

## Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream

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**SUMMARY.** Effects of forest clearcutting on rates of leaf breakdown were studied in Big Hurricane Branch, a second-order stream located at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of North Carolina, USA. Breakdown rates of leaves of three tree species were measured in the stream before, during and after the catchment was clearcut. Changes in the stream attributable to logging and associated activities—principally road building—were increased stream flow, increased sediment transport, elevated water temperatures, increased nitrate concentrations and decreased allochthonous organic inputs. Breakdown rates of all three leaf species were slowed during clearcutting and accelerated later. Following logging the breakdown rate of dogwood leaves was equal to the pre-treatment rate, and white oak and rhododendron leaves broke down faster than prior to treatment. We attribute the slow breakdown during treatment to burial of the leaf packs in sediment. Subsequent acceleration may have been due to a lack of alternative food sources for invertebrate detritivores.

### Introduction

Small headwater streams draining deciduous forests, such as those typical of the southern Appalachian Mountains, receive large inputs of allochthonous organic matter every autumn. This allochthonous material accounts for the major energy input to such streams. Once in a stream, leaves are broken down by the combined effects of microflora, leaf consuming invertebrates, chemical leaching, and physical breakage. The rate at which breakdown occurs is modified by a variety of factors, including temperature (Kaushik & Hynes, 1968, 1971; Suberkropp, Klug & Cummins, 1975; Paul,

Benfield & Cairns, 1982), stream chemistry (Egglishaw, 1968, 1972; Hynes & Kaushik, 1969; Kaushik & Hynes, 1971; Howarth & Fisher, 1976; Hart & Howmiller, 1975; Iversen, 1975; Triska & Sedell, 1976; Kirby, Webster & Benfield, 1982), stream substrate (Reice, 1974) and characteristics of the leaves themselves (e.g., Petersen & Cummins, 1974).

Some leaves, e.g. dogwood, break down rapidly, whereas other leaf species, e.g. oaks, break down slowly. Several leaf characteristics seem to be involved in these differences. Cromack & Monk (1975) found that rates of leaf breakdown in a deciduous forest floor were best correlated with the initial lignin content of leaf species. Sedell, Triska and Triska (1975), Triska, Sedell & Buckley (1975), Suberkropp & Klug (1976) and Triska & Sedell (1976) showed the same trend in streams: slower breakdown by species with higher initial lignin content. Several

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studies have also suggested a relationship between breakdown rates in streams and initial leaf nitrogen content (Kaushik & Hynes, 1971; Sedell *et al.*, 1974; Hart & Howmiller, 1975; Triska *et al.*, 1975). This relationship, however, is not strong and is based primarily on the observed rapid breakdown of alder leaves, a nitrogen-fixing species having especially high tissue nitrogen concentrations. Wallace, Woodall & Sherberger (1970), Kaushik & Hynes (1971) and Mackay & Kalff (1973) found that aquatic invertebrates feed preferentially on certain leaf species. Kaushik & Hynes (1971) and Mackay & Kalff (1973) also noted that the order of feeding preference was similar to the order of breakdown rate. This relationship may be indirect. These authors and others, especially Bärlocher & Kendrick (1973a,b, 1975a,b), have shown that invertebrates prefer microbially colonized (conditioned) leaves, and microbial colonization rates are also related to breakdown rates (Petersen & Cummins, 1974; Suberkropp & Klug, 1976).

In this study we examined the effects of forest clearcutting on leaf breakdown in a second-order stream. Logging activities directly and indirectly affect most of the factors listed above: water

temperature is usually elevated (e.g. Brown & Krygier, 1970; Swift & Messer, 1971), nutrient levels increase (e.g. Likens *et al.*, 1977; Swank & Douglass, 1977), sediment load increases (e.g. Lieberman & Hoover, 1948; Brown & Krygier, 1971; Barton, 1977; Douglass & Swift, 1977) and adversely affects stream invertebrates (e.g. Ellis, 1936; Tebo, 1955; Cordone & Kelly, 1961; Burns, 1972) and the quantity and quality of leaves entering the stream are modified. Interactions among these several factors are complex, however, so it may not be possible to predict, *a priori*, how logging will affect rates of leaf breakdown in any specific instance.

### Description of study area

This study was conducted on Catchment 7 at Coweeta Hydrologic Laboratory, Franklin, North Carolina (Fig. 1). Prior to clearcutting in 1977, the only experimental manipulation to this 58.7 ha, south-facing catchment, since the U.S. Forest Service began management in 1924, was a woodland grazing experiment. Six cows grazed the area from 1941 to 1949, but had little long-term impact on the vegetation (Johnson, 1952).

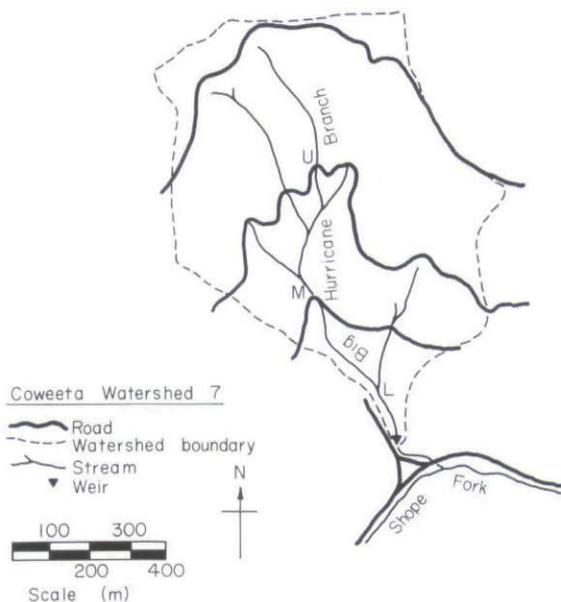


FIG. 1. Map of Catchment 7 and Big Hurricane Branch. U, M, and L indicate the upper, middle, and lower sampling sites, respectively.

Twenty-five years later there were no discernable effects of grazing on water chemistry or flow characteristics (Swank & Douglass, 1977). Pre-clearcut vegetation on the catchment could be separated into four main vegetation types. A pine-hardwood association occurred at higher altitudes and along ridges. An oak-hickory association at intermediate altitudes occurred in two distinct types based on dominant tree species, litter depth and decay rate, and soil moisture and temperature: mesic on east-facing slopes, and xeric on west-facing slopes. At lower altitudes along ravines, the vegetation was a typical cove hardwood association. *Rhododendron maximum* L. was a major understory

species, especially along the stream channel.

Catchment 7 is drained by a second-order stream, Big Hurricane Branch (Plate 1a,b). This stream has a 90° V-notch weir for continuous recording of discharge. Based on 29 years of record, pre-clearcutting discharge averaged 17.7 l s<sup>-1</sup> (data from U.S. Forest Service, Coweeta Hydrologic Laboratory). The 1225 m main channel has an average gradient of 0.191 m m<sup>-1</sup>, and varies from sections of steep exposed bedrock to short sandy reaches of low gradient and infrequent small pools. The drainage density is 42 m ha<sup>-1</sup>. Prior to clearcutting, dissolved nutrient levels in Big Hurricane Branch were quite low. Among the biologically important

TABLE 1. Leaf fall and leaf blow-in to Big Hurricane Branch before and after clearcutting. The 'other' category includes all leaf species comprising less than 3% of the total and all unrecognizable leaf fragments. Data were collected with six 0.4045 m<sup>2</sup> litter traps located over or adjacent to the stream and twelve 0.4 m wide blow-in traps located on the stream bank

Species	Percentage Composition			
	Pre-treatment		Post-treatment	
	Leaf fall*	Blow-in†	Leaf fall‡	Blow-in§
White oak <i>Quercus alba</i> L.	14.2	5.5	—	—
Red Oak <i>Quercus rubra</i> L.	13.4	11.6	—	—
Rhododendron <i>Rhododendron maximum</i> L.	11.6	16.1	26.5	22.4
Hickories <i>Carya</i> spp.	11.4	16.5	—	—
Yellow Poplar <i>Liriodendron tulipifera</i> L.	9.1	14.4	10.8	—
Birches <i>Betula</i> spp.	5.4	8.1	15.7	—
Chestnut Oak <i>Quercus prinus</i> L.	4.8	7.1	—	—
Red Maple <i>Acer rubrum</i> L.	4.8	4.6	—	57.9
Basswood <i>Tilia americana</i> L.	4.2	—	—	—
Beech <i>Fagus grandifolia</i> Ehrh.	—	4.2	—	—
Dogwood <i>Cornus florida</i> L.	—	—	3.9	—
Other	21.1	11.9	43.1	19.7
Total annual input (dry wt)	259.2 g m <sup>-2</sup>	174.8 g m <sup>-1</sup>	4.2 g m <sup>-2</sup>	38.6 g m <sup>-1</sup>

\*Measured in autumn, 1974.

†Measured in 1974–75.

‡Measured in autumn, 1978.

§Measured in 1978–79.

nutrients,  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$  and  $\text{PO}_4\text{-P}$  averaged 2, 4, and  $2 \mu\text{g l}^{-1}$ , respectively (Swank and Douglass, 1977).

Dense riparian vegetation provided heavy shading for this stream, especially during the period May–mid-October. Autochthonous primary production is extremely low in such undisturbed streams at Coweeta (J. J. Hains, personal communication). However, stream-side vegetation produced  $259.2 \text{ g m}^{-2} \text{ year}^{-1}$  of direct litter input in 1974–75, and an additional  $174.8 \text{ g m}^{-1} \text{ year}^{-1}$  of litter blow-in (Table 1). Several species of oaks, hickories and birches, as well as rhododendron, red maple and beech, were the dominant contributors of allochthonous material.

During April–June, 1976, three roads with a total length of 2.95 km were built on Catchment 7 for logging access (Plate 1d). Two of the roads crossed the main stream (Fig. 1). Approximately 5% of the catchment area was disturbed by road building. Logging began in January 1977 and was

completed in June 1977 (Plate 1c). Site preparation, i.e. clearfelling trees that remained after logging, was completed in October 1977. A mobile cable system was used for most logging; however, tractor skidding was used on more gentle slopes (about 8.9 ha). A total of 15.9 ha was not logged (but was site prepared) due to the poor quality of timber growing there. Mineral soil was exposed on less than 10% of the total catchment area. Following logging, most of the logging debris which fell in or over the stream was removed from the main channel (Plate 1b).

## Methods

Measurements of leaf breakdown rates were made in three separate periods: 1974–75, prior to any disturbances associated with logging; 1976–77, after road building but during logging; 1977–78, following completion of all logging activities

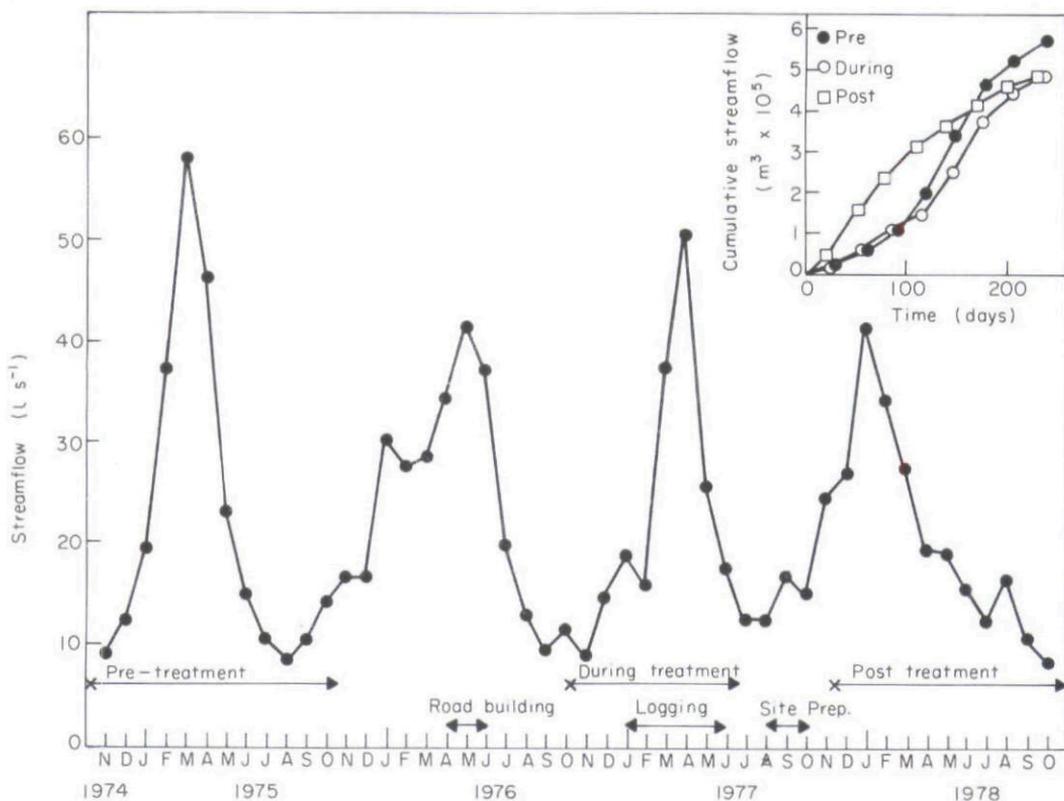


FIG. 2. Streamflow in Big Hurricane Branch during the study period. The time span of each leaf breakdown study and various logging activities are indicated. Cumulative streamflow during each leaf breakdown study is shown in the insert. Data from U.S. Forest Service, Coweeta Hydrologic Laboratory.



PLATE 1. (a) A section of big hurricane branch prior to clearcutting located 75m upstream from the weir. (b) The same site after clearcutting. (c) The cable logging operation in progress. (d) One of the roads built into the catchment for logging access.

(Fig. 2). These three periods are referred to here as pre-, during-, and post-treatment, respectively. Each autumn, senescent leaves of dogwood (*Cornus florida*), white oak (*Quercus alba*), and rhododendron (*Rhododendron maximum*) were collected from trees just prior to leaf abscission. Two to four grams (dry wt) of leaves were placed in nylon mesh bags (10 × 10 cm, 3-mm octagonal openings). Bags of leaves were air dried for 7–10 days, weighed and placed in the stream. In the pre-treatment study, sixty bags of each leaf species were placed at each of three sites: 350, 750, and 1150 m below the stream origin (Fig. 1); these sites are referred to as upper, middle and lower. In the during-treatment study, forty bags of each leaf species were placed at the lower site only. For the post-treatment study, we placed thirty bags of each species at each of the three sites. In addition, during the pre-treatment study, we exposed leaves of each species in packs loosely tied together with nylon fishing line at the lower site only.

Prior to placing bags and packs in the stream, its bed was raked to remove leaves already there and to provide more even water flow over the area. Bags and packs were then distributed over the area and tied in groups to galvanized nails inserted in the stream bed. Bags and packs were retrieved periodically (frequently at first, less often later) until the majority of leaf material had disappeared from the bags. In the laboratory, leaves were rinsed to remove attached sediment, air dried and weighed. Subsamples were ashed (495°C, 4 h) in order to correct weights to ash-free dry weights.

Leaves of each species were analysed for initial nitrogen by a micro-Kjeldahl procedure which involved digestion of 0.50 g of dried and ground (40 mesh) leaf material in 7 ml of a mixture of concentrated sulphuric and selenous acids for 2 h at 265°C, followed by dilution to 50 ml and analysis on a Technicon AutoAnalyzer II. Initial lignin content of the leaves was analysed using the spectrophotometric method of Johnson, Moore & Zank (1961). This procedure involved leaching 1.0 g of dried, ground (40-mesh) leaf material successively with hot deionized water, ethanol, acetone, and diethyl ether. The lignin was then digested by acetyl bromide (25% in glacial acetic acid) and the samples were subsequently read on a double beam spectrophotometer at 280 nm.

Throughout the 4 years spanned by this study, chemical and physical measurements of Big Hurricane Branch were made routinely by Forest Service personnel at Coweeta Hydrologic Laboratory.

## Results

### Streamflow

Compared to undisturbed streams, discharge in Big Hurricane Branch during the first year following completion of logging (July 1977–June 1978) increased about 28% (W. T. Swank, personal communication). Increased flows were especially pronounced in summer and autumn. This is a commonly observed result of clearcutting and may be attributed to the reduction in transpirational loss during summer and the lag in movement of water through the soil to the stream channel.

Comparisons among the three litter bag study periods show that the greatest cumulative streamflow occurred during the pre-treatment period (Fig. 2). Smaller and nearly equal cumulative flows occurred in the during- and post-treatment study periods. Differences in the temporal pattern of discharge were also observed. The seasonal distributions of flow were similar in the pre- and during-treatment studies. However, due to increased winter flows in the post-treatment study, much higher cumulative flows and a larger fraction of the annual flow occurred during the first 100–120 days in this study period.

### Stream temperatures

Summer water temperatures increased in Big Hurricane Branch following clearcutting (Fig. 3). Actual temperatures were 2–3°C higher than temperatures predicted from a pre-treatment regression against water temperatures in a stream draining an adjacent, forested catchment. However, cumulative degree-days were lowest in the during-treatment study and about the same in the pre- and post-treatment studies (Fig. 3). During the first 200 days of exposure, 2100, 1760 and 2250 degree-days were accumulated in the pre-, during- and post-treatment studies, respectively.

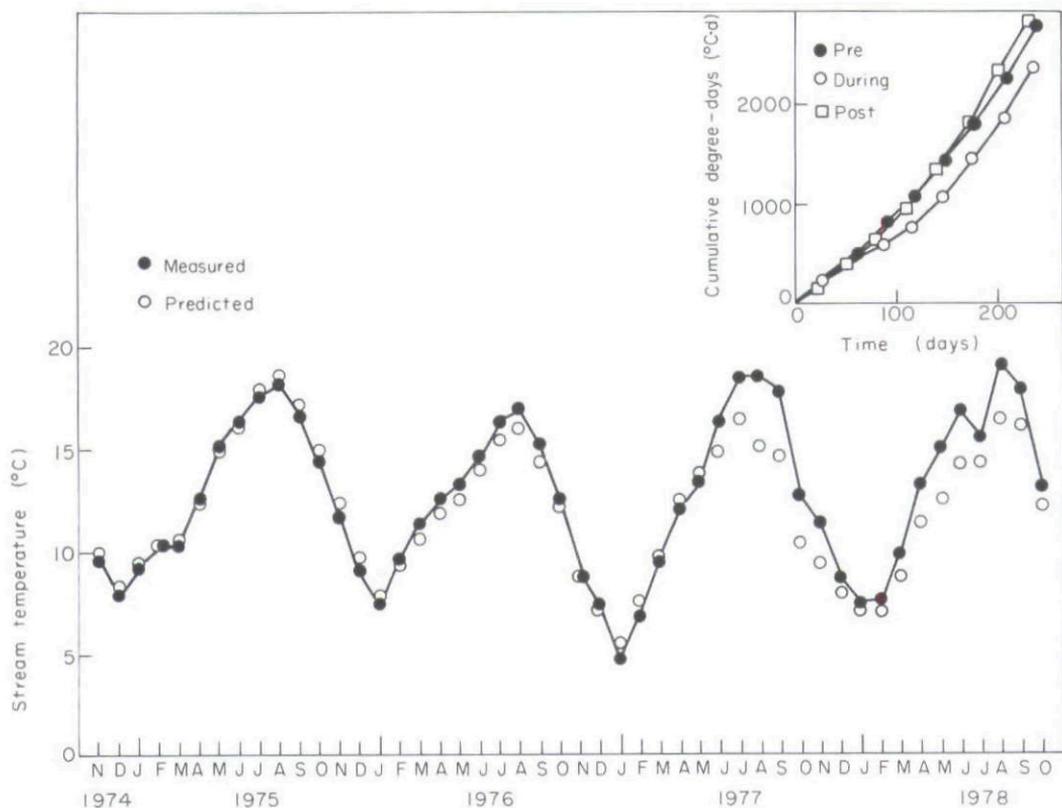


FIG. 3. Stream water temperature in Big Hurricane Branch during the study period. Actual temperatures are compared with temperatures predicted from a pre-treatment regression against water temperature in an adjacent undisturbed stream. Cumulative degree-days during each leaf breakdown study are shown in the insert. Data from U.S. Forest Service, Coweeta Hydrologic Laboratory.

#### Dissolved nutrient levels

There were small but detectable changes in concentrations of dissolved ions following treatment (data from U.S. Forest Service, Coweeta Hydrologic Laboratory). During and following road-building, but prior to clear-cutting, increases were found in concentrations of Ca,  $\text{SO}_4\text{-S}$ , K, Cl, Mg, Na and  $\text{SiO}_2$ . However,  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$  and  $\text{PO}_4\text{-P}$  showed no response during that year. In the next year, the most conspicuous change was a large increase in the concentration of dissolved  $\text{NO}_3\text{-N}$ , beginning in August 1977 (Swank & Waide, 1980). The concentration of  $\text{NO}_3\text{-N}$  subsequently increased from pre-treatment levels of  $2\mu\text{g l}^{-1}$  to  $40\mu\text{g l}^{-1}$  or higher. The concentration of  $\text{PO}_4\text{-P}$  remained near pre-treatment levels.

#### Sediment

Suspended sediments leaving the weir pond showed large increases over pre-treatment levels, principally during the road building and logging phases, when use of roads was greatest (Fig. 4). The highest suspended sediment concentration was recorded in June 1976, following two large storms (precipitation amounts of 15 and 25 cm, the second having a 100-year return frequency). Suspended sediment concentrations then declined until they again rose in the period of logging and site preparation (March–October 1977). Concentrations generally declined thereafter.

Based on accumulation of sediment in the weir pond, which comes primarily from bedload, pre-treatment sediment load averaged  $37\text{ kg day}^{-1}$ .

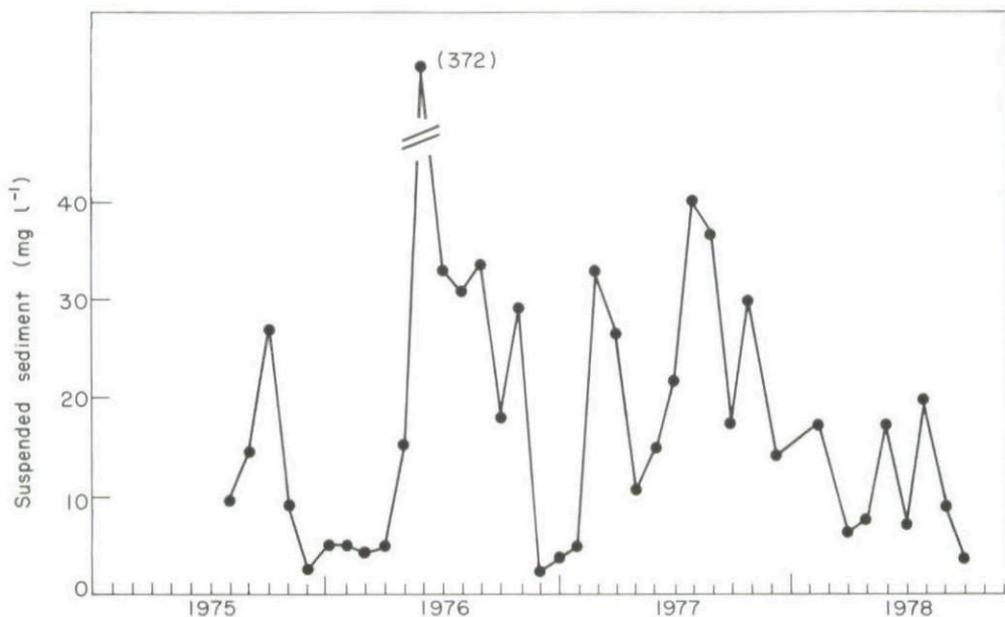


FIG. 4. Suspended concentrations in flow-proportional samples taken from water crossing the weir blade in Big Hurricane Branch. Data from U.S. Forest Service, Coweta Hydrologic Laboratory.

During road construction, this fraction of the sediment load increased to  $753 \text{ kg day}^{-1}$ . Much of this increase can be attributed to the effects of the two large storms mentioned previously which occurred as the roads were being built. These storms washed large amounts of material from roadbeds into the stream channel. In the subsequent period of road stabilization, sediment load decreased to  $47 \text{ kg day}^{-1}$ , only slightly above pre-treatment levels. For the during-treatment study period, this fraction of the sediment load increased to  $80 \text{ kg day}^{-1}$ , and it further increased to  $164 \text{ kg day}^{-1}$  in the third, post-treatment study period. In the during- and post-treatment periods, much of the increased load was in fairly large ( $>.05 \text{ mm}$ ) particles as was also reported by Gurtz, Webster & Wallace (1980).

#### Leaf breakdown rates

Breakdown rates were calculated as the slopes (absolute values) of regression equations, with the natural logarithm of the fraction of the initial weight remaining expressed as a function of exposure time measured in days (Jenny, Gessel & Bingham, 1949; Olson, 1963; Petersen &

Cummins, 1974). For all breakdown rates calculated, the regression slopes were significantly different from zero ( $P > 0.05$ ). Breakdown rates were compared using an analysis of covariance for pair-wise comparisons (Sokal & Rohlf, 1969). All differences were tested at the 5% level of significance.

*Exposure method effect.* During the pre-treatment study, breakdown rates were measured at the lower site by two exposure methods, bags and packs (Table 2). For white oak there was no significant difference between

TABLE 2. Pre-treatment breakdown rates ( $\text{day}^{-1}$ ) measured in bags and packs at the lower site. Each rate is given with its 95% confidence interval. Numbers in parentheses are the number of samples and the coefficient of determination,  $r^2$

	Bags	Packs
Dogwood	$0.0235 \pm 0.0041$ (35, 0.80)	$0.0116 \pm 0.0059$ (17, 0.55)
White Oak	$0.0080 \pm 0.0008$ (53, 0.90)	$0.0076 \pm 0.0011$ (36, 0.61)
Rhododendron	$0.0025 \pm 0.0006$ (53, 0.57)	$0.0055 \pm 0.0014$ (40, 0.85)

rates measured by the two methods at the lower site. At the lower site, dogwood leaves broke down significantly slower whereas rhododendron leaves broke down significantly faster in packs, when compared with bags. Neither method gave consistently smaller confidence intervals or larger coefficients of determination. Cummins *et al.* (1980) found that breakdown rates of packs were similar to breakdown rates of natural leaves in riffles of a low gradient stream, whereas breakdown rates for leaves confined in 1 mm mesh bags were significantly slower. However, Benfield, Paul & Webster (1979) found that the technique used to expose leaves was less important than the amount of material exposed. Because bags facilitate handling, we found the use of large mesh bags which do not restrict macroinvertebrate movement more practical for our work. All subsequent results will be discussed in terms of breakdown rates for bags only.

*Site effects.* In the pre- and post-treatment studies, leaves were exposed at three different sites (Table 3). In general, we found little consistency in differences among sites that could be

related to any measured physical or biological differences among sites. No site had consistently faster or slower breakdown rates during either study. Differences in breakdown rates among sites probably relate to the random placement of bags in relation to patterns of water flow at each site. In the rest of the paper, data from the three sites have been combined.

*Species effects.* Comparisons of composite breakdown rates of the three leaf species during the three study periods are shown in Table 3 and Fig. 5. In both the pre- and during-treatment studies, dogwood leaves broke down significantly faster and rhododendron broke down significantly slower than the other two leaf species. In the post-treatment study, dogwood breakdown was significantly fastest, but rates for rhododendron and white oak were not significantly different.

*Treatment effect.* Breakdown rates of all three leaf species were significantly slower in the during-treatment study than prior to treatment (Table 3). Dogwood and white oak were affected similarly, declining to about 60% of their pre-

TABLE 3. Breakdown rates ( $\text{day}^{-1}$ ) of the three leaf species measured during each of the three study periods. Each rate is given with its 95% confidence interval. Numbers in parentheses are the number of samples and the coefficient of determination,  $r^2$

Species	Site	Pre-treatment	During-treatment	Post-treatment
Dogwood	upper	$0.0234 \pm 0.0040$ (36, 0.80)		$0.0256 \pm 0.0035$ (30, 0.81)
	middle	$0.0196 \pm 0.0041$ (37, 0.73)		$0.0209 \pm 0.0041$ (30, 0.80)
	lower	$0.0235 \pm 0.0039$ (35, 0.80)	$0.0134 \pm 0.0023$ (45, 0.77)	$0.0186 \pm 0.0036$ (30, 0.89)
	combined	$0.0219 \pm 0.0025$ (104, 0.74)		$0.0219 \pm 0.0024$ (84, 0.81)
White Oak	upper	$0.0056 \pm 0.0009$ (51, 0.76)		$0.0107 \pm 0.0010$ (30, 0.94)
	middle	$0.0053 \pm 0.0008$ (43, 0.81)		$0.0047 \pm 0.0010$ (30, 0.78)
	lower	$0.0080 \pm 0.0008$ (53, 0.80)	$0.0038 \pm 0.0004$ (44, 0.91)	$0.0109 \pm 0.0011$ (30, 0.94)
	combined	$0.0064 \pm 0.0006$ (143, 0.78)		$0.0090 \pm 0.0010$ (84, 0.79)
Rhododendron	upper	$0.0037 \pm 0.0008$ (53, 0.61)		$0.0162 \pm 0.0021$ (30, 0.72)
	middle	$0.0047 \pm 0.0019$ (59, 0.32)		$0.0053 \pm 0.0015$ (30, 0.64)
	lower	$0.0025 \pm 0.0006$ (53, 0.57)	$0.0011 \pm 0.0003$ (45, 0.65)	$0.0082 \pm 0.0033$ (28, 0.78)
	combined	$0.0037 \pm 0.0007$ (156, 0.37)		$0.0105 \pm 0.0020$ (82, 0.59)

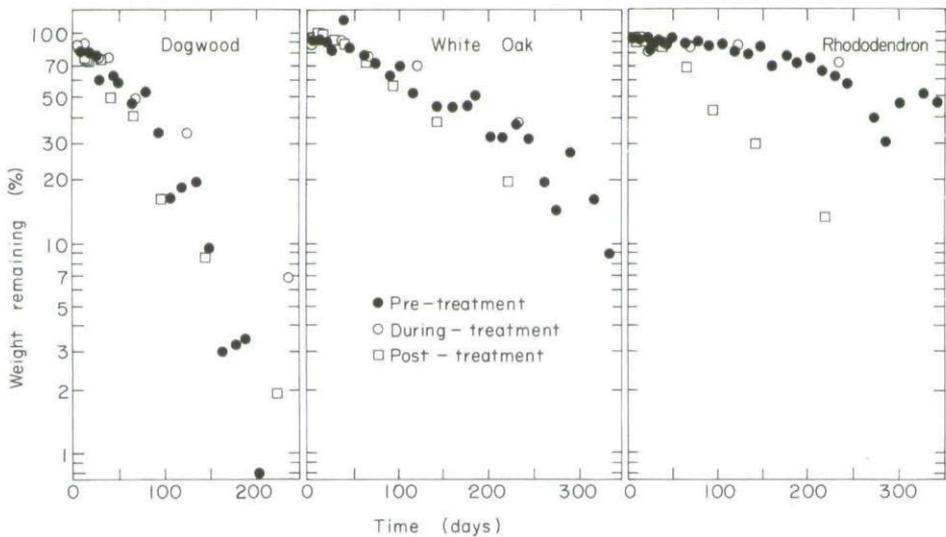


FIG. 5. Leaf breakdown plotted on semi-logarithmic scales as a percentage of the initial ash-free dry weight remaining for each of the three leaf species during each of the three studies.

treatment values. The breakdown rate of rhododendron was more strongly affected, slowing to about 30% of its pre-treatment value. In contrast, except for dogwood, breakdown rates generally increased in the post-treatment period as compared with the pre-treatment rates. Dogwood broke down at the same rate in both study periods. Breakdown of white oak increased about 40% in the post-treatment period. Again, rhododendron, the species which broke down most slowly in the pre-treatment study, was affected most. Its breakdown rate increased about 180% in the post-treated period in comparison with the pre-treatment period.

## Discussion

Forest clearcutting and road building on Catchment 7 caused a variety of physical, chemical and biological changes in Big Hurricane Branch. These changes appear to have had a complex effect on leaf breakdown rates in this stream.

Although mean and maximum stream temperatures increased in the summer following clearcutting, degree-days accumulated during the pre- and post-treatment studies were not substantially different. However, accumulated degree-days in the during-treatment period were less than in the other two study periods. Differences in breakdown rates in the three study periods were evident after 100–150 days,

especially for rhododendron (Fig. 5), yet degree-day accumulations were quite similar at that time for the pre- and post-treatment studies. Lower degree-day accumulations during treatment may have contributed to the slower breakdown rates observed at that time.

Increased stream  $\text{NO}_3\text{-N}$  concentrations in the post-treatment period may have influenced breakdown rates, although they were not a factor in the during-treatment study. Triska & Sedell (1976) found that increasing the nitrate levels in experimental streams did not significantly increase breakdown rates. However, the nitrate level in their control stream was considerably higher ( $43\mu\text{g l}^{-1}$ ) than the nitrate level in Big Hurricane Branch prior to treatment ( $2\mu\text{g l}^{-1}$ ). If the increased streamwater nitrate concentration did influence post-treatment leaf breakdown, the effect should have been greatest for rhododendron leaves as is indeed evident in Fig. 5, since these leaves have the lowest tissue nitrogen concentrations (Table 4). However, the recent study by Elwood *et al.* (1981) suggests that leaf breakdown rates in the southern Appalachian Mountains are more likely limited by phosphorus than nitrogen. Phosphorus concentrations in Big Hurricane Branch did not increase in response to clearcutting.

Changes in the initial substrate quality of the three leaf species over the different study periods also do not seem to be related to differences in breakdown rates (Table 4). In the first two study

TABLE 4. Initial characteristics of leaves used in each of the studies. TKN is total Kjeldahl nitrogen

Species	Study period	Ash (%)	TKN (%)	Lignin (%)
Dogwood	Pre-treatment	10.98	1.63	8.0
	During-treatment	10.65	1.06	8.2
	Post-treatment	11.63	1.16	8.1
White Oak	Pre-treatment	6.57	1.38	13.8
	During-treatment	6.11	1.03	13.0
	Post-treatment	4.15	0.99	12.3
Rhododendron	Pre-treatment	4.23	0.77	7.6
	During-treatment	5.23	0.74	8.2
	Post-treatment	8.05	0.73	7.2

periods, all leaf material placed into litter bags was collected on or immediately adjacent to Catchment 7. In the third study, material was collected from an adjacent undisturbed catchment so that we could specifically study changes in physical and biological conditions within Big Hurricane Branch, as they influenced leaf breakdown rates, independently of the altered quality of early successional vegetation on Catchment 7. The small variations in leaf characteristics shown in Table 4 are not of sufficient magnitude to explain either the reductions in breakdown rates in the during-treatment study or the increased rates of white oak and rhododendron breakdown in the post-treatment study.

Changes in stream flow following clearcutting may have contributed to differences in leaf breakdown rates reported here. Specifically, the increased flows observed in the post-treatment study (Fig. 2) may have accelerated breakdown during that period. However, reduced breakdown rates in the during-treatment period cannot be attributed to an alteration of stream flow.

There are two possible direct effects of sediment on leaf breakdown rates. Sediment in the stream bed may bury leaves, making them unavailable to most macroinvertebrates and possibly causing anaerobic conditions in the leaf pack (Cummins *et al.*, 1980). Alternatively, movement of sediment particles may cause abrasion and physical leaf breakdown. Based on sediment transport data from Big Hurricane Branch, it appears that a large amount of sediment entered the stream channel in late spring, 1976, due primarily to two large storms that occurred as roads were being built on the catchment. A large fraction of this sediment influx was

washed out of the stream channel immediately, but much remained, particularly the larger material, and moved downstream slowly in subsequent years. As a result leaf bags were often buried in sediment in the during-treatment study period, possibly contributing to slower leaf breakdown rates.

By the time of the post-treatment study, suspended sediment levels had declined below levels of the previous year (Fig. 4), indicating that smaller-sized sediment particles had been mostly washed out of the stream. However, transport of larger particles (>0.05 mm) which settled out in the weir pond was higher than the previous year. Movement of this material in the stream may have accelerated leaf breakdown rates by physical abrasion of the leaves. However, this possible explanation of accelerated breakdown rates in the post-treatment study does not explain why rhododendron breakdown rate was so much more accelerated than white oak or dogwood. Also, since leaf breakdown in the post-treatment study was generally accelerated most at the upper study site (Table 3), which was least affected by sediment inputs from the roads (Fig. 1), abrasion by sediment cannot be the only factor, or even the most important factor, causing accelerated breakdown rates in the post-treatment study period.

The abundance of leaf-consuming fauna available to process leaves is a final factor, potentially regulating breakdown rates, which was altered by clearcutting. Densities of *Peltoperla maria* Needham, a dominant shredder (Cummins, 1973) in Coweeta streams, declined in Big Hurricane Branch following clearcutting (M. Gurtz, personal communication). The role

of stream macroinvertebrates on rates of leaf breakdown has not been clearly quantified. Petersen & Cummins (1975), Hart & Howmiller (1975), Iversen (1975), Sedell *et al.*, (1975) and Kirby *et al.* (1982) all attributed differences in leaf breakdown rates to differences in invertebrate fauna. However, Fisher & Likens (1973) found that macroconsumers accounted for only a small fraction of energy flow in Bear Brook. Studies at Coweeta suggest that macroinvertebrates play a major role in leaf breakdown in these streams (Webster & Patten, 1979; Wallace, Webster & Cuffney, 1982). We might conclude that the decrease in shredder abundance was certainly not a factor in the accelerated breakdown of rhododendron and white oak leaves in the post-treatment study. That is, the change in shredder density was exactly opposite to what one might hypothesize in order to explain the increases in leaf breakdown rates.

However, there is an alternative interpretation. With the decrease in allochthonous input to Big Hurricane Branch after clearcutting (Table 1), our bags of leaves represented islands of a scarce food resource. In the pre-treatment study, dogwood was eaten while rhododendron leaves, and to some extent white oak leaves, were largely ignored. *Peltoperta maria* prefers to eat dogwood leaves; both rhododendron and white oak leaves are consumed more slowly than other leaf species (Wallace *et al.*, 1970). We suggest that in the post-treatment study, when our leaves were almost the only food source available to shredders, dogwood leaves were eaten as readily as before, but the less-preferred white oak and rhododendron leaves were also eaten because of the scarcity of other leaves.

Hynes (1975) emphasized the extent to which streams are influenced by their drainage basin. We have shown here how forest clearcutting and road building caused major changes in Big Hurricane Branch. As the vegetation regrows, the stream also should recover to its pre-treatment condition. We suspect that leaf breakdown rates will remain high for several years because of higher temperatures and nutrient conditions and relatively low allochthonous inputs. Also, qualitative changes in the allochthonous inputs will affect food availability to consumer organisms and hence the pattern and rate of stream recovery. In 1978, 43.1% of total litter inputs to the stream were unidentified leaves, primarily of herbaceous species (Table 1). Tree

species with increased importance following logging included birch, red maple and dogwood. All of these species break down rapidly when compared with species that dominated pre-treatment litter inputs to Hurricane Branch (Table 1). For example, one of the dominant herbaceous annuals, *Aster curtisii* T. & G., broke down at a rate of  $0.0116 \text{ day}^{-1}$  in the post-treatment period. Breakdown rates of  $0.0110 \text{ day}^{-1}$  for birch (*Betula lutea* Michx. (pre-treatment) and of  $0.0155 \text{ day}^{-1}$  for red maple (*Acer rubrum* L.) (post-treatment) have also been measured in Big Hurricane Branch. More slowly-decaying leaf species, such as the oaks, have been noticeably reduced in stream litterfall collections. Thus, not only has the breakdown rate of leaves in Big Hurricane Branch increased following treatment, but the species composition of litter inputs to the stream has also shifted towards species with more rapid breakdown rates. One of the consequences of this change in litter quality will be an alteration of the timing of leaf availability to stream fauna. Petersen & Cummins (1974) noted that the variety of leaves entering a stream presented the invertebrate community with a continuous supply of suitable (i.e. conditioned) leaves. Stream invertebrate life cycles are adapted to this temporal pattern. With the acceleration of leaf breakdown in Big Hurricane Branch, very little material is left in the stream by late spring (Fig. 5). As a result, some invertebrates may be without sufficient food at a critical time in their life cycle. How subsequent changes in litter inputs interact with successional changes in the stream fauna to regulate organic matter dynamics, with continued influence by physical changes in the stream, will remain a subject of study as Big Hurricane Branch recovers from the effects of forest clearcutting.

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