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IV. Litter Bre	akdowi	and Stre	ams	

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Long-Term Patterns in Leaf Breakdown in Streams in Response to Watershed Logging

key words: leaf breakdown, long-term, disturbance, stream response

Abstract

The watershed of Big Hurricane Branch, Coweeta Hydrologic Laboratory, North Carolina, USA, was logged in 1976. We measured breakdown rates of experimental leaf packs in this second-order stream prior to logging, during logging, soon after logging, and 3 additional times since then. Leaf breakdown was slow just after logging, apparently due to leaf burial by sediments. Thereafter, leaf breakdown rates have been consistently faster than before logging and faster than in a reference stream. These differences may be related to 3 factors. First, the post-logging nitrate concentration has been about 3–10 times higher than pre-logging values in Big Hurricane Branch and 5 times higher than in a reference stream. The high nutrient concentration may be stimulating microbial decomposition processes in leaf packs. Second, dominance of litterfall by "medium" and "fast" processing leaves from the recovering forest coupled with relatively high sediment loads during storms may hasten breakdown through physical abrasion. Third, the interaction of high nutrients and high quality leaves may be attractive to leaf-shredding invertebrates whose feeding activities may also hasten the breakdown rates.

1. Introduction

Most ecologists appreciate the value of long-term studies but many never become involved in such studies for a variety of reasons including lack of consistent long-term funding, availability of research sites, publications come too slowly, and the time span of graduate education is out of phase with funding cycles (Callahan, 1984; Elliott, 1990). Many natural processes in ecosystems occur on longer time scales than can be studied with short-term funding cycles or short-term research goals. Because we are unable to perceive slow changes in ecosystems that occur over decades, we may draw mistaken conclusions about cause and effect relationships of observed phenomena in short-term projects (Magnuson, 1990; Gosz, 1999). In addition, time lags between cause and effect in natural systems may be on temporal scales that exceed the normal duration of short-term projects and may also lead to inappropriate conclusions. Recognition of the value of long term research has spread around the world such that over 30 countries are now or are in the process of becoming involved in an international LTER (ILTER) network (Gosz, 1999). The present study was conducted at a long term ecological research (LTER) site with the benefit of sustained funding from the U.S. National Science Foundation over most of the duration of the research.

Leaf breakdown rates in streams using surrogate "leaf packs" have been examined around the world over the past 30 years or so (e.g., Webster and Benfield, 1986). There has been considerable discussion about the usefulness of surrogate leaf packs in investigating processes in streams (e.g., Boulton and Boon, 1991). Yet, surrogate leaf packs have been used to study various aspects of detritus processing in streams and lakes including microbial

decomposition processes (e.g., Suberkropp and Chavuet, 1995; Suberkropp, 1998), invertebrate-microbe interactions (e.g., Bärlocher, 1985), and predator-prey interactions (Reice, 1991; Malmovist, 1993). Surrogate leaf packs have also been used to compare leaf breakdown in streams draining forests with different management histories (e.g., Griffith and Perry, 1991; Benfield et al., 1991; Whiles and Wallace, 1998) and to evaluate other environmental disturbances to streams (Burton et al., 1985; Stout and Coburn, 1989). While there remains some uncertainty about the relative importance of various mechanisms involved in the conversion of leaf litter to fine particles (Gessner et al., 1999), few would argue with the notion that mass loss of leaf material over time is an integrative process that may reflect overall ecosystem function in streams. Most published studies of leaf breakdown in streams have been limited to 1 year or 1 season at a single site in a single stream (Webster and Benfield, 1986). The objective of this paper is to present a synthesis of leaf breakdown rates over about 20 years in a stream draining a watershed recovering from logging.

2. Site Description

The study was conducted at the Coweeta Hydrologic Laboratory (CHL) in western North Carolina, USA. CHL is a US Forest Service Experimental Field Station and a Long Term Ecological Research (LTER) site supported by the National Science Foundation and the U.S. Forest Service. The Coweeta Basin is organized in to multiple experimental watersheds (catchments) that have been the subject of various whole-watershed manipulations over the last 60 years. There are also a number of long-term reference watersheds that have not been disturbed since being logged prior to 1922, with the exception of the American Chestnut blight in the late 1930's. Historically, 26 of the watersheds were fitted with weirs and flow records for most go back to the mid 1930's.

This paper will concentrate on two watersheds at Coweeta: Watershed 7 and Watershed 14. Characteristics of the two basins are shown in Table 1. Watershed 7 was clear-cut and cable logged in 1977. Efforts were made to minimize disturbance to the soil surface by lifting logs from steep slopes to roads by an above ground cable system. However, tractor skidding was employed on gentler slopes. Three major roads crossing the mainstream and tributaries were constructed in the basin. Prior to logging in 1977, the lower part of the basin had been experimentally exposed to cattle grazing for a few months each year from 1941 to 1952 and was logged prior to 1920. The basin was essentially undisturbed from 1952 until the logging operation in 1977. Watershed 7 is drained by Big Hurricane Branch, a second-

Table 1. Selected morphometric variables of the two study streams.

Variable	Big Hurricane Branch	Hugh White Creek
Watershed	7	14
Treatment	Clear-cut	Long-term reference
Catchment basin area (ha)	59.5	61.1
Mainstream length (m)	1225	1077
Gradient (m m ⁻¹)	0.19	0.16
Mean annual discharge (1 s ⁻¹)	17.7	19.0
Max watershed elevat. (m)	1060	996
Min watershed elevat. (m)	724	708
Basin orientation	South Facing	North Facing

order, high gradient stream. Watershed 14 is one of the long-term reference watersheds at Coweeta. Like the rest of the basin, it was logged in the early 1920's but has remained undisturbed since the chestnut blight of the late 1930's. Watershed 14 is drained by Hugh White Creek, also a second-order, high gradient stream.

3. Methods

Leaf breakdown studies were conducted in Big Hurricane Branch (BHB) once before the 1977 clearcut, once during the clear-cut, and 4 times after the clear-cut. Leaf breakdown rates in Hugh White Creek (HWC) were measured simultaneously with 3 of the post-clearcutting studies in BHB, but not before or during the clear-cut. In general, the methods employed were similar but varied somewhat in exposure technique, species measured, location and number of sites, number of leaf packs per site, and pick up schedule. Leaves were picked from trees just before abscission and air-dried to constant weight. Leaf packs consisted of a standard (for each study) mass of leaves placed in mesh bags that were put into the streams in mid-to late autumn. Three to 5 packs were immediately retrieved from the streams and taken back to the laboratory to be used to account for mass loss due to handling. Three to 5 replicate leaf packs were collected from the sites after 2 weeks and then approximately monthly (for 6–8 months) until all packs were retreived. Leaf packs were placed individually into plastic bags and returned to the laboratory where they were washed to remove debris and invertebrates, air dried to constant weight in paper bags, and weighed. Sub-samples were ground to a fine powder and ashed at 500 °C for 1–4 hr to estimate ash-free dry mass (AFDM). Leaf breakdown rates (k) were estimated by regressing the natural log of percent AFDM remaining against days of incubation (PETERSEN and CUMMINS, 1974).

4. Results

The first study occurred over a 5 year period surrounding the logging operation (Webster and Waide, 1982). Three leaf breakdown experiments were done in BHB: pre-logging 1974–1975; after road construction but during logging (1976–77); and after all logging activity ceased (1978–79). Three leaf species were employed at three sites in the stream: Cornus florida L. (dogwood), Quercus alba L. (white oak) and Rhododendron maxima L. (rhododendron). Dogwood is a "fast" species in terms of breakdown rate and white oak and rhododendron are "medium" and "slow" species, respectively (Petersen and Cummins, 1974). There were no consistent significant differences among sites but there were clear differences among species (Webster and Waide, 1982). In the pre-and-during logging phases of the study, the breakdown rates were: dogwood>white oak>rhododendron (Table 2). In the post-logging phase, dogwood was faster than white oak and rhododendron which were not different from each other. Among years, all three species exhibited slower breakdown rates during logging than in pre-logging, and white oak and rhododendron were faster in post-logging than in pre-logging. Dogwood breakdown rates were the same in pre-and post-logging.

Table 2. Leaf breakdown rates (d⁻¹) for Big Hurricane Branch before, during, and after logging. (From Webster and Waide, 1982)

Species	Pre-logging 1974–75	Logging 1976–77	Post-logging 1978–79
Dogwood	0.0219	0.0134	0.0219
White Oak	0.0064	0.0038	0.0090
Rhododendron	0.0037	0.0011	0.0105

Table 3. Leaf breakdown rates (d⁻¹) in Big Hurricane Branch and Hugh White Creek, 1982-1983 (From GOLLADAY and WEBSTER, 1982).

Species	Big Hurricane Branch	Hugh White Creek
Dogwood	0.0536	0.0297
Red Maple	0.0237	0.0109
White Oak	0.0116	0.0056
Rhododendron	0.0128	0.0047

The second study was done in 1982–83 and incorporated an additional species (Acer rubrum L. Red Maple) and stream (Hugh White Creek) (GOLLADAY and WEBSTER, 1988). Dogwood leaves broke down nearly 2.5 times faster, and white oak and rhododendron leaves broke down about 1.3 times faster in BHB in 1982–83 than during the post-logging (1977–78) phase (Table 3). All three species broke down about twice as fast in BHB as in HWC in the 1982–83 study. In fact, breakdown rates for white oak and rhododendron leaves in HWC were very similar to those observed in BHB in the pre-logging phase. However, the dogwood rate in HWC was about 1.3 times faster than the pre-logging BHB rate. Red maple, a "medium" species broke down about half as fast in HWC as in BHB.

The third study (1986–87) contrasted leaf breakdown rates of red maple, dogwood, rhododendron, and Liriodendron tulipifera L. (yellow poplar – a "medium" species) among 4 streams in the Coweeta Basin including BHB and HWC (BENFIELD et al., 1991). The other two streams drained clear-cuts much older than that drained by BHB. There was no significant difference between sites for dogwood, but the other three species broke down significantly faster in BHB than in HWC (Table 4). Considering all four streams in this study, there was no significant difference among the 4 streams in dogwood leaf breakdown rate, the red maple rate was faster in all three clear-cut streams than in HWC, the yellow poplar rate was faster in 2 of the 3 clear-cut streams, and the rhododendron rate was faster in 2 of the 3 clear-cut streams than in HWC. Breakdown rates for dogwood and rhododendron were slower in BHB in 1986–87 than in the post logging-phase (1977–78) and slower for these two and for red maple than in 1982–83. Similarly, breakdown rates for dogwood, red maple, and rhododendron were also slower in HWC in 1986–87 than in 1982–83, suggesting the presence of some basin wide effect.

The most recent study was in 1994–95 in which red maple, white oak and rhododendron breakdown rates were examined at four sites in BHB and four sites in HWC. A familiar pattern emerged from comparing the mean breakdown rates between watersheds for each species: rates in BHB were significantly (2–4) times faster than in HWC (Table 5). In addition, white oak and rhododendron broke down 2–5 times faster in BHB in 1994–95 than in the pre-during-or post-logging studies of the 1970's.

Table 4. Leaf breakdown rates (d⁻¹) in Big Hurricane Branch and Hugh White Creek, 1986–87 (From Benfield *et al.*, 1991). Values with the same letter are not significantly different (ANOVA, alpha = 0.05).

Species	Big Hurricane Branch	Hugh White Creek
Dogwood	0.0185 A	0.0160 A
Yellow Poplar	0.0150 A	0.0067 B
Red Maple	0.0183 A	0.0073 B
Rhododendron	0.0079 A	0.0016 B

Table 5. Leaf breakdown rates (d⁻¹) in Big Hurricane Branch and Hugh White Creek, 1995, 96 (E. F. Benfield, unpublished data). Values with the same letter are not significantly different (ANOVA, alpha = 0.05).

Species	Big Hurricane Branch	Hugh White Creek
Red Maple	0.0314A	0.0139B
White Oak	0.0240A	0.0113B
Rhododendron	0.0184A	0.0046B

Breakdown rates of the 3 species of leaves (dogwood, white oak, and rhododendron) that were exposed in at least 5 of the 6 studies in BHB show similar trends over the years 1974–95 (Fig. 1). Rates during logging were slower than pre-logging and post logging rates. Rates were faster 5 years after logging but dipped rather sharply 4 years later (1986–87) only to rise rather sharply again some 8 years later. The sharp dip in 1985–86 may be related to the fact that stream discharge was 35% lower than the previous 10 year record (Data from the US Forest Service, CHL), and Coweeta Hydrologic Laboratory was undergoing one of the worst droughts on record (Cuffney and Wallace, 1989).

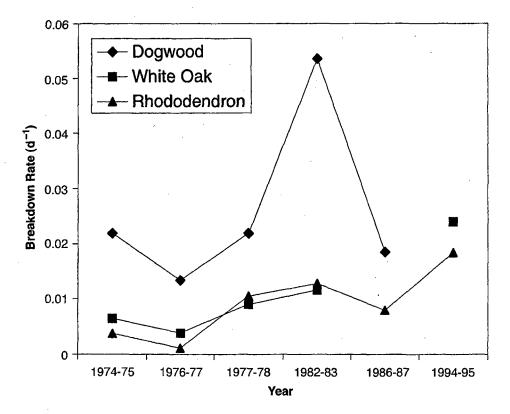


Figure 1. Breakdown rates for 3 leaf species in Big Hurricane Branch, 1974-1995.

5. Discussion

A number of changes in the basin and streams resulted from the clear-cut which have been summarized in other publications and need not be recounted in detail here (e.g., Webster et al., 1991; Webster et al., 1999). However, several significant changes that appear to impact leaf breakdown are worth mention. First, large amounts of sediment were released into BHB from roads constructed in preparing the site for logging and about 80% of the sediment was still in the stream 2.5 years later (Swift, 1988). Elevated sediment transport rates were evident in the years during and following logging and have persisted in the years since, especially during storm flows (Golladay et al., 1987). Increased sedimentation during logging resulted in burial of leaf packs and was presumed to be a major reason breakdown rates were slower than the pre-logging and post-logging rates (Webster and Waide, 1982). In the post-logging phase, much of the fine sediments had washed out of the stream but coarse sediments remained and, coupled with higher stream base-flow following logging, were thought to contribute to faster leaf breakdown rates through abrasive action (Webster and Waide, 1982).

A second major change occurring in BHB due to clear-cutting was a drastic change in the quantity and quality of litter input to the stream. "Slow" species like oaks, hickories, and rhododendron composed about 55% of litter input to BHB in the pre-logging phase and the remaining litter was "medium" and "fast" species like birches, red maple, yellow poplar and a few others (Webster and Waide, 1982). Rhododendron composed 26% of the post-logging litterfall, and the rest of the litter was composed of "medium" (yellow poplar, red maple, birches, black locust) and "fast" (dogwood, and several viney herbaceous species like blackberry and grape) species. Post-logging litterfall was reduced by about 98% and blowin by about 80% of pre-logging values (WEBSTER and WAIDE, 1982). In subsequent years, the cove-hardwood forest drained by BHB has regrown to a significant degree in terms of cover but the regrowing successional forest is dominated by yellow poplar, birches, rhododendron, black locust, eastern hemlock, dogwood, red maple, and red oak (ELLIOTT et al., 1997). Rhododendron, oaks, and hickories composed about 30% of the litterfall to BHB in 1993-94 while the bulk of litterfall was ash, birches, yellow poplar, magnolia, red maple, and grape (J. R. Webster and E. F. Benfield, unpublished data). The presence of mostly "fast" and "medium" leaves in BHB coupled with a lack of large wood and debris dams (GOLLADAY et al., 1989) to serve as retention devices results in fairly rapid loss of benthic coarse particulate organic matter (CPOM) due to transport in storms.

Microbial activity and invertebrate feeding also appear to be part of the equation. Nitrate-N concentrations in BHB have been elevated from 3 to 10 times over pre-logging values over the 20 years since logging (SWANK and VOSE, 1997). This nutrient supplement coupled with relatively labile substrates ("medium" and "fast" leaves) may well have been important in enhancing microbial decomposition processes associated with leaves in BHB. Longterm studies of invertebrates in BHB have demonstrated that most functional groups of aquatic insects have increased in abundance, standing biomass, and secondary production since logging, especially the leaf-shredding insects (STONE and WALLACE, 1998). Furthermore, total invertebrate abundance, biomass, and production are higher in BHB than in HWC, the long-term reference stream (STONE and WALLACE, 1998; STOUT et al., 1993). "Fast" and "medium" leaves are generally more rapidly microbially conditioned than "slow" leaves and are also more suitable food resources for shredders (reviewed by Webster and Benfield, 1986). Adding the nutrient supplement for microbial decomposition to the equation of leaves preferred as food by shredders and higher shredder biomass and production may be the key to understanding why leaf breakdown rates in BHB are faster since logging and further, why breakdown rates remain faster in BHB than in HWC.

Leaf-shredding invertebrates and leaf litter inputs were greatly reduced in BHB following logging (Gurtz and Wallace, 1988) but Webster and Walle (1982) speculated that remaining shredders may have been partly responsible for faster post-logging leaf breakdown rates

because the leaf packs may have served as a food source in a limited resource situation. In the years since logging, litter standing crop in BHB is greatly reduced within two months after litter fall while that in HWC remains relatively high throughout most of the year (Stout et al., 1993). Surrogate leaf packs placed in BHB may be "islands" of food resources in a limited resource situation and even "slow" species break down rapidly in this disturbed stream due to a combination of high nutrients and high shredder density. In contrast, surrogate leaf packs in HWC do not add appreciably to the normal standing biomass and thus may not be any more attractive to shredders than native leaf material and, as a consequence, break down at more "normal" rates.

Clearly, this study demonstrates that a single-year study of leaf breakdown in BHB would not have been adequate to capture the pattern of stream ecosystem response to the watershed manipulation. Furthermore, the "natural" disturbance (drought) signal was also seen in the pattern of leaf breakdown in both the disturbed and reference streams. This supports the notion that unusual environmental events that may alter the course of ecosystem processes might be missed in short-term studies.

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