

Changes in stream benthic organic matter following watershed disturbance

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Benthic organic matter was collected quarterly from streams draining a 9-yr-old clearcut, an 18-yr-old "old-field", a 25-yr-old successional forest, and two reference watersheds at Coweeta Hydrologic Laboratory in the Appalachian Mountains of North Carolina, USA. Samples were separated into large benthic organic matter (LBOM >1 mm) and fine benthic organic matter (FBOM <1 mm). An additional survey of large (>5 cm diam.) and small (1–5 cm diam.) wood was conducted. Standing stocks of LBOM ranged from 124 to 255 g AFDM m⁻² (ash free dry mass) and were significantly higher in streams draining reference watersheds and the successional forest than in either the recent clearcut or old-field. Reference sites exhibited LBOM peaks in late autumn and spring. No seasonal patterns were observed in disturbed streams. Standing stocks of FBOM averaged 113 to 387 g AFDM m⁻², and the stream draining the successional forest had significantly higher FBOM levels than the other sites. In reference streams, FBOM abundance peaked in spring. In disturbed streams, FBOM standing stocks were highest in summer or late autumn. Standing stocks of large wood ranged from 0 to 3956 g AFDM m⁻² and were significantly higher in the reference streams than in streams draining the old-field or successional forest. Small wood averaged 11 to 342 g AFDM m⁻² and was significantly lower in the stream draining the old-field than at the other sites. Comparisons of organic matter inputs with standing stocks indicated that disturbed streams at Coweeta receive less material and process it faster than reference streams. Disturbed streams also appear to be less retentive than reference streams and exhibit a gradual decline in FBOM during the winter when large, long-duration storms combined with low particle generation rates deplete accumulated FBOM.

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Introduction

Low-order temperate forest streams are closely linked to the areas they drain (Hynes 1975, Vannote et al. 1980), and the role of allochthonous organic matter as an energy base for these streams has been well documented (e.g. Nelson and Scott 1962, Minshall 1967, Kaushik and Hynes 1971, Petersen and Cummins 1974). Accumulations of leaves and wood are also important habitats for stream consumers, decrease stream power and erosiveness, and act as sites of nutrient uptake (e.g. Heede 1972, Swanson et al. 1976, Likens and Bilby 1982). In contrast to forest ecosystems, where structure

and function are internally generated by the growth of vegetation, much of the structure and function of lotic ecosystems is generated by the import of organic matter from the surrounding watershed. Thus, watershed disturbances such as forest cutting or burning induce stream disturbances which continue until predisturbance patterns of vegetation are reestablished on the watershed (e.g. Webster and Swank 1985), a process that may take 100–400 yr, depending on climate and mature forest type of the region (Likens and Bilby 1982, Swanson and Lienkaemper 1978).

During forest succession the most serious impact on stream ecosystems is probably a decline in the amount

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Tab. 1. Characteristics of the study sites. Estimates of litter input (not including wood) to Big Hurricane Branch, Sawmill Branch, Hugh White Creek, and Grady Branch are based on collections made in 1983–1984 and include litterfall + blow-in (Webster unpubl. data). Inputs to Carpenter Branch were obtained during 1985–1986 and represent litterfall only (Risley 1987).

	Big Hurricane Branch	Sawmill Branch	Carpenter Branch	Hugh White Creek	Grady Branch
Watershed#	7	6	13	14	18
Treatment	Clearcut	Old-field	Intermediate Successional	Reference	Reference
Watershed Area (ha)	58.7	8.9	16.1	61.1	12.5
Main Channel Length (m)	1225	370	604	1125	345
Gradient (mm ⁻¹)	0.19	0.24	0.19	0.15	0.20
Streambed Area (m ²)	3274	277	1330	8085	1116
Average Annual Discharge (L sec ⁻¹) ^a	18.52	2.65	5.39	19.37	4.06
Minimum Discharge (L sec ⁻¹) May 1985-Apr 1986	5.85	0.69	1.21	4.88	0.70
Maximum Discharge (L sec ⁻¹) May 1985-Apr 1986	120.92	38.09	46.12	171.30	32.86
Litterfall (g AFDW m ⁻² yr ⁻¹)	436	438	382	491	626

^aBased on a minimum of 30 yr of Forest Service Records.

of large woody debris and numbers of debris dams in stream channels (Swanson and Lienkaemper 1978, Likens and Bilby 1982, Golladay et al. 1987). Debris dams have been reported to erode rapidly following watershed logging (Fisher and Likens 1973, Bilby 1981). Small twigs and leaves, which form the internal matrix of debris dams, decay relatively rapidly, and because post-disturbance allochthonous inputs tend to be low, the matrix is not replenished. Even though larger wood may remain, breakdown of debris dam matrices may account for the increased organic matter transport observed following logging (Gurtz et al. 1980, Hobbie and Likens 1973, Webster and Golladay 1984). Eventually large woody debris dating from before the disturbance also decays. The net result is an erosion of the stream's capacity to resist downstream export of material, particularly during storms or seasons of high discharge. Thus, forest disturbance reduces the ability of streams to resist shorter term natural disturbances. In this investigation, we examined the effects of forest disturbance on the abundance of organic matter in streams by measuring standing stocks of woody debris and leaf litter in streams draining clearcut, old-field, intermediate successional, and reference watersheds.

Materials and methods

Site description

This work was conducted at Coweeta Hydrologic Laboratory, Macon County, NC, USA. Five sites were selected for study, three streams draining disturbed watersheds and two streams draining reference watersheds. Big Hurricane Branch drains Watershed-(WS)-7, a 58.7-ha experimental watershed, which was grazed by cattle from 1941–1952 and cable logged during the winter of 1976–1977. Regrowth is dominated by hardwood sprouts, herbs, vines, and seedlings (Boring et al. 1981). Carpenter Branch drains WS-13, a 16.1-ha experimental watershed. Originally hardwoods, all trees and shrubs were cut in 1939–1940 and again in 1962 (Swank and Douglass 1977). The watershed is presently covered by an intermediate successional hardwood forest dominated by yellow poplar, *Liriodendron tulipifera* L. at lower elevations and mixed oaks, *Quercus* spp. at higher elevations (Leopold and Parker 1985). Sawmill Branch (SB) drains WS-6, an 8.9-ha experimental watershed. In 1942 the riparian vegetation was removed from the streamside (12% of watershed area). In 1958 all marketable timber was removed from the watershed, and the slash was burned. The watershed was fertilized, limed, and seeded with grass in 1959. Herbicides were

Tab. 2. Fine (0.45 μm – 1 mm) and large (>1 mm) benthic organic matter in Coweeta streams. Values are means (g AFDW m^{-2}) and in parentheses \pm 95% confidence limits and sample sizes.

	FBOM Annual Mean	LBOM Annual Mean
<i>Disturbed</i>		
Sawmill Branch	157 (37,120)	129 (18,120)
Big Hurricane Branch	113 (15,240)	124 (19,239)
Carpenter Branch	387 (58,120)	255 (31,120)
<i>Reference</i>		
Hugh White Creek	166 (20,240)	213 (24,240)
Grady Branch	147 (20,120)	244 (30,120)

applied from 1960–1965 to inhibit the growth of broad-leaf vegetation. WS-6 was fertilized again in 1965, and from 1966–1968 all vegetation was killed by herbicide treatment (Johnson and Swank 1973). Finally in 1968 the watershed was permitted to begin natural succession, and today it is an old-field, with primarily black locust, *Robinia pseudoacacia* L. at lower elevations and yellow poplar at higher elevation sites. Hugh White Creek drains WS-14, a 61.1-ha watershed and Grady Branch drains WS-18, a 12.5-ha watershed. Watersheds 14 and 18 are mixed hardwood forests composed of mixed oaks, red maple *Acer rubrum* L., hickory *Carya* spp. and yellow poplar with a dense rhododendron *Rhododendron maximum* L. understory (Day and Monk 1974). Both sites are longterm reference watersheds at Coweeta. They were selectively logged prior to 1925 and, except for the chestnut blight, have been undisturbed for 60 yr (Swank and Douglass 1977). Further characteristics of the study sites are presented in Tab. 1.

Undisturbed Coweeta streams are densely shaded by riparian vegetation, have low autochthonous primary production, and receive most of their annual energy input from autumn leaf fall (Webster et al. 1983). Based on collections made in 1983–1984 and 1985–1986, annual litter inputs (excluding wood) to the streams range from 382 to 626 g AFDM m^{-2} streambed yr^{-1} (Tab. 1.) (Risley 1987, Webster unpubl. data). Coweeta streams support a diverse invertebrate fauna dominated by detritivores (Woodall and Wallace 1972, Haefner and Wallace 1981). The study sites were selected to provide a successional gradient ranging from recently disturbed to relatively undisturbed streams. The reaches sampled on each stream extended from the stream source downstream to the gauging station. Prior to treatment all of the streams drained mixed hardwood (oak/hickory) forest.

Benthic organic matter measurements

Benthic organic matter was collected from each stream on 7–12 July 1985 (summer), 21–26 November 1985 (autumn), 13–18 February 1986 (winter), and 25–29 April 1986 (spring). Hugh White Creek and Big Hurricane Branch were divided into 20 equal segments. The smaller streams, Grady Branch, Carpenter Branch, and Sawmill Branch, were divided into 10 segments. On each date a randomly selected transect within each segment was sampled for benthic organic matter using a 0.071- m^2 circular sampler. A particular transect was sampled only once during the study period. Samples were taken at 0.25, 0.5, and 0.75 of the distance across the channel on each transect. With the sampler in place, substrate was stirred to a depth of 10 cm if possible. The resultant slurry of organic matter and fine sediment was pumped with a bilge pump through a 1-mm mesh net into a 20-l bucket. Large organic material (i.e. leaves, and sticks <1 cm diam.) was removed from the sampler by hand. This material and particles >1 mm which were retained by the net (LBOM) were placed in paper bags and taken to the laboratory, dried, weighed, subsampled, ashed, and reweighed to determine organic content as ash free dry mass (AFDM). Material passing through the net (FBOM) was subsampled, returned to the laboratory, filtered (Gelman type A/E glass fiber filter), weighed, and ashed to determine organic content as AFDM.

During summer 1985, estimates of large (>5 cm diam.) and small (1–5 cm diam.) woody debris were obtained for each stream. Small and large wood standing stocks were determined in randomly selected 1-m wide cross-sections. Cross-sections were selected using a stratified random sampling regime, with one cross-section sampled per stream segment. All wood debris 1–5 cm in diameter was removed from each cross-section and weighed wet. Subsamples were returned to the laboratory, air dried to constant weight, ashed (550°C, 40 min), and the residue weighed to determine organic content as ash free dry mass. The AFDM of the original sample was estimated by correcting for moisture and ash using the laboratory measurements. The AFDM of the original sample was then divided by the transect area so fine wood standing stocks could be expressed on an areal basis (g AFDM m^{-2} stream channel).

Large woody debris (>5 cm diam.) was handled in a similar manner. Small logs were weighed individually and subsampled, and AFDM was determined as described above. For logs too large to weigh, diameter and length were measured to determine volume. Subsamples were returned to the laboratory, dried, weighed, immersed in a graduated cylinder of water to determine volume, ashed, and the residue weighed to determine AFDM. The density of the subsample and the volume of the original log were used to estimate AFDM. The weights of all logs in a particular transect were summed,

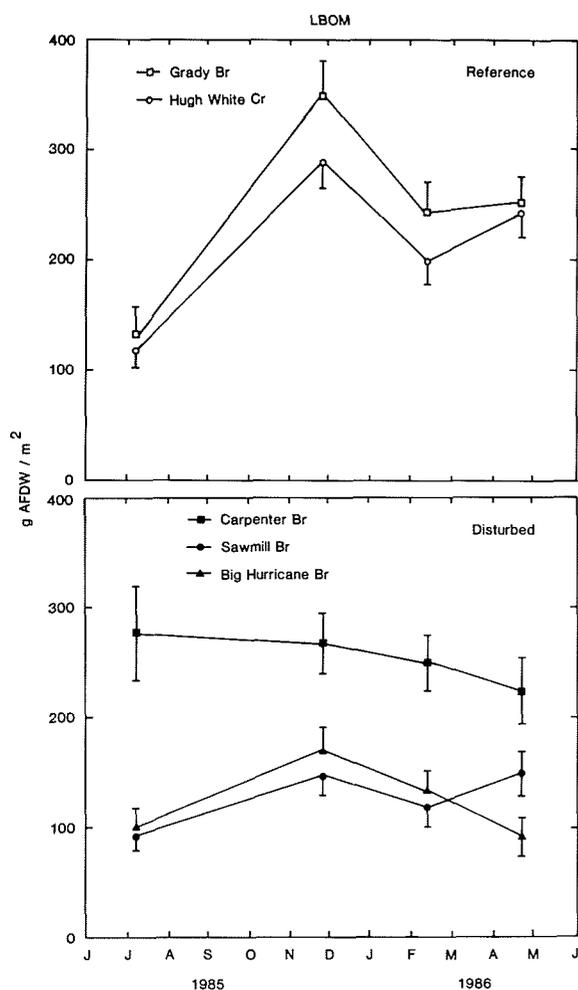


Fig. 1. Large benthic organic matter (>1 mm) in Coweeta streams. Values are means (g AFDM m⁻²) and standard errors.

then divided by transect area to determine large wood standing stock on an areal basis.

Finally, the entire main channel of each stream was surveyed for accumulations of organic matter. Three categories were recognized: 1) organic matter accumulations – accumulations of leaves and sticks supported by rocks and boulders, with no wood >5-cm diam., 2) logs – wood alone, with an average diam. >5-cm, 3) debris dams – sticks and leaves aggregated with supporting logs >5-cm diam. Only accumulations that clearly affected stream morphology, i.e. created pools or stair-step patterns of flow, were included in the survey.

Unless otherwise noted, all statistical comparisons of sites were made using analysis of variance followed by multiple comparisons of means with an alpha level of 0.05.

Results and discussion

Average annual benthic organic matter standing stock

Mean annual LBOM (averaged over all sampling sites and dates) ranged from 124 to 255 g AFDM m⁻² (Tab. 2). Grady Branch (reference), Hugh White Creek (reference), and Carpenter Branch (intermediate successional) had significantly more LBOM than Big Hurricane Branch (recently disturbed) or Sawmill Branch (old-field).

FBOM averaged 113 to 387 g AFDM m⁻² (Tab. 2). Carpenter Branch had significantly more FBOM than any of the other streams. The standing stock of FBOM in Hugh White Creek (reference) was significantly higher than in Big Hurricane Branch (recently disturbed); there were no significant differences in comparisons of the other sites.

Seasonal pattern of LBOM standing stock

Reference streams (Grady Branch and Hugh White Creek) exhibited a seasonal difference in LBOM abundance, with significantly higher standing stocks in autumn and spring than summer (Fig. 1). Of the disturbed streams, only Big Hurricane Branch had an annual distribution of LBOM similar to the reference streams. In Big Hurricane Branch, autumn LBOM standing stocks were significantly higher than those observed in spring or summer. In the other two streams there were no

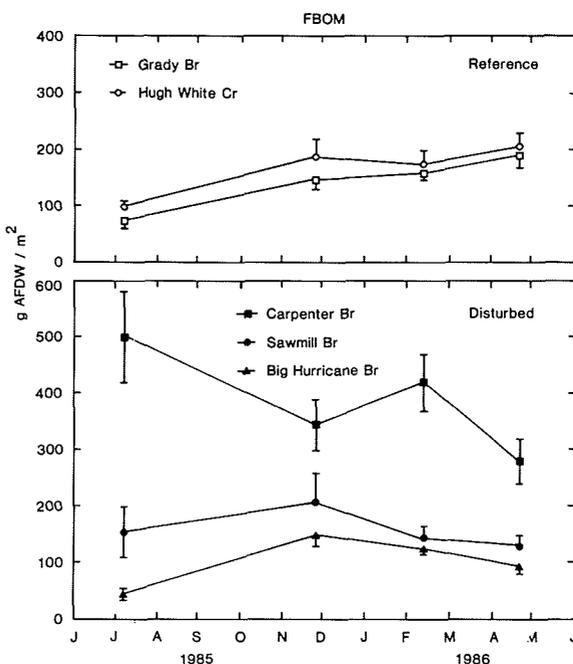


Fig. 2. Fine benthic organic matter (0.45 μ m – 1 mm) in Coweeta streams. Values are means (g AFDM m⁻²) and standard errors.

Tab. 3. Estimates and confidence intervals (95%) for small woody debris in Coweeta streams. Estimates were obtained using arithmetic means and confidence limits based on the t-statistic and nonparametrically using the Hodges-Lehman procedure. Values are g AFDW m⁻² of stream channel.

	Parametric		Non-parametric		n	Range
	mean	C.L.	Median	C.L.		
<i>Disturbed</i>						
Sawmill Branch	78	(0,229)	11	(1,338)	10	(0-675)
Big Hurricane Branch	383	(238,528)	342	(213,540)	20	(0-1080)
Carpenter Branch	261	(81,441)	196	(121,486)	10	(61-911)
<i>Reference</i>						
Hugh White Creek	312	(173,451)	284	(133,452)	20	(0-1048)
Grady Branch	300	(169,431)	270	(182,448)	10	(94-734)

significant differences in LBOM standing stocks over the study period.

Seasonal pattern of FBOM standing stock

In the reference streams, FBOM levels were highest in spring samples and lowest in summer (Fig. 2). In Grady Branch FBOM levels observed during summer were significantly lower than those observed during any other season, and no significant differences in FBOM standing stocks were measured on the other dates. In Hugh White Creek, FBOM standing stocks in autumn and spring were significantly higher than summer levels. In the disturbed streams there was no consistent pattern of FBOM distribution. In Sawmill Branch (old-field) there were no significant differences in FBOM levels over the

year. In Big Hurricane Branch (recently disturbed), autumn FBOM levels were significantly higher than those observed at any other date. The FBOM standing stocks measured in winter and spring were significantly higher than those collected during summer. In Carpenter Branch (intermediate successional), FBOM levels were significantly greater in summer than in other seasons.

Distribution of woody debris

The amount of wood measured in cross-sections within each stream varied over several orders of magnitude. Nonparametric methods were used to compare amounts of woody debris in the streams. Arithmetic means and confidence intervals based on the t-statistic are pre-

Tab. 4. Estimates and confidence intervals (95%) for large woody debris in Coweeta streams. Estimates were obtained using arithmetic means and confidence limits based on the t-statistic, and non-parametrically using the Hodges-Lehman procedure. Values are g AFDW m⁻² of stream channel.

	Parametric		Non-parametric		n	Range
	mean	C.L.	Median	C.L.		
<i>Disturbed</i>						
Sawmill Branch	1457	(0,4608)	0	(0,6991)	10	(0-13981)
Big Hurricane Branch	2833	(515,5151)	1241	(339,4145)	20	(0-20370)
Carpenter Branch	232	(0,506)	138	(0,593)	10	(0-1185)
<i>Reference</i>						
Hugh White Creek	5134	(930,9338)	2462	(184,7530)	20	(0-34500)
Grady Branch	4578	(0,9209)	3956	(119,8280)	10	(0-15527)

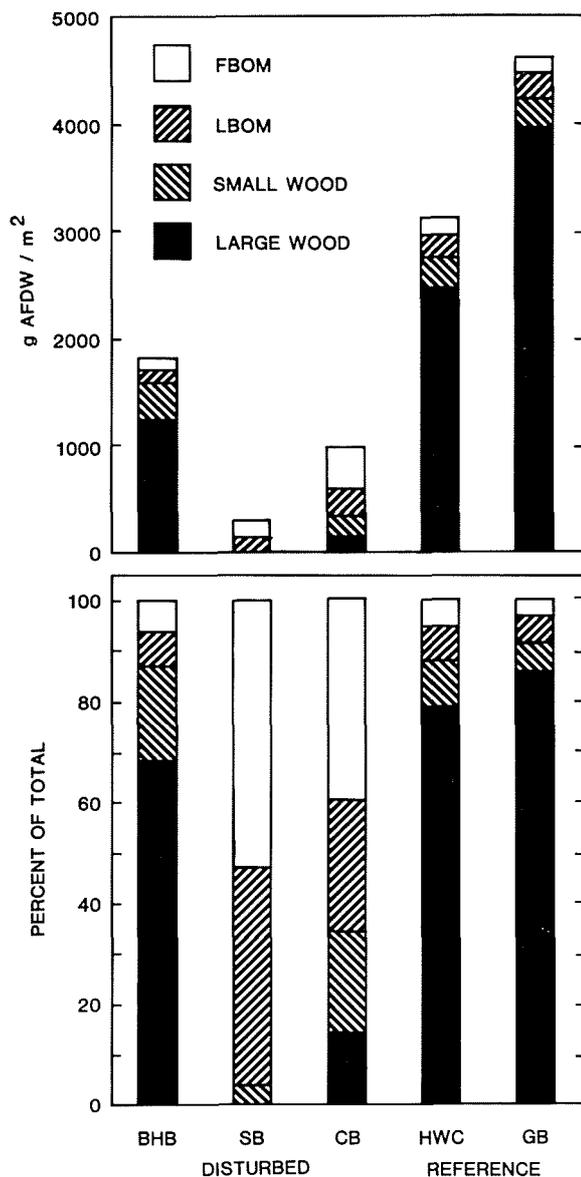


Fig. 3. Contributions of various organic fractions to total organic matter standing stock in Coweeta streams; BHB-Big Hurricane Branch, SB-Sawmill Branch, CB-Carpenter Branch, HWC-Hugh White Creek, GB-Grady Branch. Nonparametric estimates of wood standing stocks were used in calculations, but other values are means.

sented for purposes of comparison with other studies and with nonparametric procedures. However, we feel that these estimates are biased by the asymmetrical distribution of the data (distribution is skewed toward high wood standing stocks).

Standing stocks of small wood debris ranged from 11 to 342 g AFDM m⁻² (Tab. 3, values are based on the Hodges-Lehman procedure, e.g. Hollander and Wolfe 1973). Sawmill Branch (old-field) had significantly

lower standing stocks of small woody debris than the other streams (Kruskal-Wallis Test, followed by a protected Wilcoxon Rank-Sum LSD, $p < 0.05$). There were no significant differences in the amount of small wood among the other streams.

Standing stocks of large woody debris in Coweeta streams ranged from 0 to 3956 g AFDM m⁻² (Tab. 4, values based on Hodges-Lehman procedure). The reference streams, Grady Branch and Hugh White Creek, had significantly greater amounts of large wood than both Carpenter Branch (intermediate successional) and Sawmill Branch (old-field) (Kruskal-Wallis Test, followed by a protected Wilcoxon Rank-Sum LSD, $p < 0.05$). Standing stocks of large wood in Big Hurricane Branch (recently disturbed) were not significantly different from either reference streams or the other disturbed streams.

Percent composition of organic matter standing stocks

Total organic matter standing stocks were estimated for each stream by summing average annual standing stocks from each organic matter category. Total organic matter in reference streams was 3126 g AFDM m⁻² (HWC) and 4347 g AFDM m⁻² (GB). The dominant fraction in both streams was large woody debris (79% in HWC and 90% in GB) (Fig. 3). Total organic matter standing stocks in Big Hurricane Branch (recently disturbed) was 1820 g AFDM m⁻², with 68% as large woody debris. Streams draining the old-field and intermediate successional forest appeared to have substantially lower total organic matter standing stocks than the other sites; total organic matter standing stock was 297 g AFDM m⁻² in Sawmill Branch and 978 g AFDM m⁻² in Carpenter Branch. Large wood constituted only 14% of total organic matter in Carpenter Branch (intermediate successional) and was essentially absent in Sawmill Branch (old-field); the dominant form of organic matter in these two streams was FBOM (0.45 μ m - 1 mm). In Big Hurricane Branch (recent clearcut) the dominant form of organic matter was large wood; however its importance (as percent composition and absolute amount) was lower than in the reference streams. These findings suggest that watershed disturbance has resulted in decreases in the amount of large woody debris in stream channels.

The predominance of large woody debris is not unique to Coweeta streams. Naiman and Sedell (1979a) reported that over 90% of total organic matter in first and third order Oregon Cascade Mountain streams was large woody debris (>10 cm diam.). Estimates of large wood standing stock in Cascade streams range from 15 to 45 m⁻² (Keller and Swanson 1979, Naiman and Sedell 1979a, Swanson et al. 1982), considerably higher than observed in Coweeta streams.

Tab. 5. Distribution of organic debris in Coweeta streams. Values are means and 95% confidence limits.

	Disturbed			Reference	
	Big Hurricane Branch	Sawmill ^a Branch	Carpenter Branch	Hugh White Creek	Grady Branch
Organic Accumulations (no. per 25 m)	1.1 (0.4)	2.2 (0.9)	1.9 (0.7)	2.7 (0.6)	5.1 (1.4)
Debris Dams (no. per 25 m)	0.1 (0.1)	0.0 (0.0)	0.2 (0.2)	0.4 (0.2)	0.6 (0.5)
Logs (no. per 25 m)	2.6 (0.5)	0.3 (0.5)	0.6 (0.4)	2.3 (0.6)	2.3 (0.8)
Log diameter	20.7 (2.1)	–	20.4 (13.5)	22.6 (2.4)	19.2 (3.0)

^aData originally collected for 10 m reaches, then converted to 25 m reaches.

Aggregation and distribution of benthic organic matter

Debris dams (sticks and leaves aggregated with logs >5 cm diam.) are not common in first and second order Coweeta streams because streamflows of sufficient magnitude to move and consolidate large woody debris are rare. Thus, logs generally remain in position where they fall into the stream. The reference streams had significantly more debris dams than Big Hurricane Branch, the recently disturbed stream; there were no differences in the number of debris dams in Carpenter Branch (intermediate successional) when compared with the other sites (Tab. 5). Organic matter accumulations (accumulations of leaves and sticks with no wood >5 cm diam.) were the most common morphological features in undisturbed Coweeta streams. Grady Branch had significantly more organic matter accumulations than any other stream. Hugh White Creek had more organic matter accumulations than Big Hurricane Branch; there were no significant differences in the number of organic matter accumulations in Carpenter Branch compared with the other sites.

Logs (>5 cm diam.) were also common in Coweeta streams. Carpenter Branch, the stream draining intermediate successional forest, had significantly fewer logs than the other streams. There was no significant difference in the average diameter (approx. 20 cm) of logs in the different streams. Sawmill Branch was not surveyed for distribution of organic debris in the present study. However, a similar survey conducted in 1983 revealed an average of 2.17 organic matter accumulations, 0.33 logs, and no debris dams per 25 m reach.

A regression analysis of benthic organic matter standing stock versus distance upstream from the weir ponding basin indicated that organic matter standing stocks were not substantially greater near the headwaters of either disturbed or reference streams. This has several implications. First, instream processing for most LBOM probably occurs near the site of introduction. If transport of LBOM represented a significant loss from these

streams, one would expect a depletion of LBOM at downstream sites, where average discharge is highest. Second, FBOM losses are balanced by processes generating particles. If this was not the case, downstream sites which have greatest fluctuations in discharge, would have less FBOM. A similar analysis for small (1–5 cm diam.) and large (>5 cm diam.) woody debris showed no consistent upstream changes over the reaches studied.

Comparison of standing stocks with inputs of organic matter

Much of the LPOM in low-order streams tends to remain and be processed near points of entry. Canopy density combined with retention characteristics of very short reaches may determine LPOM standing stocks. Certainly the input of wood is determined by the presence of trees adjacent to streams and the occurrence of stochastic events (wind, fire, ice storms, bank cutting, and debris avalanches) that fell trees into stream channels (Keller and Swanson 1979). We examined the relationship between litter input and standing stock based on collections (litterfall + blow-in) made in 1983–1984 from Big Hurricane Branch, Hugh White Creek, Grady Branch, and Sawmill Branch (Tab. 1). Measurements of litterfall (1985–1986) on WS-13 were used to estimate litter input to Carpenter Branch.

Estimates of LBOM turnover were obtained by dividing total litterfall by mean annual LBOM standing stock. In the reference streams the turnover rate was 2.3 yr⁻¹ for Hugh White Creek and 2.6 yr⁻¹ for Grady Branch. In Sawmill Branch (old-field) and Big Hurricane Branch (recent clearcut) turnover rates were 3.4 yr⁻¹ and 3.5 yr⁻¹, respectively. In Carpenter Branch (intermediate successional) the turnover rate was either 1.5 yr⁻¹ for litterfall alone or 1.8 yr⁻¹ when a correction was applied to estimate blow-in (average 19.9% of total input to the other streams).

Because travel distances for leaf material in streams are relatively short (Dance et al. 1979, Speaker et al.

1984, Webster et al. 1987), the differences between reference and disturbed streams probably cannot be attributed to differences in downstream transport. However, litter is processed faster in disturbed streams because early successional vegetation, which dominates the litterfall in recently disturbed streams, breaks down more rapidly than litter from mature forests (Webster and Benfield 1986). Also, decay rates of all litter types appear to be accelerated in Coweeta streams following logging (Webster and Waide 1982, Golladay and Webster 1988). Carpenter Branch (intermediate successional) receives less litter from its watershed and maintains relatively high LBOM standing stocks, which result in relatively low turnover compared with reference streams. These findings indicate that reference streams receive greater litter inputs and retain a greater proportion as LBOM, whereas disturbed streams receive lower litter inputs and process a greater proportion into FBOM.

FBOM standing stocks were strongly influenced by litter input and the presence of LBOM. In general, reference streams had higher levels of FBOM than disturbed streams. In Sawmill Branch and Big Hurricane Branch (disturbed streams), FBOM standing stocks were highest in November, following a period during which litter inputs and subsequent particle generation rates were at annual maxima (e.g. Webster 1983). During winter and spring, FBOM standing stocks declined in disturbed streams, corresponding to a period when particle generation rates were at annual minima (e.g. Webster 1983). Also, disturbed streams appear to be less retentive of fine organic material than reference streams and lose larger amounts material during storms (Golladay et al. 1987). Reduced retentiveness probably accounts for the gradual decline in FBOM observed during winter in disturbed streams when large long-duration storms combined with low particle generation rates resulted in depletion of FBOM accumulated during late summer and autumn. In the reference streams, standing stocks of FBOM remained high from autumn through spring, apparently reflecting the slower processing rate of litter from mature forests. Reference streams were also more retentive than disturbed streams and thus less susceptible to large losses of FBOM during storms (Golladay et al. 1987).

Carpenter Branch had anomalously high levels of FBOM and did not exhibit strong seasonal variation in FBOM standing stocks. The reasons for this are uncertain, but WS-13 was once the site of a homestead (W. T. Swank, pers. comm.), and sections of Carpenter Branch are deeply incised with steep dirt banks and fine sediment substrata typical of a pastureland stream. Also the middle portion (200–300 m) of the stream is relatively low gradient. Perhaps the high FBOM levels are artifacts of soil erosion resulting from homesteading and atypical streambed morphology.

Changes in stream organic matter abundance following watershed disturbance

In many streams, distinct seasonal patterns of organic matter abundance can be linked to patterns of organic matter input from surrounding vegetation. In temperate regions, LBOM standing stocks are highest in late autumn following the period of highest annual litterfall (e.g. Naiman and Sedell 1979a, Wakefield et al. 1980, Short and Ward 1981, Iversen et al. 1982, Minshall et al. 1982, Barlocher 1983, King et al. 1987). LBOM standing stocks then gradually decline throughout the rest of the year as coarse organic matter is processed into smaller particles (FBOM).

In areas where substantial snowpack develops during winter, streams ice over, and discharge remains relatively constant (e.g. Likens et al. 1967). Under such conditions FBOM standing stocks may increase due to relatively low transport of fine particles (Short and Ward 1981). With spring snowmelt, streamflows increase and substantial scouring and downstream transport may occur, reducing FBOM standing stocks (Fisher and Likens 1973, Naiman and Sedell 1979b, Short and Ward 1981, Minshall et al. 1982). At Coweeta extensive snowpacks seldom develop but streams are subject to scouring during large, long duration storms that occur from late autumn through early spring. Resistance to downstream transport of material during this period is determined by the size and frequency of retention structures in stream channels. Even small debris dams and organic accumulations retain material during low flows; however, at some discharge any debris dam will erode, releasing material into the water column (Heede 1972, Fisher and Likens 1973).

Forest logging appears to have decreased the resistance of Coweeta streams to organic matter export in several ways. The gradual decline in wood standing stocks following logging has resulted in a decrease in the size and frequency of retention structures in disturbed streams. Small infrequent retention structures are not efficient at retaining material during storms. The altered chemical quality of litter following forest logging has resulted in faster processing of litter and an apparent conversion of coarse to fine material earlier in the season. Increased processing combined with reduced litter input means that proportionally more organic material is in a readily transportable form and less material is available to be incorporated into retention structures just prior to the season when export of organic matter is most likely to occur.

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References

- Barlocher, F. 1983. Seasonal variation of standing crop and digestibility of CPOM in a Swiss Jura stream. – *Ecology* 64: 1266–1272.
- Bilby, R. E. 1981. Role of organic debris in regulating the export of dissolved and particulate matter from a forested watershed. – *Ecology* 62: 1234–1243.
- Boring, L. R., Monk, C. D. and Swank, W. T. 1981. Early regeneration of a clear-cut southern Appalachian forest. – *Ecology* 62: 1244–1253.
- Dance, K. W., Hynes, H. B. N. and Kaushik, N. K. 1979. Seasonal drift of solid organic matter in two adjacent streams. – *Arch. Hydrobiol.* 87: 139–151.
- Day, F. P. Jr. and Monk, C. D. 1974. Vegetation patterns on a southern Appalachian watershed. – *Ecology* 55: 1064–1074.
- Fisher, S. G. and Likens, G. E. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. – *Ecol. Monogr.* 43: 421–439.
- Golladay, S. W. and Webster, J. R. 1988. Effects of clearcut logging on wood breakdown in Appalachian Mountain Streams. – *Am. Midl. Nat.* 119: 143–155.
- , Webster, J. R. and Benfield, E. F. 1987. Changes in stream morphology and storm transport of seston following watershed disturbance. – *J. North Am. Benthol. Soc.* 6: 1–11.
- Gurtz, M. E., Webster, J. R. and Wallace, J. B. 1980. Seston dynamics in southern Appalachian streams: effects of clear-cutting. – *Can. J. Fish. Aq. Sci.* 37: 624–631.
- Haefner, J. D. and Wallace, J. B. 1981. Production and potential seston utilization by *Parapsyche cardis* and *Diplectrona modesta* (Trichoptera: Hydropsychidae) in two streams draining contrasting southern Appalachian watersheds. – *Environ. Ent.* 10: 433–441.
- Heede, B. H. 1972. Influences of a forest on the hydraulic geometry of two mountain streams. – *Wat. Resources Bull.* 8: 523–530.
- Hobbie, J. E. and Likens, G. E. 1973. Output of phosphorus, dissolved organic carbon, and fine particulate carbon from Hubbard Brook watersheds. – *Limnol. Oceanogr.* 18: 734–742.
- Hollander, M. and Wolfe, D. A. 1973. Nonparametric statistical methods. – Wiley, New York.
- Hynes, H. B. N. 1975. The stream and its valley. – *Verh. Int. Ver. Limnol.* 19: 1–15.
- Iversen, T. M., Thorup, J. and Skriver, J. 1982. Inputs and transformation of allochthonous particulate organic matter in a headwater stream. – *Holarct. Ecol.* 5: 10–19.
- Johnson, P. L. and Swank, W. T. 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds of contrasting vegetation. – *Ecology* 54: 70–80.
- Kaushik, N. K. and Hynes, H. B. N. 1971. The fate of dead leaves that fall into streams. – *Arch. Hydrobiol.* 68: 463–515.
- Keller, E. A. and Swanson, F. J. 1979. Effects of large organic material on channel form and fluvial processes. – *Earth Surface Processes* 4: 361–380.
- King, J. M., Day, J. A., Davis, B. R. and Henshall-Howard, M. P. 1987. Particulate organic matter in a mountain stream in the south-western Cape, South Africa. – *Hydrobiologia* 154: 165–187.
- Leopold, D. J. and Parker, G. R. 1985. Vegetation patterns on a southern Appalachian watershed after successive clear-cuts. – *Castanea* 50: 164–186.
- Likens, G. E. and Bilby, R. E. 1982. Development, maintenance and role of organic debris dams in New England streams. – In: Swanson F. J., Janda, R. J., Dunne, T. and Swanston, D. N. (eds), *Sediment budgets and routing in forested drainage basins*. USDA Forest Serv., Gen. Tech. Rep. PNW-141, Portland, Oregon, pp. 122–128.
- , Bormann, F. H., Johnson, N. M. and Pierce, R. S. 1967. The calcium, magnesium, potassium, and sodium budgets for a small forested ecosystem. – *Ecology* 48: 772–785.
- Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland spring brook community. – *Ecology* 48: 139–149.
- , Brock, J. T. and LaPoint, T. W. 1982. Characterization and dynamics of benthic organic matter and invertebrate functional feeding group relationships in the Upper Salmon River, Idaho (USA). – *Int. Rev. Gesamten Hydrobiol.* 67: 793–820.
- Naiman, R. J. and Sedell, J. R. 1979a. Benthic organic matter as a function of stream order in Oregon. – *Arch. Hydrobiol.* 87: 404–422.
- and Sedell, J. R. 1979b. Characterization of particulate organic matter transported by some Cascade Mountain streams. – *J. Fish. Res. Bd Can.* 36: 17–31.
- Nelson, D. J. and Scott, D. C. 1962. Role of detritus in the productivity of a rock outcrop community in a Piedmont stream. – *Limnol. Oceanogr.* 7: 396–413.
- Petersen, R. C. and Cummins, K. W. 1974. Leaf processing in a woodland stream. *Freshwat. Biol.* 4: 343–368.
- Risley, L. S. 1987. Acceleration of seasonal leaf fall by herbivores in the southern Appalachian. – Ph. D. dissertation, Univ. of Georgia, Athens, GA.
- Short, R. A. and Ward, J. V. 1981. Benthic detritus dynamics in a mountain stream. – *Holarct. Ecol.* 4: 32–35.
- Speaker R., Moore, K. and Gregory, S. 1984. Analysis of the process of retention of organic matter in stream ecosystems. – *Verh. Int. Ver. Limnol.* 22: 1835–1845.
- Swank, W. T. and Douglass, J. E. 1977. Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina. – In: Correll, D. L. (ed.), *Watershed research in eastern North America*. Smithsonian Inst., Wash., D.C., pp. 343–362.
- Swanson, F. J. and Lienkaemper, G. W. 1978. Physical consequences of large organic debris in Pacific Northwest streams. – USDA. Forest Serv. Tech. Rep. PNW-69, Portland, OR.
- , Lienkaemper, G. W. and Sedell, J. R. 1976. History, physical effects, and management implications of large organic debris in western Oregon streams. – USDA Forest Serv. Gen. Tech. Rep. PNW-56, Portland, Oregon.
- , Gregory, S. V., Sedell, J. R. and Campbell, A. G. 1982. Land-water interactions: the riparian zone. – In: Edmonds, R. L. (ed.), *Analysis of coniferous forest ecosystems in the western United States*. Hutchinson Ross, Stroudsburg, PA, pp. 233–266.
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. and Cushing, C. E. 1980. The river continuum concept. – *Can. J. Fish. Aq. Sci.* 37: 130–137.
- Wakefield, R. H., Harrison, A. D. and Kovaiak, W. P. 1980. Seasonal changes in the quantity and nitrogen content of coarse detritus in a southern Ontario stream. – *Int. Rev. Gesamten Hydrobiol.* 65: 883–888.
- Webster, J. R. 1983. The role of benthic macroinvertebrates in detritus dynamics of streams: a computer simulation. – *Ecol. Monogr.* 53: 383–404.
- and Waide, J. B. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. – *Freshwat. Biol.* 12: 331–344.
- and Golladay, S. W. 1984. Seston transport in streams at Coweeta Hydrologic Laboratory, North Carolina, U.S.A. – *Verh. Int. Ver. Limnol.* 22: 1911–1919.
- and Swank, W. T. 1985. Within – stream factors affecting nutrient transport from forested and logged watersheds. – In: Blackmon, B. G. (ed.), *Proceedings of forestry and water quality: a mid-south symposium*. Univ. of Arkansas, Monticello, AR, pp. 18–24.
- and Benfield, E. F. 1986. Vascular plant breakdown in

- freshwater ecosystems. – *Ann. Rev. Ecol. Syst.* 17: 567–594.
- , Gurtz, M. E., Hains, J. J., Meyer, J. L., Swank, W. T., Waide, J. B. and Wallace, J. B. 1983. Stability of stream ecosystems. – In: Barnes, J. R. and Minshall, G. W. (eds), *Stream ecology*. Plenum, New York, pp. 355–395.
- , Benfield, E. F., Golladay, S. W., Hill, B. H., Hornick, L. H., Kazmierczak, R. F., Jr. and Perry, W. B. 1987. Experimental studies of physical factors affecting seston transport in streams. – *Limnol. Oceanogr.* 32: 848–863.
- Woodall, W. R., Jr. and Wallace, J. B. 1972. The benthic fauna of four small southern Appalachian streams. – *Am. Midl. Nat.* 88: 393–407.