dbh) in a fixed radius (2.36 m) subplot at each point were also recorded. All seedlings (<1.5 m tall) in four randomly located, permanent, 1-m^2 seedling plots within a 10-m radius of each plot were identified to species.

Differences among least-square means of soil redox potential, porewater salinity, and characteristics of trees ≥12.5 cm dbh in each zone were tested with randomized block ANOVA, with zone and river as main effects, using the Mixed Procedure in SAS 6.12. Comparisons were made with the Tukey-Kramer method for unequal cell sizes. Differences between zones were considered significant if $P<0.05$.

Table 1. Magnitude and significance of environmental variables in fringe, riverine, and basin zones of mangrove forests along four rivers, Kosrae, Federated States of Micronesia. Data are least squares mean and standard error.

Variable and Zone	$\bar{x} \pm$ SE (*n*)
Porewater salinity (o/oo)	
Fringe	39.6±4.12 (30)
Riverine	25.9±3.60 (37)
Basin	21.1±3.36 (40)
F	6.17 ($P=0.08$)
Soil redox potential (mV)	
Fringe	9±30.0 (72)
Riverine	11±24.3 (122)
Basin	−6±24.4 (100)
F	0.14 ($P=0.87$)

RESULTS

There were no significant differences among fringe, riverine, and basin zones in porewater salinity ($F=6.17$, $P=0.08$) or soil redox potential ($F=0.14$, $P=0.87$) (Table 1). Nor were there significant differences among the four rivers (porewater salinity: $F=1.53$, $P=0.36$; soil redox potential: $F=0.43$, $P=0.74$).

Five of the six species of mangrove trees found on Kosrae were located on our plots as seedlings, saplings, and/or mature trees (Fig. 1). Only *L. littorea*, which is prized for its wood and therefore rare in these forests, was not represented. All five species were found as seedlings, saplings, or trees in all three zones, but only *B. gymnorrhiza* was found in all three stages in all three zones. All three stages of *R. apiculata* and *R. mucronata* were found only in the basin and fringe zones, respectively. Although *S. alba* trees were found in all three zones, seedlings were found only in basin and riverine zones, and there were no saplings. There were no *X. granatum* trees; saplings occurred in all three zones, but seedlings were found only in the basin zone. Although not all species were evenly distributed among the four rivers, there were no significant differences in sizes of trees or characteristics of stands among them.

Even though the impacts of harvesting were minimized in establishing the plots, 40% of the points in the riverine zone and 25% of the points in the basin zone had one or two stumps within 20 m of the point centre. There were no stumps around the fringe zone points. Because most trees are harvested for firewood, neither very large nor very small trees are taken, so that only 8% of the trees at the riverine zone were

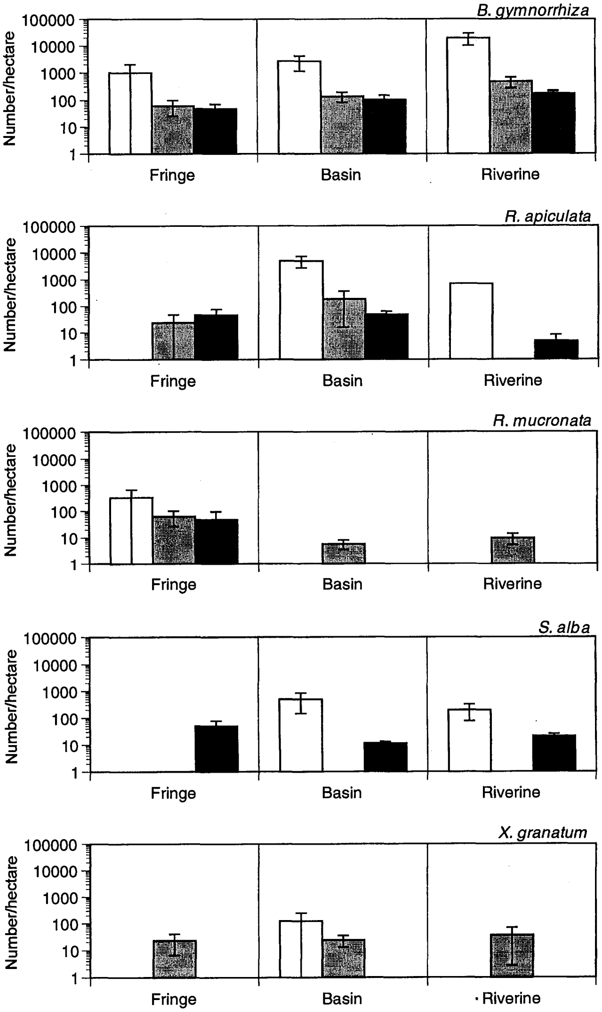

Fig. 1. Densities of trees at different stages of growth among three zones in mangrove forests in Kosrae, Federated States of Micronesia. White bars = seedlings, grey bars = saplings (stems >2.5 and <12.5cm dbh), dark bars = trees (≥12.5cm dbh).

pole-sized (≥12.5 and <27.5cm dbh), compared to 20% at the basin zone and 24% at the fringe zone.

Trees were significantly taller in the basin zone than in the fringe zone and, for *R. apiculata*, than in the riverine zone as well (Table 2). In addition, *S. alba* trees were significantly denser in the fringe zone than in riverine and basin zones, and they were significantly smaller in dbh in the fringe zone than in the basin zone. *B. gymnorrhiza* trees had significantly greater basal area in the riverine zone than in the fringe zone.

DISCUSSION

The absence of significant differences in porewater salinity and soil redox potential among fringe, riverine, and basin zones and the lack of restriction of any of the common mangrove tree species to any one of these zones suggest that hydrogeomorphic zones do not exist in mangrove forests in Kosrae. However, significant differences in tree height, particularly between fringe and basin zones, indicate instead that our experimental

Table 2. Magnitude and significance of characteristics of mangrove trees in three zones along four rivers on the island of Kosrae. Data are least squares $\bar{x}\pm$SE. Significant differences ($P\leq 0.05$) among zones are indicated by different lower-case letters.

Species and zone	Number of plots	Density (trees/ha)	Basal area (m^2/ha)	Volume (m^2/ha)	Dbh (cm)	Height (m)
Sonneratia alba						
Fringe	3	50.2±7.2a	17.9±3.0a	124.7±24.7a	57.3±10.8a	21.0±1.7a
Riverine	5	20.7±5.5b	15.3±2.3a	119.6±18.8a	98.3±8.2ab	25.6±1.3ab
Basin	4	11.7±6.0b	14.4±2.5a	109.5±20.4a	120.6±8.9b	30.7±1.4b
F		8.68 ($P=0.02$)	0.41 ($P=0.68$)	0.13 ($P=0.88$)	10.24 ($P=0.01$)	9.83 ($P=0.01$)
Bruguiera gymnorrhiza						
Fringe	3	27.5±42.7a	1.6±4.7a	9.7±28.7a	37.6±4.5a	17.3±1.2a
Riverine	5	186.8±32.5a	19.8±3.5b	118.4±21.9a	36.4±3.4a	19.0±0.9a
Basin	4	105.1±35.3a	14.7±3.9ab	91.3±23.8a	42.6±3.7a	23.9±1.0b
F		4.27 ($P=0.07$)	4.59 ($P=0.06$)	4.35 ($P=0.07$)	0.82 ($P=0.48$)	10.19 ($P=0.01$)
Rhizophora apiculata						
Fringe	2	84.4±21.5a	1.8±2.0a	15.4±17.7a	15.3±8.6a	19.5±1.0a
Riverine	3	27.2±21.5a	1.8±2.0a	19.1±17.7a	36.8±8.6a	28.5±1.0b
Basin	4	48.3±12.4a	4.6±1.1a	44.9±10.2a	34.1±5.0a	26.9±0.6b
F		2.72 ($P=0.27$)	1.00 ($P=0.50$)	1.23 ($P=0.45$)	2.76 ($P=0.27$)	34.45 ($P=0.03$)
Rhizophora mucronata						
Fringe	1	144.3	5.6	52.6	20.2	16.8
All trees						
Fringe	3	53.9±27.2a	8.5±3.2a	57.3±21.4a	40.5±13.7a	18.8±1.5a
Riverine	5	86.7±21.4a	14.5±2.5a	98.2±16.8a	61.8±10.8a	23.4±1.1b
Basin	4	55.0±21.1a	11.2±2.4a	81.9±16.6a	65.8±10.6a	27.2±1.1b
F		0.69 ($P=0.51$)	1.16 ($P=0.33$)	1.09 ($P=0.35$)	1.13 ($P=0.34$)	10.34 ($P=0.0005$)

design (and perhaps the environmental parameters we chose) was inappropriate for the detection of these zones. In fact, porewater salinity was significantly higher in fringe mangrove forests than in basin mangrove forests when a subset of our data was used to determine the effect of gap formation in those two zones (Ewel *et al.*, in press). Because of favourable growing conditions (high rainfall, absence of seasonality, and low frequency of natural gap-forming events), Kosrae presents a conservative test of the hypothesis that hydrogeomorphic zones exist. Differences in vegetation structure indicate that growing conditions vary among zones, and differences in soil structure or nutrient availability may have a greater influence than soil redox potential or porewater salinity in these forests.

The magnitude of average redox values in the Kosraean mangrove forests suggests that long inundation periods are mitigated by high turnover rates. Redox values were higher than those reported for northern Australia (−115 to −162mV; Boto & Wellington, 1984) and Belize (−45 to −212mV; McKee, Mendelssohn, & Hester, 1988) and for a monospecific basin mangrove forest in Florida, USA (−158mV at 1cm and −202mV at 15cm; McKee, 1993), but lower than values reported from another basin forest in Florida with a mixture of two species (292mV at 1cm to 273mV at 15cm; McKee, 1993). In the Australian study, the highest values were associated with sites with high plant biomass, and the lowest values (reflecting the most anaerobic conditions) were recorded at higher elevations where inundation was less frequent. At the Belize site, where elevation differences were small, proximity to trees that oxidize the rhizosphere, especially *Rhizophora*, increased redox values significantly (McKee, 1993). In Kosrae, moderate densities of tall trees in all three zones, relatively frequent flooding even in the basin zone, and perhaps variation in soils and other geomorphologic characteristics among the rivers, may have prevented differences from being detected between the three zones.

Porewater salinity in the Kosraean mangrove forests is likely to be moderated by high rainfall and groundwater flow from freshwater forested wetlands upstream from the mangrove forests. Groundwater flow and surface runoff rates may be buffering the mangrove forests from extremes of salinity, particularly in the basin forests. The highest porewater salinity measured was only 45 o/oo, which was recorded in both fringe and riverine plots, whereas 32 o/oo was the maximum measured in the basin plots. Low porewater salinities have also been reported in some basin swamps in high intertidal zones in Australia, where rainfall, runoff, and groundwater seepage are abundant (Semeniuk, 1983) and on islands behind dunes where groundwater seepage exceeds tidal inflow (Cintrón *et al.*, 1978).

Taller trees in the basin zone and shorter trees in the fringe zone characterized Kosraean mangrove forests (Table 2). This is probably not due to differences in harvesting patterns, as no stumps were found in the fringe plots. Moreover, *B. gymnorrhiza* and *R. apiculata*, the two species most commonly harvested (Ewel *et al.*, in press), did not differ significantly in dbh among the zones. *S. alba* was significantly larger in both diameter and height in the basin zone, but fringe zone trees were still very large and gnarled: they are not likely to be younger. *S. alba* dominated in volume in all three, whereas *B. gymnorrhiza* comprised more than half the trees in riverine and basin zones. Differences in stature, the greater abundance of *R. apiculata* regeneration in basin forests, and the nearly complete confinement of *R. mucronata* to fringe forests (but at only one of the three fringe plots), are the main discriminating features among the three zones.

Differences in tree height are often related to porewater salinity. Stunted tree growth is associated with hypersalinity, usually defined as levels greater than sea strength (FAO, 1994). None of the mangrove species in Kosrae is considered very salt tolerant (Clough, 1992), and the most common (*S. alba*, *B. gymnorrhiza* and *R. apiculata*) are probably widespread because of generally low salinities throughout all the zones. Although both porewater salinity and soil redox potential may have occasionally been high enough to affect establishment of propagules, other factors such as interspecific competition, nutrient limitation, predation on propagules, and soil type and texture, may have been just as important in restricting the distribution of the three less common species. In these relatively benign mangrove forests, porewater salinity does not appear to vary enough to impose readily identifiable zonation in tree distribution.

The pattern of tree species distribution we recorded conflicts with an earlier description by Hosokawa, Tagawa, & Chapman (1977), who recognized three types of mangrove forests in Kosrae and Pohnpei, the next major island to the west. One type was dominated by *S. caseolaris* (now agreed to be *S. alba* [e.g. Stemmermann, 1981]), which grew near the seaward edge of a mangrove forest; another was dominated by *R. mucronata* (sometimes mixed with *R. apiculata*) along the mouths of streams; and a third was dominated by *B. gymnorrhiza*, which occurred along the banks further upstream as well as in interior parts, sometimes continuous with freshwater forested wetlands or upland forests.

Our data present a different picture, with *B. gymnorrhiza* being a more consistent member of the species complement in the fringe swamp and *R. apiculata* more common than *R. mucronata*. Our plots included only one stand of *R. mucronata*. Some of the discrepancy in these two reports may be due to the gradual loss of *S. alba* over the last two decades, perhaps due to natural mortality, as suggested by the paucity of seedlings and saplings. This species is widely recognized as a pioneer species (Tomlinson, 1988), can reproduce vegetatively, and is clearly maintaining dominance in the Kosrae forests. However, *B. gymnorrhiza* and *R. apiculata*, the two species most commonly harvested, are more likely to invade these small gaps (median $= 92\,\text{m}^2$, formed both by harvesting and by large *S. alba* branches falling; Ewel *et al.*, in press). Loss of *S. alba* from the fringe zone could have significant consequences, as this large, spreading tree, which branches close to the ground where it is open-grown (F. Putz, pers. comm.), may be particularly important in breaking the force of storm tides. It is also commonly covered with epiphytes and hosts a diversity of invertebrates, lizards, and birds.

In spite of Kosrae's small size, its mangrove forests are comparable to Malaysian mangroves in standing stock volume [$237\,\text{m}^3$/ha in Kosrae *v.* $217\,\text{m}^3$/ha before the largest and most intact mangrove stand in Malaysia at Perak was harvested (Noakes, 1955)]. They also show less of an impact from harvesting than in Malaysia, in spite of increasing harvesting rates. Two *R. apiculata* stands in Sabah, Malaysia, that had been selectively harvested 6–7 years before they were measured, had volumes of $154\,\text{m}^3$/ha and $182\,\text{m}^3$/ha, but with trees averaging only 12 cm dbh and 10 m in height (Liew, 1970). The average diameter of *R. apiculata* at 18 other managed sites in Malaysia was 9.4 cm (Gong, Ong &

Wong, 1991, cited in Chan *et al.*, 1993), much smaller than in Kosrae (Table 2).

Management policies in Kosraean mangrove forests, as in any mangrove forest, should protect the riverine zone from harvesting because of the likelihood of subsequent erosion followed by sediment deposition in seagrass beds and the coral reef. Harvesting in the fringe zone should also be discouraged, because of its importance in protecting against coastline erosion, but this appears to be less of a problem in Kosrae than in many other localities. Whereas regeneration of *B. gymnorrhiza* is abundant in all three zones, replanting *R. apiculata*, particularly where it has been harvested from riverine forests, may be advised. Concentrating harvesting in basin zones may have the advantage of opening up large enough gaps to permit survival of planted seedlings of *S. alba*. Determining how to delineate the boundaries of fringe and riverine zones for enforcement of harvesting regulations, for example, may be a useful next step.

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