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Decomposition and Mass of Woody Detritus in the Dry Tropical Forests of the Northeastern Yucatan Peninsula, Mexico[1]

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ABSTRACT

The decomposition rates and mass of fine (<10-cm-diameter) and coarse (>10-cm-diameter) woody detritus were measured in the dry tropical forests of the northeastern Yucatan Peninsula. The smallest mass of woody detritus was found in undisturbed stands: fine fractions averaged 4.7 Mg ha^{-1} and coarse fractions ranged between 13 and 38 Mg ha^{-1}. The largest mass of fine woody detritus (32.2 Mg ha^{-1}) was found in a hurricane-disturbed forest; whereas, the largest mass of coarse woody detritus (99.5 Mg ha^{-1}) was found in stands disturbed by catastrophic fires. A decomposition time-series study installed in 1989 indicated that decomposition rates varied greatly among species and diameters of branch segments. Over a 4-year period, the decomposition rate constant for fine woody detritus ranged from 0.151 to 1.019 $year^{-1}$ and that for coarse woody detritus ranged from 0.008 to 0.615 $year^{-1}$. The half-life of woody detritus increased 33-fold (among pieces ranging from 1 to 30 cm in diameter) for the most decay-resistant species (*Manilkara zapota*) but was relatively constant for the least decay-resistant species (*Bursera simaruba*). The wide range in decomposition rates observed in these forests indicates that the poor substrate quality of some species may override climatic (*e.g.*, warm temperatures) and biotic (*e.g.*, termites) factors favorable to rapid decomposition, leading to a substantial accumulation of woody detritus.

RESUMEN

Las tasas de descomposición y almacenamiento de detrito de madera fina (<10 cm de diámetro) y gruesa (>10 cm de diámetro) fueron medidos en bosques tropicales secos del noroeste de la Península de Yucatán, México. Las acumulaciones mas pequeñas de detrito de madera fueron encontrados, en rodales no perturbados: las partículas finas promediaron 4.7 Mg ha^{-1} y las fracciones gruesas variaron de 13 a 38 Mg ha^{-1}. Las acumulaciones mayores de detrito de madera fina (32.2 Mg ha^{-1}) se localizaron en un bosque perturbado por un huracan, mientras que las acumulaciones mas grandes de detrito de madera gruesa (99.5 Mg ha^{-1}) fueron encontrados en rodales perturbados por incendios catastróficos. Se estableció un estudio de series de tiempo de la descomposición en 1989 que indicó que los intervalos de descomposición variaron grandemente entre especies y diametros de partículas de madera. Después de un período de 4 años la constante de la tasa de descomposición para detrito de madera fina varió de 0.151 a 1.019 $año^{-1}$ y para detrito de madera gruesa de 0.008 a 0.615 $año^{-1}$. La vida media del detrito de madera se incrementó 33 veces entre partículas de 1 a 30 cm de diámetro para las especies más resistentes a la descomposición (*Manilkara zapota*) pero fué relativamente constante para las menos resistentes (*Bursera simaruba*). La gran variación de las tasas de descomposición observada en estos bosques indica que la calidad pobre del sustrato de algunas especies se debe a la nulificación de factores climaticos (ej. temperatura elevada) y bióticos (ej. termitas) que favorecen la descomposición rápida y la acumulación elevada del detritus de madera.

Key words: *coarse woody debris; decay; decomposition; fine woody debris; fire; hurricane; organic matter; tropical forests.*

DECOMPOSING DETRITUS IN FORESTS contributes to ecosystem functioning by reducing erosion and helping build soils (McFee & Stone 1966), providing wildlife habitat, and serving as stores of nutrients and water (Harmon *et al.* 1986, Franklin *et al.* 1987, Harmon & Chen 1991). It is also a major source of energy flow, serves as a seedbed for plants

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(Harmon & Franklin 1989), and is a major habitat for decomposers and heterotrophs (Graham 1925, Ausmus 1977, Harmon *et al.* 1986). Furthermore, woody detritus plays a major role in the global carbon cycle, both in terms of amount and function. Steady-state estimates (the only type of calculation possible given the paucity of data) indicate that 25–230 Pg of woody detrital carbon have not been included in current global inventories (Harmon & Chen 1991, Harmon *et al.* 1993). This omission takes on added significance because most of the carbon released to the atmosphere by forest clearing is the result of either the burning or decomposition of woody detritus (Harmon *et al.* 1993).

Despite the importance of woody detritus in forest ecosystems, this topic has, until recently, evoked little research. Most recent research on this subject has focused on the temperate zone, where in old-growth forests woody detritus comprises up to 14–22 percent of the aboveground biomass and 48–81 percent of the aboveground detritus (Grier & Logan 1977, Tritton 1980). Although there are less data for tropical ecosystems, it appears that dead wood can comprise up to 55–93 percent of the aboveground detritus in these forests as well (Edwards & Grubb 1977, Uhl & Kauffman 1990). In addition, tropical forests can store high absolute amounts of woody detritus. Values up to 20–50 Mg/ha have been recorded (Edwards & Grubb 1977, Uhl & Kauffman 1990). Such values are surprising given the general perception that decomposition rates of tropical wood are extremely high. One explanation for this apparent contradiction is that the earliest published studies on wood decomposition in tropical ecosystems are biased toward low-density, non-resistant species (Lang & Knight 1979) or small material expected to decompose rapidly (Hopkins 1966, Odum 1970, Collins 1981).

The overall objective of our study was to understand the dynamics of fine and coarse woody detritus in dry tropical forests and its role in the recovery of these forests from major disturbances such as hurricanes and fires. As no published work existed on woody detritus in this particular forest region, we began by examining the degree to which human-caused and natural disturbances influence the mass of such detritus there. Our hypothesis was that the greatest amount of woody detritus occurs in recently disturbed forests. This is a departure from the generally accepted view that woody detritus is greatest in the oldest forests (see Schlesinger 1977). We also were interested in systematically quantifying the range of decomposition rates for the dominant species in this ecosystem, with the underlying hypothesis that the chemical and physical nature of the wood (*i.e.*, substrate quality) could override favorable climatic and biotic factors and lead to low decomposition rates for many species. Finally, we examined woody detritus in a range of diameters to test the hypothesis that decomposition rate in these forests decreases with increasing diameter.

STUDY AREA

The general study area was located in the northeastern portion of Quintana Roo, Mexico (20°N, 88°W) (Fig. 1). The climate is seasonally dry, with a mean annual temperature of 25°C and precipitation of 1100 mm per year (Whigham *et al.* 1990). Precipitation is highly variable seasonally and from year to year (Whigham *et al.* 1991). The climate would support tropical dry to very dry forest in the Holdridge life zone system (Holdridge *et al.* 1971). The forests were classified as Selva mediana subperennifolia by Miranda (1958) and have a canopy height between 10 and 20 m. Although there are over 200 species attaining tree stature in the area, the common species in order of dominance include *Manilkara zapota* (L.) van Royer, *Talisia olivaeformis* (HBK.) Radlk., *Gymnanthes lucida* Swartz, *Brosimum alicastrum* Swartz, *Drypetes lateriflora* (Swartz) Drug & Urban, *Blomia cupanioides* Mir., *Coccoloba diversifolia* Jacq., *Beaucarnea pliabilis* (Baker) Rose, *Bursera simaruba* (L.) Sarg., and *Myrcianthes fragrans* (Sw.) McVaugh (all of which will hereafter be referred to by genus). The topography has low relief, and elevations are generally less than 25 m. Soils are shallow, highly organic, classified as lithosol-redzina (Whigham *et al.* 1990), and are derived from Miocene and Pliocene limestones (Back & Hanshaw 1970, Escalante Rebolledos 1986).

Prior to the extensive damage caused by Hurricane Gilbert in 1988 (Olmsted *et al.* 1989) and fires in 1989, the main use of the forest stands studied appears to have been limited to the extraction of *Manilkara* sap and the removal of palms (*Thrinax radiata* Lodd. ex. J. A. Schult, *Coccothrinax readii* Quero) and small understory trees such as *Gymnanthes* for local construction materials. Until recently, there has been little agricultural clearing in this part of the Yucatan except for shifting agriculture.

Four forest stands were sampled that were representative of a range of forest compositions and past disturbances (Fig. 1 and Table 1). Chunyxche, located 29 km south of Tulum, was the least dis-

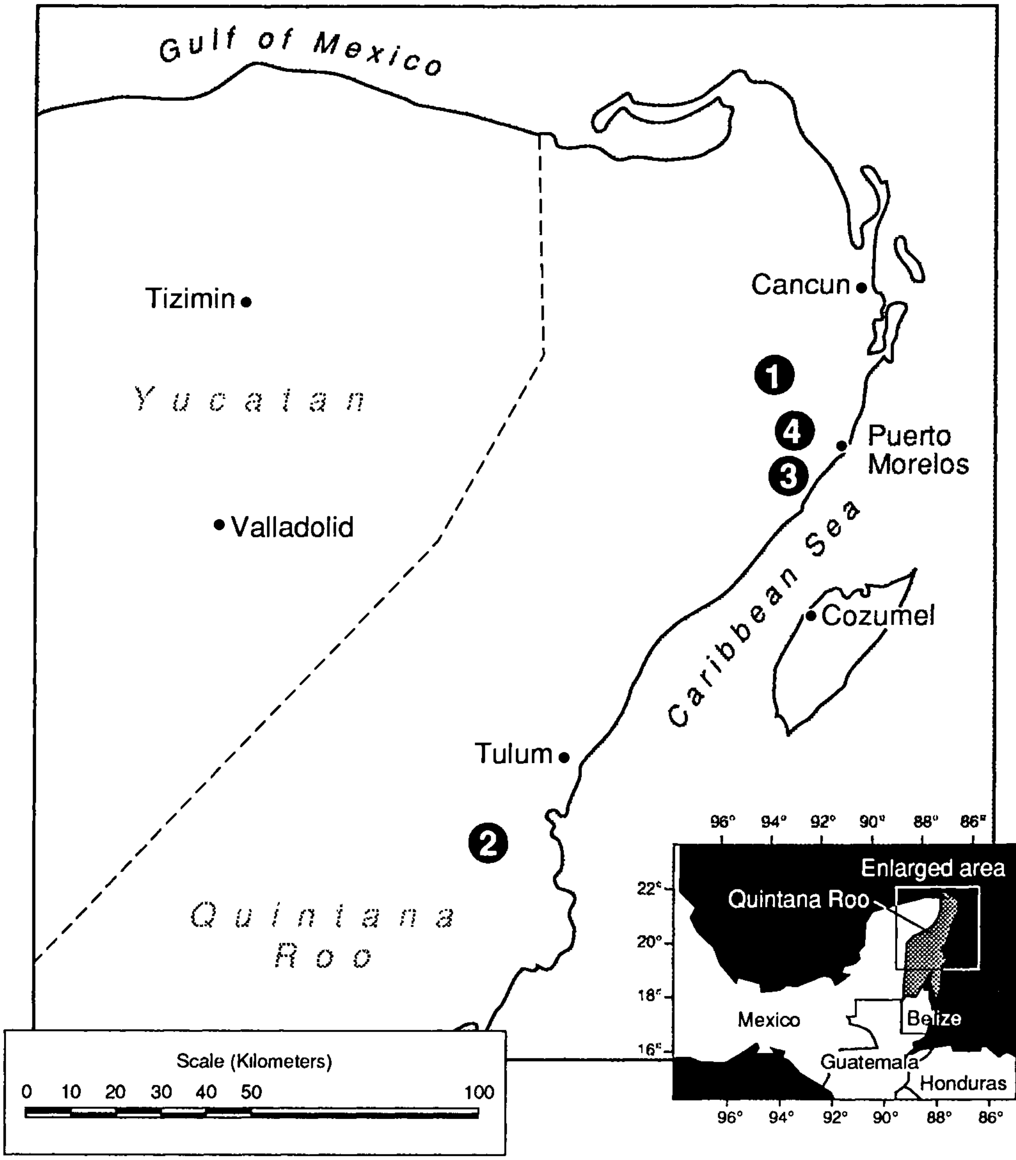

FIGURE 1. Location of the forest stands within the Quintant Roo, Mexico, study area (1) Bosques de Cancun, (2) Chunyxche, (3) Rancho San Filipe, and (4) Vallarta Road.

turbed and probably most productive forest. Rancho San Filipe, located 10 km south of the village of Puerto Morelos, had been moderately disturbed by Hurricane Gilbert (Whigham *et al.* 1991) and more severely by a subsequent fire that burned the northernmost portion of the ranch in September 1989. Bosques de Cancun, located 27 km southwest of Cancun, had been subjected to moderate hurricane and moderate fire damage that killed about half the trees. The Vallarta Road stand, located 10 km west of Puerto Morelos, had been subjected to little hurricane damage but severe fire damage that killed all the trees. Of the forest stands sampled, Vallarta Road was the only one with evidence of major clearing within the last 50 years.

METHODS

MASS OF FINE WOODY DETRITUS.—Mass of fine woody detritus (FWD) (<10 cm in diameter) on the forest

TABLE 1. *Mean predisturbance basal area and aboveground biomass per unit area of the stands sampled.*[a]

Stand	Basal area (m^2/ha)	Live biomass[b] (Mg/ha)	Date sampled	Number of plots
Bosques de Cancun	24.0 (1.0)[c]	112 (28)	1991	4
Chunyxche	39.7 (6.4)[c]	209 (22)	1991	2
Rancho San Filipe	26.9 (0.9)[d]	133 (6)	1989–90	12
Vallarta Road	28.5 (3.4)[c]	94 (16)	1991	4

[a] Values are give in terms of the mean (and standard error).
[b] Estimated with equations of Brown *et al.* (1989) for diameters at breast height within 40 m × 40 m plots.
[c] I. Olmsted, pers. obs.
[d] D. Whigham, pers. obs.

floor was sampled during February 1992 in the unburned stands at Bosques de Cancun, Chunyxche, Rancho San Filipe, and Vallarta Road. In each stand all FWD was removed and weighted from 20 randomly located 1 m × 1 m quadrats. Subsamples were removed to determine moisture content.

It was not possible to use small plots to measure suspended FWD. For trees defoliated and killed by the hurricane but left standing, we estimated the mass of suspended FWD by measuring the diameters of such trees in the same 40 m × 40 m plots used to measure coarse woody detritus (CWD) and applying the equation of Brown *et al.* (1989) for dry tropical forests. We then assumed that 20 percent of the aboveground woody mass per unit area was <10 cm in diameter.

In the burned plots, mass of FWD was also estimated by measuring the diameters of the trees killed by the fire in 40 m × 40 m plots and then applying the equation of Brown *et al.* (1989). As most the FWD present on the forest floor at the time of the fires was presumably consumed, we assumed that most of the FWD present on the floor after the fires came from trees killed thereafter. As with our estimates for hurricane-killed trees, we assumed that 20 percent of the total aboveground woody biomass was <10 cm in diameter.

MASS OF COARSE WOODY DETRITUS.—Unlike the case with FWD, weighing each log and snag to estimate mass of CWD was impractical. An alternative approach was to define decay classes and sample these for density, then use measured dimensions of dead trees in quadrats to calculate the volume in each decay class (Harmon *et al.* 1986). Mass of CWD (expressed as mass per unit area) was sampled within 40 m × 40 m quadrats. CWD was defined as >10 cm in diameter and >1 m in length. For each log, the species, decay class, length, and diameter at the large and small end and at the midpoint were recorded. Log length was determined to the nearest 0.1 m with a meter tape, and diameters were measured to the nearest 1 cm with calipers. In the case of logs with elliptical cross-sections, both the long and short axes were recorded.

Measurements were similar for snags (standing, dead trees), except that the midpoint diameter was not measured. The large-end diameter was taken at breast height to the nearest 1 cm with a diameter tape, and the small-end diameter for broken snags was measured from the log formed by the fallen top. If the top was not found, the snag small-end diameter was visually estimated. When snags were intact, the total height was estimated from a diameter-height relationship developed from a sample of 95 trees. When a snag was broken, the height was visually estimated. This method was fairly accurate because most broken snags were less than 3 m tall and estimates were periodically checked with a clinometer.

A set of logs of the dominant species was examined for external, visual characteristics that indicated the degree of decomposition (Harmon *et al.* 1986). As species was difficult to determine for extremely decomposed logs, the latter were sampled separately. External characteristics noted included the presence of leaves, twigs, branches, bark on branches, casehardening, lichens, mosses, fungal fruiting bodies, ants, and termites. Bark cover, cross-sectional shape, and friability of sapwood and heartwood were also noted.

Within each species, logs and snags were subjectively assigned to 1 of 5 decay classes (Harmon *et al.* 1986). Class 1 logs and snags were the least decayed, had the most extensive bark cover, and had leaves and fine twigs. Class 2 logs and snags were relatively undecayed but had no leaves and few fine twigs, and bark had started to fall off. Class 3 logs and snags had no bark and only a few branch stubs remained; although in this class the sapwood was decaying, the heartwood was relatively undecayed, and branch stubs did not move when pushed or pulled. Class 4 logs had no branches or bark cover, the outer portions of the wood were often casehardened, and the inner wood was decomposing. Class 5 logs were elliptical in cross-section (indicative of advanced decay) and in many cases the wood was scattered across the soil surface.

For each sampled log, density was determined from 4 cross-sections spaced evenly along its length. Entire cross-sections were removed; for those that would disintegrate after cutting, the dimensions were recorded prior to removal. Density was computed from the dry weight and volume of each cross-section. Because large drying ovens were unavailable, we weighed each cross-section in the field to determine the fresh weight and then removed subsamples to determine moisture content. These subsamples were first dried in a small solar oven in the field, then dried in an electric oven at 55°C for 7 days and weighed.

Stores of CWD were computed by multiplying the volume of each species and decay class by the mean density. Log volume was determined by Newton's formula. The formula used to calculate snag volume was that for the frustrum of a cone. The densities of logs and snags in each decay class were assumed to be equal. To separate CWD present before Hurricane Gilbert, we assumed that in 1989 logs and snags of decay class 1 and in 1990–91 logs and snags of decay class 2 were added by the storm. The CWD mass prior to the hurricane was therefore assumed to be decay class 2–5 wood in 1989 and decay class 3–5 in 1990–91. Fragments present on the ground before fires were identified as class 3 to 5 logs with char along the length and not just at the base.

Decomposition rates.—Decomposition rates of FWD and CWD were measured at Rancho San Filipe by establishing a time series study in February 1989. The overall experimental design for FWD was a split-plot with 6 blocks, 2 diameter classes, and 6 tree species. The 2 diameter classes were ≤ 1 cm and 4–8 cm. The 6 tree species studied, *Blomia, Brosimum, Bursera, Gymnanthes, Manilkara,* and *Talisia,* were the dominants at this location.

The segments of branches used in the FWD study were taken from trees that had been felled along a firebreak 2–4 weeks previously. The 1-cm-diameter branch segments were 20 cm long, and the 4- to 8-cm branch segments were 40 cm long. Total fresh weight was determined for each segment after a subsample had been removed to determine moisture content. The average moisture content for each size-species combination was used to determine initial dry weight for that combination. Each segment was identified by a numbered aluminum tag tied on with nylon line. All branch samples were placed beneath the forest canopy and in contact with the litter layer. At harvest, the total wet weight of each branch segment was determined in the field. The 1-cm branch segments and extremely decomposed, larger branch segments were dried in a solar oven, then reweighed to determine moisture content. In the case of less decomposed, larger branch segments, subsamples were removed from the center and the ends for drying in the solar oven. These subsamples were then oven-dried at 55°C for 7 days to estimate their initial water content. All calculations of losses in mass of FWD were based upon oven-dry weights.

In the case of the branch segments ≤ 1 cm in diameter, the sampling interval was 6 months for the first 3 years and 1 year thereafter. For branch segments < 4 cm in diameter, the sampling interval was 1 year, with 4 sample times. At each sample time, a single branch segment of each species and size was removed from each of the blocks.

In addition to examining detritus of the previously mentioned species in both diameter classes, we also set out 4- to 6-cm-diameter segments of *Beaucarnea, Carica papaya* L., *Cecropia peltata* L., and *Coccothrinax readii* stems. The growth form of these species prevented us from examining them in a full range of sizes. *Beaucarnea* stem segments were set out in 1989, and segments from the other 3 species were added in 1990.

For the CWD study, it was not possible to follow a split-plot experimental design because the sample logs were so heavy that they had to be left where they were found throughout the forest. All logs examined were beneath the forest canopy. For each species and size class examined, 4–8 logs were left in each location. Logs 15 cm in diameter and 1 m long of *Beaucarnea, Blomia, Brosimum, Bursera, Talisia,* and *Tabebuia chrysantha* (Jacq.) Nicholson and logs 30 cm in diameter and 2 m long of *Brosimum, Bursera, Manilkara,* and *Myrcianthes* were used in the time series. Length, end diameters, and bark cover were measured for each of these logs. Disks were removed from these logs initially, and one log of each species was sampled at 1-year intervals to determine changes in density. The methods used to measure density were the same as those used for sampling decay classes, except that 3 cross sections were removed from each decomposing log sampled in the time-series study.

Statistical analysis.—Analysis of variance with a split-split-plot experimental design was used to test the effects of species, branch segment diameter, time since placement, and their interactions upon loss in mass for FWD.

Decomposition rate constants for FWD were calculated from the linear regressions of the mean percentage of mass per branch segment remaining, transformed into natural logarithms (ln), versus time. The slope of these regressions was the decomposition rate constant. In the case of CWD, we used ln-transformed mean relative density as the dependent variable. Relative density was calculated as the current density divided by the mean initial density. As with FWD, we fit logarithmic-transformed regressions to the data. The half-life of each species and size combination was calculated from these regressions.

All statistical tests were performed by procedure GLM of SAS Institute, Inc. (1985). Statistical tests were judged significant if $0.05 > P > 0.01$ and highly significant if $P < 0.01$.

TABLE 2. *Mass of fine woody detritus (FWD) suspended in standing dead trees and on the forest floor at Quintana Roo, Mexico.*[a]

Stand and disturbance	Mass (Mg/ha^{-1}): Suspended in standing dead trees	Mass (Mg/ha^{-1}): On the forest floor
Bosques de Cancun		
Hurricane	0.0 (0.0) 2[b]	14.2 (3.4) 20[c]
Fire	9.7 (1.1) 2[b]	0.0 (0.0) 2[b]
Chunyxche		
Undisturbed	0.4 (0.1) 2[b]	4.3 (1.0) 20[c]
Rancho San Filipe		
Hurricane	0.6 (0.2) 12[b]	10.0 (2.3) 20[c]
Fire	24.2 (3.2) 4[b]	0.0 (0.0) 4[b]
Vallarta Road		
Hurricane	0.0 (0.0) 2[b]	7.5 (1.6) 20[c]
Fire	19.1 (3.0) 2[b]	0.0 (0.0) 2[b]

[a] Values given include the mean (and standard error), followed by number of samples.
[b] Sampled in 40 m × 40 m plots.
[c] Sampled in 1 m × 1 m plots.

RESULTS AND DISCUSSION

MASS OF FINE WOODY DETRITUS.—Mass of FWD was strongly influenced by the degree of disturbance (Table 2). At Chunyxche, the site with the least disturbance, total FWD amounted to 4.7 Mg ha^{-1}. Even 3 years after Hurricane Gilbert, storm-damaged stands had considerably more FWD than did those at Chunyxche: mass ranged from 7.5 Mg ha^{-1} at Vallarta Road to 14.2 Mg ha^{-1} at Bosques de Cancun.

Although we do not have data on total FWD on the forest floor at all the sites immediately after the hurricane, we can correct our 1992 values to account for decomposition losses. Whigham *et al.* (1991) have determined that, immediately after Hurricane Gilbert, 18.0 ± 1.9 Mg ha^{-1} ($\bar{x}$ ± SE, $N = 60$) of fresh FWD had been added to the forest floor at Rancho San Filipe. Adding this amount to the value we recorded at Chunyxche (the least disturbed stand) would indicate that 22.7 Mg ha^{-1} had accrued there immediately after the storm. Our recorded value of 10.0 Mg ha^{-1} of FWD on the forest floor in 1992 at Rancho San Filipe indicates that decomposition losses from 1989 through 1992 amounted to about 56 percent. Adjusting the values recorded for the relatively undisturbed forests at Vallarta Road and Bosques de Cancun to reflect these decomposition losses indicates that FWD immediately after the storm amounted to 17.0 Mg ha^{-1} at the former and 32.2 Mg ha^{-1} at the latter. An alternative calculation incorporating the average decomposition rate for 2- to 10-cm-diameter wood weighted by size class and abundance of the dominant species indicates a loss of 57 percent in 3 years. Correcting our 1992 values in accordance with this percentage indicates that the post-storm mass of FWD ranged from 17.6 to 33.3 Mg ha^{-1} for these same two stands.

Immediately after the fires, FWD ranged from 9.7 Mg ha^{-1} at Bosques de Cancun to 24.2 Mg ha^{-1} at Rancho San Filipe. This range is below that estimated for forests immediately after moderate to severe hurricane damage. These differences may stem from the fact that fires removed most of the FWD on the forest floor; whereas, the hurricane added to the predisturbance FWD.

The type of disturbance also influenced the proportion of FWD suspended in standing dead trees relative to that on the forest floor. Most FWD in undamaged or hurricane-damaged forests was on the forest floor. For example, at Rancho San Filipe, where numerous *Brosimum* were defoliated and killed by Hurricane Gilbert, only 6 percent of the total FWD was suspended in standing dead trees. In contrast, almost all FWD in fire-damaged stands at this location was suspended in standing dead trees because the fires had removed most of the FWD on the forest floor and had left many such trees.

TABLE 3. *Mass of logs, snags, and total coarse woody detritus in Quintana Roo, Mexico.*[a]

Stand and disturbance	Mass (Mg/ha)		
	Logs	Snags	Total
Bosques de Cancun			
Hurricane[b]	31.5 (3.1)	2.8 (1.7)	34.3 (4.9)
Fire[b]	26.3 (5.5)	46.1 (0.7)	72.4 (9.4)
Chunyxche			
Undisturbed[b]	20.5 (0.2)	12.8 (8.9)	33.3 (9.2)
Rancho San Filipe			
Hurricane[c]	37.3 (4.1)	12.9 (2.4)	50.2 (4.2)
Fire[d]	1.6 (0.7)	96.7 (12.9)	98.3 (11.5)
Vallarta Road			
Hurricane[b]	13.7 (0.5)	6.8 (4.7)	20.5 (5.2)
Fire[b]	25.8 (7.8)	73.7 (16.2)	99.5 (24.0)

[a] Values are given in terms of the mean (and standard error) for 40 m × 40 m plots.
[b] $N = 2$.
[c] $N = 16$.
[d] $N = 4$.

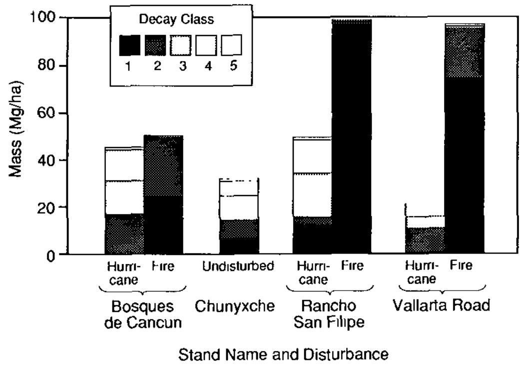

FIGURE 2. Distribution of CWD mass by stand, disturbance, and decay class.

MASS OF COARSE WOODY DETRITUS.—Hurricane-disturbed forests contained between 20.5 and 50.2 Mg/ha of CWD (Table 3) with a corresponding volume of 33.0 to 74.8 m^3/ha. As almost all the class 1 and 2 wood (depending upon the year of the inventory) was added by Hurricane Gilbert, subtracting these classes indicated that undisturbed wood in these forests had a mass between 13.0 and 37.8 Mg/ha.

The largest amount of CWD was in fire-disturbed forests. The fire at Vallarta Road was extremely intense, killing all the trees and increasing the mass of postfire CWD to 99.5 Mg/ha and the volume to 125.9 m^3/ha, despite the fact that the fire appeared to have removed most of the prehurricane wood (Fig. 2). Within classes 3 to 5, for example, mass of CWD in the unburned Vallarta Road plot was 7.5 Mg/ha; whereas, that in burned plots at this location was 0.6 Mg/ha. A similar pattern occurred at Rancho San Filipe and Bosques de Cancun. Assuming that the prefire stores of CWD in the burned forests were similar to those in the adjacent unburned forests would indicate that 92 to 99 percent of the class 3 to 5 wood was consumed by fires.

Kind and severity of disturbance in plots dramatically affected the ratio of snags to logs (Table 3). At Rancho San Filipe, 98 percent of the CWD in burned forests was snags; whereas, in the forests heavily damaged by Hurricane Gilbert 74 percent of the CWD was logs. In the undisturbed forests at Chunyxche and in those moderately damaged by Hurricane Gilbert at Vallarta Road, from 8 to 33 percent of the CWD was snags—proportions that may be more typical of undisturbed forests in this region.

Our data indicate that a considerable mass of woody detritus can be found in dry tropical forests. The estimated range for undisturbed forests of 17.7–42.7 Mg/ha greatly exceeds the mass found in surface litter (9.2 ± 0.2 Mg/ha, $N = 36$) but is less than the mass of organic matter found in the very shallow but highly organic soil (156.2 ± 9.7 Mg/ha, $N = 36$) (D. Whigham, pers. obs.). In forests disturbed by fire, which consumes much of the litter and organic soil in this forest type, woody detritus can become the dominant store of organic matter and carbon.

Although our estimates of the mass of woody detritus in a dry tropical forest are surprisingly large, they are probably low for two reasons. We did not consider the wood associated with dead coarse roots. Including these roots could increase our estimates up to 20 percent (Santantonio *et al.* 1977), depending on the degree of sprouting in top-killed trees and the difference between decomposition rates above and below ground. We did not consider wood buried within the soil and forest floor. Excavations made at Rancho San Filipe before the onset of Hurricane Gilbert in soil pits extending to the depth of solid rock indicated that 5.0 ± 0.8 Mg/ha ($\bar{x}$ ± SE, $N = 36$) of decayed wood fragments were buried in the soil (D. Whigham, pers. obs.). Adding in these "missing" pools indicates that our estimates of total mass of woody detritus could be low by as much as 30–50 percent in undisturbed forests.

TABLE 4. *Density according to decay classes for coarse woody detritus (CWD) of dominant tree species in Quintana Roo, Mexico.*[a]

Species	Density (g/cm³) in decay class—				
	1	2	3	4	5
Beaucarnea pliabilis	0.25 (0.01) 8	0.19 (0.02) 3	0.06 (0.01) 12	—	—
Blomia cupanioides	0.79 (0.01) 3	0.82 (0.02) 3	—	—	—
Brosimum alicastrum	0.62 (0.01) 8	0.47 (0.05) 21	—	—	—
Bursera simaruba	0.33 (0.01) 14	0.23 (0.03) 6	0.11 (0.02) 15	—	—
Ceiba aesculifolia	0.51 (0.02) 8	—	—	—	—
Krugiodendron ferreum	—	0.62 (0.02) 3	—	0.49 (0.05) 3	—
Manilkara zapota	0.81 (0.02) 15	0.84 (0.02) 22	0.81 (0.16) 3	0.54 (0.05) 16	—
Myrcianthes fragrans	—	0.73 (0.05) 9	0.50 (0.13) 3	—	—
Tabebuia rosea	0.76 (0.09) 6	0.65 (0.04) 10	—	—	—
Talisia olivaeformis	0.79 (0.03) 8	0.65 (0.03) 9	0.57 (0.04) 6	—	—
Unknown	—	—	0.67 (0.09) 4	0.64 (0.09) 6	0.22 (0.02) 11

[a] For each decay class within a species, values given include the mean (and standard error) and, below, the number of cross-sections sampled.

DENSITY CHANGES OVER TIME.—There were two major patterns of decomposition observed in CWD. In those species with decay-resistant heartwood (*e.g.*, *Manilkara*), density tended to remain constant until the later stages of decomposition (Table 4), even though some tissues such as the inner bark and sapwood had definitely decreased in mass. In contrast, in species with non-resistant heartwood (*e.g.*, *Beaucarnea, Brosimum, Bursera*), density continually decreased as decomposition proceeded, and sloughing of the outer layers did not greatly affect overall density.

DECOMPOSITION RATES.—The split-split-plot analysis of variance indicated that there were highly significant effects of species, branch segment diameter (size), and time on the percentage of mass of FWD branch segments remaining. In addition, the interaction terms of time × size and time × species × size were highly significant. This analysis indicates that the way these factors influence the percentage of mass remaining is complex. For example, the ranking of species (as indicated by the decomposition rate constants in Table 5) was not the same for the various branch segment diameters tested.

The woody detritus of many of the examined species did not decompose linearly with time (Fig. 3), although such decomposition is often assumed when using the negative exponential decomposition model (Wieder & Lang 1982). Unfortunately, we did not have enough degrees of freedom (*i.e.*, sample times) to fit a more complex model than this one. Some information about the temporal deviation from this exponential model, however, is revealed by the Y-intercept of the linear ln-transformed regression (Harmon *et al.* 1990a, b). For example, species with Y-intercepts of less than 100 percent are likely to have a period of rapid decomposition followed by a period of slower decomposition (*Carica* in Fig. 3 and Table 5). Many of the species with this pattern were attacked by termites. In leaf litter, this pattern is usually caused by rapid leaching and decomposition of labile fractions (Harmon *et al.* 1990b), but such causes are highly unlikely for wood because it is very low in water-soluble matter (Harmon *et al.* 1986). A contrasting temporal pattern was exhibited by species with a Y-intercept greater than 100 percent (*Coccothrinax* in Fig. 3 and Table 5): here, there was an initial period with little decomposition followed by a period of more rapid decomposition.

There were substantial differences in decomposition rates among species even when size was similar (see the K values in Table 5). For example,

TABLE 5. *Coefficients of regressions used to estimate decomposition rate constants for selected species and branch segment diameters of woody detritus, Quintana Roo, Mexico.*

Species	Segment diameter (cm)	Regression coefficients[a] Y_0 (%)	k ($year^{-1}$)	r^2	*N*
Beaucarnea pliabilis	4	60.0	0.235	0.87*	5[b]
Beaucarnea pliabilis	15	95.2	0.531	0.29	5[c]
Blomia cupanioides	1	129.2	0.381	0.96**	7[b]
Blomia cupanioides	6	115.0	0.178	0.93*	4[b]
Blomia cupanioides	15	102.8	0.024	0.33	4[c]
Brosimum alicastrum	1	100.6	0.458	0.92**	7[b]
Brosimum alicastrum	6	83.3	0.237	0.94*	4[b]
Brosimum alicastrum	15	110.1	0.172	0.87*	5[c]
Brosimum alicastrum	30	103.1	0.107	0.59	4[c]
Bursera simaruba	1	87.9	0.369	0.80**	7[b]
Bursera simaruba	6	61.6	0.487	0.80	4[b]
Bursera simaruba	15	75.0	0.372	0.80*	5[c]
Bursera simaruba	30	143.3	0.615	0.91*	5[c]
Carica papaya	4	56.6	1.019	0.93	3[b]
Cecropia peltata	4	72.9	0.641	0.84	3[b]
Coccothrinax readii	4	132.7	0.489	0.99	3[b]
Gymnanthes lucida	1	119.5	0.623	0.97**	7[b]
Gymnanthes lucida	6	100.0	0.199	0.92*	4[b]
Manilkara zapota	1	121.6	0.343	0.91**	7[b]
Manilkara zapota	6	108.3	0.151	0.85	4[b]
Manilkara zapota	30	102.9	0.008	0.03	5[c]
Myrcianthes fragrans	30	100.0	0.052	—	2[c]
Tabebuia rosea	15	98.7	0.061	0.49	4[c]
Talisia olivaeformis	1	106.6	0.414	0.83**	7[b]
Talisia olivaeformis	6	106.8	0.207	0.99**	4[b]
Talisia olivaeformis	15	95.8	0.030	0.28	4[c]

[a] The regression was of the form $Y_t = Y_0 e^{-kt}$ where Y_t is the percentage of the mass remaining at time t (years), Y_0 is the initial mass in percent dry weight, and k is the decay rate constant. * $0.05 > P > 0.01$; ** $P < 0.01$.
[b] Each data point represents the mean of 6 branch segments.
[c] Each data point represents the mean of 3–8 cross sections.

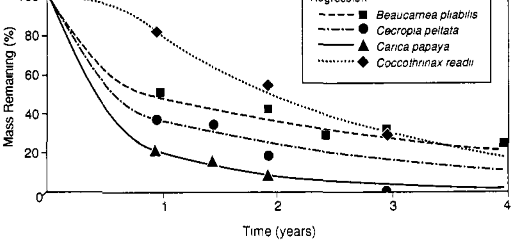

FIGURE 3. Change in remaining mass of branch segments with time for 4 selected species with 4-cm segment diameters of FWD at initial placement. The lines are values predicted from regressions in Table 5 except that the initial values (time = 0) are forced through 100% mass remaining.

decomposition rate constants for branch segments of intermediate diameter ranged from 0.151 $year^{-1}$ in *Manilkara* to 1.019 $year^{-1}$ in *Carica*. On the basis of the average mass remaining after 4 years of decomposition, *Brosimum, Bursera,* and *Gymnanthes* generally decomposed most rapidly; whereas, *Blomia, Manilkara,* and *Talisia* decomposed most slowly. Rankings of these species changed as branch diameter increased. Most notable in this regard was *Gymnanthes,* which decomposed fastest in the 1-cm diameter class but was intermediate in the 6-cm diameter class, largely because the heartwood in the larger segments was very resistant to decomposition.

Most species exhibited a clear increase in half-life as branch segment diameter increased (Fig. 4). This pattern was most dramatic for species with decay-resistant heartwood. For example, the half-life of *Manilkara* increased from 2.6 years at 1-cm

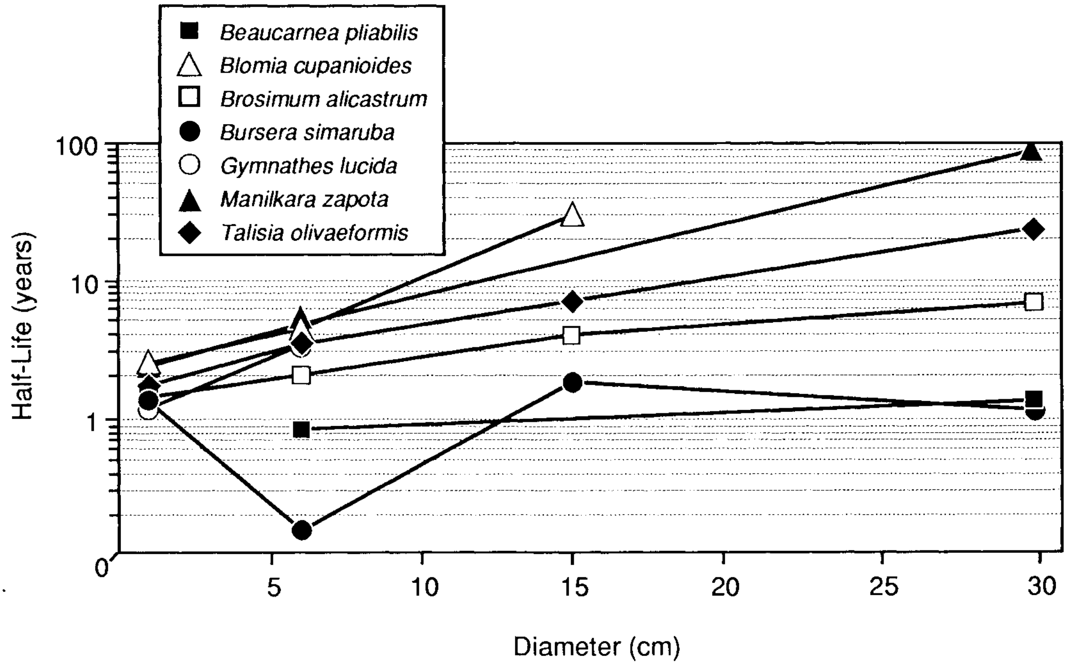

FIGURE 4. Effect of branch segment diameter on the decomposition half-life of woody detritus from the dominant tree species of Quintana Roo, Mexico.

diameter to 86 years at 30-cm diameter. For species such as *Brosimum* with less decay-resistant heartwood, there was a smaller increase in half-life with increasing diameter. The only exception to the overall pattern was *Bursera*, whose half-life changed little with increasing diameter.

The range in decomposition rates among trees we observed is larger than previously reported for tropical forests. Particularly interesting is the fact that several species decompose at rates slower than the 0.1–0.2 year^{-1} observed by Odum (1970) and Kira (1978), respectively. These differences are probably not due to climate, as the less decay-resistant species decompose at rates exceeding the 0.461 year^{-1} estimated by Lang and Knight (1979). This pattern suggests that substrate-quality factors such as extractives may be overriding climatic controls.

Factors affecting mass of woody detritus.—The general perception seems to be that because of increased temperature, moisture, and insect activity, woody detrital mass should decrease as one approaches the equator. Comparison of our data in Table 3 with data from other major biomes indicates, however, that this perception may not be true. The amounts of CWD we measured in undisturbed dry tropical forests exceed those reported for deciduous forests in warm temperate climates, where 20–25 Mg/ha is typical (Harmon *et al.* 1986, Harmon & Chen 1991, Muller & Liu 1991, Onega & Eickmeier 1991). Dry tropical forests appear more comparable to cold deciduous forests, where mass of CWD ranges from 30 to 49 Mg/ha (Tritton 1980, Gore & Patterson 1986, Harmon *et al.* 1986), or to pine-dominated conifer forests, where 29–42 Mg/ha of CWD have been reported (Fahey 1983, Harmon *et al.* 1986). Our estimates also fall within the amounts reported for total woody detritus in moister tropical forests, where 5–51 Mg/ha occur (Edwards & Grubb 1977, Kauffman *et al.* 1988, Uhl & Kauffman 1990). In contrast, woody detrital mass in dry tropical forests is much smaller than in Pacific Northwest conifer forests, which range between 200 and 550 Mg/ha (Grier & Logan 1977, Agee & Huff 1987, Spies *et al.* 1988). Thus, these comparisons suggest that there is no simple correlation between mass of woody detritus and latitude.

The mass of woody detritus has been shown to depend upon a number of factors including the productivity of the ecosystem, climate, substrate quality, and organisms degrading the material (Harmon *et al.* 1986). As latitude increases, the production rate of woody detritus should decrease along with the overall productivity of the forest, leading to lower mass of such detritus (Harmon *et al.* 1993). This trend is, however, partially offset by a decrease in the decomposition rate with increasing latitude, a relation caused by the decrease in temperature and macroinvertebrate abundance (*e.g.*, termites). Decomposition rates of wood are also highly dependent upon the presence of toxic extractives (Scheffer & Cowling 1966), which may not be correlated with latitude and for some species may be more important than climatic factors.

Disturbance also plays a major role in determining the amount of woody detritus in forests. The most obvious effect of disturbances is to increase the amount of such detritus (although there seems to be a common misperception that woody detrital mass is highest in the oldest forests). In the forests we studied, levels of woody detritus were increased 1.5- to 1.7-fold by hurricanes and 2.5- to 3.8-fold by fires. These increases are similar to those in a fire-killed *Pseudotsuga/Tsuga* forest in which woody detritus increased 2.7-fold (Agee & Huff 1987) and in a logged tropical forest in which woody detritus increased 3.4-fold (Uhl & Kauffman 1990).

As the time since disturbance increases, the amount of woody detritus in these dry tropical forests should decrease dramatically. Given the decomposition rates observed here, we would expect most of the disturbance-generated wood to disappear within 30 to 150 years, depending upon the species composition of the forest. At this point, it is difficult to judge whether the mass of woody detritus in these disturbed dry tropical forests will decrease below the levels found in old-growth forests (Gore & Patterson 1986, Spies *et al.* 1988) or will asymptote to old-growth levels (Lambert *et al.* 1980). The factor determining how woody detrital mass changes over time appears to be the relative timing of decomposition and post-disturbance production (Harmon *et al.* 1986). Additional data on how the production of woody detritus changes over a succession in dry tropical forests will be required before such changes in disturbed forests of this type can be accurately predicted.

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