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Woody Debris in the Mangrove Forests of South Florida[1]

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ABSTRACT

Woody debris is abundant in hurricane-impacted forests. With a major hurricane affecting South Florida mangroves approximately every 20 yr, carbon storage and nutrient retention may be influenced greatly by woody debris dynamics. In addition, woody debris can influence seedling regeneration in mangrove swamps by trapping propagules and enhancing seedling growth potential. Here, we report on line-intercept woody debris surveys conducted in mangrove wetlands of South Florida 9–10 yr after the passage of Hurricane Andrew. The total volume of woody debris for all sites combined was estimated at 67 m^3/ha and varied from 13 to 181 m^3/ha depending upon differences in forest height, proximity to the storm, and maximum estimated wind velocities. Large volumes of woody debris were found in the eyewall region of the hurricane, with a volume of 132 m^3/ha and a projected woody debris biomass of approximately 36 t/ha. Approximately half of the woody debris biomass averaged across all sites was associated as small twigs and branches (fine woody debris), since coarse woody debris >7.5 cm felled during Hurricane Andrew was fairly well decomposed. Much of the small debris is likely to be associated with post-hurricane forest dynamics. Hurricanes are responsible for large amounts of damage to mangrove ecosystems, and components of associated downed wood may provide a relative index of disturbance for mangrove forests. Here, we suggest that a fine:coarse woody debris ratio ≤ 0.5 is suggestive of a recent disturbance in mangrove wetlands, although additional research is needed to corroborate such findings.

Key words: Avicennia germinans; *disturbance; downed wood; Everglades National Park; Hurricane Andrew;* Laguncularia racemosa; *necromass;* Rhizophora mangle; *Rookery Bay National Estuarine Research Reserve; Ten Thousand Islands National Wildlife Refuge.*

Woody debris provides an often overlooked, yet potentially important component of mangrove ecosystems (Harmon *et al.* 1986). The slow decomposition of woody debris following a major disturbance (Spies *et al.* 1988), for example, has led to speculation that coarse woody debris serves to promote the long-term persistence and supply of nutrients in a forest ecosystem (Harmon & Hua 1991). Similarly, woody debris can persist for many years in tropical mangrove forests (Robertson & Daniel 1989) and can provide erosion control, promote soil pedogenesis, increase site water retention, serve as a potential source of fuel, serve as nursery beds for germinating seeds, and provide habitat for heterotrophic communities (Harmon *et al.* 1986). Specific to mangroves, woody debris may trap propagules (Pinzón *et al.* 2003), promote sedimentation (Krauss *et al.* 2003), and, as mentioned in Allen *et al.* (2000), potentially increase growth of seedlings proximal to debris stores.

Accordingly, mangrove wetlands in South Florida support diverse food webs, assist with water quality improvement, and protect coastlines against tropical storm surges (Odum *et al.* 1982, Twilley 1998). Coastal wetland communities are especially important in the Caribbean where tropical storm frequency is high. An estimated 38 storms impacted some part of the Everglades region since 1886 (Doyle and Girod 1997), while shifts in the carbon balance of coastal systems are expected under scenarios of greater storm frequency in the Caribbean (Scavia *et al.* 2002). The frequency of disturbance in mangrove wetlands is particularly important in comparing ecosystem properties across sites to avoid attributing changes to the wrong environmental gradient.

Disturbances to forests greatly influence the amount of woody debris on the forest floor (Sturtevant *et al.* 1997, Allen *et al.* 2000). Determining forest structural changes in response to different environmental impact scenarios (*e.g.*, hurricane, lightning strike), similarly, continues to be an effective way to model ecosystem response (Doyle & Girod 1997, Chen

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& Twilley 1998). Including woody debris in these assessments may be useful in accounting for site differences in productivity, community dynamics, or carbon biogeochemistry (Harmon & Hua 1991).

Jiménez *et al.* (1985) report on cases of mangrove tree mortality throughout the Caribbean, but do not include estimates of downed wood. Downed wood as a component of mangrove forest structure has been reported in only two other investigations (Robertson & Daniel 1989, Allen *et al.* 2000); both studies were from the old world tropics. The purpose of this study, therefore, is to provide an estimate of downed wood for the hurricane-prone mangrove wetlands of South Florida by testing whether the volume of downed wood varied with proximity to the path of a hurricane.

METHODS

STUDY SITES.—Downed woody debris was sampled from 23 mangrove sites spanning from Rookery Bay National Estuarine Research Reserve in southwestern Florida, to the Taylor River and Joe Bay areas in southeastern Florida (Fig. 1). All locations were initially selected based upon proximity to the path of Hurricane Andrew, which impacted the study region in August of 1992. The reported maximum sustained windspeed from Hurricane Andrew was 232 km/h (Armentano *et al.* 1995), and the eyewall of the storm was over the Everglades landscape for at least 4 h (Platt *et al.* 2000), with peak wind gusts, probably associated with tornado activity, ranging from 253 to 333 km/h. (Wakimoto and Black 1994). The strongest sustained winds from a hurricane generally occur around the eyewall (Jordan *et al.* 1960), yet tornadoes or unpredictable turbulent eddies spawning in areas to the immediate right of a storm's path (*cf.*, Novlan and Gray 1974) often register the greatest amount of damage (Shea and Gray 1973, Wakimoto and Black 1994). In order to understand potential differences in woody debris stores relative to the hurricane's path, we stratified our sampling locations into five regions. These regions included two that were of low hurricane impact, with RB-Right actually having lower sustained wind speeds than the other regions and TAY-Left escaping much of the wind damage by having a reduced forest stature. ENP-Left, ENP-Eye, and ENP-Right correspond to the immediate left (0–35 km), eyewall, and immediate right (0–35 km) of Hurricane Andrew's path, respectively (Table 1, Fig. 1).

All sites were interior forest locations associated with either a nearby river, creek, or embayment; overwash mangrove islands were not sampled. Forests were composed of three principal tree species: *Rhizophora mangle* L., *Avicennia germinans* L., and *Laguncularia racemosa* Gaertn. f. These species make up the majority of the surveyed downed woody debris. Trees of the mangrove associate, *Conocarpus erectus* L., were sparse and present only in TAY-Left and one site (SRU) along the Shark River.

Rainfall in the region is between 1010 and 1650 mm/yr depending upon location, occurrence of periodic droughts, and aperiodic tropical storms (McPherson *et al.* 2000). Prior to Hurricane Andrew, no major storm impacted our survey sites since 1960 (Hurricane Donna) and 1965 (Hurricane Betsy) (Craighead & Gilbert 1962, Doyle *et al.* 1995). Likwise, no major storm has impacted survey sites since 1992.

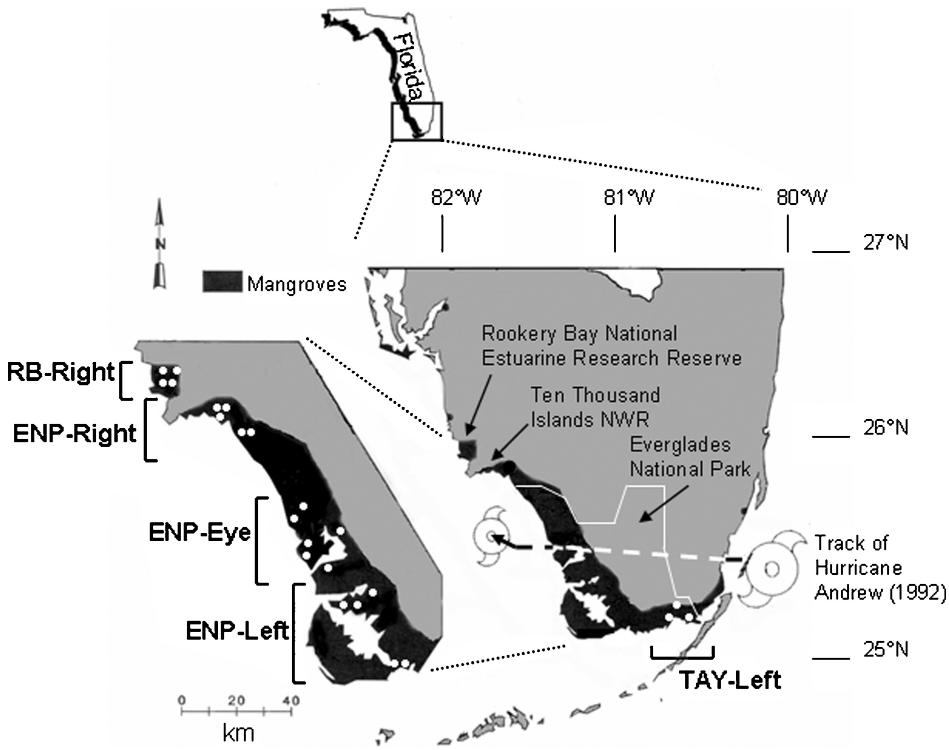

FIGURE 1. Location of field sampling sites along the southern and southwestern coasts of Florida, including Rookery Bay National Estuarine Research Reserve, Ten Thousand Islands National Wildlife Refuge, and Everglades National Park (*after* Doyle *et al.* 1995).

TABLE 1. *Mean total woody debris volume, mean forest canopy height, and mean percentage forest cover at 1 m above the ground by region, site, and location relative to the path of Hurricane Andrew (1992) for South Florida mangrove forests.*

Region	Site	Descriptor	Location relative to the path of Hurricane Andrew	Mean woody debris volume (m^3/ha, ±1 SE)	Mean canopy height (m, ±1 SD)	Mean percentage cover (%, ± 1 SD)
RB-Right	Rookery Bay 1	RB1	Right	19.6 ± 3.4	11.8 ± 1.2	91.7 ± 2.8
RB-Right	Rookery Bay 2	RB2	Right	47.4 ± 10.0	10.1 ± 2.0	90.6 ± 2.9
RB-Right	Henderson Creek 1	HC1	Right	64.5 ± 23.8	10.8 ± 1.6	92.5 ± 3.4
RB-Right	Henderson Creek 2	HC2	Right	33.7 ± 6.2	10.3 ± 2.1	94.5 ± 1.6
ENP-Right	Ten Thousand Islands 1	TI1	Right	65.2 ± 19.8	11.5 ± 2.7	94.8 ± 0.8
ENP-Right	Ten Thousand Islands 2	TI2	Right	31.7 ± 4.8	11.8 ± 2.0	93.8 ± 2.2
ENP-Right	Ten Thousand Islands 3	TI3	Right	62.2 ± 8.5	11.9 ± 2.4	88.3 ± 3.6
ENP-Right	Everglades City 1	EC1	Right	147.9 ± 7.4	10.5 ± 1.1	85.2 ± 2.1
ENP-Right	Everglades City 2	EC2	Right	181.1 ± 36.7	10.4 ± 0.7	86.7 ± 7.2
ENP-Eye	Second Onion Bay	SOB	Eyewall	119.0 ± 38.4	9.9 ± 4.1	93.8 ± 2.5
ENP-Eye	Lostman's Key South	LKS	Eyewall	139.6 ± 47.4	12.4 ± 2.1	97.4 ± 1.0
ENP-Eye	Johnson Mound Creek	JMC	Eyewall	56.0 ± 3.9	6.5 ± 1.6	95.3 ± 1.8
ENP-Eye	North Highland Beach	NHB	Eyewall	166.2 ± 55.4	8.3 ± 1.3	95.6 ± 1.3
ENP-Eye	Broad River Middle	BRM	Eyewall	156.2 ± 42.6	9.9 ± 1.8	87.8 ± 5.1
ENP-Eye	Broad River Lower	BRL	Eyewall	157.3 ± 22.5	9.6 ± 1.2	90.1 ± 5.5
ENP-Left	Shark River Upper	SRU	Left	38.2 ± 6.2	6.8 ± 0.6	97.1 ± 1.0
ENP-Left	Shark River Middle	SRM	Left	45.5 ± 9.8	12.3 ± 1.3	96.9 ± 2.2
ENP-Left	Shark River Lower	SRL	Left	77.9 ± 13.5	18.2 ± 2.0	95.8 ± 0.8
ENP-Left	Flamingo 1	FL1	Left	55.3 ± 13.6	15.8 ± 1.4	95.8 ± 1.5
ENP-Left	Flamingo 2	FL2	Left	28.7 ± 8.6	15.8 ± 1.8	95.1 ± 1.0
TAY-Left	Taylor River Upper	TRU	Left	23.1 ± 5.1	1.9 ± 0.8	0.2 ± 0.0
TAY-Left	Taylor River Middle	TRM	Left	12.6 ± 3.4	1.9 ± 0.7	0.2 ± 0.0
TAY-Left	Joe Bay	JBA	Left	14.0 ± 3.6	1.6 ± 0.6	0.2 ± 0.0

WOODY DEBRIS MEASUREMENTS.—Downed wood was measured from May 2001 to October 2002 using a line-intercept technique originally described by Van Wagner (1968) and Brown (1974), and later applied to mangroves (Allen *et al.* 2000). On most sites, four 20-m-long transects were demarcated from two random azimuth offsets at 15 m from an established plot center. For Shark and Taylor River sites, between 6 and 12 nonoverlapping transects were established from fixed points 10 m apart along a systematic grid. Survey sites were separated into five regions as described above; between 16 and 31 transects were analyzed for each region.

Coarse woody debris >7.5 cm in diameter, intersecting the line at any location, was measured to 0.1 cm with metal calipers and categorized as sound, intermediate, or rotten. Rotten and intermediate classes were indicative of trees and debris downed by Hurricane Andrew, with classes being assigned based upon penetration ease of the metal calipers similar to Robertson and Daniel (1989). Volume adjustments were made for downed, rotten logs containing hollow cores by measuring the width of the remaining outside shell and subtracting the inner decomposed core volume. Fine woody debris between 1 and 7.5 cm was tallied as numeric counts over the first 4 m of the transect and separated into two diameter categories (1–2.5 cm; 2.5–7.5 cm). Fine debris with a diameter <1 cm was subsampled as numeric counts over the first 2 m of each transect.

Volume for fine woody debris from numeric count data and for coarse woody debris >7.5 cm in diameter was calculated as follows (Van Wagner 1968, Allen *et al.* 2000):

$$v = \frac{\pi^2\left(\sum d_i^2\right)}{8L} \times k \quad (1)$$

with v representing woody debris volume (m^3/ha), d_i as the diameter of an individual piece of woody debris (m), L as the sample line length (m), and k as the per hectare conversion constant (10,000 m^2/ha).

Approximate conversions from woody debris volume to mass were made to compare woody debris estimates among forests. We used density data for mangroves from Robertson and Daniel (1989), and from Polit and Brown (1996) we used relative scaling relationships of 0.5 t/m^3 for woody debris <7.5 cm and of 0.5, 0.35, and 0.2 t/m^3 for large woody debris classified as sound, intermediate, and rotten, respectively. Components of woody debris could not be identified conclusively to species and prevented our use of species-specific densities.

Average canopy height was measured on at least three codominant individuals per species on each site using a laser height device (Impulse 200, Laser Technology, Inc., Englewood, CO), and overstory canopy density was determined from four readings per plot at cardinal directions with a spherical densiometer (Model A, Forest Densiometers, Bartlesville, OK).

Statistical analysis.—The analysis was conducted as a split-plot design, since volume of downed wood within a sample region was not independent. An analysis of variance (ANOVA) with a nested error structure (*i.e.*, site within region) was used to determine if differences existed in combined downed woody debris volume (coarse + fine debris) among regions and for coarse woody debris volume and fine woody debris volume, separately, among regions. All data were log-transformed (+0.5) to improve normality and homogeneity of residual variances. Statistical groupings were determined with a Tukey's Studentized range test ($\alpha = 0.05$). Relationships between volume of downed wood and canopy height for a given range of predicted windspeeds were determined through linear regression. Windspeed estimates were derived for each site based on a hurricane simulation model (HURASIM) designed to simulate wind trajectory, magnitude, and circulation of Hurricane Andrew (Doyle 1998).

RESULTS

The average woody debris volume for all five regions was 67 m^3/ha. Differences in total woody debris volume (*i.e.*, coarse + fine debris) by sample region were significant ($F_{4,18} = 13.74$; $P \leq 0.001$), with large mean volumes (98–132 m^3/ha) associated with eyewall and immediate right-side impact zones of Hurricane Andrew (ENP-Eye and ENP-Right; Table 2). Total woody debris volume for these regions, however, differed statistically only from TAY-Left. Eastern Everglades sites (TAY-Left) around Joe Bay and the Taylor River Slough contained the smallest woody debris volume of 16 m^3/ha but were also characterized by very small trees (1.6–1.9 m) and an open canopy (0.2% canopy coverage; Table 1).

Differences were less pronounced when coarse and fine woody debris were analyzed separately. Although both coarse woody debris ($F_{4,18} = 9.10$; $P \leq 0.001$) and fine woody debris ($F_{4,18} = 7.09$; $P = 0.001$) estimates differed significantly for sample regions, comparative groupings among components varied slightly. In particular, coarse woody debris volume from only one region, TAY-Left, differed from all other regions. The same general trend was true for fine woody debris volume, with the exception that TAY-Left did not differ from fine woody debris estimates in either RB-Right or ENP-Left. There was greater consistency for fine woody debris estimates among sites than for coarse woody debris (Fig. 2).

Variation in total woody debris volume by region suggested a fairly strong damage signature from Hurricane Andrew even 9–10 yr following impact. Sites located in the storm's eyewall (ENP-Eye) and immediately to the right of the eyewall (ENP-Right) had from 32 to 181 m^3/ha (mean = 117 m^3/ha) of total woody debris, while all other sites contained a range for woody debris estimates of 13–78 m^3/ha (mean = 38 m^3/ha; Table 1). The relative proportion of fine woody debris versus coarse woody debris also shifted near the storm's eyewall, with larger pieces occurring in the region associated with tall trees and maximum sustained Hurricane Andrew windspeeds exceeding 220 km/h (ENP-Eye and ENP-Right; Fig. 2). Coarse debris comprised the largest percentage of downed wood in most surveyed mangrove stands, with a ratio of fine:coarse debris ranging from 0.37 to 0.82 on RB-Right, ENP-Right, ENP-Eye, and ENP-Left sites. Large standing woody stems are absent from scrub mangroves of TAY-Left and, therefore, sites have a reduced relative coarse woody debris composition (ratio of fine:coarse = 3.0; Fig. 2).

With the exception of the TAY-Left region, JMC, and SRU, surveyed stands had a canopy height of approximately 8–15 m (Table 1). No relationship existed between tree height and combined woody debris volume for plots experiencing maximum sustained windspeeds of 200–205 km/h, while a slightly positive relationship resulted from identical comparisons at higher windspeeds (Fig. 3). All forest understories of RB-Right, ENP-Right, ENP-Eye, and ENP-Left were nearly completely

TABLE 2. *Mean volume of woody debris (±1 SE) in South Florida mangrove forests. For volume sub-totals or overall totals, values followed by the same letter in the same row are not significantly different at $\alpha = 0.05$.*

Diameter/ decay class	Mean volume (m^3/ha)					
	RB-Right	ENP-Right	ENP-Eye	ENP-Left	TAY-Left	Mean
Coarse (>7.5 cm)						
Sound	0.00	0.26	0.00	0.15	0.00	0.09
	(–)	(0.26)	(–)	(0.15)	(–)	
Intermediate	9.47	11.22	11.54	11.29	1.36	9.28
	(3.00)	(3.50)	(2.76)	(2.02)	(0.68)	
Rotten	14.12	56.12	85.34	16.83	2.74	34.00
	(5.15)	(10.60)	(14.77)	(4.35)	(0.93)	
Subtotal	23.6 [a]	67.6 [a]	96.9 [a]	28.3 [a]	4.1 [b]	
Fine (≤7.5 cm)						
0.0–1.0 cm	1.41	2.53	1.16	1.03	0.19	1.20
	(0.16)	(0.54)	(0.12)	(0.09)	(0.04)	
1.0–2.5 cm	3.78	5.15	4.49	4.31	3.95	4.35
	(0.45)	(0.92)	(0.46)	(0.42)	(0.97)	
2.5–7.5 cm	12.53	22.36	29.88	17.79	8.06	18.48
	(1.98)	(3.62)	(3.54)	(2.44)	(1.72)	
Subtotal	17.7 [ab]	30.0 [a]	35.5 [a]	23.1 [ab]	12.2 [b]	
Total	41.3 b	97.6 ab	132.4 a	51.4 ab	16.3 c	67.4

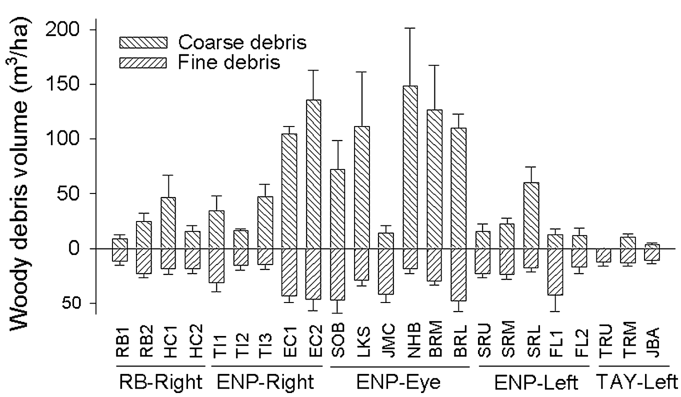

FIGURE 2. Distribution of fine and coarse woody debris by site and region (±1 SE) from South Florida mangrove wetlands.

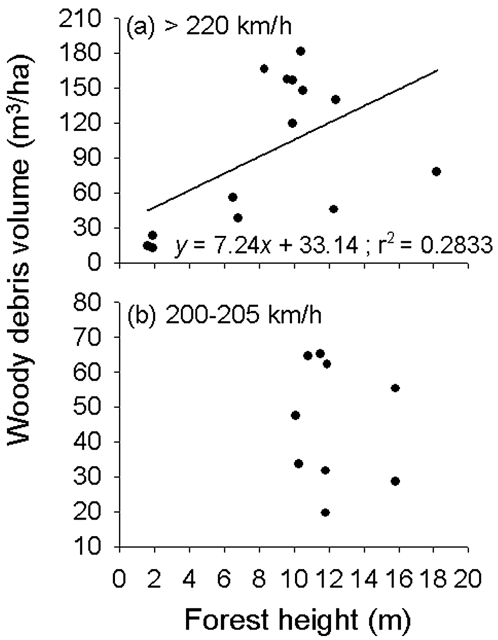

FIGURE 3. Relationship between woody debris volume (m^3/ha) and forest height for two ranges of HURASIM model-projected Hurricane Andrew windspeeds (a: >220 km/h; b: 200–205 km/h) from South Florida mangrove wetlands.

shaded by undamaged vegetation or by vegetative regrowth by the time woody debris surveys were conducted (85–97%; Table 1), indicating a high level of storm resiliency among South Florida mangroves. The scrub stature of TAY-Left vegetation did not provide shading at any of the sites.

DISCUSSION

Forest height confounds a relationship between maximum projected hurricane wind speeds and volume of woody debris (Fig. 3). In ENP-Eye, the reduced forest stature of JMC corresponded to less woody debris and was suggestive of a potential relationship between forest height and downed wood (Table 1). However, only 28 percent of the variation in the volume of woody debris can be explained by the linear relationship of woody debris with forest height in some areas (Fig. 3a). Similarly, forest height and woody debris are not correlated for plots with maximum estimated windspeeds of 200–205 km/h (Fig. 3b).

Sites associated with the greatest Hurricane Andrew storm winds had, as expected, larger amounts of woody debris. Transects that were run perpendicular to the prevailing azimuth of downed wood orientation resulted in large estimates of woody debris, which may have biased surveys for some transects. Within the eyewall, defined azimuths of downed logs were less pronounced (Doyle *et al.* 1995) and may have been influenced less by sampling with a random azimuth. The few transects that were established in Everglades City, just outside the eyewall, may have been affected slightly by this artifact. It is unlikely, however, that estimates were skewed greatly since wood volume was visibly high on these sites. Everglades City plots were also isolated as a noncontinuous forest patch. Not only were decomposition rates potentially lower on these drier sites, but also hurricane winds were fairly unimpeded by surrounding forests and may have resulted in greater impact than HURASIM-predicted maximum windspeeds of 220 km/h indicated. Overall, however, these results suggest that woody debris, which is associated with tropical storm activity, can be fairly high in South Florida mangrove ecosystems.

Downed wood represents a large carbon and potential nutrient pool in mangrove wetlands (Robertson & Daniel 1989, *cf.*, Harmon *et al.* 1986). Some 9–10 yr following Hurricane Andrew, woody debris is still prevalent on South Florida sites. Much of the downed wood, especially in the eyewall and areas to the immediate right of the storm path, were large trees and, therefore, had much slower decay rates relative to smaller woody debris. Mangrove trunk wood, for example, was still present in the understory after falling 15 yr previously (Robertson & Daniel 1989). Mangrove trees killed by Hurricane Donna (1960) in South Florida had stumps present in 1993, and many *R. mangle* boles were not completely decomposed even after 30 yr (T. Doyle, pers. obs.). The distrubution of downed wood in this investigation (Fig. 2) suggests that much of the intersected coarse woody debris, especially in ENP-Eye and ENP-Right, resulted directly from Hurricane Andrew. As a consequence of either the distance from Hurricane Andrew's influence or lower forest stature, respectively, estimates from RB-Right or TAY-Left may provide a better idea of background woody debris levels under a reduced relative hurricane incidence regime in South Florida.

Our survey technique, which differed slightly from Allen *et al.* (2000) in that we estimated wood that rotted away internally from large downed logs, accounted for overestimating woody debris based upon outside diameter measurements only. Since the majority of debris on our surveys was categorized as rotten (Table 2), and much of what was remaining was of downed logs likely to be around for many additional years, it was important to subtract the debris that had already disappeared. This was not a major consideration for surveys conducted by Allen *et al.* (2000) in Micronesia, since most downed logs were fully intact (J. Allen, pers. comm.). Long-term woody debris persistence has been noted in other surveys from tropical areas, but with trees remaining erect during the earlier stages of decomposition (*cf.*, Delaney *et al.* 1998, Santiago 2000). Most mortality in South Florida mangroves was not associated with attrition of large trees with a standing decomposition period, as in Jiménez *et al.* (1985), but rather from strong winds, with most decomposition occurring on the ground after tree or branch fall. Tree mortality due to lightning strikes (Smith *et al.* 1994) and single-tree attrition cannot be discounted, especially in RB-Right and TAY-Left plots. Shifts in the relative percentage of coarse woody debris versus fine woody debris by region (Table 2; Fig. 2) and the decomposition state of larger wood further indicates that the majority of the coarse woody debris in ENP-Eye and ENP-Right sites may have been from Hurricane Andrew. In fact, a fine:coarse woody debris ratio of 0.37 and 0.44 for ENP-Eye and ENP-Right, respectively, indicates that lower ratios may indicate a more recent disturbance when compared to sites of similar forest stature. Fine-to-coarse woody debris ratios exceeded 0.75 for RB-Right and ENP-Left; TAY-Left sites (3.0) were not comparable on the basis of a much reduced relative forest stature. A low fine-to-coarse woody debris ratio of 0.11 was found on mangrove sites on Kosrae, Federated States of Micronesia, under an accelerated individual tree harvest regime relative to mangrove forests of Pohnpei (0.56) and Yap (0.61: Allen *et al.* 2000). Such analyses of components of downed wood may provide a relative index of disturbance among similar mangrove forests in a geographical region; however, the variation in this metric indicates that more research is warranted.

Accordingly, fine woody debris comprised 36 percent of the total debris on a per volume basis (Table 2). At least that percentage of woody debris is probably not associated with direct hurricane influence, although delayed mortality of trees and subsequent woody debris fall cannot be discounted (Whigham *et al.* 1991, Smith *et al.* 1994, Sherman *et al.* 2001). Converting volume of fine woody debris into biomass equates to about 12.0 t/ha over all sites, or approximately one half of the total biomass of combined woody debris, which is estimated at 23.8 t/ha. Roughly, 14.1 t/ha of fine woody debris and 16.3 t/ha of coarse woody debris were recorded from eyewall and immediate right-side impact regions of Hurricane Andrew. Any disparity in percentages of volume and mass is associated with the large amount of coarse woody debris (>7.5 cm) categorized as rotten; decomposed mangrove wood is assumed to weigh 60 percent less than sound wood (Allen *et al.* 2000). Therefore, woody debris mass is not expected to follow the same patterns depicted for volume (as in Fig. 2). If surveys had been conducted just after the passage of Hurricane Andrew, much greater biomass of woody debris would have been likely on some sites (>40 t/ha). Even those projected values would have been quite low compared to some estimates as high as 550 t/ha from coniferous forests in the U.S. Pacific Northwest (Harmon *et al.* 1986). Much larger tree size and potentially slower decomposition rates in Harmon *et al.* (1986) can account for some differences relative to South Florida mangroves.

Volume and biomass of woody debris from South Florida mangroves represent high levels in some regions (*i.e.*, ENP-Eye, ENP-Right) and low to intermediate levels in others relative to published accounts from other mangrove wetlands. Robertson and Daniel (1989) reported 9.5 t/ha of woody debris in Australian mangrove wetlands, considerably less than our estimate from South Florida. However, woody debris volume and biomass from RB-Right, ENP-Left, and TAY-Left regions were less than debris stores from mangrove forests on Kosrae, Micronesia. A measured downed wood volume of 104 m^3/ha in Allen *et al.* (2000) exceeded levels found in areas impacted only moderately by Hurricane Andrew, but was similar to the volume of 98–132 m^3/ha reported from ENP-Eye and ENP-Right regions (Table 2). Large amounts of woody debris on Kosrae were attributed to forest stature, with tree DBH ranging from 15 to 130 cm and height ranging from 19 to 27 m (Ewel *et al.* 1998), and to an accelerated harvest rate (Allen *et al.* 2000). In South Florida, we can attribute the large volume of woody debris in some locations to a direct hurricane effect.

In general, mangrove wetlands support less woody debris than upland forests (Allen *et al.* 2000). Hydrological conditions of mangrove wetlands, which include a diversity of tide, precipitation, and river-flow regimes, can complicate direct comparisons with upland forests. Polit and Brown (1996) indicate that lowered stocks of woody debris may be partially explained by the higher decomposition rates of woody debris in wetlands. Also, decay of fallen mangrove wood may be quick at first, relative to most temperate systems, due in part to consistently higher temperatures, a prolonged wet season, and a combined terrestrial and marine fungal community in mangroves (*cf.*, Kathiresan & Bingham 2001). Although we did not have comparable upland sites in this investigation, our sites in Everglades City were much dryer than in other locations and were partially isolated hydrologically by a nearby road. These sites also supported some of the highest estimated levels of woody debris. Yet, a reduced moisture-related decomposition rate is not supported by Harmon *et al.* (1987), who reported an inverse relationship between woody debris decay and precipitation by geographic region. It may be difficult, however, to compare a trend based upon freshwater moisture in an upland environment with one based upon saltwater moisture from tidal inundation. Plus, soil waterlogging, as measured through soil oxidation–reduction, did not seem to influence the large volumes of woody debris (estimated at 136–428 m^3/ha) in a Hawaiian montane cloud forest (Santiago 2000).

Forest height was only a moderate predictor of woody debris in South Florida mangrove forests, even after stratifying forests by maximum sustained Hurricane Andrew windspeeds (Fig. 3). Total stand volume of a mangrove forest can also be a poor indicator of downed wood (Allen *et al.* 2000), yet the relationship between forest basal area and coarse woody debris can be strong (Santiago 2000). Increases in downed wood with an increase in maximum hurricane windspeed relative to preimpact standing biomass may be a more useful predictor of downed woody debris, since this method may account for three-dimensional aspects of tree and forest structure. Determining a more appropriate metric to predict the volume of downed wood in Florida mangrove forests may involve intensive studies on plot-level variation within forests and should be a focus of future woody debris research efforts on long-term ecological research plots.

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