

Wood Decomposition Following Clearcutting at Coweeta Hydrologic Laboratory

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Introduction

Most of the forest on Watershed (WS) 7 was cut and left on site to decompose (figure 7.1). This chapter describes the rate and manner of wood decomposition and also quantifies the fluxes from decaying wood to the forest floor on WS 7. In doing so, we make the case that wood and its process of decomposition contributes to ecosystem stability. We also review some of the history of wood decomposition and place our results in the context of detrital organic matter pools on the watershed.

Much of our understanding of wood decay has come out of studies on how to prevent decay (reviewed by Hunt and Garratt 1938; Campbell 1952; Cartwright and Findlay 1958). Indeed, the prevention of wood decay is still a big business—for example, the Forest Products Laboratory of Madison, Wisconsin, estimates that “billions of dollars” are spent each year to replace wood products destroyed by wood decay fungi. We now also recognize the positive aspects of wood decay. With the promotion of an ecosystem perspective as a way to study nature (e.g., Odum 1969), decomposition began to be recognized as an important part of nutrient cycles and energy flow. The development of the ecosystem perspective helped to stimulate studies of the role of wood and its decomposition under natural conditions (McFee and Stone 1966; Swift 1977) and more studies of wood decomposition under natural conditions began to appear in the literature.

As reviews of wood decay began to appear (Spaulding and Hansbrough 1944; Aho 1974; Kaarik 1974; Swift 1977), it became apparent that reported wood decay rates were highly variable. The extensive review by Harmon et al. (1986) perhaps best demonstrates the wide variability in wood decay rates, where 26 reviewed studies of wood in situ (i.e., in the forests as opposed to laboratory studies) showed

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Figure 7.1 Wood on WS 7 at year 1. Nearly 100 t/ha of wood was left on WS 7 following clearcutting. The volumes and densities were measured in 4 x 4 m plots during year 1 and provided the basis for remeasurements in years 6 and 11. (USDA Forest Service photo)

ranges of decay rates of more than 100-fold. It appeared difficult to draw meaningful quantitative relationships because even decay rates for the same species from the same region could vary by up to 25-fold. Most reviews have described specific details of various studies about the wood or site conditions and offered speculations on why decay rates may have been low or high in specific instances. But no relative comparison or ordering of the potential factors controlling wood decay had been attempted in most of these reviews, giving the impression that wood decay may be hopelessly variable. Meentemeyer (1984), however, developed a statistical model that explained 80% of the variation in decay of fine litter material over continental scales as a function of annual actual evapotranspiration (AET) combined with lignin content. This same analysis was performed for 67 reported wood decay rates (weight loss or density loss) by Meentemeyer's graduate student (Smith 1988), and she found that just over 50% of the reported wood decay rates could be explained by AET alone. Wood type explained another 8% (e.g., conifers decayed at 80% the rates of hardwoods) but diameter of the wood pieces, surprisingly, did not contribute to the model. She noted variability in methods as contributing significant sources of variation. Long-term regional studies of wood decay that control many of these methodological sources of variation have been conducted (e.g., Schowalter et al. 1998).

One method that probably has not served wood decay studies very well is the adoption of Olsen's (1963) "k" value to quantify the rate of change in density or mass. This method presumes that decay occurs in a rather orderly fashion and that the same proportion of the material is decayed each year. This technique allowed

researchers to measure decay rates in several different ways (e.g., by calculating mass loss over relatively short time periods or using simple estimates of flux into or out of a decaying "pool"). But use of a single exponent has been criticized as being too simple for substrates that were actually mixtures of substance of variable decomposability (Minderman 1968). Calculation of k using estimates of annual inputs divided by estimates of standing stock was noted to produce the highest reported rates of decay (Smith 1988) because standing stocks can be temporarily depressed due to non-steady-state conditions. Another innovation to quickly assess decay rates was the use of chronosequences (a series of sites in which the ages of the decaying wood was known or derived). Errors can arise in assigning ages to logs, and fragmentation from logs can be difficult to estimate. Probably the most accurate way to measure wood decay is to follow fresh logs through time and make repeated measures over the entire course of decay. Few wood decay studies have had this luxury, and none have followed the piece through complete decay. Given that the methods used to quantify wood decay rates can introduce variation, it perhaps should not be so surprising that highly variable rates can come out of different studies.

Despite the interest in the decay rates, it may be that it is more important to understand where the organic matter or carbon (C) goes following decay. Nutrient fluxes from decaying wood have been recently studied (Palviainen et al. 2004; Hafner et al. 2005) as have been C fluxes to the soil (Hafner et al. 2005; Zalamea et al. 2007). The role of wood is being considered in detrital C pools (Harmon and Hua 1991; Liu et al. 2006). Regional C budgeting attempts would be greatly aided if a general factor could be derived for wood that partitions the C flux from wood during decay between that which returns immediately to the atmosphere as CO_2 and that which enters the forest floor and soil and contributes to the "long-term" soil organic matter pools. Kononova (1966) suggested such a factor as ranging from 0.3 to 0.5 for all plant material, but this has never been tested to our knowledge. On a site level, organic matter and nutrient fluxes to the soil during wood decay should increase soil water storage, nutrient availability, and beneficial microbial populations. These, in turn, should benefit plant growth and may be one way of stabilizing the ecosystem during forest regrowth.

Our study of wood decay on WS 7 is different from most studies of wood decomposition in that it follows wood decomposition via repeated samples on individual logs over an 11-year period. This is a sufficiently long period to assess over half the wood mass loss at Coweeta. It includes measures of both solution and gaseous losses during decay. Because it follows measured logs from the start, we are able to make relatively reliable estimates of fragmentation rates. Estimates of fragmentation and solution fluxes allow us to estimate fluxes of organic matter and nutrients to the forest floor.

Site Description

Coweeta Hydrologic Laboratory (lat. 35° 03' N, long. 83° 25' W) is located in the southern Appalachian Mountains in western North Carolina. Coweeta forests are characterized as mixed-aged, oak-hickory hardwoods on steep slopes. Compared

to other temperate forests of North America, Coweeta is considered to have a relatively humid (annual precipitation of 180 cm per year, evenly distributed) and moderately warm climate (mean temperature 13°C, with monthly mean temperatures ranging from 2°C to 20°C annually). WS 7 drains a 59-ha basin and was clearcut in 1977. Saw logs were removed and remaining stems, along with slash, were left in place to decompose. Details of the management are given by Swank and Webster (see chapter 1, this volume). Slopes on WS 7 range from 20% to 80%; aspect varies due to the incised valley of the drainage network, but is generally south. The elevation ranges from 772 m at the gage to over 1000 m at the top of the ridge. Soils are Humic Hapludults on the lower elevations and Typic Distrochrepts on the higher elevations. Forest floors are composed of L, F, and H layers with thick H layers forming particularly on sites with *Kalmia latifolia* understory.

Methods

Green volumes of large wood (logs > 5 cm diameter) and densities of selected disks from logs were measured in a series of 4 x 4 m plots during year 1 following clearcutting of the WS 7 forest. Eighty-eight individual logs from 12 different species of trees from the first-year study were relocated in years 6 and 7 (Mattson 1986; Mattson et al. 1987). The logs that could be relocated were tagged and a series of measures made in years 6 and 7. The logs were revisited and measured in year 11 to provide a long-term data set on individual logs as they underwent decomposition.

Selected logs were measured for gaseous fluxes of CO₂ and solution fluxes of C and nutrients. Logs were fitted with 10-cm-diameter chambers attached to the wood surface in which CO₂ efflux was measured monthly via the static method of absorption into NaOH solution (Anderson 1982). Solution flux to the forest floor was estimated by fitting a collection trough beneath entire logs. Leachate volume was periodically measured and subsamples were analyzed for organic C and nutrients. Fragmentation losses were estimated by the assessment of volume losses from the individual logs where volume was measured in year 1. Wood nutrient concentrations were also followed over time. Mass of small wood (diameter < 5 cm) was measured at year 1 and 7 on 2 x 2 m plots. No measures were made at year 11, as all the small wood had decayed by then.

Results and Discussion

The overall density loss from the individual logs generally showed a linear decline; but some logs showed highly variable changes in density over time (figure 7.2). The difference in the slopes of the slowest and fastest logs suggest up to 3-fold differences in decay rates. The differences among species appear to be minor, except the decay-resistant black locust has clearly a slower rate of decay. The individual logs in figure 7.2 are highly variable (increasing and decreasing over time), showing that individual disks cut from the same log can produce highly variable rates of density

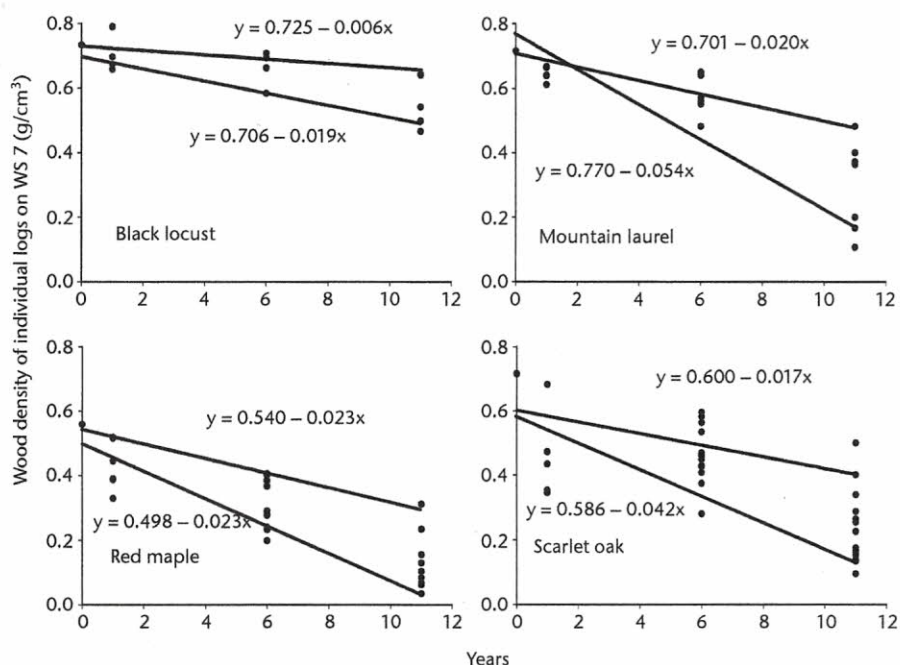


Figure 7.2 Density loss from individual logs and linear regressions of the slowest and the fastest decay shown by individual logs (solid lines). These four major species groups show within-species variation.

loss. Schowalter et al. (1998) also observed highly variable rates of loss over time for oak logs, and they suggest a two-phase pattern of rapid decay of inner bark followed by slower decay of sapwood and heartwood. Our data of density, determined on individual disks destructively sampled over time, shows that the density at any single point along a log can be highly variable once decay has started. Our data point out the need to have multiple samples from individual logs in order to assess decay rates. State of decay within an individual log has been shown to be variable spatially (Swift 1977; Graham et al. 1980; Pyle and Brown 1999). Most of the variation in our log decay appeared to be associated only somewhat with species but at least as much with individual conditions of the logs and likely reflect individual wood variation or contact with the soil or even the colonization patterns by decomposers.

The mass of large wood at four time periods (years 0, 1, 6, and 11) was calculated as the product of individual species volume and density for each period. Volume of large wood was measured for each tree species of wood at year 1. This volume was assumed to be equal to year 0 volumes and was corrected for observed volume loss or fragmentation loss by species at each time period (years 6 and 11). Each species volume was multiplied by the mean of its density for that time period. The mass was then summed over all species to get total wood at each time period. Small wood was simply collected and weighed at two time intervals (table 7.1). The

Table 7.1 Wood decomposition on WS 7 over the first 11 years following clearcutting of the forest.

	Amount remaining			
	Year 0	Year 1	Year 6	Year 11
Large wood*				
Green volume (cm ³ /m ²)	17,609	17,609	15,963	10,391
Green density (g/cm ³)	0.5176	0.4248	0.3321	0.2021
Dry mass (g/m ²)	9,114	7,481	5,302	2,100
Small wood**		Year 1	Year 7	
Dry mass (g/m ²)		2,100	780	

* Large wood > 5 cm diameter

** Small wood < 5 cm diameter

interacting patterns of density loss and volume loss, and the resulting decline of the entire large wood mass are shown in figure 7.3. The mass-weighted density of large wood was calculated as the ratio of summed mass divided by total volumes from table 7.1. This mass-weighted density declined in a negative exponential fashion while volume showed no changes and then began to decline at an increased pace. These two different processes contribute to mass loss that appeared to be linear over time as has been suggested for slow decay material such as wood (Taylor and Parkinson 1988).

The relationship of increasing fragmentation occurring as wood density decreased is shown for year 11 data in figure 7.4. Most fragmentation of logs did

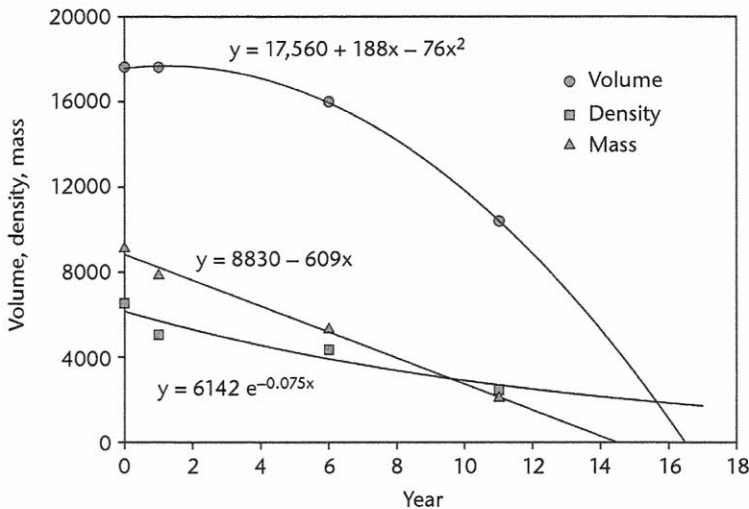


Figure 7.3 Wood decomposition on WS 7 versus time since clearcutting. The processes of density loss and fragmentation are compared to show how each contributes to mass loss. Solid lines are curve fits to the four data points. These are extrapolated to year 17. Density is the mass-weighted mean density of all measured wood pieces. The data have been scaled to allow plotting on the same axis: volume (cm³/m²), mass (g/m²), and density (g/cm³ x 10,000).

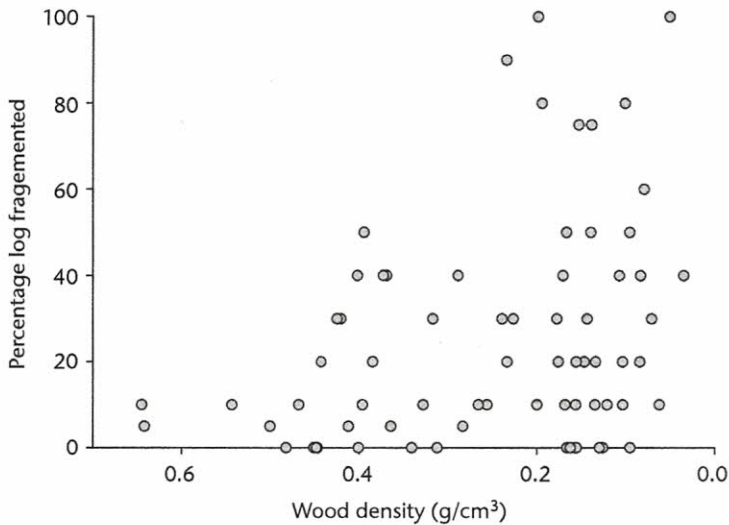


Figure 7.4 Degree of fragmentation of log versus density of wood for wood pieces on WS 7 at year 11. Degree of fragmentation is the percent of the original log that had completed fragmented or disintegrated. The mean wood density of class 3 and class 4 logs, or those that showed signs of complete structural loss, was 0.176 g/cm^3 . This was used as an estimate of wood density when the remaining logs would be considered to have entered the forest floor via fragmentation or collapse.

not begin to occur until after wood densities fell below 0.5 g/cm^3 and many pieces underwent complete fragmentation at densities as high as 0.25 g/cm^3 . The point at which fragmentation begins to occur is particularly important as it represents the point where the woody material contributes significantly to the forest floor organic matter.

Most wood decay studies do not address the later stages of decay; but in our study, wood was placed on the ground as a single "cohort," where age was known, and because the wood decayed rapidly, we were able to project the complete collapse of a volume of large wood in about 16 years (figure 7.3). Gore and Patterson (1986) assembled wood data from four studies of the clearcutting of hardwood forests of the northeast United States. Their projections match figure 7.3 closely, but their rates of loss were slower; initial wood masses of $10,500 \text{ g/m}^2$ declined to minimums of less than $2,000$ by year 30. Afterward, they showed that wood would begin to recover mass as inputs from wood litterfall began to accumulate. They projected steady-state masses of $4,000 \text{ g/m}^2$.

We partitioned the flux of C from wood as it decayed during years 7 through 11. We used our CO_2 effluxes, solution fluxes, and fragmentation rates to show that two-thirds of the C losses from wood went to the atmosphere as CO_2 and one-third entered the forest floor as either fragmentation or solution fluxes (table 7.2). The CO_2 fluxes from wood measured at years 6 and 7 (table 7.2) were 30% higher than the losses of C if we used the overall density losses (table 7.1). Using these data, we show the patterns of C fluxes shift over time as going mostly to the atmosphere

Table 7.2 Annual carbon fluxes associated with wood* on WS 7 estimated for years 7–11.

Flux	kg C ha ⁻¹ –yr ⁻¹
Solution inputs from canopy throughfall	+27
Solution outputs via leaching	–145
Outputs via fragmentation	–1190
Outputs via CO ₂	–2715
Net change	–4023

* Wood was assumed to be 50% C.

in the first years, and then going mostly to the forest floor in the later years (figure 7.5). When we integrated the two regression equations in figure 7.5 and solved for the time period between year 0 and year 16.5 (the point of projected complete collapse), we obtained the following total projected fluxes of wood organic matter: 9,700 g/m² of total loss and 4,100 g/m² of flux to the forest floor. This gives a slightly higher partition coefficient of 40% of the total loss of wood transferred to the forest floor. In either case, these fluxes to the forest floor agree with the general humus “coefficient” proposed by Kononova (1966); that is, 0.3 to 0.5 of the mass of fresh plant material contributes to humus formation. Graham et al. (1980) partitioned fragmentation and density loss from dead balsam fir in chronosequences of fir-waves and calculated a partition twice as high as ours. They estimated that two-thirds of their wood fragmented and entered the forest floor and one-third was lost to density decreases.

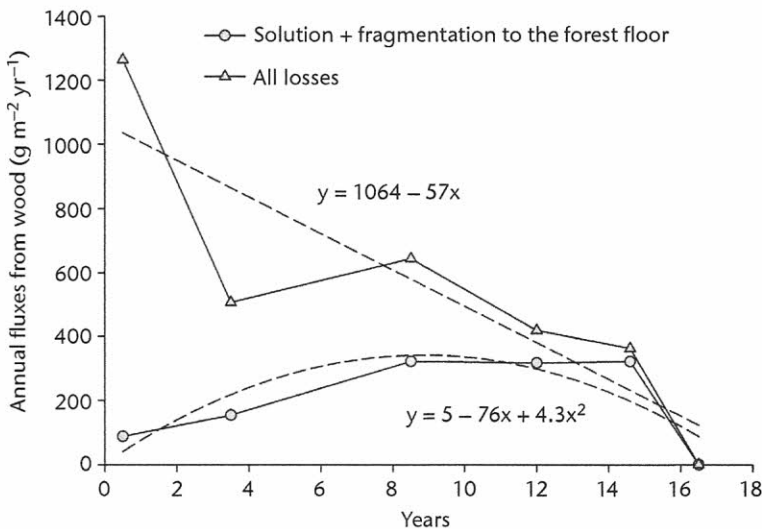


Figure 7.5 Annual fluxes of organic matter from wood during decomposition on WS 7. The two sets of symbols indicate the total losses from wood and those losses that go to the forest floor, respectively. The dashed lines are regressions. The area between the two dashed lines is the loss going to the atmosphere as CO₂; the area under the bottom dashed line is the flux to the forest floor.

Table 7.3 Nutrients in large wood on WS 7 with comparison to other studies.

	Nutrient concentration (% by weight)			Nutrient mass (g/m ² of watershed area)		
	Year 6	Year 11	Range of published values ¹	Wood Year 6	Wood Year 11	Live boles on WS 18 ²
N	0.186	0.317	0.14–0.30	9.86	6.62	26
P	0.008	0.012	0.002–0.02	0.40	0.25	11
Ca	0.159	0.273	0.02–0.26	8.42	5.70	8
K	0.060	0.038	0.01–0.10	3.19	0.79	14
Mg	0.010	0.100	0.01–0.03	0.53	2.09	1.8
Na	0.001	0.008	0.001	0.04	0.16	–

Note: Concentrations are for samples of large wood tissue (not bark). Mass estimates were extrapolated to both wood and bark (assuming bark concentrations were similar to wood concentrations).

¹ Grier (1978), Graham et al. (1980), Foster and Lang (1982), Barber and Van Lear (1984), Schowalter et al. (1998).

² Monk and Day (1988). Live wood mass on WS 18 was 13,400 g/m²; dead wood masses on WS 7 were 5,300 and 2,100 g/m² for years 6 and 11, respectively.

The major nutrients contained in the wood at years 6 and 11 were low, as expected of wood (table 7.3). Compared to other studies, our concentrations were slightly high in nitrogen (N), calcium (Ca), and magnesium (Mg), and low in phosphorus (P) and potassium (K). The concentrations of nutrients generally increased from year 6 to year 11, except for a slight decrease in K concentration. K decrease may reflect greater solubility and its loss may reflect physical leaching. The increase in concentration of the other nutrients, particularly N, indicates at least passive, or more likely active, retention by decomposing fungi. Organic N has been known to increase wood decay rates in laboratory studies (Campbell 1952; Cowling and Merrill 1966), and rates of microbial N fixation have been shown to increase in proportion to the degree of wood decay (Jurgensen et al. 1984). In general, other studies have shown that most nutrients increase in concentration during the course of wood decay, except for K, which has been observed to decrease (Grier 1978; Foster and Lang 1982; Fahey 1983; Keenan et al. 1993; Barber and Van Lear 1984).

Despite the low concentrations of nutrients in the wood, the mass of nutrients was still relatively large because of the large mass of wood. The mass of nutrients in the live boles on WS 18 (table 7.3) show how nutrients are conserved or lost in the wood. The mass of wood was considerably smaller than the mass of live boles on WS 18, but N was somewhat conserved as were Ca and Mg. P and K were considerably reduced, as these did not seem to be conserved in wood.

Estimates of element transfers from wood to the forest floor via leaching were collected in a set of logs placed onto modified throughfall collectors (table 7.4). The solution collected was often a brown color, indicating high content of dissolved organic C. The average concentration of dissolved organic C in year 7 was quite high at 115 mg/L, with the highest concentration of 490 mg/L from the most highly decayed logs. The calculated fluxes of dissolved nutrients (Ca, Mg, K) appeared to be relatively important to the soil directly beneath the logs, but since the projected cross sectional area of the logs equaled only 14% of the surface of the watershed, the fluxes on a watershed level were small. For example, Ca flux in solution to the

Table 7.4 Concentrations (mg/L) of dissolved organic carbon (DOC) and elements in solution passing into and out of wood and the resulting net flux to the forest floor for year 7 on WS 7.

	Canopy throughfall	Wood leachate	Net change in concentration	Flux from wood to forest floor (g m ⁻² yr ⁻¹)
DOC	5–24	56–180	76	102
N-NO ₃	0.11	0.08	-0.03	0.0
N-NH ₄	0.10	0.17	0.07	0.1
P-PO ₄	0.05	0.07	0.02	0.0
Ca	0.73	3.32	2.59	2.7
K	2.30	3.71	1.41	1.5
Mg	0.26	0.68	0.42	0.4

Note: Fluxes were calculated using the net increase in concentration from throughfall to wood and a measured annual solution throughput of 136 cm through wood. The fluxes represent the transfer to forest floor area directly below the wood, which is 14.25% of the total forest floor area. To get fluxes to the entire watershed, the fluxes must be multiplied by 0.1425.

entire watershed was 0.4 g m⁻² yr⁻¹ and equal to about 7% of the estimated forest uptake rates (5.4 g m⁻² yr⁻¹) for a reference forest on nearby WS 18 (Monk and Day 1988). The fluxes of nitrate, phosphate, and ammonium were negligible, due to the low concentrations and apparently conservative nature of the decomposing wood for these nutrients. This pattern of nutrient fluxes is similar to that observed for slash measured in year 1 after cutting. Generally, N uptake was observed and base cation leaching was substantial (Knoepp et al., chapter 4, this volume).

The flux of organic C in solution was not a large loss or a large flux to the detrital C pools. For example, the annual flux of dissolved C at year 7 from wood was calculated at 11 gC/m² of watershed area. This was less than 1% of the soil C content of the top 10 cm of soil (1,806 gC/m², Mattson and Swank 1989) as measured in year 7. Therefore solution fluxes from wood could not readily be the cause for the observed large, but short-lived, increase of concentrations of organic matter in the soil during the first two years following clearcutting of WS 7 (Waide et al. 1988; Knoepp and Swank 1997; see Knoepp et al., chapter 4, this volume). Still, the solution flux of dissolved C and nutrients are likely important as they create small micro-sites of nutrient enrichment. The leachate from wood is not uniformly distributed over the woody material but instead drips from distinct points and areas of contact with the soil.

While the transfers of material via solution from wood to the forest floor were relatively small, the transfers via fragmentation of the wood were notably greater (table 7.5). The total inputs of wood to the forest floor over the entire wood decomposition cycle, estimated to be about 16.5 years, was 4,135 g/m², for an average rate of input of 250 g m⁻² yr⁻¹. This input is 60% of the annual litterfall inputs to the forest floor at year 6 (420 g/m²; Mattson 1986) and clearly should have affected organic matter pools. Indeed, the forest floor measures on WS 7 showed a trend of increasing mass following clearcutting. Precut forest floor mass (L and F layers only) was 816 g/m² versus first-year postcut mass of 970 g/m² (Seastedt and Crossley 1981). By year 6, the forest floor (L and F layers) of WS 7 was 1158 g/m² versus

Table 7.5 Estimated transfers (g/m^2) of dry mass and nutrients to the forest floor from fragmenting wood on WS 7.

	Years 0–6	Years 6–11	Years 11–17	Total
Large wood*	570	1190	1410	3170
Small wood**	1120	780	0	1900
N	3.14	4.95	4.47	12.57
P	0.14	0.20	0.17	0.50
Ca	2.69	4.26	3.85	10.79
K	1.01	0.97	0.54	2.52
Mg	0.17	1.08	1.41	2.66
Na	0.02	0.09	0.11	0.22

* Large wood > 5 cm diameter

** Small wood < 5 cm diameter

equivalent measures on nearby uncut WS 2 of $880 \text{ g}/\text{m}^2$ (Mattson 1986). Increase in the forest floor is, in part, attributed to a temporary reduction in decomposition rates due to extremes of surface temperatures and desiccation during the first few years following the clearcut (Seastedt and Crossley 1981; Abbott and Crossley 1982). The inputs of wood are considered an important and perhaps larger cause of the observed forest floor increases. However during year 20, Vose and Bolstadt (2007) did not detect larger forest floor mass (L, F, and H layers) on WS 7 versus WS 2 based on only three sample sites.

Seven years after clearcutting, soil C was measured in WS 7 and adjacent WS 2 (Mattson and Swank 1989). The 0–10 cm layer contained $1806 \text{ g}/\text{m}^2$, a value close to that on WS 2 ($2106 \text{ g}/\text{m}^2$) and also similar to values 8 years after cutting ($1647 \text{ g}/\text{m}^2$) reported by Knoepp et al. (see chapter 4, this volume). The response of soil cations, C, and N are presented over a 33-year period after cutting WS 7 by Knoepp et al. (chapter 4, this volume).

The flux of nutrients to the forest floor from fragmenting small and large wood was substantial (table 7.5). The combined fragmentation of large and fine wood turns out to be relatively constant input of nutrients as small wood and bark fragmented early and large wood fragmented later. In this calculation, small wood and bark were assumed to have the concentrations shown for large wood (table 7.3). The total flux for the entire decay cycle divided by 16.5 years (the approximate time for wood to completely enter the forest floor) gives average annual flux rates that were equal to about one-quarter the amounts in litterfall on nearby control WS 18. For example, calculated N flux of fragmented wood averaged $0.76 \text{ g m}^{-2} \text{ yr}^{-1}$ compared to reported litterfall N flux of $3.3 \text{ g m}^{-2} \text{ yr}^{-1}$ for control WS 18 (Monk and Day 1988). Average Mg fluxes were 0.16 versus $0.65 \text{ g m}^{-2} \text{ yr}^{-1}$ for litterfall on WS 18.

Synthesis

The decomposition rate of the mass of wood on WS 7 was rapid but similar to that found in other reports from the southeastern United States for hardwood decay

(Abbott and Crossley 1982; Harmon 1982) or pine decay (Barber and Van Lear 1984). Wood mass loss is about twice as fast in the southeast versus the northeast United States (Gore and Patterson 1986) and several-fold faster than rates from the Pacific Northwest (Harmon et al. 1986). The interaction of early density loss and later fragmentation loss produced a generally linear rate of mass loss. Most wood decay studies have not followed individual pieces of wood over time but have instead attempted to derive decay rates from existing pieces of wood by estimating the time the wood had been decaying (i.e., chronosequences) and these studies may have underestimated fragmentation losses. But despite this difference, wood density loss was also high in our study.

The conditions of the wood substrate may be one reason for high rates of wood decay at Coweeta. The pieces of wood were relatively short and small in diameter. Average diameter was 12 cm, and few pieces were more than 25 cm. Lengths were typically 1 to 4 meters, and many pieces were cut in two during repeated sampling. Smaller wood has generally been shown to decay more rapidly as a result of greater proportion of nonresistant sapwood (Aho 1974); to have high surface-to-volume ratio, more readily exposing the inner wood to the elements and to decay organisms; and to have greater diffusion rates (Boddy 1983). Smaller pieces of wood also tend to have greater contact with the soil, which promotes moisture, decay fungi, and insects (Barber and Van Lear 1984). Hardwood species have lower lignin contents than conifers (Cote 1977), and lignin is known to be resistant to decay (Campbell 1952). The class of fungi called "white rots" can degrade lignin and are generally present in hardwood while "brown rots" cannot degrade lignin and are predominant in conifer wood (Rypacek et al. 1986). Finally, excessive wood moisture content has been noted as reducing decay in conifers (Progar et al. 2000). Perhaps a more important factor responsible for high wood-decay rates at Coweeta is the high and frequent rainfall in combination with the warm temperatures (Swift et al. 1988). Higher rates of wood decay are reported in warm moist regions, and the highest rates are from the tropics (Lang and Knight 1979; Smith 1988).

It may be important to clarify that the high fragmentation rate was actually a measure of "loss" of wood, and was not precisely "decomposition." We assumed the wood fragments that fell to the forest floor were equivalent to density loss in contributing to wood decay. This may overestimate decomposition rates of wood because wood pieces that fragment may still be composed of partially sound wood. Therefore, fragmentation may be considered as simply moving wood from logs to the forest floor, where it may persist. On the other hand, the fragments are clearly smaller and of lower density than logs and, once in the forest floor, act more as humus. Regardless of the terminology, it is important to differentiate between the loss of C to the atmosphere and the transfer of organic matter to the forest floor. Our data suggest that up to two-thirds of the mass is lost as CO_2 and that one-third or more enters the forest floor and soil as wood fragments. The transfer of wood to the forest floor contributes to refractory organic matter and nutrients. The forest floor increased in mass on WS 7 by year 6. Much of this increase may have been due to wood fragments. For example, wood fragments comprise up to 30% of forest-floor volume in forests in the Adirondak Mountains of New York State (McFee and Stone 1966). In our study, wood fragmentation was approximately equal to 50% of

litterfall during the period from 6 to 11 years after clearcutting. The inputs of wood would also be expected to be incorporated into the soil organic matter pool and contribute to long-term C storage

Wood decomposition is not conceptually difficult to measure, and the measured rate is a good integrator of a basic ecosystem process. The wood decomposition rate should reflect the tendency of a system to accumulate organic matter. Ecosystems have often been characterized by the accumulation of organic matter on site (Odum 1969; O'Neill et al. 1975; Waide 1988). Organic matter accumulation is in turn the result of the balance between the rates of primary production and decomposition. Coweeta forests and most forests of the southeastern United States do not typically have large accumulations of wood. The co-occurrence of moisture and warm temperatures create favorable conditions for rapid wood decay. In contrast, the accumulations of woody organic matter in the coniferous forests of the Pacific Northwest can exceed 300 Mg/ha where wood decomposition rates are among the lowest reported (e.g., k of 0.005 yr^{-1} ; Harmon and Hua 1991). Globally, the rates of primary production appear to be more narrowly constrained by climate than are the rates of organic matter decay (Meentemeyer 1984; Harvey 1989). This would mean that accumulations of organic matter are under greater control by decomposition rates that vary more than the production rates. Decomposition rates have a stronger exponential relationship with temperature than do plant growth rates. Therefore, one may expect that in areas of at least moderate primary production, such as a forest, the decay rate of resistant organic matter will be the primary determinant of the accumulation of organic matter.

Decaying wood acts as a slow-release fertilizer, releasing nutrients bound in the wood as the surrounding forest grows. The nutrient content in the wood on WS 7 was generally conserved and nearly equal to the pools in the forest floor. Also, the flux of N, Ca, and Mg in fragmenting wood was to be about one-quarter that of fluxes in litterfall.

Thus wood contributed to ecosystem resilience through woody debris decomposition and the subsequent flux of both organic matter and nutrients to the forest floor, increasing the nutrient content of detrital pools and supplying nutrients to the regrowing forest. As organic matter in wood decomposed into CO_2 and was lost from the system, the regrowth of new vegetation fixed CO_2 into new plant matter. Regrowth of new vegetation during the first two years of regrowth on WS 7 was estimated to be between 2.1 and 3.7 t/ha of biomass (Boring et al. 1988). This rate certainly increased over the first 11 years and surpassed the rate of organic matter loss from wood ($5 \text{ t ha}^{-1} \text{ yr}^{-1}$) as measured by woody CO_2 loss at year 6.

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