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DOWNED WOOD IN MICRONESIAN MANGROVE FORESTS

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Abstract: Dead, downed wood is an important component of upland forest and aquatic ecosystems, but its role in wetland ecosystems, including mangroves, is poorly understood. We measured downed wood in ten sites on the western Pacific islands of Kosrae, Pohnpei, and Yap, all located within the Federated States of Micronesia. Our goals were to examine patterns of variability in the quantity of downed wood in these mangrove ecosystems, provide a general characterization of downed wood in a region with no previously published accounts, and investigate the relationship between harvesting practices and the amount of downed wood. The overall mean volume of downed wood at our study sites was estimated to be 60.8 m^3 ha^{-1} (20.9 t ha^{-1}), which is greater than most published data for forested wetlands. There were significant differences among islands, with the sites on Kosrae (104.2 m^3 ha^{-1}) having a much greater mean volume of downed wood than those on Pohnpei (43.1 m^3 ha^{-1}) or Yap (35.1 m^3 ha^{-1}). Part of the difference among islands may be attributable to differences in stand age and structure, but the most important factor seems to be the greater amount of wood harvesting on Kosrae, coupled with a low efficiency of use of cut trees. Of a total of 45 cut trees examined on Kosrae, no wood had been removed from 18 (40%); these are believed to be trees cut down because other, more valuable, trees were caught on them as they were felled. Of the other 27 trees, only 24 to 42% of the stem volume (to a 10 cm top) was removed from the forest, the amount varying by species. The impacts of current harvesting practices are unknown but may include important effects on tree regeneration and the abundance and species composition of crab populations.

Key Words: coarse woody debris, Federated States of Micronesia, harvesting impacts, Kosrae, Pohnpei, Yap

INTRODUCTION

Dead, downed wood is an important component of upland forest and aquatic ecosystems. In upland forests, downed wood provides animal habitat, serves as a substrate for plant establishment, influences nutrient cycling and organic matter dynamics, and affects geomorphic processes on at least a microtopographic scale (Harmon et al. 1986, McMinn and Crossley 1993). In streams, downed wood alters flow patterns, thereby generating a diversity of habitats, and it traps dissolved and particulate material (Bilby and Likens 1980, Benke et al. 1985, Gregory et al. 1991).

The role of downed wood in forested wetlands, however, remains poorly understood. Because of the intermediate position of forested wetlands in the continuum from dry uplands to permanently flooded aquatic systems, the function of downed wood may differ from ecosystems at either end of the continuum (Harmon et al. 1986). Among the factors that may be substantially different are wood decomposition rate, the primary decomposers, mobility of the downed wood, and its role in overall nutrient budgets (Harmon et al. 1986, Cragg 1993, Polit and Brown 1996).

The role of downed wood in mangrove forests, in particular, has been largely ignored (Robertson et al. 1992) despite evidence that it may be significant. For instance, the gradual breakdown of downed wood in a mature *Rhizophora* spp.-dominated forest in north Queensland, Australia proved to be nearly as important as leaf litter consumption by crabs in overall carbon flux patterns on the forest floor (44 vs. 62 g C m^{-2} yr^{-1}; Robertson and Daniel 1989a).

The amount of downed wood within a particular forest type, and therefore possibly its ecological importance, has been shown to vary considerably based on factors such as stand age, past management practices, insect and disease outbreaks, and the frequency of storms (Spies et al. 1988, Green and Peterken 1997, Lee et al. 1997, Sturtevant et al. 1997, Wei et al. 1997, Kirby et al. 1998). Mangrove forests also show variations in the quantity of downed wood, although such variation has seldom been documented. Robertson and Daniel (1989a), for example, found an order of magnitude less downed wood in a young stand of mangroves than in an older stand with larger trees and a higher total aboveground biomass. Tropical cyclones, by causing periodic large pulses of downed wood to enter mangrove ecosystems, can be another important source of spatial and temporal variation (Jiménez et al. 1985, Smith et al. 1994).

In our study, we measured downed wood in mangrove stands on three small western Pacific islands. Our primary goals were (1) to examine patterns of variability in the quantity of downed wood in mangrove ecosystems with generally similar species composition but different stand histories, (2) to provide a general characterization of downed wood in a region with no previously published accounts, and (3) to investigate the relationship between harvesting practices and the amount of downed wood.

METHODS

Study Areas

Downed wood was measured on the islands of Kosrae (5° 19′ N, 163° E), Pohnpei (6° 54′ N, 158° 14′ E), and Yap (9° 33′ N, 138° 09′ E) in the Federated States of Micronesia (Figure 1). Kosrae and Pohnpei are high volcanic islands of about 11,200 and 35,500 ha, respectively. The mountainous, heavily forested interiors of these islands are surrounded by relatively narrow coastal plains on which most of the people, roads, and agricultural developments are found. Annual rainfall is approximately 5,000 to 6,000 mm, and there is no pronounced dry season. Kosrae and Pohnpei are on the edge of the tradewind belt and are rarely affected by typhoons; none have passed closer than 90 km to either island since 1945 (Ray 1997). Yap consists of four metamorphic, volcanic islands that are older and not so high or rugged as Kosrae and Pohnpei. Their total area is about 9,700 ha. Annual rainfall on Yap averages about 3,000 mm; the driest months of the year are February to April, when rainfall averages less than 180 mm per month. Typhoons are a much more frequent occurrence on Yap; 11 typhoons passed within 50 km of the islands from 1945–1996, and another 10 passed between 50 and 100 km (Ray 1997).

Mangroves occupy approximately 14% of the land area of Kosrae, 15% of Pohnpei, and 12% of Yap (MacLean et al. 1988). The three most common mangrove species on all three islands are *Bruguiera gymnorrhiza* (L.) Lam., *Sonneratia alba* J.E. Sm., and *Rhizophora apiculata* (Jack) Voigt. Seven (Kosrae and Pohnpei) to eleven (Yap) other mangrove species are present but are generally much less common (MacLean et al. 1986, Whitesell et al. 1986, Falanruw et al. 1987, Duke 1999).

On Kosrae, downed wood measurements were carried out in the immediate vicinity of the 12 cluster plots described in Ewel et al. (1998a). These plots are located in four small river basins, two on the northern side of the island and two on the southern side. Each cluster plot consists of five sampling points spread over an area of approximately 1.2 hectares. The plots are characterized as occurring within fringe, riverine, or interior hydrogeomorphic zones (*sensu* Woodroffe 1992), depending on their location within the river ba-

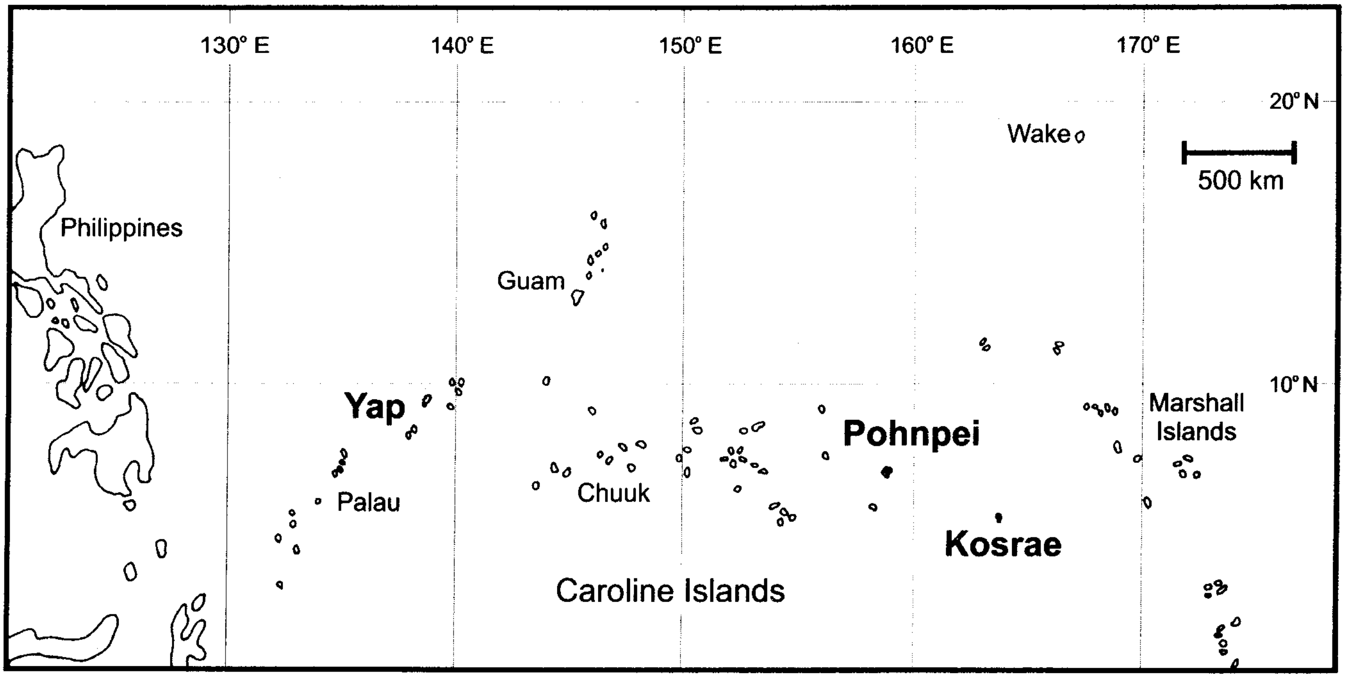

Figure 1. Location of Kosrae, Pohnpei, and Yap, Federated States of Micronesia.

sins. On Pohnpei, measurements were made in the three plots of Fujimoto et al. (1995). These plots are all located on the southeastern part of the island. Two are 1 ha (50 × 200 m) in size (PE1 and PC2), and one is 0.18 ha (30 × 60 m; PE2). PE1 and PE2 are described as occurring in an estuary environment, while PC2 is described as a coral reef environment (Fujimoto et al. 1995). On Yap, three previously unstudied stands were selected, one on the east side of the islands (Dechumur) and two on the west (Gurung and Maa). All three stands would be classified as the coral reef type by Fujimoto et al. (1995). All the sites on Pohnpei and Yap have both fringe and interior characteristics *sensu* Woodroffe (1992).

The selected stands (Table 1) are believed to be representative of the mature and old-growth forests found on each of the islands. The stands on Kosrae are most likely the oldest but have been disturbed more by harvesting than those on Pohnpei and Yap (Devoe 1994). On Kosrae, mangrove wood is used extensively for fuel and as a source of poles for construction of cooking huts and other structures (Lal 1990, Devoe 1994, Naylor and Drew 1998). Many households harvest wood for their own subsistence needs, and there are also several commercial harvesters (Lal 1990, Naylor and Drew 1998). Harvesting most frequently is done by removing one to a few trees from any one location. Gaps created by harvesting average only 164 m^2 (SE = 56) in size (Ewel et al. 1998b), but there is some indication that harvested gap size is increasing (Pinzón 1998). *Rhizophora* spp. are strongly preferred for fuelwood on Kosrae because of their clean-burning properties and the flavor they impart to food, but *Bruguiera gymnorrhiza* and *Xylocarpus granatum* König are also used occasionally (Lal 1990).

The stands on Pohnpei are well-developed forests that may have originated following the major typhoon that struck the island in 1905 (Hezel 1995, Cole et al. 1998). The stands on Yap have been subject to fairly frequent typhoons and are shorter in stature than those on the other two islands. One recent typhoon, Fern, struck Yap seven months before this study was conducted, with sustained winds of 148 km hr^{-1} and gusts up to 185 km hr^{-1}.

Downed Wood Measurement

The quantity of downed wood was estimated using the line-intersect technique (Van Wagner 1968, Brown 1974). On Kosrae, two 100-m transects were established within the 1.2-ha area comprising each of the 12 cluster plots. On Pohnpei and Yap, one or two transects were established at each site; the length varied depending on the size and shape of the stand or plot. Along all transects, a 20-m sampling line was established every 25 m on a randomly selected azimuth. At least six sampling lines were established at each site; most sites were sampled with ten or more sampling lines. Along the entire 20-m length of the sampling line, the diameter of every piece of downed wood greater than 7.5 cm in diameter was measured and classified into three decay classes (sound, intermediate,

Table 1. Characteristics of sampled stands within mangrove wetlands on the Islands of Kosrae, Pohnpei, and Yap, Federated States of Micronesia.

Location	Dominant Species	Tree ha^{-1}	BA (m^2 ha^{-1})	Mean diameter (cm)	Mean canopy height (m)
Kosrae					
Finkol	SOAL, BRGY, RHAP[1]	1444	27.4	9.3	7.7
Okat	SOAL, BRGY, RHAP	502	32.7	20.7	15.2
Utwe	SOAL, BRGY, RHAP	443	36.1	21.8	12.5
Yela	SOAL, BRGY, RHAP	454	36.4	25.3	14.2
Pohnpei[2]					
PC1	RHAP, SOAL, BRGY	604	49.5	17.9	16.6
PE1	SOAL, BRGY, XYGR	800	59.7	26.2	18.7
PE2	XYGR, RHAP, BRGY	1481	72.9	22.8	15.9
Yap					
Maa	SOAL, RHMU, BRGY	901	44.2	25.4	n.d.
Gurung	SOAL, RHMU, BRGY	907	41.3	19.8	n.d.
Dechumur	RHAP, BRGY[3]	1071	43.9	21.5	n.d.

[1] Species arranged in descending order from left to right based upon stand volume of each species. SOAL = *Sonneratia alba*; BRGY = *Bruguiera gymnorrhiza*; RHAP = *Rhizophora apiculata*; RHMU = *R. mucronata*; XYGR = *Xylocarpus granatum.*
[2] Data from surveys of R. Tabuchi, Shikoku Research Center, Kochi, Japan.
[3] Only two species present in stand.

and rotten). Three classes of fine downed wood were subsampled over shorter portions of the sampling line. Wood in the 0–1 cm class was sampled over the first 2 m of each line, and wood in the 1–2.5 cm and 2.5–7.5 cm classes were sampled over the first 4 m.

The volume of downed wood was calculated for each class using the equation $v = \pi^2\Sigma d^2/8l$, where v is volume (m^3/m^2), d is diameter of piece (m) and l is length of sampling line (m) (Van Wagner 1968). Mass was calculated using conversions of 0.5 tons m^{-3} for wood $<$ 7.5 cm and 0.5, 0.35, and 0.20 tons m^{-3} for larger wood in the sound, intermediate, and rotten categories, respectively. Lack of on-site facilities precluded calculating conversion rates from wood samples, so the conversions we used are based on results reported for similar species by Robertson and Daniel (1989a) and on observed relationships between decay classes reported by Polit and Brown (1996).

Estimation of Wood Remaining After Harvesting

Wood remaining from trees that had been harvested was sampled in 9 of the 12 cluster plots on Kosrae. This survey was done during May–August 1997, and each of the plots was sampled once. In some cases, harvested trees are caught by neighboring trees during felling operations; the neighboring trees are then felled but not necessarily to be cut into shorter pieces and removed. Because these cut, but unharvested trees are considered part of the ‘‘felling event,’’ they were also measured. Trees that were sampled lay within 5 m of a 30-m-long transect along a random azimuth from one of the 5 points within each cluster plot (Ewel et al. 1998a). Because stems are usually cut into shorter pieces right where they lay after being felled, we were able to measure the length of the stem that had been removed. By measuring the length and diameter of the stump and of successive parts of the stem that had been left on the site, we obtained estimates of the percent of stem volume (to a 10 cm top diameter) that had been removed.

Statistical Analysis

A nested ANOVA was used to compare downed wood levels among islands, with site (i.e., the four river basins in Kosrae, the three plots in Pohnpei, and the three stands in Yap) nested within island. Islands were treated as fixed effects and sites as random effects for this analysis. In addition, a randomized complete block design was used to analyze for differences in downed wood amongst the three types of hydrogeomorphic zones (fringe, riverine, and interior) on Kosrae, with zones (fixed effect) as treatments and river basins (random effect) as blocks. Because the volumes per line ranged over three orders of magnitude, the data (+0.5) were log-transformed to improve the homogeneity of variances. Differences among means were compared using Tukey’s studentized range test.

Table 2. Mean total volume and mass of woody debris (± 1 s.e.) on sample plots within mangrove wetlands on the Islands of Kosrae, Pohnpei, and Yap, Federated States of Micronesia. Values followed by the same letter within a particular variable are not statistically different at α = 0.05.

Diameter/Decay Class	Mean volume (m^3 ha^{-1})				Mean mass (tons ha^{-1})			
	Kosrae	Pohnpei	Yap	Mean	Kosrae	Pohnpei	Yap	Mean
Fine (≤ 7.5 cm)								
0.0–1.0 cm	0.37c	0.79b	0.91a	0.69	0.19b	0.39a	0.46a	0.35
	(0.03)	(0.10)	(0.08)		(0.01)	(0.05)	(0.04)	
1.0–2.5 cm	1.83b	5.15a	6.07a	4.35	0.92b	2.58a	3.03a	2.17
	(0.16)	(0.51)	(0.65)		(0.08)	(0.26)	(0.32)	
2.5–7.5 cm	8.03a	9.55a	6.49a	8.02	4.02a	4.77a	3.25a	4.01
	(0.91)	(1.59)	(1.29)		(0.45)	(0.80)	(0.64)	
Coarse (> 7.5 cm)								
Sound	8.80a	2.02a	1.18a	4.00	4.40a	1.01a	0.59a	2.00
	(2.43)	(1.01)	(0.72)		(1.22)	(0.51)	(0.36)	
Intermediate	30.69a	7.34b	4.97b	14.33	10.74a	2.57b	1.74b	5.02
	(6.36)	(2.31)	(1.50)		(2.23)	(0.81)	(0.52)	
Rotten	54.49a	18.26b	15.98b	29.58	13.62a	4.57b	3.99b	7.39
	(9.45)	(5.60)	(4.57)		(2.36)	(1.4)	(1.14)	
TOTAL	104.22a	43.11b	35.10b	60.81	33.88a	15.89b	12.89b	20.89

RESULTS

Quantity and Composition of Downed Wood

The mean total volume of downed wood for all sites was 60.8 m^3 ha^{-1} (Table 2). Large, rotten wood accounted for the largest quantity (49% of the mean total volume). Large, intermediate (24%), and small wood (<7.5 cm diameter; 22%) accounted for smaller proportions, while large sound wood was of minor importance (7%). The spatial distribution of the downed wood was highly variable. Some sampling lines intersected almost no downed wood (<1 m^3 ha^{-1}), whereas one line on Kosrae intersected a very large, fallen *S. alba* and several other large logs and had a calculated volume of 1009 m^3 ha^{-1}.

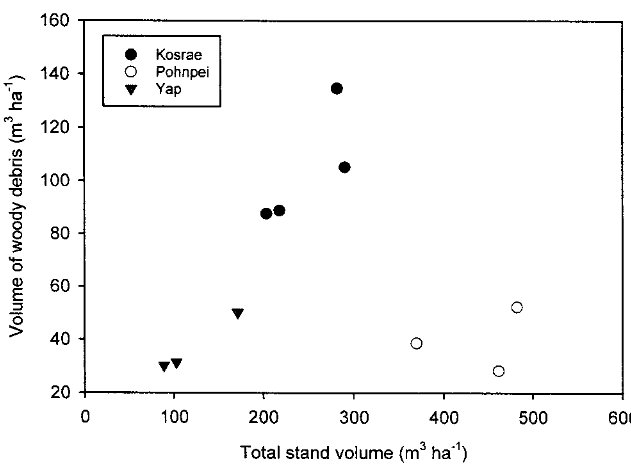

Figure 2. Relationship between total standing wood volume and volume of downed wood.

The mean total mass of downed wood was 20.9 t ha^{-1} (Table 2). Large, rotten wood again accounted for the largest proportion of the total, but due to its smaller mass per unit volume, its proportion of total mass (36%) was lower than for volume. Partly because of its higher mass-to-volume ratio, wood less than 7.5 cm diameter accounted for nearly as much biomass as large, rotten wood (32%).

The sites on Kosrae had more than twice the mean volume of downed wood found on Pohnpei or Yap, a highly significant difference ($F_{2,7}$ = 11.67, p ≤ 0.0001). There were also significant differences among islands in the volumes of all classes of downed wood except the 2.5–7.5 cm class of smaller wood and large, sound wood (Table 2).

Relationship of Standing Wood Volume to Downed Wood

There was no linear correlation between the total volume of standing wood and the volume of downed wood (r = 0.00017, p = 0.9996). Substantially different relationships between the amounts of standing and downed wood are evident among the islands (Figure 2). The sites on Yap have relatively low volumes of both types of wood, whereas sites on Kosrae have intermediate standing volumes and high volumes of downed wood, and those on Pohnpei have high stand volumes and low amounts of downed wood.

Variation Among Hydrogeomorphic Zones on Kosrae

For the island of Kosrae, where data were collected within the context of hydrogeomorphic zones, there

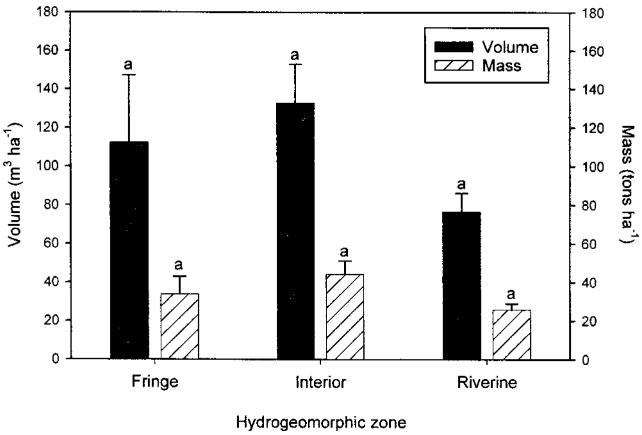

Figure 3. Volume and mass of downed wood by hydrogeomorphic zone for Kosrae study sites.

appeared to be less downed wood in the riverine zone (Figure 3), but mean total volume and mass among zones were not significantly different for mean total volume ($F_{2,5} = 3.04$, $p = 0.0517$) and for mean total mass ($F_{2,5} = 2.30$, $p = 0.1963$).

Wood Remaining Following Harvesting on Kosrae

Only the three most common species were represented among the 45 trees that were felled: 29 *B. gymnorrhiza,* 14 *R. apiculata,* and 2 *S. alba* (Table 3). Fourteen of the *B. gymnorrhiza* trees were not cut up after felling, nor were one *R. apiculata* and one *S. alba,* suggesting that these trees were felled because they had snagged another. Among the trees that were cut up, 39% and 42% of the stem volume of wood from *R. apiculata* and *B. gymnorrhiza* were removed, respectively. There was no difference among species in mean diameter of the felled trees (Table 3).

Table 3. Characteristics of trees felled (± 1 s.e.) on Kosrae, Federated States of Micronesia.

	Trees censused		Trees cut after felling		
Species	Number	Diameter (cm)	Number	Diameter (cm)	Percent stem volume removed
BRGY[1]	29	27.9 (1.7)	13	25.5 (1.7)	42
RHAP	14	27.7 (1.6)	13	27.7 (1.7)	39
SOAL	2	32.1 (4.9)	1	39.0 (n.d.)	24

[1] See species abbreviations for Table 1.

DISCUSSION

The amount of downed wood found in this study is not exceptional when compared to mature and old-growth upland forests in both temperate and tropical regions. Downed wood in temperate deciduous forests typically ranges from 20 to 49 t ha^{-1}, 5 to 51 t ha^{-1} have been reported for moist tropical forests, and conifer forests in the Pacific Northwest may have from 200 to 550 t ha^{-1} (Harmon et al. 1986, 1995).

Compared to both temperate and tropical forested wetlands, however, the quantity of downed wood in the Micronesian mangrove forests is relatively large, especially on Kosrae. The overall mean of 20.9 t ha^{-1} is considerably greater than the 6.6 t ha^{-1} estimate for an Illinois floodplain forest (Polit and Brown 1996) and the 9.5 t ha^{-1} reported for a mature *Rhizophora* spp. dominated forest in north Queensland (Robertson and Daniel 1989a). In general, mangroves and other forested wetlands seem to have relatively low amounts of downed wood compared to upland forests, possibly due to higher rates of decomposition and organic matter export (Polit and Brown 1996, Lugo 1997), although this remains to be demonstrated for most types of forested wetlands.

There are at least two reasons why the quantity of downed wood in Micronesian mangroves might be greater than at the north Queensland mangrove site (which is the most comparable site for which downed wood data is available). First, the stature of the forests is larger in Micronesia. As a first approximation, downed wood might be expected to be positively correlated with living biomass (Robertson and Daniel 1989a, Harmon and Hua 1991). Although the mean heights of the trees on Kosrae and Pohnpei are similar to the height range of the mangroves in Queensland (10–15 m; Robertson and Daniel 1989a), many of the trees on Kosrae and Pohnpei exceed 25 m. Also, exceptionally large *Sonneratia alba* trees occurred at some of the Micronesian sites, many of which have a dbh well in excess of 1 m (Cole et al. 1998). These trees occasionally fall and frequently shed branches larger than many whole trees; these very large pieces of wood were shown to contribute significantly to the total amount of downed wood in some sites.

Second, the relatively high level of cutting occurring in some of the Micronesian swamps may be adding substantially to the amount of downed wood. Evidence of cutting is particularly conspicuous in Kosrae. The north Queensland site, on the other hand, is described as "generally unaffected by human activities" (Robertson and Daniel 1989a) and no tropical cyclones have struck the area in over 50 years (Smith and Duke 1987). While harvesting can lead to decreases in downed wood in some managed forests (Harmon et al.

1986, Green and Peterken 1997), the relatively large amounts of downed wood in Kosrae seem to be due primarily to harvesting practices on that island, which result in a large quantity of felled but un- or underutilized, trees. No wood at all had been removed from just over one-third of the cut trees we sampled on Kosrae and, of those that had been cut up, less than half of the stem volume was removed from the forest. Harvesting practices on Kosrae seem to be the single biggest factor causing the overall difference in downed wood between the Micronesian and north Queensland sites.

The impact of such harvesting practices on ecosystem functions is unknown but may include several important effects. Density of mangrove seedlings is higher on microsites adjacent to downed wood, due perhaps to the trapping of propagules by the downed wood and protection of seedlings from floating debris and wave action (Pinzón 1998). Seedlings adjacent to downed logs also may have higher growth rates, especially adjacent to well-decayed logs, where nutrient availability may be greater.

The effect of downed wood on quantity and species composition of crabs, including the interaction of downed wood and increased exposure of substrates to direct sunlight, should be investigated. Mangrove crabs play a major role in processing detritus in some mangrove ecosystems (Robertson 1986, Robertson and Daniel 1989b), and in Micronesia, they are also an important source of cash or in-kind income (Lal 1990, Naylor and Drew 1998). Some mangrove crab species (e.g., *Scylla* spp.) Seem to have a tendency to locate their burrows near logs and stumps. It is possible that altering the pattern and availability of downed wood might influence the numbers and species composition of crabs, which in turn might cause differences in litter processing, nutrient cycling, and propagule predation.

The importance of downed wood and the effect of anthropogenic changes in its amount may vary among hydrogeomorphic zones. Although differences in the amount of downed wood among the three zones on Kosrae were not statistically significant, the high spatial variability (partly because of harvesting; Pinzón 1998) may have masked biologically important differences. The high rainfall in Micronesia apparently reduces the difference in site characteristics such as porewater salinity and redox potential (Ewel et al. 1998a), but differences among the zones in other regions have been found for factors such as net primary productivity, litterfall, and form of organic matter exported (Twilley et al. 1986). Future studies on the role of downed wood in mangrove ecosystems might be effectively conducted within the hydrogeomorphic zone context.

The relationships among stand structure, disturbance history, and amounts of downed wood at our sites are complex and merit further investigation. The reason for the lack of correlation between amounts of standing wood and downed wood among our sites is not clear, particularly for the sites on Pohnpei and Yap, where disturbance from harvesting is less than on Kosrae. It is possible, due to the catastrophic typhoon of 1905 (Hezel 1995), that the sites on Pohnpei, despite their high volume of standing wood, are younger than the others and have not yet begun to produce large amounts of downed wood from natural mortality.

The amount of downed wood on Yap, while high compared to forested wetlands in other regions, is lower than might be expected given the recent passage of a typhoon. Forests that have experienced multiple wind disturbance events may be more resistant to damage in later events (Everham and Brokaw 1996). One possible mechanism for increased resistance on Yap is the development of a lower, more uniform canopy. Although we did not collect height data from our sites on Yap, canopy height on that island tends to be 5 to 10 m shorter than on Kosrae and Pohnpei (T.G. Cole, U.S.D.A. Forest Service, unpublished data), and there are very few large, emergent trees. Also, trees susceptible to windthrow may be eliminated more quickly on Yap, thereby reducing the number of such trees available for destruction in any single storm.

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