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A tropical freshwater wetland: I. Structure, growth, and regeneration

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Abstract

Forested wetlands dominated by *Terminalia carolinensis* are endemic to Micronesia but common only on the island of Kosrae, Federated States of Micronesia. On Kosrae, these forests occur on Nansepsep, Inkosr, and Sonahnpil soil types, which differ in degree of flooding and soil saturation. We compared forest structure, growth, nutrition, and regeneration on two sites each on Nansepsep and Inkosr soils and one site on the much less common Sonahnpil soil type. *Terminalia* tree sizes were similar on all three soil types, but forests differed in total basal area, species of smaller trees, and total plant species diversity. *Terminalia* regeneration was found only on the Inkosr soil type, which had the highest water table levels. Other *Terminalia* species are relatively light demanding, and *T. carolinensis* exhibited similar characteristics. It is therefore likely that *Terminalia* requires periodic, but perhaps naturally rare, stand-replacing disturbances (e.g., typhoons) in order to maintain its dominance, except on the wettest sites, where competition from other species is reduced. *Terminalia* swamps in the Nansepsep soil type appeared to be at the greatest risk of conversion to other uses, but swamps on all three types may face greater pressure as Kosrae's population increases and the island's infrastructure becomes more developed.

Introduction

Freshwater forested wetlands are found on many of the high islands of Micronesia. The less disturbed wetlands are characterized by closed canopies of large trees in genera such as *Campnosperma*, *Calophyllum*, *Metroxylon*, and *Terminalia*. Heights that often exceed 25 m, large buttresses, pneumatophores, and extensive epiphyte communities (Hosokawa 1952, 1954; Maxwell 1982) make these wetlands some of the most impressive and distinctive forests in the region. Nevertheless, remarkably little is known about them.

Freshwater forested wetlands usually cover no more than 3–6% of the total land area of a Micronesian island (e.g., Whitesell et al. 1986; MacLean et al. 1988), but their ecological and socioeconomic importance is likely to be much greater than their areal extent would suggest (Drew et al. in press). Because these wetlands are generally located in the lower reaches of streams and rivers between uplands and mangrove forests, they are likely to play important roles in trapping sediments and, therefore, in protecting sensitive seagrass beds and coral reefs. Other possible functions include floodwater retention, improvement of water quality, provision of habitat for fish and wildlife, carbon sequestration (Chimner and Ewel, in press), and production of wood, thatching material, food, and medicines. Despite their importance, these wetlands may be the most threatened forest type in Micronesia, as development pressures bring opportunities for conversion to agriculture and other types of land uses (Drew et al. in press).

On the island of Kosrae, Federated States of Micronesia (Figure 1: 5°19′ N, 163°00′ E), forested wetlands dominated by *Terminalia carolinensis* Kanehira are found on three soil types, all of which have similar parent materials and soil texture but vary in depth of water table and flood frequency. Our primary goal in this study was to determine the effects of soil type and hydrologic regime on plant species composition, stand structure, regeneration, and tree growth in *Terminalia* forests on Kosrae. We also wanted to evaluate the conservation-related implications of any differences we found among the three soil types for this exceedingly rare, poorly understood, and seriously threatened type of forested wetland.

Swamps dominated by Terminalia carolinensis

Terminalia carolinensis is a large tree (up to 35 m tall) with distinctive pagoda-like crown architecture and buttresses that can rise several meters above the ground. Although most common in low-lying, wet sites, the species, which is classified as a facultative wetland plant (Stemmermann and Proby 1978a), can also be found in riparian areas at higher elevations. Although the genus *Terminalia* has a pantropical distribution, *T. carolinensis* occurs only in Kosrae, Pohnpei (Stemmermann and Proby 1978a; Fosberg et al. 1979), and possibly Palau (E. Waguk and K. Rengulbai, personal communication).

Terminalia carolinensis was described in 1932, when it was recognized as being very similar to *Terminalia crassiramea* Merr. but distinguishable "by its fewer-nerved leaves which are much more acute at the base and also by its large somewhat compressed fruits" (Kanehira 1932, p. 673). *Terminalia crassiramea* is now treated as a synonym for *T. copelandii* Elmer (Sosef et al. 1995). In a report on a visit to Kosrae in 1827, F.H. Kittilitz included a drawing of a tree named 'ka' (the Kosraean name for *T. carolinensis)*, which he apparently thought was 'an especially stately specimen' of *T. catappa* L. (Ritter and Ritter 1982, p. 210–211). The latter is a much more common, but superficially similar, strand species that has a beach form and a taller river-bottom form (Whitford 1911). *Terminalia catappa* can also reach a height of 35 m and develop massive plank buttresses, and it occurs in both strands and upper terraces (George et al. 1993). The river-bottom form has been regarded as a separate species, *T. cattapoides* C.T. White & Francis (Kraemer 1951), which is now regarded as another synonym for *T. copelandii* (Sosef et al. 1995). Both Kosraeans and Pohnpeians distinguish *T. catappa* from *T. carolinensis*, giving different names to each (Falanruw et al. 1990).

Botanical descriptions of Terminalia *swamps*

A more rigorous description of the forested wetlands dominated by *T. carolinensis* (hereafter referred to as *Terminalia)* appeared a century after Kittilitz' notes; it called attention to epiphytic vegetation and recognized the "*Terminalia carolinensis* consociation of the *Horsfieldia nunu*-*Cyclosorus heterocarpus* association" (Hosokawa 1952, 1954). More recent descriptions noted the prominence of *Terminalia*, and listed associates such as *Horsfieldia nunu* Kanehira, *Neuburgia celebica* (Koord.) Leenh., *Barringtonia racemosa* (L.) Bl, and *Hibiscus tiliaceus* L.; vines or herbaceous species such as *Derris trifoliata* Lour., *Freycinetia* spp., and *Sciropodendron ghaeri* (Gaertn.) Merr.; and common ferns and epiphytes (Stemmerman and Proby 1978b; Maxwell 1982). No study has examined the relationships between soils or hydrology and stand dynamics in these forested wetlands.

Study sites

The island of Kosrae in the western Pacific Ocean is approximately 109 km^2, and has a rugged,

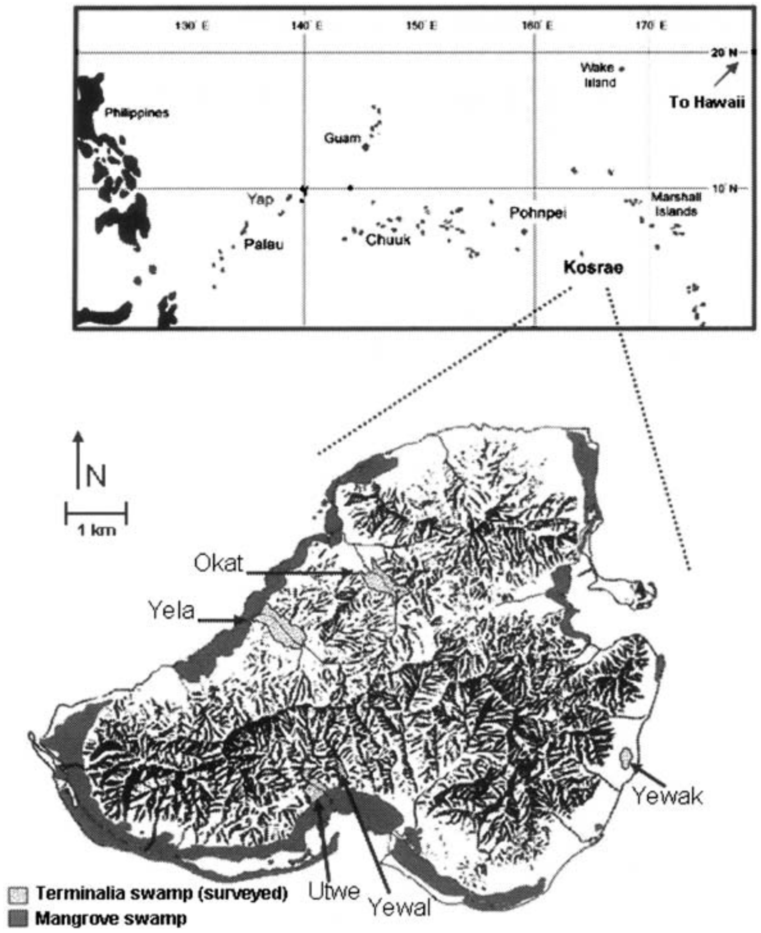

Figure 1. Location of study sites on Kosrae, Federated States of Micronesia. Boundary lines sometimes extend beyond a study area, which occupied only the soil type surveyed. Island size on insert map is slightly exaggerated.

heavily forested interior fringed by a narrow coastal plain. High annual rainfall (5050 mm) and flat coastal topography facilitate the development of extensive forested wetlands. Approximately 14% of the land area on Kosrae is covered by mangrove forests and at least 5% by freshwater forested wetlands (Whitesell et al. 1986). Another 5% of the island may have been covered by freshwater forested wetlands that have been converted to agroforests (Laird 1983).

All three soil types that characterize *Terminalia* forests are found in poorly drained areas with slopes of 5% or less (Laird 1983). Inkosr soils (silty clay loam, 0–2% slopes) are deep and extremely wet; Nansepsep soils (silty clay loam, 0–2% slopes) are also very deep and somewhat poorly drained; and Sonahnpil soils (very stony silty clay loam, 0–5% slopes) are generally similar in texture but include cobble and larger stones (Laird 1983). Whitesell et al. (1986) mapped roughly equal amounts of *Terminalia* forest on Inkosr and Nansepsep soils, with fewer hectares on Sonahnpil associations. Nansepsep soils are considered the most suitable of the three for agriculture (Laird 1983). The likelihood of anthropogenic disturbance is reduced in most Inkosr and Sonahnpil associations because of flooding or rocky substrates, respectively. For our project, we selected two *Terminalia* forest stands located on Inkosr soils in Yela and Yewak and two on Nansepsep soils in Utwe and Okat. A fifth stand was located on a Sonahnpil association in Yewal (Figure 1).

Materials and methods

In April 2000, four 0.04-ha circular plots were established systematically along each of two transects at each of five stands, for a total of eight plots per site. Plot centers were permanently marked by tagging the closest witness tree at its base with aluminum tags. The two 120-m transects were arranged parallel to each other, and plots were located 30 m apart. Four 1-m^2 quadrats were established 2 m from each plot center in each cardinal direction.

Environment

Light levels were measured on a single day between 09:00 and 16:00 at ~0.4 m above the soil surface at the center point of each plot and over each 1-m^2 quadrat by using an integrating line quantum sensor (Li-191 SA, Li-Cor, Lincoln, Nebraska, USA) and a datalogger (Li-1400, Li-Cor, Lincoln, Nebraska, USA). A second line quantum sensor and datalogger placed in an open location (e.g., a large canopy gap or home site) near each stand allowed us to calculate percent light penetration.

A 1-m-deep borehole was dug near each plot center. The water table level was measured after it had stabilized. Near every other plot center on all sites (n = 4 per site), a single soil sample was collected from a depth of 10–15 cm, placed in a plastic bag, and kept cool. The samples were oven-dried on Kosrae (~60 °C) and shipped to the Cooperative Extension Service at Louisiana State University (Department of Agronomy, Baton Rouge, Louisiana, USA) for analyses of pH, extractable nutrients (Ca, Na, Mg, P, K), and soil texture (sand:silt:clay).

Vegetation measurements

Within each 0.04-ha main plot, each tree ≥5.0 cm in diameter was identified to species and measured at 1.3 m or 30 cm above the highest buttress (*sensu* Avery and Burkhart 1994). The crown class of each tree (dominant, codominant, intermediate, and overtopped, *sensu* Smith 1986) was also determined, and total height was measured on the three codominant trees nearest each plot center by using a laser height device (Impulse 200, Laser Technology, Inc., Englewood, Colorado, USA).

A single 0.01-ha subplot with the same center point was established within each main plot to identify and measure saplings and shrubs, defined as woody stems > 1.3 m in height and < 5.0 cm DBH. In addition, all woody stems within each 1-m^2 quadrat < 1.3 m in height were identified, tallied, and assigned to one of three height classes (i.e., < 30 cm, 30–90 cm, or > 90 cm). Percent cover of herbaceous plants in each quadrat was estimated by species.

At one of the Nansepsep soil types (Utwe) and one of the Inkosr soil types (Yela), dendrometer bands were installed on 15 *Terminalia* trees. Bands were made of stainless steel to prevent corrosion. Each tree was marked with a numbered tag, scraped lightly with a rasp at approximately 30 cm above the highest buttress to ensure a tight band fit against the tree cambium, and fitted with a dendrometer band (cf., Cattelino et al. 1986; Keeland and Sharitz 1993). Dendrometer bands were measured quarterly in 1997 and 1998 and then approximately monthly in 1999 and 2000. Data were analyzed as individual tree basal area increments to account for any differences in tree size when studies were initiated.

Height, diameter at 1.3 m (i.e., DBH), species (where possible), and decay class (*sensu* Spetich et al. 1999) were recorded for each snag or stump in each main plot. In addition, two 20-m transects were established along random azimuths from the center point of each main plot. Downed wood intersecting the transect was measured as described by Allen et al. (2000), with decay classes determined by bark condition, wood texture and color, and presence of twigs (Spetich et al. 1999). Formulas for calculating woody debris volume are according to methods by Van Wagner (1968) and are a function of woody debris diameter, numeric counts at each diameter class, and sample line length.

Statistical analyses

Forest structure variables, woody debris volume, and soil chemical properties were compared among the three soil types in separate analyses by using a one-way analysis of variance (ANOVA), with soil type being treated as a fixed-effect experimental unit. Dendrometer increment was first converted to basal area increment and then analyzed with a one-way ANOVA as a comparison between two sites (Yela vs. Utwe). Mean annual basal area increment was determined through a regression analysis (see Figure 5). Non-normal data were either square root or natural log transformed to improve normality and homoscedasticity of residual variances. Statistical groupings were determined with a Tukey's Studentized Range Test ($\alpha = 0.05$). All analyses were performed using SAS version 8.02 (SAS Institute Inc. 1999).

Results

Environment

The amount of light transmitted to understory species in *Terminalia* forests on Kosrae averaged 3% of available light; there were no significant differences in light penetration among soil type ($F_{2,36} = 0.03$; $p = 0.972$). Soil types differed significantly in four physicochemical parameters (Table 1): water depth ($F_{2,36} = 18.93$, $p < 0.001$), pH ($F_{2,18} = 22.20$, $p < 0.001$), Na ($F_{2,18} = 17.23$, $p < 0.001$), and K ($F_{2,18} = 4.15$, $p = 0.033$). Water tables were closest to the surface on Inkosr soils, where they were above the surface on many plots, whereas Sonahnpil water tables were so deep below the soil surface (> 1 m) that at times they could not be located through the rocky substrate. pH was slightly acidic on all soil types but especially on flooded Inkosr soils. Na, likewise, was high on Inkosr soils, and K was low for Sonahnpil soils relative to Inkosr soils (Table 1). No differences in soil texture were found.

Live vegetation

Overall, the tree diameter distributions were similar among soil types (Figure 2). But, only Inkosr and Sonahnpil soils supported trees > 80 cm DBH. There were no significant differences in mean height ($F_{2,35} = 4.30$; $p = 0.021$) or mean DBH ($F_{2,35} = 0.14$; $p = 0.867$) of dominant and codominant *Terminalia* among all stands (Table 2). Basal area of stands on the Sonahnpil soil type was significantly greater than on Inkosr and Nansepsep soil types ($F_{2,35} = 5.95$; $p = 0.006$). This difference is at least partially due to the greater tree density on Sonahnpil soils (Table 2: $F_{2,35} = 5.49$; $p = 0.008$). For trees smaller than 5.0 cm DBH, there were no differences among soil types for either mean basal area ($F_{2,36} = 0.93$; $p = 0.402$) or tree density ($F_{2,37} = 1.07$; $p = 0.353$) (Table 2).

Among trees ≥5.0 cm DBH, *Terminalia* and *Horsfieldia nunu* had the highest relative basal areas (Figure 3). Species richness of trees ≥5.0 cm DBH was lowest on the Inkosr soil type, where only six species were positively identified. Aside from the two dominant overstory species, only *Barringtonia racemosa* was common on the Inkosr soil type. *Dendrocnide kusaiana*, *Campnosperma brevipetiolata* Volkens, and *Inocarpus fagifer* (Parkinson) Fosberg each accounted for 3–5% of the relative basal area of the Nansepsep and Sonahnpil soil types, which had 16 and 15 tree species, respectively.

Table 1. Physical and chemical properties (± 1 SE) of three soil types in *Terminalia* swamps on Kosrae, Federated States of Micronesia. Soil types followed by the same lowercase letter for a particular variable are not significantly different at $\alpha = 0.05$.

Variable	Nansepsep	Inkosr	Sonahnpil
Water depth (cm)	−36.8 b (9.2)	2.2 a (2.0)	−65.9 c (8.8)
pH	5.8 b (0.05)	5.2 c (0.11)	6.4 a (0.20)
P (mg L^{-1})	203.5 a (62.9)	306.6 a (62.1)	265.2 a (27.9)
Na (mg L^{-1})	92.3 b (5.5)	160.6 a (15.7)	71.0 b (4.5)
K (mg L^{-1})	213.3 ab (33.4)	314.0 a (32.4)	190.2 b (24.0)
Mg (g L^{-1})	1.35 a (0.114)	1.23 a (0.109)	1.28 a (0.281)
Ca (g L^{-1})	4.34 a (0.406)	4.61 a (0.369)	4.09 a (0.820)
% sand	44.6 a (2.2)	48.6 a (3.4)	51.9 a (3.0)
% silt	11.7 a (2.8)	13.3 a (3.3)	14.9 a (3.2)
% clay	43.7 a (2.6)	38.1 a (4.1)	33.2 a (3.1)

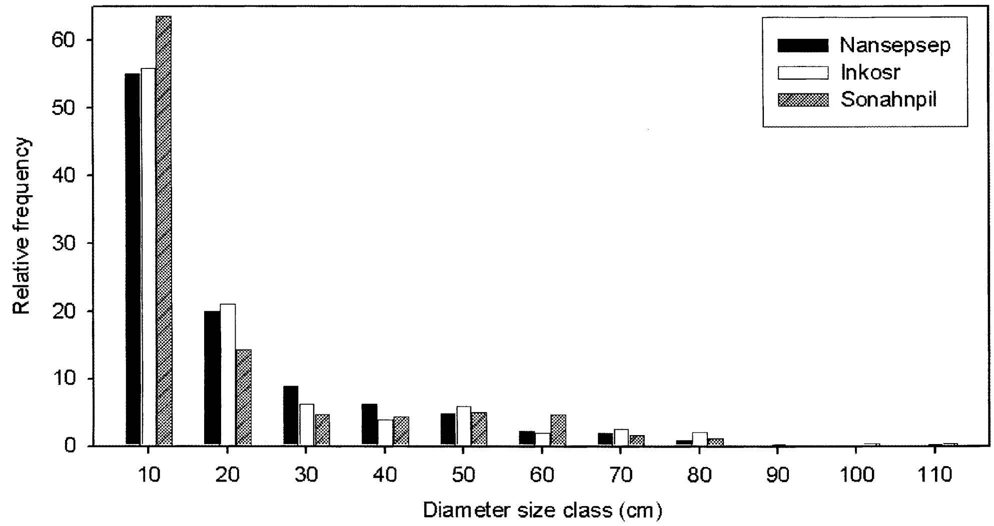

Figure 2. Diameter size class distribution (dbh ≥5.0 cm) for all tree species in *Terminalia* forests on three soil types on Kosrae, Federated States of Micronesia.

The species composition in the smaller size classes of trees (< 5.0 cm DBH) differed considerably from that of the larger trees. *Terminalia* did not dominate the smaller size classes on any of the soil types (Figure 4). *Horsfieldia nunu* had the highest relative basal area on the Nansepsep soil type, and *B. racemosa* on the Inkosr soil type. Although *D. kusaiana* had a high relative basal area on the Sonahnpil soil type, four additional species *(H. nunu, Hibiscus tiliaceus* L., *N. celebica*, and *Ficus tinctoria* Forst.) contributed nearly 50% of the relative basal area on this soil type. Except for four individuals of *Terminalia* on only 1 of 16 Nansepsep forest plots, this species was totally absent from the < 5.0 cm DBH size class on both Nansepsep and Sonahnpil soil types.

There were no differences among soil types in woody seedling density in quadrats ($F_{2,36}$ = 1.75; p = 0.188: Table 2). Across all soil types, seedlings of *H. nunu* were present in 19–39% of quadrats, while *Terminalia* seedlings were less frequently encountered and even completely absent from the Sonahnpil soil type (Table 3). *Barringtonia racemosa* was also a common seedling, though only in the Nansepsep and Inkosr soil types. *Dendrocnide kusaiana* seedlings were only present in large quantities on the Sonahnpil association (Table 3). The lowest woody seedling diversity was found on the Inkosr soil type, but this trend among soil types was not upheld for seedling density (Table 2).

The most indicative species for the Inkosr soil type was the herbaceous *S. ghaeri* (Table 3). Nansepsep or Sonahnpil soil types were most easily identified by the presence of *Zingiber zerumbet* (L.) Smith and *Cyclosorus heterocarpus* Ching. Although agroforest species composition varied somewhat, all three soil types were used to some degree for crop production (Table 3).

Tree diameter growth was approximately four times greater on Nansepsep soils than on Inkosr soils ($F_{1,41}$ = 24.95; $p < 0.001$). Growth was linear but slower in 1997–1998 during an El Niño-related drought on Kosrae (Figure 5).

Stumps and dead wood

The number of cut trees did not differ significantly by soil type ($F_{2,35}$ = 1.58; p = 0.220), reflecting high variation in stump counts among plots (Table 2). Density of cut stumps was as high as 448 ha^{-1} on some plots in the Nansepsep soil type and nonexistent on other plots. Likewise, four and five out of eight plots on the Okat and Utwe sites (Nansepsep soils), respectively, were associated with agroforest gaps, while no more than two agroforest gaps were associated with plots on either Inkosr or Sonahnpil soil types. Agroforestry

Table 2. Characteristics (±SE) of *Terminalia* forests on three soil types on Kosrae, Federated States of Micronesia. Means followed by the same lowercase letter for a particular variable are not significantly different at $\alpha = 0.05$.

Soil type	Number of plots	Main plot (dbh ≥5.0 cm)					Subplot (dbh < 5.0 cm)		Quadrat
		Mean height (m)	Mean dbh (cm)	Mean basal area (m^2 ha^{-1})	Tree density (# ha^{-1})	Cut tree density (# ha^{-1})	Mean basal area (m^2 ha^{-1})	Tree density (# ha^{-1})	Seedlings (# m^{-2})
Nansepsep	16	28.3 a (0.6)	20.3 a (1.5)	29.0 b (1.5)	577 b (3.5)	43.6 a (27.8)	0.9 a (0.2)	2912 a (421)	1.5 a (0.4)
Inkosr	16	24.6 a (1.1)	21.9 a (1.5)	33.0 b (3.0)	555 b (54)	6.2 a (6.2)	0.7 a (0.1)	2246 a (494)	1.3 a (0.2)
Sonahnpil	8	27.5 a (1.3)	20.8 a (2.4)	46.5 a (10.2)	804 a (157)	6.2 a (6.2)	0.8 a (0.1)	1916 a (400)	0.5 a (0.1)

activity was more prevalent on the Nansepsep soil type.

The mean volume of woody debris was low (30.5 m^3 ha^{-1}: Table 4). Sonahnpil soils had significantly less woody debris than Nansepsep soils ($F_{2,75} = 3.45$; $p = 0.037$), and neither site was significantly different from the Inkosr soil type. Most coarse woody debris was classified as rotten, while most fine woody debris was in the 2.5–7.5 cm size class.

Discussion

Soil type and hydrologic regime

Although soil texture, slope, parent material, and most nutrients were similar among the three soil types (Table 1; Laird 1983), the sites located on the Inkosr soil type were clearly the wettest, and the Sonahnpil soil type had the lowest water table. The high pH of the Sonahnpil soil type may have been associated with dryness; Sonahnpil soils have been described previously as being more acidic (cf. Laird 1983) than we found them to be.

The Inkosr soil type also had significantly higher Na concentrations than the other two (Table 1). This difference may have been related more to lower elevation and proximity of the Inkosr sites to seawater than to mean water table depth. Both coastal storms and occasional influxes of seawater during El Niño-related droughts may have influenced Na levels. During the 1997–1998 El Nino-related drought, a reversal of groundwater flow from mangroves into the seaward fringe of the Yela *Terminalia* forest (on the Inkosr soil type) would have exposed freshwater soils to salt water (Drexler and Ewel 2001).

The lower plant species richness (Table 3, Figures 3 and 4) and the much slower growth rate of the *Terminalia* trees on the Inkosr soil type (Figure 5) duplicated patterns in other forested wetlands such as in southern USA (Mitsch and Ewel 1979; Conner and Buford 1988) and northeastern USA (Golet et al. 1993). Lower oxygen availability is often associated with longer periods of flooding and limits the number of species that can reproduce and survive (Mitsch and Gosselink 2000).

Whereas some of the differences in *Terminalia* forest structure are probably related to hydrologic regimes, other differences may be related more to

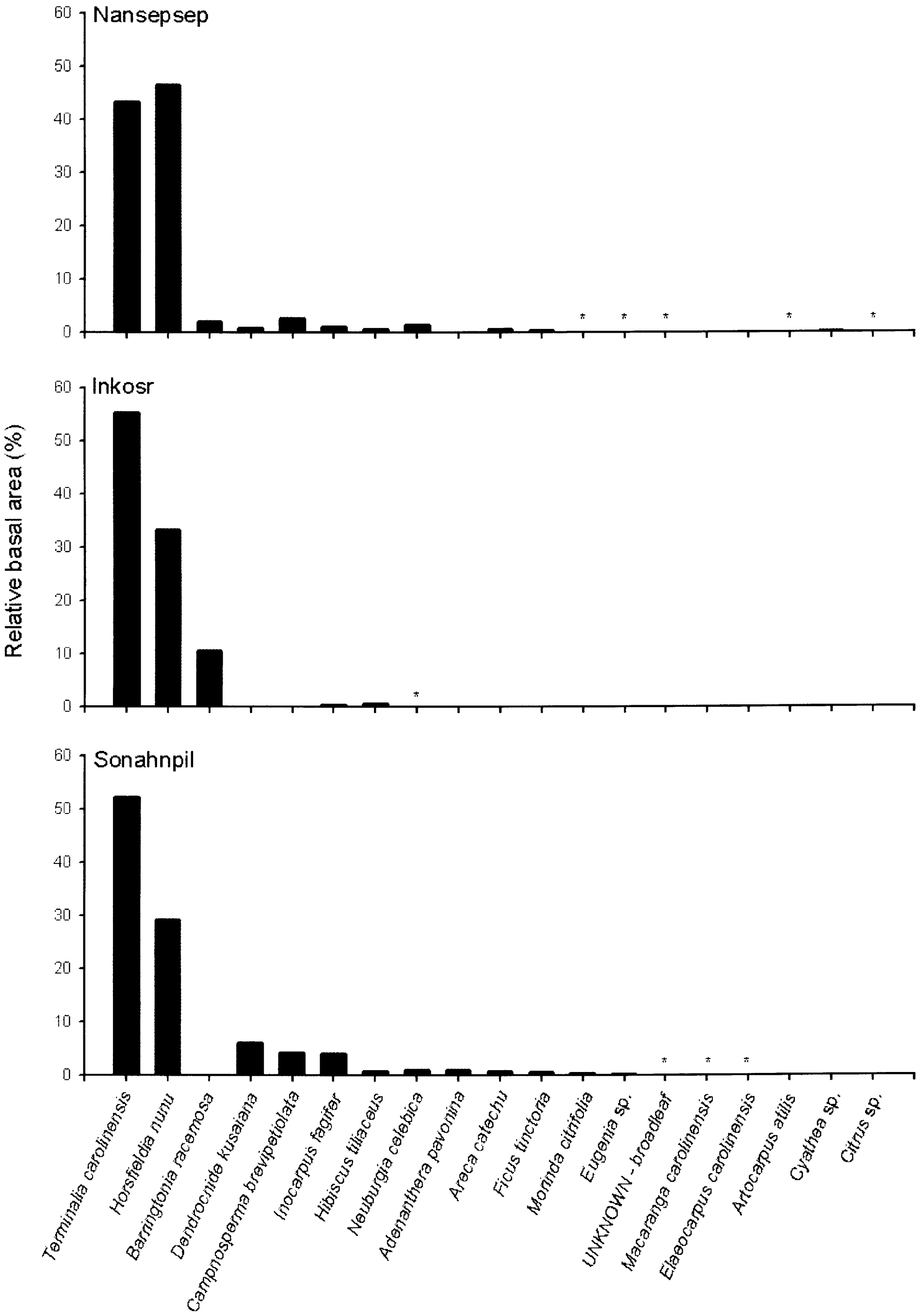

Figure 3. Relative basal area distribution (dbh ≥5.0 cm) of species by soil type in *Terminalia* forests on three soil types on Kosrae, Federated States of Micronesia. Species designated by an asterisk (*) were represented in at least one plot but had a very low basal area.

human use. The Nansepsep soil type is regarded as more suitable for agriculture than the Inkosr soil type because of its lower water table level (Laird 1983). These Nansepsep sites were more likely to have agroforestry species in the understory (Table 3) and appeared to have more tree harvesting. Nevertheless, the amount of downed wood was similar on both soil types. Some downed

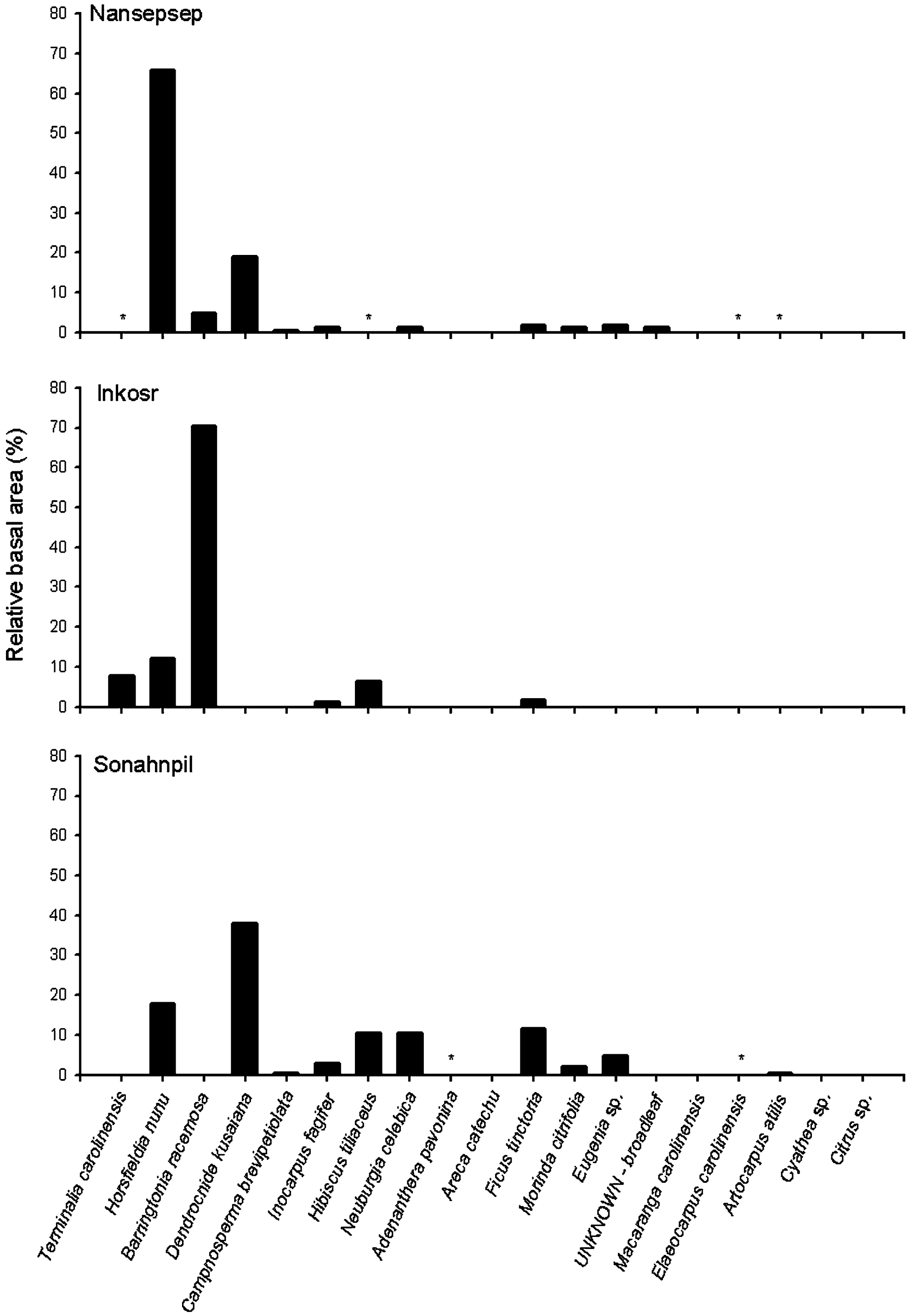

Figure 4. Relative basal area distribution (dbh ≤ 5.0 cm) of species by soil type in *Terminalia* forests on three soil types on Kosrae, Federated States of Micronesia. Species designated by an asterisk (*) were represented in at least one plot but had a very low basal area.

wood is likely to have been logged from or burned off of Nansepsep soils during maintenance of agroforestry plots. Yet, despite the impressive forest stature of *Terminalia* forests growing on all three soil types, the woody debris volume was relatively low. Mangrove forests just seaward of

Table 3. Percent of 1-m^2 quadrats where a particular plant species occurred in the understory, and mean percent quadrat coverage by that species for each *Terminalia* forest soil type on Kosrae, Federated States of Micronesia.

Species	Nansepsep		Inkosr		Sonahnpil	
	% quadrats	% coverage	% quadrats	% coverage	% quadrats	% coverage
Tree/shrub species						
Areca catechu	3.1	17.5			3.1	20.0
Barringtonia racemosa	12.5	7.5	39.1	9.4		
Campnosperma brevipetiolata					9.4	6.7
Dendrocnide kusaiana	1.6	40.0			12.5	< 5.0
Eleocarpus carolinensis	1.6	< 5.0				
Eugenia sp.	3.1	< 5.0				
Hibiscus tiliaceus	1.6	< 5.0				
Horsfieldia nunu	39.1	6.2	34.4	8.0	18.8	10.0
Inocarpus fagifer	3.1	15.0	1.6	< 5.0	3.1	< 5.0
Ixora casei	1.6	10.0				
Morinda citrifolia			1.6	10.0	3.1	< 5.0
Terminalia carolinensis	12.5	9.4	20.3	11.9		
Herbaceous species						
Chromolaena odarata	1.6	10.0				
Curcuma sp.	1.6	13.0			12.5	6.3
Dioscorea bulbifera	6.3	16.3				
Lycopodium cernuum	3.1	< 5.0	1.6	< 5.0		
Scirpodendron ghaeri	1.6	< 5.0	18.8	45.4		
Smythea lanceata					3.1	< 5.0
Zingiber zerumbet	21.9	18.2			25.0	27.5
Unknown species[a]	7.8	5.8			15.6	13.4
Fern species						
Asplenium nidus	3.1	< 5.0	14.1	12.2		
Cyathea sp.	1.6	< 5.0				
Cyclosorus heterocarpus	75.0	23.1			28.1	29.4
Nephrolepis hirsutula	28.1	18.3	3.1	< 5.0	37.5	15.0
Other epiphytic ferns[b]	15.6	8.5	1.6	10.0	3.1	< 5.0
Other ferns[c]	15.6	9.0	4.7	10.0	40.6	21.2
Liana species						
Derris sp.	15.6	< 5.0	12.5	5.6	9.4	< 5.0
Freycinetia sp.	12.5	5.6				
Merremia sp.	10.9	5.7	9.4	< 5.0	12.5	< 5.0
Piper ponapense	31.3	5.5	3.1	< 5.0	40.6	6.2
Agroforestry species						
Cyrtosperma chamissonis	14.1	20.6	9.4	40.8		
Manihot esculenta	1.6	30.0			12.5	57.5
Musa sp.	1.6	20.0	1.6	20.0	12.5	15.0

[a] Unknown herbaceous plant species included two weedy herbs, one grass, and at least one representative of the Melastomataceae family

[b] Epiphytic ferns were mostly *Anthrophylum* sp.

[c] Additional fern species present in plots probably included *Davillia solida*, *Microsorium scolopendria*, and *Pteris spinescens* (c.f., Maxwell 1982); however, identifications could not be confirmed.

Terminalia forests on Kosrae, for example, have 88–135 m^3 ha^{-1} of downed wood (Allen et al. 2000), two to three times the volume in the *Terminalia* forests (Table 4). The volume of woody debris in *Terminalia* forests is also much lower than volumes reported from other tropical forests in the Pacific (e.g., 136–428 m^3 ha^{-1}: Santiago 2000).

Forest succession

Light available for germination and photosynthesis of young seedlings was low in *Terminalia* forest understories (3.0–3.5%), although well within the 0.5–5.0% range reported for other forests (Chazdon and Pearcy 1991) and even higher than for wet forests in Costa Rica (1.2–2.1%: Nicotra et al.

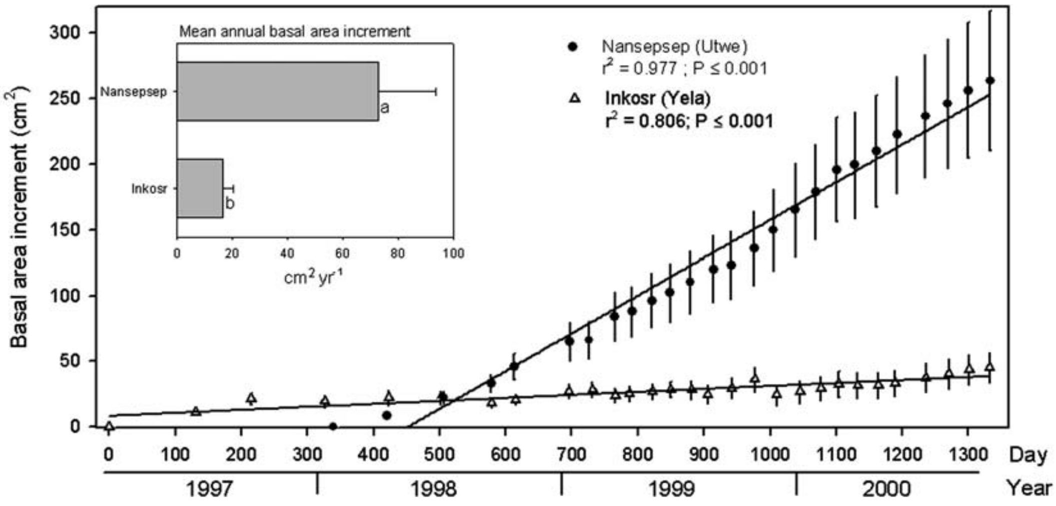

Figure 5. Cumulative basal area increment and mean annual basal area increment of representative codominant *Terminalia* trees on Nansepsep and Inkosr soil types on Kosrae, Federated States of Micronesia. Regression analysis was applied to the mean increment among subsequent time points. Means followed by the same lowercase letter for a particular variable are not significantly different at $\alpha = 0.05$.

1999). Openings in *Terminalia* swamps tended to be dominated by *H. nunu* or *H. tiliaceus* in spite of prolific *Terminalia* seed production (Miller 1984; personal observations). Though woody seedlings were present (Table 2), few apparently survive and grow into the sapling size classes, especially on Sonahnpil soil types (Figure 4). *Horsfieldia nunu's* high relative basal area in the smaller size classes (Figure 4) suggested that it is more shade tolerant (or less light demanding) than *Terminalia* and therefore better suited to growing in small gaps created by treefalls or cutting. It apparently is outcompeted by *Terminalia* on more open sites and also may be a less effective competitor on the wettest sites (i.e., Inkosr soils). Inkosr soils are the only sites where *Terminalia* seems to be able to maintain itself, perhaps because of its greater tolerance of soil saturation than that of *H. nunu*. The slow growth rates of trees on this soil type indicate how important a factor flooded soils can be in constraining succession.

Terminalia now dominates sites with the least recent disturbance, but it is not clear how it would have gotten started on these sites. We believe that our study sites, with the possible exception of Yewal, were heavily logged during the Japanese occupation of Kosrae (i.e., from 1914 to 1945). It is also possible that a typhoon in 1905 destroyed

Table 4. Mean total volume of woody debris(±SE) on sample plots in *Terminalia* forests with different soil types on Kosrae, Federated States of Micronesia. Means followed by the same lowercase letter for a particular variable are not significantly different at $\alpha = 0.05$.

Diameter/Decay class	Mean volume (m^3 ha^{-1})			
	Nansepsep	Inkosr	Sonahnpil	Mean
Fine (≤ 7.5 cm)				
0.0–1.0 cm	0.24 (0.04)	0.27 (0.05)	0.14 (0.07)	0.22
1.0–2.5 cm	1.80 (0.29)	1.68 (0.32)	1.59 (0.40)	1.69
2.5–7.5 cm	6.26 (1.40)	4.10 (1.54)	4.34 (1.72)	4.90
Coarse (> 7.5 cm)				
Sound	0.41 (0.41)	0.00 (–)	0.00 (–)	0.14
Intermediate	13.65 (9.24)	6.63 (6.14)	0.53 (0.36)	6.94
Rotten	15.21 (4.07)	26.12 (11.75)	8.59 (2.75)	16.64
Total	37.6 a	38.8 ab	15.2 b	30.5

most of the trees on some parts of the island Sarfert 1919; Allen et al. 2001). Either of these events could have created open environments that would have favored the development of stands that are still dominated by *Terminalia*. This pattern is consistent with silvicultural recommendations for other *Terminalia* species, which call for the creation of open, high-light environments during the first several years of stand establishment (e.g., Kitajima 1994; Norgrove and Hauser 2002).

Prospects for the future of Terminalia *swamps on Kosrae*

Terminalia forests are likely to have been common once on Pohnpei, but they are now common only in one remote watershed. Freshwater swamps dominated by other species are still found in Pohnpei, but many of these wetlands have been converted to open taro patches of *Cyrtosperma chamissonis* Schott. Merr., *Alocasia macrorrhiza* (L.) G. Don, or *Colocasia esculenta* (L.) Schott. *Terminalia* forests have been used for agroforestry by Kosraeans for nearly 2000 years (Athens et al. 1996); their endurance as both wetlands (with apparently unaltered hydrology) and agroforests is probably unique among the wetlands of the world (Chimner and Ewel 2004). Because these forests are so important to the people of Kosrae (Drew et al. unpublished manuscript), their continued use seems certain, as long as subsistence agriculture is important in Kosrae's economy.

One of our study sites, the Yela forest, was identified as one of 14 'Areas of Biological Significance' by The Nature Conservancy during a recent assessment of biodiversity in the Federated States of Micronesia (Raynor et al. n.d.) and has been recommended for inclusion in the UNEP World Conservation Monitoring Centre's Protected Areas and World Heritage Programme. Among our other study sites, those located on the Nansepsep soil type are probably at the greatest immediate risk, but forests on all three types may face continued pressure for conversion to other uses. Extension of a circumferential road into a previously isolated village has already traversed several small *Terminalia* forests that were used as agroforests. Completion of that road would provide access to and perhaps exploitation of the Yela forest, which is privately owned. Other recent proposals for development projects on the island have included drainage of wet sites for more intensive agriculture, which could affect local wetlands regardless of whether they are used as agroforests or not. At present, *Terminalia* forests in Kosrae provide a valuable snapshot of major characteristics and sources of variation in a rare, tropical forested wetland. Understanding how other Pacific island wetlands differ from those on Kosrae (e.g., *Terminalia richii* A. Gray forests in Samoa: Pouli et al. 2002), why they may have been less attractive as agroforestry sites, and how they differ from one island to another should be the next step in using these forests to help us better understand the full range of characteristics of and services provided by tropical forested wetlands.

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