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Decomposition of fine woody debris in a deciduous forest in North Carolina[1]

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FASTH, B. G., M. E. HARMON, J. SEXTON (Department of Forest Ecosystems and Society, 321 Richardson Hall, Oregon State University, Corvallis OR, 97331), AND P. WHITE (North Carolina Botanical Garden, University of North Carolina, Chapel Hill, NC, 27599). Decomposition of fine woody debris in a deciduous forest in North Carolina. J. Torrey Bot. Soc. 138: 192–206. 2011.—We examined the effect of position with respect to the soil surface, species, and piece size on the decomposition rate of fine woody debris ($<$ 15 cm diameter) in a North Carolina forest disturbed by hurricane. To examine year-to-year trends, pieces of two species (*Carya tomentosa* ((Lam.) Nutt.) and *Quercus alba* (Lam.)) in four size classes were placed on the forest floor and collected annually for ten years. In addition, to examine position effects samples of the same species and sizes were suspended in the air and buried underground at a depth of 20 cm and collected at years 2, 4, and 8. Nine other species were placed on the forest floor and collected at years 2, 4, and 8 to determine the range of variability among species. Decomposition was slower the first year than subsequent years, therefore the lag exponential equation was used to determine time trends and an integrated decomposition rate-constant (k_I) reflecting the overall decomposition rate-constant was calculated. The k_I for *C. tomentosa* and *Q. alba* ranged from 0.17–0.25 year^{-1} with a significant interaction between species and size. The buried and suspended samples generally decomposed more slowly than the samples on the surface and k_I ranged from 0.11–0.24 year^{-1} and from 0.10–0.18 year^{-1}, respectively. There was a significant interaction between position and size; while drying limited decomposition of suspended pieces regardless of size, high moisture may have limited decomposition in the largest buried pieces. The k_I for all eleven species and sizes averaged over all size classes ranged from 0.06–0.33 year^{-1}. There was a highly significant interaction between species and size with the smaller sizes tending to decompose faster than the larger sizes and in general species with the most decay-resistant heartwood having the largest response to increases in size. Our experiments and comparison to other studies suggests that the interactions between species, size, and position relative to soil surface are highly complex and dependent on site climate.

Key words: branches, decomposition rate, dual exponential model, fine woody debris, lag exponential model, single exponential model size effect, species effect, temperate forest.

Fine woody debris (FWD), typically $<$ 10 cm in diameter, is an important, but understudied part of forested ecosystems (Woodall and Liknes 2008). Formed from dead branches attached to or free from stems, woody roots, and small woody stems, this material stores carbon and nutrients (Wei et al. 1997), provides a food source and habitat for vertebrates, invertebrates and fungi (Nordén et al. 2004), and is a source of soil organic matter in forest ecosystems (Chen et al. 2001). This material also is an important fuel for forest fires as it is far more likely to burn than coarse woody debris (CWD) (Rienhardt et al. 1991).

The fraction of total carbon stores comprised of FWD in undisturbed forests is likely small, but there are surprisingly few studies to quantify this number. Harmon et al. (2004) found that FWD of all forms ranging from dead branches to coarse roots comprised 4.1% of total carbon stores in an old-growth Douglas-fir/western hemlock forest. Smithwick et al. (2002) reported that attached dead wood and downed FWD on the forest floor comprised 2–5% of total carbon stores in forests within the Pacific Northwest. If the FWD attached to dead stems and dead coarse roots had been included, the fraction com-

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prised of FWD would likely have been 4–7% for these same forests assuming ratios of FWD types found by Harmon et al. (2004). Klinge et al. (1975) found 0.4% of total tropical forest carbon stores comprised of FWD, but this also excluded FWD attached to dead stems and dead coarse roots, the addition of which might have more than doubled the store to 1% of the ecosystem total.

Despite the small fraction stored in FWD (even with corrections for missing types of FWD), there are two reasons this material is likely to be important in the carbon cycling of forests. First, the low store of FWD is caused in part by its relatively high decomposition rate compared to coarse woody debris (> 15 cm diameter) (Harmon et al. 1995); hence, the store does not reflect the contribution to carbon flux. For example, while FWD formed 4.1% of the carbon store, it contributed 13% of the heterotrophic respiration of an old-growth forest (Harmon et al. 2004). Second, most of the reported FWD stores are for forests that have not been disturbed for considerable time. The amount of FWD within a forest is strongly influenced by disturbances such as harvest, fire, insects, wind, rain, and snow. Given the typical fraction of live carbon comprised of materials that could form FWD, a stand replacing disturbance might increase the proportion of total carbon stored in FWD as much as 6-fold. In cases in which large wood is removed such as timber harvest, the proportional increase in FWD (including coarse dead roots) could be even higher (Wei et al. 1997).

Despite the importance of FWD in forest ecosystem function there have been relatively few studies on the dynamics of this material. In general the decomposition of FWD is higher than that of CWD (Harmon et al. 1995), although in dry, warm sites this may not be true (Erickson et al. 1985). Estimates of annual loss rates from FWD have ranged from 0.5–99% (Proctor et al. 1983, Erickson et al. 1985); likely a wider range than observed for leaf litter. Factors explaining this wide range of decomposition rates include species, size, position relative to the soil surface, and climate. Conifer species appear to decompose slower than angiosperm ones (Abbott and Crossley 1982, Erickson et al. 1985), although few comprehensive species level comparisons have been conducted within any region. Decomposition rates generally appear to decrease with increasing size, although Erickson et al. (1985) found that suspended small diameter pieces could decompose slower than larger ones. The cause of increasing decomposition rates with size is likely related to excessive drying of small wood and therefore may only be apparent in dry microenvironments. Buried FWD appears to decompose faster than suspended FWD, although this too is likely a function of the dryness of the climate at a site (Chen et al. 2001, Harmon et al. 2004). Tropical decomposition rate-constants of FWD (0.151–4.6 year^{-1}; Proctor et al. 1983, Harmon et al. 1995) appear higher than temperate ones (0.01–0.452 year^{-1}; Boddy and Swift 1984, Erickson et al. 1987) which are in turn higher than boreal rates (0.045–0.119 year^{-1}; Palviainen et al. 2004, Keane 2008). This suggests that temperature is an important control, although these trends are likely confounded with precipitation and microsite effects that influence FWD moisture. For example, exposure to direct sunlight can lead to high temperatures and rapid drying (Erickson et al. 1985). Therefore, shading from the canopy is likely to increase decomposition rates. However, it must be acknowledged that many of these controls interact in ways that have yet to be elucidated.

The objective of this study was to examine several of the key factors that appear to control FWD decomposition including, species, size, and position relative to the soil surface in a warm temperate forest. Hurricane Fran passed through the Chapel Hill area of North Carolina on September 6, 1996. Many large trees were uprooted throughout this forested area creating an excellent opportunity to collect samples of fresh FWD to study decomposition rates. Ultimately this information will be critical to understanding how hurricane disturbed forest ecosystems respond.

Materials and Methods. SITE DESCRIPTION. This study was conducted at the North Carolina Botanical Garden, a 242-ha tract of oak-hickory-pine forest (Braun 1950, Greller 1988) in Chapel Hill, North Carolina (35°53′ N, 79°2′ W). The development, dynamics, and environment of the Piedmont hardwood forest of North Carolina have been well studied (Oosting 1942, Peet and Christensen 1980). Mature vegetation, including the forests sampled in this project, are dominated by mixed hardwoods with beech (*Fagus grandifolia*

Table 1. Species, position, and harvesting time (in years) of FWD samples.

Scientific name	Common name	Incubation period (years)									
		1	2	3	4	5	6	7	8	9	10
*Quercus alba**	White oak	O	OBS	O	OBS	O	O	O	OBS	O	O
Carya tomentosa *	Mockernut Hickory	O	OBS	O	OBS	O	O	O	OBS	O	O
Acer rubrum	Red maple		O		O				O		
Fagus grandifolia	American beech		O		O				O		
Juniperus virginiana	Eastern redcedar		O		O				O		
Liquidambar styraciflua	Sweetgum		O		O				O		
Liriodendron tulipifera	Tuliptree		O		O				O		
Pinus echinata	Shortleaf pine		O		O				O		
Pinus taeda	Loblolly pine		O		O				O		
Quercus rubra	Northern red oak		O		O				O		
Sassafras albidum	Sassafras		O		O				O		

* species used in temporal trend and position experiments.
Position: O; on the surface, B; below ground, S; suspended above ground.

Ehrh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and red oak (*Quercus rubra* L.) on the moist lower slopes and white oak (*Quercus alba* Lam.), red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), post oak (*Quercus stellata* Wangenh.), and other hardwoods on dryer mid and upper slopes. It is an area defined by undulating topography, soils of poor to good quality and a temperate climate. Soils of the study area include Wedowee sandy loam and Goldston slaty silt loam (Dunn 1977). The climatic regime of the area fits Thornthwaite's (1948) humid mesothermal class, with a mean annual temperature of 14.6 °C and a mean annual precipitation of 122 cm in the 1971–2000 period (State Climate Office of North Carolina). Precipitation is uniformly distributed throughout the year. The mean temperatures in January and July are 3.5 and 25.3 °C, respectively. The elevation ranges from 103–150 m.

Much of the dead wood used in this study was created when Hurricane Fran, a category three storm, passed through the region on the morning of September 6, 1996. The eye of this storm passed about 7 km east of the study area. Wind data from the closest meteorological station at Raleigh-Durham International Airport 40 km east of Chapel Hill indicated sustained winds of 72 km hr^{-1} and gusts of up to128 km hr^{-1} during the storm (NOAA, unpublished data).

Our study was established in four plots. Two of the four plots were located within an 88-acre area known as the Piedmont Nature Trails, adjacent to the North Carolina Botanical Garden in Chapel Hill. The area is typical of central North Carolina Oak-Hickory forest with a diversity of hardwood and evergreen trees and shrubs. The lower elevation plot was located along the Streamside Trail that crosses Meeting-of-the-Waters Creek. The second plot was located in the hillier portion of the Oak-Hickory Trail. The other two plots were located in the Mason Farm Biological Reserve (MFBR) which is located east and south of the North Carolina Botanical Garden. One of plots was located in Big Oak Woods, a 65-acre (0.263 km^2) hardwood bottomland, while the other was in a nearby upland site.

EXPERIMENTAL DESIGN. Three sets of experiments were conducted. The first, termed the time trend experiment, examined the temporal pattern of decomposition for FWD. Two species, white oak (*Quercus alba*) and mockernut hickory (*Carya tomentosa*), were used in this experiment. The mass of FWD remaining each year for a total of 10 years was determined for samples placed on the forest floor surface. At each time four diameter size classes (1, 2, 4, and 8 cm) were examined. The second experiment, called the species experiment, examined the effect of species on the rate of decomposition. In addition to white oak and mockernut hickory, nine other common species (*Acer rubrum*, *Fagus grandifolia*, *Juniperus virginiana* (L.), *Liquidambar styraciflua* (L.), *Liriodendron tulipifera* (L.), *Pinus echinata* (Mill.), *Pinus taeda* (L.), *Quercus rubra*, and *Sassafras albidum* (Nutt.) Nees) (Radford et al. 1968) were placed out and retrieved at years 2, 4, and 8 (Table 1). As with the time trend experiment, four size classes were used for all species. In addition for some species a 15 cm size class was added depending on the availability. The third experiment, called the position experiment, examined the effect of position relative to the soil surface on decomposition rates. The same species as the time trend experiment (i.e., white oak and mockernut hickory), were used in the position experiment. Sample pieces were placed on the forest floor surface, buried in the top 20 cm of mineral soil, or suspended above the forest floor at a height of approximately 1.5 m. Samples from this experiment were retrieved at years 2, 4, and 8; four size classes were used. All of the experiments used a random factorial design with four plots that were close to each other (maximum distance between plots was about 5 km) and they had similar soil types.

FWD Sample Preparation and Placement. The study was established in November 1996. Of the eleven species examined, three were coniferous and eight were deciduous and were chosen based on abundance within the forest. Entire or partial branches were collected from fallen trees using chainsaws, handsaws, and pruners. If not enough downed branches were available for a particular species, then a small live tree was cut. Individual FWD samples were cut to a specific length based on branch diameter size-class (class 1: 15 cm, class 2: 20 cm, class 4: 20 cm, class 8: 30 cm, class 15: 30 cm) using a radial-arm saw. Multiple samples were removed from single branches when possible. The diameter, length, and field wet weight were recorded for each sample and an aluminum tag with a unique number was attached with a UV resistant cable tie. In between each FWD sample along a branch being cut, a piece approximately 1 cm in length was removed and combined with others from the same branch to determine the moisture content of the samples from that branch. Moisture samples were weighed, oven dried at 55 °C until the weight was stable, and re-weighed to determine the moisture correction factor for the FWD samples from that branch. The inverse of the proportion of moisture obtained from the branch samples was multiplied by each FWD sample wet mass to estimate the FWD sample oven dry mass. Initial moisture content variation within a species-size class combination was ~1% of the initial dry mass. The cut ends of the samples were painted with an exterior grade latex paint to decrease moisture exchange and slow the colonization of decomposing organisms through the cut surface.

The FWD samples on the forest floor surface that were to be harvested at the same time were placed approximately 20 cm from each other in a row along the ground and connected together with a length of nylon line that was tied to a stake flag at each end of the row. The belowground samples were encased in 1 mm nylon mesh litterbags. These samples were tethered together with a nylon line and then buried in the soil at a depth of 20 cm alongside the samples lying on the surface to be harvested at the same time. To reduce soil disturbance a slit was cut in the soil at a 45 degree angle with a shovel, the sample slid into place, and then the soil was lightly pressed back into place. The suspended samples were hung using cable ties and nylon string hanging down from a 20 cm long wooden board that was attached perpendicular to the tree bole at approximately DBH (1.5 m high).

Mass Loss Determination. The mass loss of FWD samples was determined from changes in the dry mass over the time interval between placement and harvest. The FWD samples of *Carya tomentosa* and *Quercus alba* on the forest floor surface were harvested ten times over ten years, and those of the other species, belowground and suspended positions were harvested three times during the same period. At harvest each sample was cut from the nylon line and placed into a plastic bag to prevent sample loss. Samples were then returned to the laboratory and carefully cleaned of any attached debris and weighed before and after being dried to a constant mass at 55 °C. Final moisture content for each sample was determined by dividing the moisture weight by the final dry weight.

Statistical Analysis. Although a single negative exponential equation is often used to model decomposition, we were interested in determining if other forms such as the dual exponential and an exponential with a time lag might be more appropriate for FWD. We therefore conducted three tests to assess if the single negative equation was appropriate. First, the single-exponential model was used to estimate k (i.e., decomposition rate constant) and the initial mass of the FWD for the average of the samples for each time:

$$Y_t = Y_0\, e^{-kt}$$

Where Y_0 is the initial mass of material, Y_t is the proportion of mass remaining at time t, and k is the decomposition rate constant. For this analysis proportion mass remaining was used as the Y variable. The k and Y_0 values were calculated from the linear regressions of the mean remaining mass that had been transformed into natural logarithms ($\ln Y$) versus time. Second, for the time trend experiment we used a t-test to determine whether the estimated initial mass was significantly different from 1. In the case of the species and position experiments, there were too few times for a significant result regardless of the actual temporal pattern. Therefore, we compared the estimated initial mass to the variation caused by initial moisture contents. If the initial mass was higher or lower than would have been caused by this experimental error, we assumed that the single negative exponential was not appropriate. Our third test was based on the assumption that the single negative exponential has a constant proportion lost for each time step. We therefore tested if the rate-constants (k_t) estimated for each time the samples were collected differed:

$$k_t = -ln(Y_t)/t$$

where Y_t is the proportion of mass remaining at time t. In these calculations we estimated the k_t for each individual sample. An analysis of variance was run to determine if there was a statistically significant difference among the k_t for different times.

When the single negative exponential model was appropriate, we used the results of our initial test as the estimate of k. When the initial mass was significantly higher than the experimental error in moisture contents warranted, we used a lag-exponential model to estimate k:

$$Y_t = 1 - \{1 - exp(-kt)\}^L$$

where Y_t is the mass remaining at time t, k is the decomposition rate constant, and L is a dimensionless lag parameter.

When the initial mass was significantly lower or was lower than the experimental error in moisture contents warranted, we used a dual exponential equation to estimate k:

$$Y_t = \left(Y_0\ e^{-kft}\right) + \left(1 - Y_0\ e^{-kst}\right)$$

where Y_t is the mass remaining at time t, Y_0 is the initial proportion of the fast fraction, kf is the fast fraction decomposition rate constant, and ks is the slow fraction decomposition rate constant.

When the lag-negative exponential or the dual exponential equations are used, the decomposition rates are not directly comparable to that estimated using the single exponential equation. This is because the latter two equations do not assume a constant proportion of mass is lost each time step. We therefore calculated a comparable "average" or integrated decomposition rate constant (k_I) for the lag-negative exponential and the dual exponential equations using the method of Harmon et al. (2009). The predicted mass remaining for each at time steps of 0.1 years was summed. The sum of these masses over time represents the theoretical accumulation of FWD that one would expect given a constant input and the modeled decomposition curve. By then assuming that this represented the steady-state mass (where the input and output fluxes are equal) and that the input was 100 units of mass (i.e., our models were expressed in percent mass remaining), we calculated the time integrated average decomposition rate k_I using the method of (Olson 1963):

$$k_I = 100/M_{ss}$$

Where k_I is the time integrated average decomposition rate-constant and M_{ss} is the estimated steady-state mass of FWD.

For the analysis of variance of k_I in the species-size and position experiments individual sample k_I was utilized (with the assumption that for each species and size at a repetition the k_I determined from the regressions of times 2, 4, and 8 constitutes one individual sample). Furthermore, to determine the effect of species when there was a significant species and size interaction, we calculated the slope of the line representing the effect of size on k_I within a species to create a variable by which to rank the size effect amongst species.

All statistical tests were performed by the GLM, MIXED, and NLIN procedures of SAS (SAS Institute Inc.). Statistical tests were significant if $0.05 > P > 0.01$ and highly significant if $P \leq 0.01$.

Results. TIME TREND EXPERIMENT. With the exception of the largest size class (8 cm), most of the FWD mass had completely decomposed over the 10 year time trend experiment (Fig. 1).

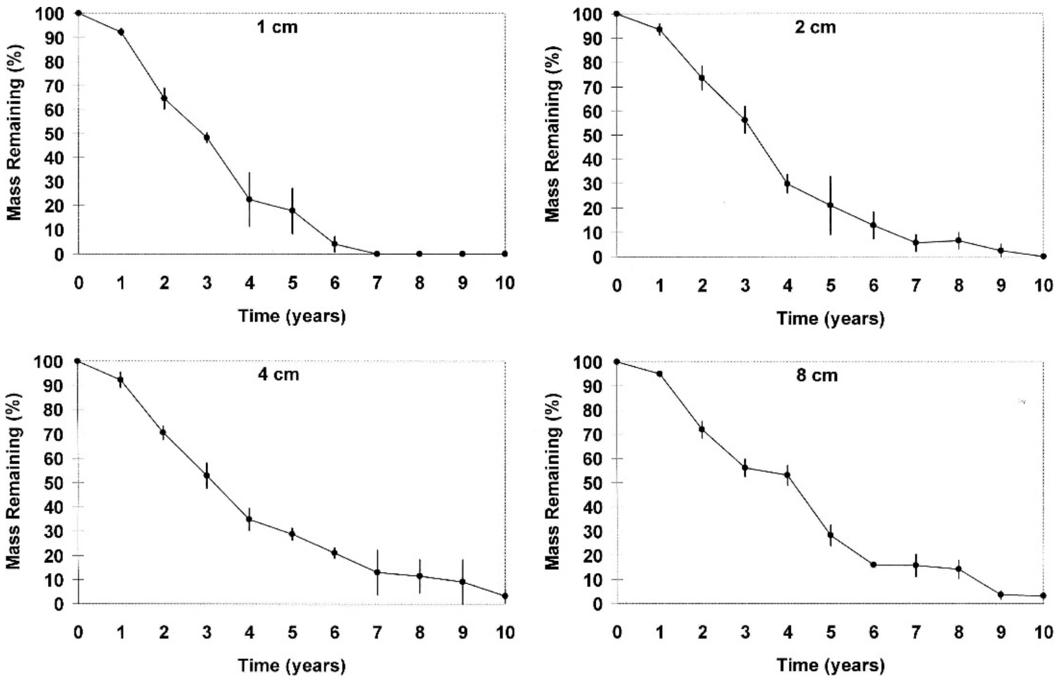

FIG. 1. Change in mean remaining mass of *Carya tomentosa* with time for four size classes. Bars represent standard errors.

Despite the relatively rapid rate of decomposition, it appeared that FWD decomposition was slower the first year than the next three to six years. Several lines of evidence support this observation. The single exponential intercept values were above 100% (105–170%) and beyond the values expected from variation in the initial moisture content, indicating a lag period. The *k*'s calculated for each time step were statistically significantly different ($P < 0.001$), indicating that *k* increased. Therefore, the lag exponential equation was selected as the most appropriate (Fig. 2). The *k* of the lag exponential equations ranged from 0.28–0.67 year^{-1} and the lag parameter ranged from 2.42–7.96. In general, the higher the lag parameter was, the higher the associated *k*. Integrated decomposition rate-constants (k_I) ranged from 0.17–0.25 year^{-1} and thus were less variable than the *k*'s for the single negative exponential or the lag-exponential equations (Table 2). Analysis of variance indicated that there was a highly significant interaction between species and size ($P = 0.000$), caused by the fact *Quercus alba* had no differences among sizes classes, whereas for *Carya tomentosa* there was a decrease in k_I with increased size.

POSITION EXPERIMENT. The buried and suspended samples generally decomposed less than the samples on the forest floor surface during the same 8 year time period. The buried samples of *Carya tomentosa* had remaining masses ranging from 18–39% and *Quercus alba* had remaining masses between 12 and 46%. The suspended samples of *C. tomentosa* had remaining masses ranging from 29–44% and *Q. alba* had remaining masses between 12 and 36%. For both species and all sizes decomposition appeared to be slower during the first two years than in subsequent years for the same reasons as stated previously in the time trend experiment; therefore, the lag exponential equation was selected. The *k* of the lag exponential equations for buried *C. tomentosa* samples ranged from 0.22–0.30 year^{-1} and the lag parameter ranged from 1.87–2.58 (Table 3). For buried *Q. alba* samples the *k* of the lag exponential equations ranged from 0.11–0.56 year^{-1} and the lag parameter ranged from 1.05–5.02. The *k* of the lag exponential equations for suspended *C. tomentosa* samples ranged from 0.14–0.25 year^{-1} and the lag parameter ranged from 1.70–3.09 (Table 3). For suspended *Q. alba* samples the *k* of the lag exponential equations

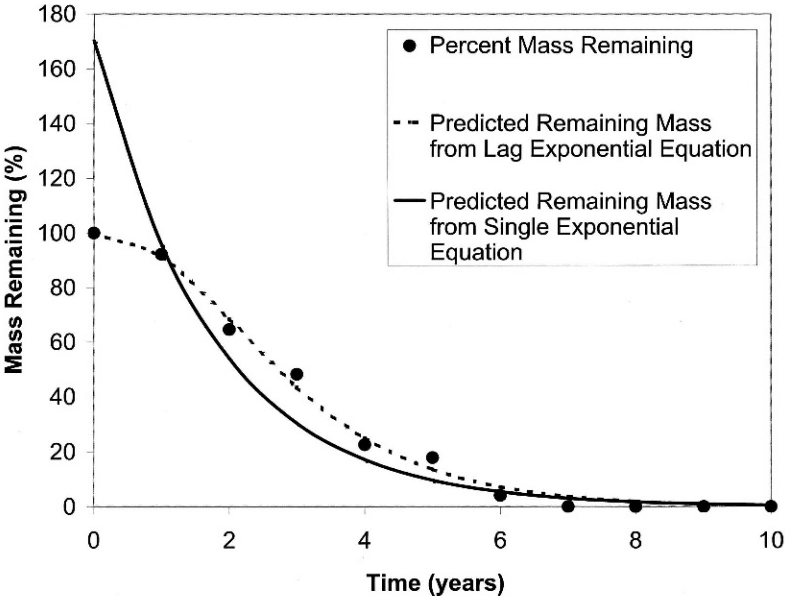

FIG. 2. Observed change in remaining mass for *Carya tomentosa* size class 1 and predicted remaining mass using single exponential and lag exponential regression. The lines are values predicted from regressions in Table 2.

ranged from 0.17 to 0.60 year^{-1} and the lag parameter ranged from 1.65–16.18. The k_I for buried samples of both species ranged from 0.11–0.24 year^{-1} and for suspended samples the range of values was between 0.10 and 0.18 year^{-1} (Fig. 3). Analysis of variance indicated that there was a significant interaction between position and size ($P = 0.035$). This interaction was likely due to differences in moisture content. Suspended samples were drier than those placed on the forest floor surface or buried in the soil. However, for buried samples the effect of moisture content may be influenced by size, specifically larger diameter pieces decomposed more slowly than smaller ones.

SPECIES EXPERIMENT. Similar to the time trend results, most of the FWD mass had decomposed over the 8 year time period of this experiment, with the exception of the conifer species (*Juniperus virginiana*, *Pinus echinata*, and *Pinus taeda*) and *Sassafras albidum,* which had remaining masses ranging from 5–22% for the smallest sizes and 18–64% of initial mass for the larger sizes. For the majority of species and sizes, decomposition appeared to be slower during the first two years than in subsequent years and therefore the lag exponential equation was selected for most of these species. There were three instances where the single exponential intercept values were within the expected variation (Table 4) and therefore that equation was used. Similarly, there were two instances where the single exponential intercept value was significantly below the expected value, indicating a period of initial rapid decomposition, and a dual exponential equation was used. There was one instance (*Liriodendron tulipifera*, size 1) where the intercept was significantly below the expected value, yet a visual assessment of the dual exponential equation showed that the single exponential equation would be more realistic, and therefore was used. The k of the lag exponential equations ranged from 0.12–1.01 year^{-1} and the lag parameter ranged from 2.22–11.96 (Table 4). As noted in the time trend experiment, in general, the higher the lag parameter the higher the associated k. The k of the single exponential equations ranged from 0.06–0.21 year^{-1} with intercepts ranging from 79–102. The k of the faster portion of the dual exponential equations ranged from 0.33–0.67 year^{-1} and the slower portion ranged from 0.04–0.11 year^{-1} with intercepts ranging from 63–98. The k_I of all the species and sizes ranged from 0.06–0.33 year^{-1}. Analysis of variance showed a highly significant interac-

Table 2. Coefficients of regressions used to estimate decomposition and integrated decomposition rate constants for two species and four sizes of fine woody detritus placed on soil surface over a ten year time period.

Species	Size (cm)	$Y_{0\ single}$	$k_{\ single}$	$r^2_{\ single}$	$k_{I\ single}$	$k_{\ lag}$	L	$r^2_{\ lag}$	$k_{I\ lag}$
Carya tomentosa	1	170.15	0.57	0.92*	0.34	0.67	7.96	1.00*	0.25
	2	162.25**	0.44	0.95*	0.27	0.58	7.16	1.00*	0.22
	4	123.19**	0.30	0.98*	0.24	0.41	3.63	1.00*	0.21
	8	140.23	0.33	0.94*	0.24	0.42	4.25	1.00*	0.19
Quercus alba	1	164.34	0.49	0.88*	0.30	0.48	3.89	1.00*	0.23
	2	107.56	0.29	0.94*	0.27	0.45	3.87	1.00*	0.22
	4	144.45	0.43	0.92*	0.30	0.52	4.79	1.00*	0.23
	8	156.22	0.43	0.94*	0.27	0.46	3.84	1.00*	0.23

Y_0 *single* is the initial mass in percent dry weight, k single is the decay rate constant derived from the single exponential equation, and k_{I} single is the integrated decay rate constant utilizing $Y_{0\ single}$ and k_{single}. K_{lag} is the decay rate constant derived from the lag equation, L is the lag coefficient, and $k_{\mathrm{I}\ lag}$ is the integrated decay rate constant utilizing k lag and L. *Denotes model P-value ≤ 0.05 **intercept significantly different than 100.

tion between species and size ($P = 0.0023$) with the smaller sizes tending to decompose faster than the larger sizes. The more decay resistant genera (*Pinus, Juniperus* and *Sassafras*) tended to decompose more slowly than the others (Fig. 4). When species were ranked based on the slope of the line representing size effect within that species, *J. virgininana* and *S. albidum* displayed the most variation amongst sizes, while the *Pinus* species had a slightly inverted size effect with larger sizes decomposing slightly faster than smaller ones (Fig. 4).

Discussion. The FWD decomposition rate for samples located on the forest floor, which ranged from 0.06–0.33 year^{-1} in our North Carolina study, was low compared to the observed global maximum of 4.6 year^{-1} (Proctor et al. 1983), but within the values found at other temperate forests which range from 0.01 (Erickson et al. 1985) to 0.452 year^{-1} (Boddy and Swift 1984). Despite considerable range in decomposition rates within sites, there is a clear increase with mean annual temperature that is consistent with a Q10 of 3 to 4 (Fig. 5). However, below a mean annual temperature of 15 °C much of the variation appears to be related to species, size, and microenvironment differences. Surprisingly, FWD decomposition rates on moist sites with low temperatures (Vávřová et al. 2009) can exceed those found on much warmer, but drier sites (Erickson et al. 1985) which indicates moisture can be

Table 3. Coefficients of regressions used to estimate decomposition and integrated decomposition rate constants for two species, four sizes and three positions of fine woody detritus with three collections over an eight year time period.

Carya tomentosa					*Quercus alba*				
Size (cm)	Position	k	L	k_I	Size (cm)	Position	k	L	k_I
1	O	0.69	7.72	0.26	1	O	0.49	4.28	0.23
2	O	0.51	4.58	0.23	2	O	0.48	4.04	0.23
4	O	0.41	3.29	0.21	4	O	0.54	5.08	0.24
8	O	0.38	4.76	0.17	8	O	0.57	5.62	0.24
1	B	0.29	2.2	0.18	1	B	0.56	5.02	0.24
2	B	0.26	1.87	0.18	2	B	0.31	2.62	0.18
4	B	0.30	2.58	0.18	4	B	0.39	4.09	0.19
8	B	0.22	1.92	0.15	8	B	0.11	1.05	0.11
1	S	0.19	2.36	0.12	1	S	0.17	1.65	0.13
2	S	0.22	2.91	0.12	2	S	0.60	16.18	0.18
4	S	0.25	3.09	0.13	4	S	0.45	7.29	0.17
8	S	0.14	1.7	0.10	8	S	0.23	1.98	0.15

Position: O, on the surface; B, belowground; S, suspended aboveground. k is the decay rate constant derived from the lag equation, L is the lag coefficient, and k_{I} is the integrated decay rate constant.

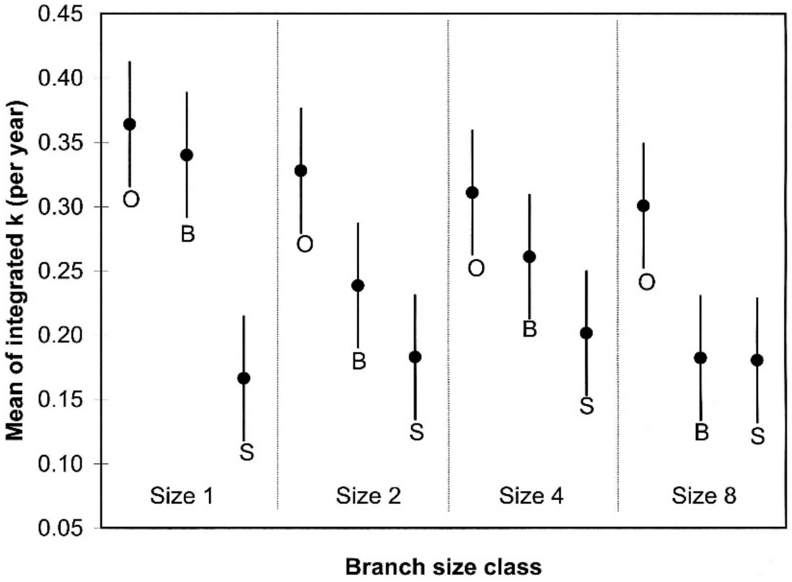

FIG. 3. Estimated mean of integrated k for *Carya tomentosa* and *Quercus alba* combined with upper and lower confidence limits ($\alpha = 0.05$) by position (O, on the surface; B, below ground; S, suspended above ground) and size class (1, 2, 4, 8 cm).

limiting in some forests regardless of temperature. The 5-fold range in decomposition rates we observed was typical of that observed at sites that had examined multiple species (Gosz et al. 1973, Lang 1974, Boddy and Swift 1984) indicating that species characteristics have considerable influence on decomposition of this material.

The diameter of a piece of FWD has long been hypothesized to have an effect on decomposition rate, although this effect is likely more complex than often conceived. The most common hypothesis is that as diameter size increases the surface area to volume ratio decreases and decomposition rates decrease (Swift et al. 1976). Abbott and Crossley (1982), Harmon et al. (1995), Frangi et al. (1997), Keane (2008), and Vávřová et al. (2009) all found an inverse relationship between FWD diameter and decomposition rate supporting the surface area to volume hypothesis (Fig. 6). In contrast Erickson et al. (1985) reported that smaller samples had slower rates, presumably because their moisture content was lower. This suggests that while surface area to volume ratio is important, its effect depends on the amount of moisture. Water can be too scarce or too abundant to support decomposition (Griffin 1977). At low moisture contents, water is held too tightly by the substrate, whereas at high moisture contents oxygen diffusion is limited because of the so-called waterlogging effect. Therefore in areas with sufficient to excess moisture, increasing surface area to volume ratios lead to an increase in decomposition rates because the effect of size is driven not directly by water, but by other factors such as gas exchange and decomposer colonization. However, in drier regions or microenvironments increasing the surface area to volume ratio may lead to excessive drying in small pieces, leading to an increase in decomposition rate with increasing size. It follows that the response of decomposition rate to changes in FWD size depends on the climate of the site. At sites where moisture is not limiting, it is likely that the size effect is largely caused by changes in the surface area to volume ratio and changes in substrate quality with increasing size. In sites where moisture is extremely limiting, it may be possible that decomposition increases with size. The site we studied in North Carolina appears to lie between these two extremes. A logical hypothesis is that exposed small pieces of FWD appeared to be moisture limited, but as soon as they are buried beneath leaves their decomposition rate increases greatly. For larger pieces, moisture limitation was apparently less important;

Table 4. Coefficients of regressions used to estimate decomposition and integrated decomposition rate constants for eleven species and four or five sizes of fine woody detritus placed on forest floor surface with three collections over an eight year time period. Rank indicates the relative decomposition rate of the species with 1 the fastest.

Species/rank	Size (cm)	Equation used	k	L	Y_0	kf	ks	k_I
Acer rubrum/3	1	lag	0.69	5.13				**0.30**
	2	lag	0.75	7.81				**0.28**
	4	lag	0.39	3.07				**0.21**
	8	lag	0.66	11.41				**0.22**
Carya tomentosa/6	1	lag	0.69	7.72				**0.26**
	2	lag	0.60	7.18				**0.23**
	4	lag	0.43	3.65				**0.21**
	8	lag	0.31	2.75				**0.17**
	15	lag	0.34	3.73				**0.17**
Fagus grandifolia/4	1	lag	0.80	7.22				**0.31**
	2	lag	0.51	4.76				**0.23**
	4	lag	0.38	3.79				**0.19**
	8	lag	0.55	8.92				**0.19**
Juniperus virginiana/9	1	lag	0.63	11.49				**0.20**
	2	lag	0.24	4.16				**0.11**
	4	lag	0.32	4.74				**0.14**
	8	single	0.06		102			**0.06**
	15	lag	0.24	7.27				**0.09**
Liquidambar styraciflua/2	1	single	0.24		79			**0.30**
	2	lag	0.69	7.87				**0.26**
	4	lag	0.68	8.02				**0.25**
	8	lag	0.58	4.90				**0.25**
Liriodendron tulipifera/1	1	lag	0.76	5.13				**0.33**
	2	lag	1.01	11.91				**0.33**
	4	dual			63	0.67	0.11	**0.22**
	8	lag	0.89	12.63				**0.28**
	15	single	0.21		100			**0.21**
Pinus echinata/7	1	lag	0.30	3.37				**0.15**
	2	lag	0.38	5.63				**0.16**
	4	lag	0.29	2.90				**0.16**
	8	single	0.21		101			**0.21**
Pinus taeda/7	1	lag	0.48	7.18				**0.18**
	2	lag	0.61	8.46				**0.22**
	4	lag	0.18	2.48				**0.11**
	8	lag	0.27	2.22				**0.17**
Quercus alba/5	1	lag	0.49	4.28				**0.23**
	2	lag	0.40	3.52				**0.20**
	4	lag	0.54	5.08				**0.24**
	8	lag	0.58	5.75				**0.24**
	15	lag	0.28	2.42				**0.17**
Quercus rubra/4	1	lag	0.76	8.40				**0.28**
	2	dual			98	0.33	0.04	**0.28**
	4	lag	0.66	11.96				**0.21**
	8	lag	0.45	4.44				**0.20**
Sassafras albidum/8	1	lag	0.40	4.60				**0.18**
	2	lag	0.56	5.43				**0.24**
	8	lag	0.12	2.97				**0.06**

k is the decay rate constant derived from equation type, L is the lag coefficient, Y_0 is the initial mass in percent dry weight for the single exponential equation or initial mass in percent dry weight applied to the fast fraction of the dual exponential equation, kf is the faster fraction decay rate constant of the dual exponential equation and ks is the slow fraction. k_I is the integrated decay rate constant.

however, the other effects of increased size such as colonization rates may limit their decomposition rates. The result is that small and large pieces of FWD have fairly similar rates of decomposition depending on their position relative to the forest floor.

However, even this level of complexity may not capture the entire effect of size on decomposition rates of FWD because substrate quality can also change with size. When the diameter size of FWD is taken into consideration we observed a significant de-

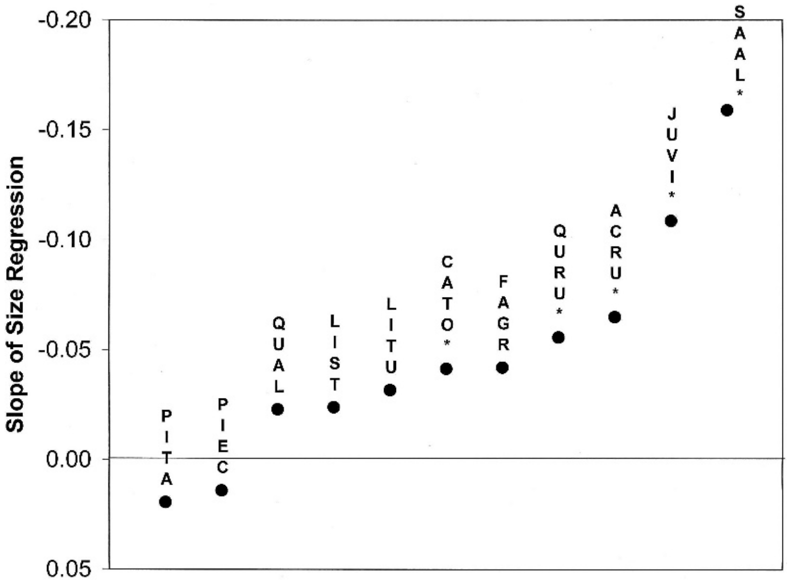

FIG. 4. Slope of the regression of k_I by size within a species. Species exhibiting a significant or highly significant size effect are denoted with a *. Species codes: ACRU *Acer rubrum,* CATO *Carya tomentosa*, FAGR *Fagus grandifolia,* JUVI *Juniperus virginiana,* LIST *Liquidambar styraciflua,* LITU *Liriodendron tulipifera*, PIEC *Pinus echinata,* PITA *Pinus taeda,* QUAL *Quercus alba,* QURU *Quercus rubra,* and SAAL *Sassafras albidum.*

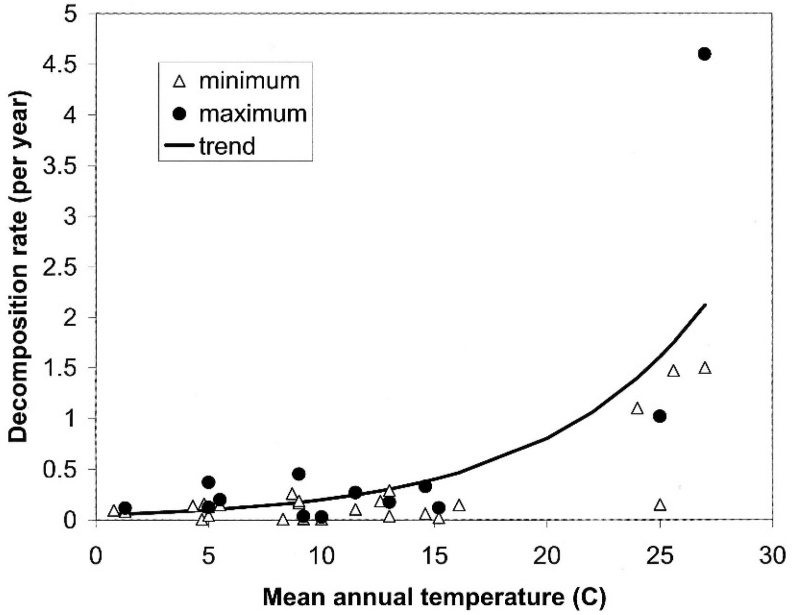

FIG. 5. Minimum and maximum FWD decomposition rates that have been observed globally versus mean annual temperature. Source of data includes: this study, Abbott and Crossley (1982), Boddy and Swift (1984), Brown et al. (1996), Christensen (1977), Erickson et al. (1987), Frangi et al. (1997), Gosz et al. (1973), Harmon et al. (1995), John (1973), Keane (2008), Lang (1974), Matson et al. (1987), O'Connell (1997), Palviainen et al. (2004), Proctor et al. (1983), Swift et al. (1976), Upadhyay and Singh (1985), Vávřová et al. (2009).

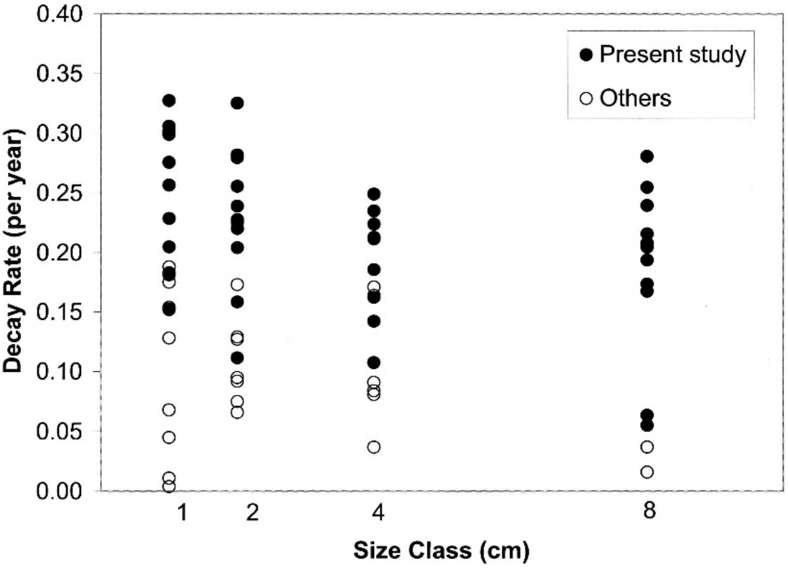

FIG. 6. The effect of piece diameter size classes (cm) on the decomposition rates of FWD from forest floor samples. Other studies include Abbott and Crossley (1982), Erickson et al. (1987), Matson et al. (1987), Swift et al. (1976), Vávřová et al. (2009).

crease of decomposition rate with increasing size for five of our eleven species, suggesting that physical size alone is not the only factor. Of the remaining six species studied, four showed moderately significant decreases with size and the two pine species had a moderate increase in rate with size (Fig. 5). We observed a greater decrease of rate with size in species with decay-resistant heartwood (e.g., *Juniperus virginiana* and *Sassafras albidum*) than those without which is similar to Harmon et al. (1995). This is because as the size of the former species increases, more decay-resistant material is added slowing down the overall decomposition rate.

Location relative to the forest floor (suspended above, resting upon, or buried below) in our study had a highly significant effect on decomposition rates of FWD of different sizes (Fig. 3). This complex pattern is probably driven by differences in moisture content interacting with size (Fig. 7). Buried FWD had the highest moisture content and showed the largest variation of rate with size, with the smallest samples decomposing at a rate equivalent to the forest floor samples then progressively slowing up to the largest size at which point the value was equivalent to samples suspended in the air. A higher moisture content would increase the rate for smaller FWD, but increasing moisture possibly becomes a limiting factor as size increases because the larger the diameter, the farther oxygen has to diffuse to support respiration. Changes in moisture regime might also explain why for pieces on the forest floor, the smallest diameters of FWD tended to have longer time lags to reach maximum decomposition rates, but when the maximum was reached the decomposition rate was faster relative to those sizes with shorter lags. The initial low rate of decomposition may have been related to excessive drying of the smaller exposed samples. However, once the forest floor samples were covered by fallen leaves, the drying rate decreased and decomposition proceeded relatively rapidly.

The observation that decomposition rates of FWD are dependent on the position of the material has several implications. The first is that since disturbances leave FWD in different positions, the time trend of carbon release could differ. A windstorm which places the majority of FWD near or on the soil surface would be expected to release carbon faster than a fire or insect outbreak which leaves the majority of FWD suspended above the soil surface. When disturbances leave standing dead wood, the faster decomposition rates of coarse roots compared to dead branches attached to standing stems could lead to a second pulse of carbon release once standing

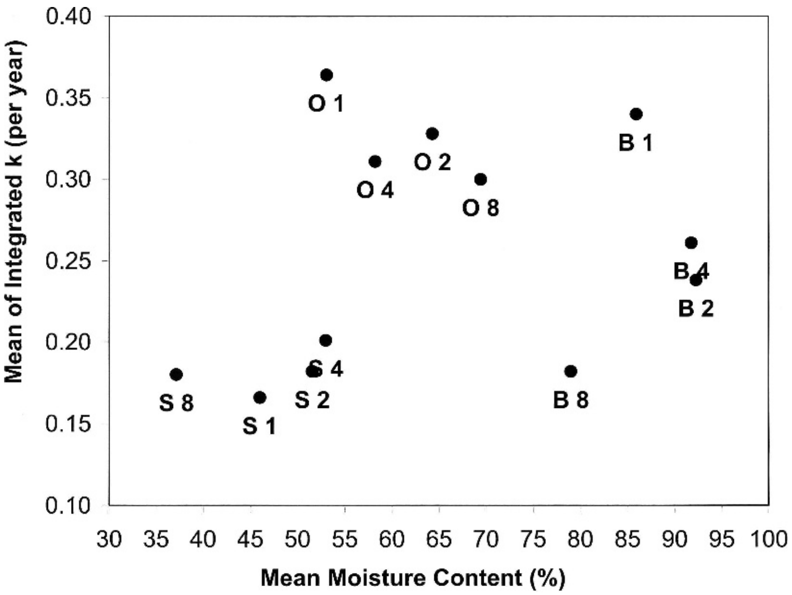

FIG. 7. Mean percent moisture content (*Carya tomentosa* and *Quercus alba* combined) and mean of integrated *k* by position (O, on the surface; B, below ground; S, suspended above ground) and size class (1, 2, 4, 8 cm).

stems eventually fall to the ground (Harmon et al. 2011). These differences in position also suggests that placing FWD as close to the soil surface as possible after logging would speed the decomposition of this material and more quickly reduce fire hazard.

Our experiments indicate that within a decade of a hurricane, the majority of FWD input by the storm had largely decomposed. Observations 10 years after the storm confirm our experimental results as most of the branches on downed trees $<$ 10 cm diameter had visually disappeared. This loss has caused the main stems of downed trees to settle onto the forest floor changing their microclimate and degree of interaction with the forest floor and quite possibly has increased decomposition rates of CWD. Based on the amount of live wood carbon added (Busing et al. 2009) and assuming FWD input in the form of branches and coarse roots was equivalent to half the mass of CWD, the cumulative 10-year pulse of carbon from FWD would have been on the order of 25 Mg ha^{-1}. The decomposition losses from the CWD estimated by Busing et al. (2009) for this same period were 35–45 Mg ha^{-1}. Combined, these losses would have exceeded the wood production of this forest over this period by almost a factor of two, indicating this hurricane may have caused this forest to be a carbon source to the atmosphere for 5–10 years.

Conclusions. Experiments examining the effect of position relative to the soil surface, size, and species on the decomposition rate of FWD indicated complex interactions among these factors. FWD on the soil surface tended to decompose the fastest, although the smallest pieces buried in the soil had comparable rates. While drying limited decomposition of suspended pieces, high moisture content may have limited decomposition of the largest pieces of FWD that were buried. Species had an important effect on decomposition rate of FWD, but it also influenced the response to increases in size, with the species with the most decay-resistant heartwood having the largest response to increases in size. The observed rates of decomposition indicate that most of the FWD input by Hurricane Fran had decomposed within the first 10 years leading to possibility of a substantial outflux of carbon from this forest.

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