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Retention of coarse organic particles in streams in the southern Appalachian Mountains

J. R. WEBSTER

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

A. P. COVICH

Department of Fisheries and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523 USA

J. L. TANK AND T. V. CROCKETT[1]

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

Abstract. Retention of coarse particulate organic matter (CPOM) is essential to the efficient use of organic matter in streams supported by allochthonous inputs. To measure retention and to study factors affecting retention, we conducted both long-term and short-term experiments using small dowels as indices of stick retention and pieces of paper as indices of leaf retention. These experiments were done in streams at Coweeta Hydrologic Laboratory. In general, we found that both types of CPOM were efficiently retained in all streams. Factors that affected CPOM transport and retention were storms, stream size, stream depth, and the abundance of retention structures in the streams. After initial transport, woody CPOM was transported only during storms. Retention was greater in smaller streams and in shallower stream sites. Rocks, boulders, and woody debris were the most important retention structures. In the stream draining a logged catchment, lower CPOM retention was associated with lower abundance of woody debris dams.

Key words: stream, large particulate organic matter, wood, retention, debris dams.

Streams draining forested areas have two dominating characteristics: dependence on allochthonous energy sources and downstream transport of material. If the allochthonous material were transported directly downstream at the speed of the flowing water, there would be minimal use of this organic energy source. Thus the efficient use of energy in these stream ecosystems depends on mechanisms that retain organic matter particles (Bilby and Likens 1980, Winterbourn et al. 1981, Cummins et al. 1989). These mechanisms include rocks, logs and small woody material, pools and backwaters, and instream and bank vegetation. Considerable evidence suggests that retention of coarse particulate organic material (CPOM, i.e., leaves and sticks) is very high. Budget studies have shown that although most organic matter enters streams as large particles, most export is small particles (e.g., Fisher and Likens 1973, Webster and Patten 1979, Webster et al. 1990, Wallace et al. 1991), suggesting that CPOM travels only short distances and is processed (i.e., broken or chewed into small particles or metabolized to CO_2) very close to where it enters a stream (Dance et al. 1979). This has been confirmed by studies directly measuring CPOM retention and travel distances (Young et al. 1978, Speaker et al. 1984, Webster et al. 1987, Lamberti et al. 1988, Cummins et al. 1989, Smock et al. 1989, Covich and Crowl 1990, Trotter 1990, Jones and Smock 1991, Prochazka et al. 1991, Snaddon et al. 1992, Ehrman and Lamberti 1992).

To gain a better understanding of the mechanisms involved in CPOM retention, we compared retention in three streams: an undisturbed reference stream, a stream draining a clearcut catchment, and another reference stream at a higher elevation and with much more extensive accumulations of woody debris.

[1] Present address: 1123 Wormley Creek Dr., Yorktown, Virginia 23692 USA.

TABLE 1. Characteristics of the three study streams.

Stream	Catchment area (ha)[a]	Catchment treatment	Weir elevation (m)	Stream gradient (m/m)	Mean discharge (L/s)[a] (Nov 89–Oct 90)
Hugh White Creek	61.1	Reference	710	0.15	26.5
Big Hurricane Branch	58.7	Logged 1977	724	0.19	26.2
Upper Ball Creek	38.8	Reference	1035	0.25	24.6

[a] Data from US Forest Service, Coweeta Hydrologic Laboratory.

Study Site

We conducted experiments in three streams at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of western North Carolina, USA (Table 1). Hugh White Creek drains a 61.1-ha reference catchment of mixed hardwood forest. This catchment has been undisturbed since it was logged before 1925; however, chestnut blight in the 1930s caused significant vegetation change and added many logs to the stream. The stream is 2nd order with substrate dominated by sand and cobble. Heavy shading keeps primary production very low and the stream community is dominated by insect shredders and collectors that depend on allochthonous energy sources.

Big Hurricane Branch is also 2nd order and drains a 58.7-ha catchment, which was logged in 1977. Forest regrowth was rapid, and at the time of this study the stream was covered in most areas by a closed canopy of successional trees such as black locust (*Robinia pseudoacacia*) and rapidly growing sprouts from the original forest. This stream is physically similar to Hugh White Creek, although it still has considerable deposits of sediment that apparently entered the stream as a result of road building and logging. Shortly after logging a burst of autochthonous production was accompanied by a change in the invertebrate community (Gurtz and Wallace 1984); but now the stream is again dominated by shredders and collectors.

Ball Creek begins in a high-elevation reference catchment of 38.8 ha. Here, the mixed hardwood and northern hardwood forest vegetation includes many hemlocks (*Tsuga canadensis*) and an extensive understory of rhododendron (*Rhododendron maximum*). The upper 900 m of this stream is referred to as Upper Ball Creek. Downstream, Ball Creek primarily drains reference forest but also receives tributaries from experimental catchments. Ball Creek joins Shope Fork to form Coweeta Creek, a 4th-order stream. Discharge in Ball Creek increases from a long-term annual average of 20.5 L/s (Upper Ball Creek) to nearly 600 L/s in Coweeta Creek (Fig. 1).

All three streams contain large amounts of CPOM and woody debris (Table 2). Because techniques for estimating numbers of debris dams are highly subjective, it is difficult to make comparisons among studies. However, the data show similar numbers of logs in Big Hurricane Branch and Hugh White Creek, although in Big Hurricane Branch the logs are smaller and less likely to function in debris retention (Golladay et al. 1989). Upper Ball Creek has more large woody debris and many very large logs in the stream (Huryn and Wallace 1985, 1987).

Methods

In each of five experiments we dropped large particles of organic matter into a stream and recorded how far they traveled, either short term (5 min) or long term (over a year). We used two types of particles—pieces of paper and wooden dowels. These were not intended to be artificial leaves and sticks but rather inexpensive, uniform material that could be readily monitored and used as indices of how leaves and sticks might behave in a stream. However, we refer to the pieces of paper as artificial leaves for convenience.

The artificial leaves consisted of pieces of waterproof paper (from "Rite in the Rain" field notebooks, J. L. Darling Corporation, Tacoma, Washington). We used either 13.4- × 3.8-cm

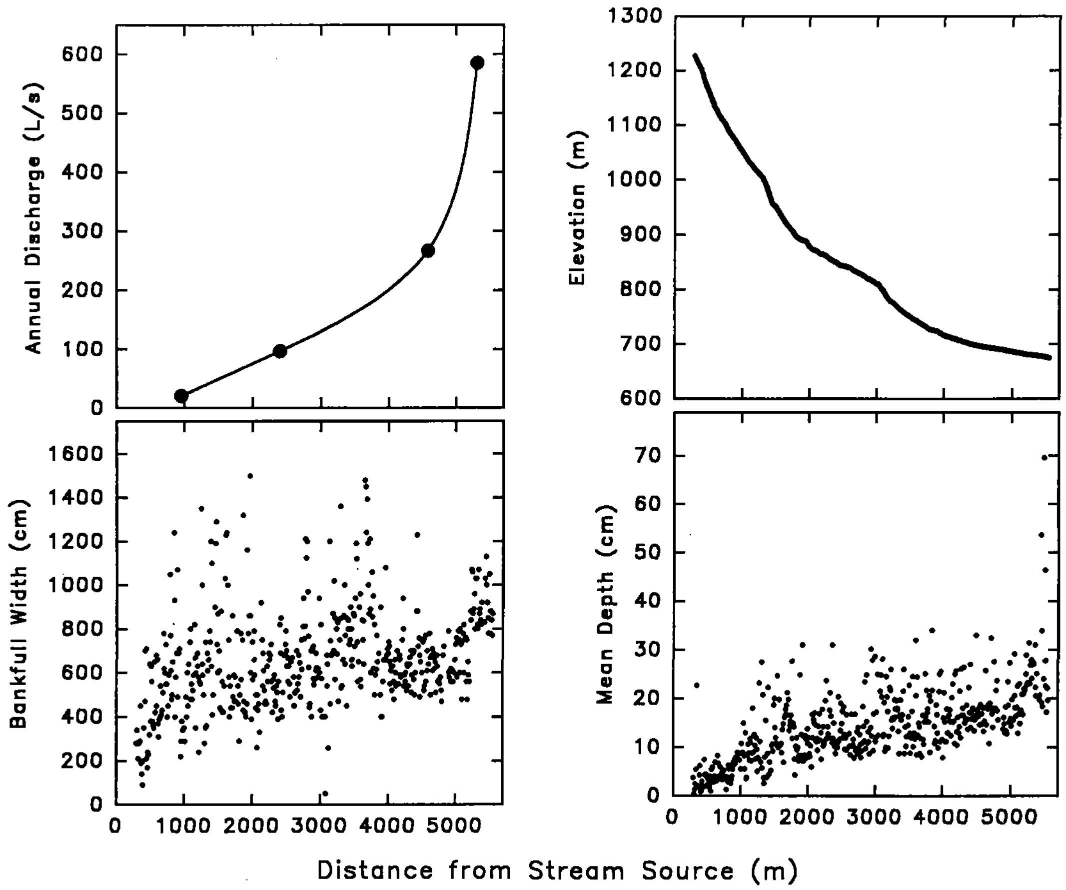

FIG. 1. Discharge, elevation, bankfull width, and mean depth along Ball Creek–Coweeta Creek. Annual discharge was calculated from US Forest Service data using 47 years of records for one site (Upper Ball Creek) and more limited records and regression of catchment area and discharge for other sites. Other data are from a survey made in 1989 with data collected every 10 m along the entire stream length.

rectangles or triangles with 4.4-cm sides. These sizes were chosen to be within the range of natural leaves and leaf fragments and, for practical reasons, to be in a size range that would move but not move too far or be lost. We used the triangular artificial leaves at smaller stream sites where the movement of rectangular artificial leaves was too restricted to provide useful information. Downstream, the triangular artificial leaves moved rapidly and were often lost.

For stick retention experiments, we used two sizes of commercial dowels. Large dowels were 60 cm long and 1.5 cm in diameter. Small dowels were half as long (30 cm) and 0.6 cm diameter. The dowels had an initial density of 0.65 g/cm^3. Lab studies with the larger dowels showed that they absorbed water and sank in about 5 d. In the long-term experiments, we did not always find all of the dowels that had been released. Since we were more likely to miss dowels that had moved long distance, our results may be slightly biased towards shorter travel distances.

Most data were statistically analyzed using a general linear model (GLM, SAS Institute 1991) with CPOM travel distance a function of various independent variables.

Detailed Methods and Results

Experiment 1—Large dowel retention

The objective of our first experiment was to compare dowel retention in the three different

TABLE 2. Debris dams and benthic organic matter in the three study streams. Complete debris dams spanned the entire channel; partial debris dams did not extend the full width of the channel. Small wood was 1–5 cm diameter; large wood was >5 cm diameter.

	Number of debris dams per 100 m					Benthic organic matter (g/m²)[b]		
		1985–86[b]		1990[c]				
Stream	1982[a]	Logs	Debris dams	Complete	Partial	CPOM	Small wood	Large wood
Hugh White Creek	23.1	9.2	1.6	2.8	5.6	213	312	5,134
Big Hurricane Branch	25.4	10.4	0.4	2.9	4.6	124	383	2,813
Upper Ball Creek	—	16.6		—	—	156	308	22,500

[a] Webster and Swank (1985).
[b] Hugh White Creek and Big Hurricane Branch from Golladay et al. (1989); Upper Ball Creek from Huryn and Wallace (1987). The number for Upper Ball Creek is for "complete debris dams".
[c] Webster, unpublished.

streams. Fifty large dowels were placed in a single location each in Hugh White Creek, Big Hurricane Branch, and Upper Ball Creek. The distance traveled by each dowel was measured at least 10 times over the next year, October 1989 through October 1990 (Fig. 2). The distance traveled by individual dowels over the course of the experiment ranged from 1 to 22 m; however, in general, the dowels did not move very far in any of the streams. After some initial transport, the dowels became stable and subsequently moved only during large storms. The pulse of transport in Big Hurricane Branch and Hugh White Creek in February occurred during a large storm (Fig. 2). However, another large storm in March caused no further transport. There was little dowel transport in Upper Ball Creek where the dowels were released in a small pool below a waterfall but were mostly retained in a debris dam at the base of the pool. This experiment clearly pointed to the need for replication of sites within streams.

Experiment 2—Effect of stream size on large dowel retention

In our second experiment, our objective was to see how retention of dowels was affected by stream size. Twenty-five large dowels were placed in four sites in Ball Creek that were 599, 883, 1100, and 1830 m downstream from the source of the stream. These dowels were placed in the stream in March 1990 and were followed through October 1990. After an initial pulse of transport caused mainly by the March storm (Fig. 2), we found most of the dowels in exactly the same place for the rest of the experiment (Fig. 3). This place ranged from 2.5 m to as much as 135 m from the point of release at the farthest downstream site. A pulse of transport at the

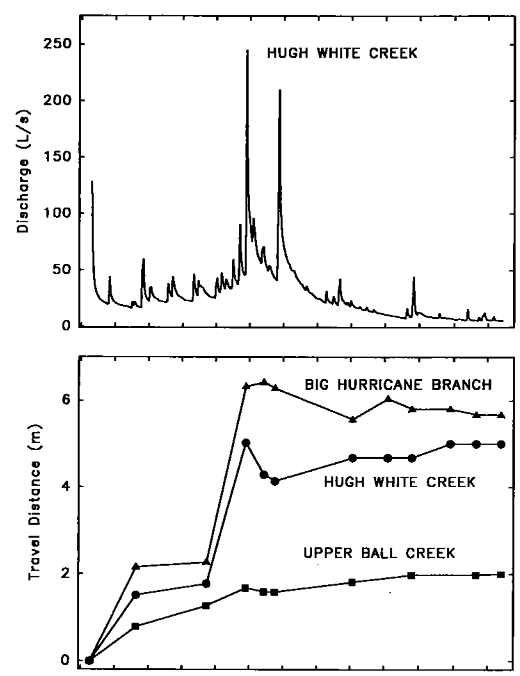

FIG. 2. Upper panel: Mean daily discharge in Hugh White Creek from October 1989 through October 1990. Data from US Forest Service, Coweeta Hydrologic Laboratory. Lower panel: Average cumulative distance moved by large dowels (60 cm long) at sites in the three study streams. Apparent upstream movements are the result of not finding all dowels on each sampling date.

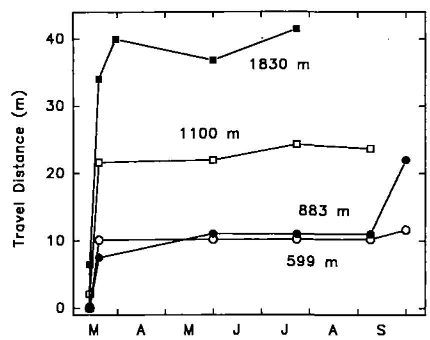

FIG. 3. Mean cumulative travel distance for large dowels (60 cm long) released at four sites in Ball Creek. Sites are identified by their distance from the stream source.

883-m site in September was caused by the breakup of a group of 14 dowels. In October only five of these were in the same location as they had been for the previous six months. In this experiment, as in the first experiment, we found that the large dowels were efficiently retained near the point where they were placed in the stream. For the movement that did occur, there was a clear tendency for greater initial travel distance at the more downstream sites (Fig. 3).

Experiment 3—Small dowel retention

Our objectives in this experiment combined our objectives of the previous experiments, that is, to compare streams and to look at the effect of stream size on retentiveness; however, in this experiment we used the smaller sized dowels. We placed 25 small dowels in each of four sites in Hugh White Creek, Big Hurricane Branch, and Upper Ball Creek in March 1990. In each stream, the four sites were progressively farther from the stream source, ranging from 100 m (site 1) to 1052 m (site 4) from the headwaters, and these distances were similar among streams. The dowels were followed through January 1991.

By the end of this experiment, individual dowels had traveled from 0.4 to 80 m from the site of release. Mean travel distances of the small dowels varied among the four sites in each stream (GLM, $p < 0.05$) with a general trend of increasing travel distance downstream. As with the larger dowels, little transport occurred after the dowels became stable at specific sites (Fig. 4). Based on statistical analysis using a GLM of log-transformed travel distances with stream, site (distance from stream source), and date as independent variables, travel distances were longest (i.e., retention was least) in Big Hurricane Branch (5.9 m) and shortest in Hugh White Creek (3.0 m). Travel distances in Upper Ball Creek were intermediate (4.0 m) and not statistically different from the other two ($p > 0.05$).

Experiment 4—Short term dowel retention

In July 1991 we conducted a short-term experiment to examine the effect of stream size on dowel retention. This experiment was done at 13 sites along Ball Creek–Coweeta Creek, ranging from 883 m to 5420 m from the stream source (Fig. 5). We dropped 25 small dowels in the stream at each site, and after 5 min we recorded the distance moved by each dowel and the type of obstacle retaining each dowel.

This experiment was conducted during a period of low flow, and at the upstream sites there was no movement at all (i.e., the dowels stayed where they were dropped). Proceeding downstream there was an exponential increase in travel distance (regression, $r^2 = 0.939$, $n = 10$) including one dowel at one of the downstream sites that moved 90 m before it was stopped. Throughout the length of the stream, most dowels were retained by rocks and boulders, but woody debris (logs, sticks, and debris dams) was also important in retaining the dowels (Table 3).

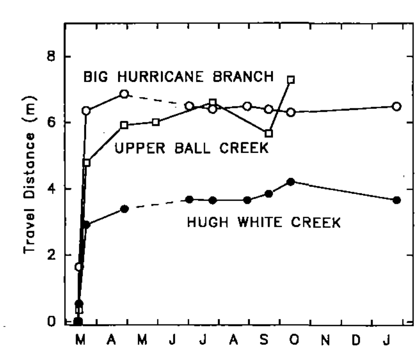

FIG. 4. Mean cumulative travel distances of small dowels (30 cm long) in each of the study streams. The dashed lines indicate missing data.

Experiment 5—Artificial leaf retention

The objective of this experiment was to compare artificial leaf retention in two of the streams and to look at the effect of stream size on retention. The experiment was done at 10 sites each in Hugh White Creek and Big Hurricane Branch. The sites were at 100-m intervals ranging from 250 m to 1150 m from each stream source. The experiment was repeated approximately monthly from February 1990 through January 1991. We placed 25 artificial leaves one at a time into the stream and recorded the distance each traveled before it was retained on some object. Retention always occurred within 5 min but ranged from 1 cm to 22 m from the release point. In downstream reaches we used paper rectangles, but nearer the source we used the smaller paper triangles. On all occasions rectangles and triangles were used together at one or more sites. After each experiment, we measured and recorded mid-stream depths over the reach traveled by the artificial leaves.

The data were analyzed by GLM with the natural logarithm of mean travel distance as the dependent variable; date, stream, site (distance from source), and shape (rectangle or triangle) were independent variables. Shape did not have a significant effect ($p > 0.05$) on travel distance when the other factors were included in the statistical model. Date, stream, and site did significantly affect travel distance ($p < 0.001$ in each case). Travel distance was shorter in summer and longer in winter (Fig. 6A). Also, travel distance increased downstream (Fig. 6B). These trends were consistent in both streams. Overall, travel distances were longer in Big Hurricane Branch than in Hugh White Creek.

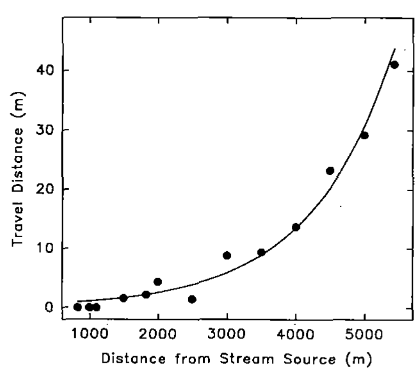

FIG. 5. Short term travel distances for small dowels (30 cm long) released at 13 sites in Ball Creek–Coweeta Creek. The regression line is based on log transformed data. The three upstream sites were not included in the regression.

TABLE 3. Obstacles retaining small dowels (30 cm long) in Ball Creek–Coweeta Creek (Experiment 4). Twenty-five dowels were released at each site, but the total number of obstacles recorded was often greater than 25 because of dowels being lodged against multiple obstacles. "Other" includes eddies, weeds, roots, and bank.

Site (distance from source, m)	Boulders	Rocks	Logs	Sticks	Debris dams	Leaves	Other
883		25					
1000		25					
1100		25					
1500	15	10					
1830	22	3		1			
2000	11	20		3			
2500	17	9	6	6			1
3000	13		2	3	3		3
3500	21	16	15		3		
4000	2	20		3		14	
4500	8	11	6	14			4
5000	6	12		6			3
5420		8	3	3			11[a]
Total	115	184	32	39	6	14	24

[a] Nine "roots".

These differences in travel distances were closely related to stream depth. Using a GLM, we found that depth was significantly related to date, site, and stream ($p < 0.0001$ in each case). Like travel distance, depth was greater in winter than in summer, increased downstream, and was greater in Big Hurricane Branch than in Hugh White Creek. Based on linear regression, travel distance increased significantly as a function of depth (Fig. 7; $r^2 = 0.27$, $n = 145$, for rectangles; $r^2 = 0.56$, $n = 63$, for triangles).

Two abnormalities are apparent in Figure 6. First, travel distance was greater in Hugh White Creek than in Big Hurricane Branch on the last sampling date (Fig. 6A). These data were collected during a rainstorm, and it is likely that high flow masked differences between streams at that time. Second, the only two sites where travel distances were greater in Hugh White Creek than in Big Hurricane Branch (850 m and

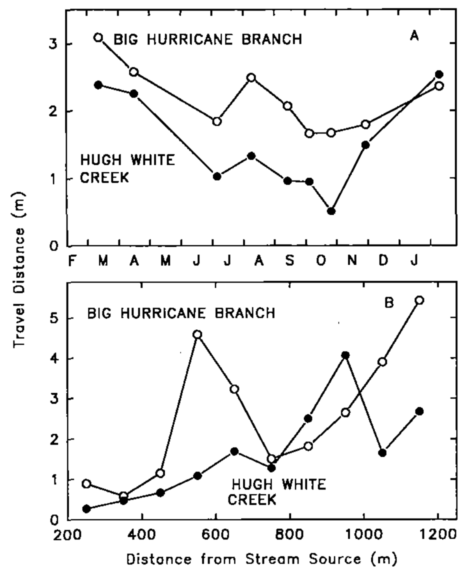

FIG. 6. Average travel distances of artificial leaves released in Big Hurricane Branch and Hugh White Creek. Data are averaged over site (A) or date (B).

950 m from the stream source; Fig. 6B) were sites where Hugh White Creek has high gradient and runs over mostly bedrock substrate. High-gradient bedrock also formed the substrate at two sites in Big Hurricane Branch (550 m and 650 m from stream source) where travel distances were exceptionally long (Fig. 6B).

Discussion

The efficient use of allochthonous organic matter in streams is the result of a balance between two processes: downstream transport and organic matter breakdown, including both fragmentation to smaller particles and metabolism to CO_2. In many ways these two processes oppose each other. For significant breakdown to occur, organic material must be retained rather than transported. On the other hand, as material is broken down into smaller particles, it becomes more easily transported. Small particles may be transported long distances and lost from the upper reaches of a stream (Cushing et al. 1993). Furthermore, breakdown reduces the retentiveness of a stream, accelerating transport and loss of material. Our experiments confirmed what has already been shown in a variety of other studies: CPOM does not move very far in streams. In addition we have identified some of the important mechanisms affecting this efficient retention.

Differences among streams

Streams at Coweeta vary in their retention of CPOM. In our comparisons of streams draining logged and reference catchments, we found that Big Hurricane Branch (catchment logged in 1977) was less retentive (Figs. 2, 4, 6) than the other two streams. Similar reduced CPOM retention resulting from logging was shown by Speaker et al. (1988). Many studies have demonstrated that CPOM retention is related to the amount of large woody debris in streams (Bilby and Likens 1980, Speaker et al. 1984, Smock et al. 1989, Trotter 1990, Jones and Smock 1991, Ehrman and Lamberti 1992), and low retention in Big Hurricane Branch may be related to reduced levels of large wood (Table 2) (Golladay et al. 1987, 1989). Webster et al. (1992) predicted that it will be many years, perhaps even centuries, before large wood enters and accumulates in this stream. Throughout this time, the

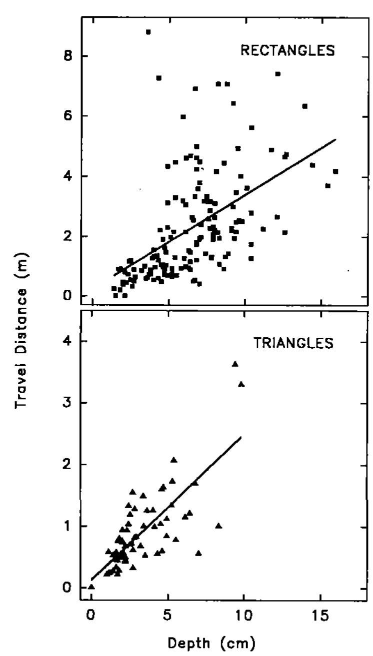

FIG. 7. Average travel distances of rectangular and triangular artificial leaves for all sites in both Hugh White Creek and Big Hurricane Branch combined. Lines are based on linear regression.

stream will have low retention and inefficient use of allochthonous energy input relative to undisturbed streams.

Other factors also contribute to low CPOM retention in Big Hurricane Branch. Leaf inputs from successional forests are low (Webster et al. 1990), and the leaves break down rapidly (Webster and Waide 1982, Benfield et al. 1991). Small sticks also break down more rapidly in logged streams (Golladay and Webster 1988). Lower input and faster breakdown means fewer leaves and sticks in the stream, further reducing retention. Higher discharge (e.g., Hewlett and Hibbert 1961) and higher storm flows (e.g., Hewlett and Helvey 1970) in logged streams also contribute to low retention. Additionally, sediment from roads and skid trails may embed the rocky substrate and smooth the streambed, further reducing retention. The net result of all these factors is that less CPOM enters logged streams, and what does enter breaks down rapidly or is washed out. Very little of the autumnal input of leaf litter remains in Big Hurricane Branch by the following summer (Golladay et al. 1989).

In contrast, we found relatively high retention in Upper Ball Creek. This stream drains a somewhat smaller catchment than the other two streams (Table 1), but has similar annual discharge because of higher rainfall and lower evapotranspiration at higher elevation. However, discharge is more flashy and the stream has a high gradient, factors that should lower retention. Based on our observation of relatively high retention, these factors are apparently balanced by the large amounts of woody debris in the stream (Table 2).

Stream size

Several studies have shown that large streams are less retentive of POM than small streams (Wallace et al. 1982, Minshall et al. 1983, Naiman et al. 1987, Minshall et al. 1992). In studies of CPOM retention, longest travel distances (i.e., least retention) have been recorded for larger streams (Young et al. 1978). Our studies at Coweeta clearly show that CPOM retention decreases with increasing stream size (Figs. 3, 5, 6). This trend has been related to a decrease in retention structures downstream (e.g., Wallace et al. 1982) and specifically to a decrease in woody debris (e.g., Naiman et al. 1987). This is certainly a very important factor, although we did not find any significant change in the types of structures retaining dowels in our short term studies. It would probably be necessary to extend the study to larger streams to document this relationship.

Larger stream size and discharge are generally accompanied by higher velocity, power, and depth. Streams with greater discharge have been shown to have lower CPOM retention (Speaker et al. 1988, Prochazka et al. 1991, Snaddon et al. 1992), but the mechanism affecting retention is not clear. Velocity does not change greatly with stream size because while depth increases gradient decreases (Leopold et al. 1964). Though stream power theoretically controls particle transport in streams (e.g., Bagnold 1966), empirical studies have shown only weak relationships between power and POM transport when comparing sites of different size (Sedell et al. 1978, Naiman and Sedell 1979, Naiman 1982). Also Minshall et al. (1992) concluded that power is not a good predictor of retention. We suggest that the effect of discharge on retention is closely related to depth (Fig. 7). Except in small, low gradient streams (Jones and Smock 1991), CPOM retention is not passive, that is, particles do not simply settle to the stream bed (e.g., Lamberti et al. 1988, Prochazka et al. 1991). Rather, retention depends on the probability that a particle hits an obstruction such as a log or a rock. This probability increases with increasing frequency of obstructions and decreases with increasing depth of the water column. However, the relationship between retention and depth is much more complex. The presence of channel obstructions also increases hydraulic roughness, decreases velocity, and increases depth. This complexity is probably the reason for the high unexplained variance in the regression relationships between travel distance and depth (Fig. 7).

Within-stream site differences

In addition to general patterns related to catchment characteristics and stream size, we saw several examples of specific sites with unusual retention characteristics in our experiments with dowels (Figs. 2, 4) and artificial leaves (Fig. 6). In their study of Upper Ball Creek, Huryn and Wallace (1987) pointed out that streams are mosaics of habitat types with different retention characteristics. Also, Lamberti et al. (1988) showed differences in CPOM retention between constrained and unconstrained sites. The biggest differences we saw were in sites where streams ran over bedrock (e.g., 550-m site in Big Hurricane Branch, Fig. 6). Despite the shallow depth of these areas, high gradient, high velocity, and the lack of obstructions greatly reduced retention. Lamberti et al. (1988) also found low retention in bedrock areas.

Seasonal patterns and storms

In our leaf retention study, we saw a distinct seasonal pattern with greater retention in summer and fall and less retention in winter and spring (Fig. 6). This pattern is undoubtedly related to the seasonal pattern of discharge (Fig. 2) and depth, but the abundance of leaves on the streambed may also be important. The very high retention of artificial leaves in Big Hurricane Branch in October (Fig. 6) was associated with the many freshly fallen leaves at that time. Once these leaves aggregated into packs, broke down, or were washed out, their effect on particle retention diminished.

We saw no seasonal pattern in dowel retention. After an initial pulse of movement, the dowels stabilized, and we saw no further movement unless caused by a storm (Fig. 2). Other studies have also shown increased CPOM transport (or lower CPOM retention) during storms (e.g., Webster 1977, Cuffney and Wallace 1989, Smock et al. 1989, Covich and Crowl 1990, Jones and Smock 1991). As flow increases, increased power and expansion of the stream in its channel increases entrainment, and increased depth reduces subsequent retention. Higher flows may break debris dams, releasing more material and further reducing retention (e.g., Fisher and Likens 1973), and under extreme conditions debris torrents may cause complete scouring of the streambed (Swanson et al. 1982). On the other hand, Covich and Crowl (1990) found that Hurricane Hugo caused a large input of organic debris (about 4× normal annual litterfall) to a stream in Puerto Rico. This litter formed debris dams and increased dowel retention over what had been expected for a storm of that magnitude.

In summary, retention of CPOM in small mountain streams of the southern Appalachians is related primarily to the number of obstructions and the depth of the water. These variables directly influence the probability that a particle encounters an obstruction. There are many obstructions in these shallow headwater streams, including rocks, boulders, logs, and sticks. Retention is very high and most particles travel only a few metres when they initially enter the stream, though further movement may occur during storms. As stream size increases downstream, retention decreases. This decrease is the result of fewer obstructions and greater depth. Although some disturbances such as hurricanes, tree diseases, or insect outbreaks may increase instream obstruction, logging has been shown to decrease retention in mountain streams. Because of the extent of logging throughout the southern Appalachians, these streams are probably much less retentive and thereby less productive than they were several hundred years ago. However, large inputs of woody debris resulting from the death of American chestnut (*Castanea dentata*) may have partially offset reduced retention resulting from logging (Webster et al. 1992).

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Literature Cited

BAGNOLD, R. A. 1966. An approach to the sediment transport problem of general physics. U.S. Geological Survey Prof. Paper 422-I.

BENFIELD, E. F., J. R. WEBSTER, S. W. GOLLADAY, G. T. PETERS, AND B. M. STOUT. 1991. Effects of forest disturbance on leaf breakdown in southern Appalachian streams. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 24:1687–1690.

BILBY, R. E., AND G. E. LIKENS. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61:1107–1113.

COVICH, A. P., AND T. A. CROWL. 1990. Effects of hurricane storm flow on transport of woody debris in a rain forest stream (Luquillo Experimental Forest, Puerto Rico). Tropical Hydrology and Caribbean Water Resources 1990:197–205.

CUFFNEY, T. F., AND J. B. WALLACE. 1989. Discharge-export relationships in headwater streams: the influence of invertebrate manipulations and drought. Journal of the North American Benthological Society 4:331–341.

CUMMINS, K. W., M. A. WILZBACH, D. M. GATES, J. B. PERRY, AND W. B. TALIAFERRO. 1989. Shredders and riparian vegetation. BioScience 39:24–30.

CUSHING, C. E., G. W. MINSHALL, AND J. D. NEWBOLD. 1993. Transport dynamics of fine particulate organic matter in two Idaho streams. Limnology and Oceanography 38:1101–1115.

DANCE, K. W., H. B. N. HYNES, AND N. K. KAUSHIK. 1979. Seasonal drift of solid organic matter in two adjacent streams. Archiv für Hydrobiologie 87:139–151.

EHRMAN, T. P., AND G. A. LAMBERTI. 1992. Hydraulic and particulate matter retention in a 3rd-order Indiana stream. Journal of the North American Benthological Society 11:341–349.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

GOLLADAY, S. W., AND J. R. WEBSTER. 1988. Effects of clearcut logging on wood breakdown in Appalachian mountain streams. American Midland Naturalist 119:143–155.

GOLLADAY, S. W., J. R. WEBSTER, AND E. F. BENFIELD. 1987. Changes in stream morphology and storm transport of organic matter following catchment disturbance. Journal of the North American Benthological Society 6:1–11.

GOLLADAY, S. W., J. R. WEBSTER, AND E. F. BENFIELD. 1989. Changes in stream benthic organic matter following catchment disturbance. Holarctic Ecology 12:96–105.

GURTZ, M. E., AND J. B. WALLACE. 1984. Substrate-mediated response of stream invertebrates to disturbance. Ecology 65:1556–1569.

HEWLETT, J. D., AND J. D. HELVEY. 1970. Effects of forest clear-felling on the storm hydrograph. Water Resources Research 6:768–782.

HEWLETT, J. D., AND A. R. HIBBERT. 1961. Increases in water yield after several types of forest cutting. Quarterly Bulletin of International Association of Scientific Hydrology 6:5–16.

HURYN, A. D., AND J. B. WALLACE. 1985. Life history and production of *Goerita semata* Ross (Trichoptera:Limnephilidae) in the southern Appalachian Mountains. Canadian Journal of Zoology 63:2604–2611.

HURYN, A. D., AND J. B. WALLACE. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology 68:1932–1942.

JONES, J. B., AND L. A. SMOCK. 1991. Transport and retention of particulate organic matter in two low-gradient headwater streams. Journal of the North American Benthological Society 10:115–126.

LAMBERTI, G. A., S. V. GREGORY, L. R. ASHKENAS, R. C. WILDMAN, AND A. D. STEINMAN. 1988. Influence of channel geomorphology on retention of dissolved and particulate matter in a Cascade Mountain Stream. Pages 33–39 *in* D. G. Abell (editor). Proceedings of the California Riparian Systems Conference, Davis, California. Forest Service General Technical Report PSW-110, Berkeley, California.

LEOPOLD, L. B., M. G. WOLMAN, AND J. R. MILLER. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco.

MINSHALL, G. W., R. C. PETERSEN, T. L. BOTT, C. E. CUSHING, K. W. CUMMINS, R. L. VANNOTE, AND J. R. SEDELL. 1992. Stream ecosystem dynamics of the Salmon River, Idaho: an 8th-order system. Journal of the North American Benthological Society 11:111–137.

MINSHALL, G. W., R. C. PETERSEN, K. W. CUMMINS, T. L. BOTT, J. R. SEDELL, C. E. CUSHING, AND R. L. VANNOTE. 1983. Interbiome comparison of stream ecosystem dynamics. Ecological Monographs 53:1–25.

NAIMAN, R. J. 1982. Characteristics of sediment and organic carbon export from pristine boreal forest catchments. Canadian Journal of Fisheries and Aquatic Sciences 39:1699–1718.

NAIMAN, R. J., J. M. MELILLO, M. A. LOCK, T. E. FORD, AND S. R. REICE. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68:1139–1156.

NAIMAN, R. J., AND J. R. SEDELL. 1979. Characterization of particulate organic matter transported by some Cascade Mountain streams. Journal of the Fisheries Research Board of Canada 36:17–31.

PROCHAZKA, K., B. A. STEWART, AND B. R. DAVIES. 1991. Leaf litter retention and its implications for shredder distribution in two headwater streams. Archiv für Hydrobiologie 120:315–325.

SAS INSTITUTE. 1991. SAS user's guide: statistics, version 6. 4th edition. SAS Institute, Inc., Cary, North Carolina.

SEDELL, J. R., R. J. NAIMAN, K. W. CUMMINS, G. W. MINSHALL, AND R. L. VANNOTE. 1978. Transport of particulate organic material in streams as a function of physical processes. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 20:1366–1375.

SMOCK, L. A., G. M. METZLER, AND J. E. GLADDEN. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. Ecology 70:764–775.

SNADDON, C. D., B. A. STEWART, AND B. R. DAVIES. 1992. The effect of discharge on leaf retention in two headwater streams. Archiv für Hydrobiologie 125:109–120.

SPEAKER, R., K. MOORE, AND S. GREGORY. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1835–1841.

SPEAKER, R. W., K. J. LUCHESSA, J. F. FRANKLIN, AND S. V. GREGORY. 1988. The use of plastic strips to measure leaf retention by riparian vegetation in a coastal Oregon stream. American Midland Naturalist 120:22–31.

SWANSON, F. J., R. L. FREDRICKSEN, AND F. M. MCCORISON. 1982. Material transfer in a western Oregon forested catchment. Pages 233–266 *in* R. L. Edwards (editor). Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross, Stroudsburg, Pennsylvania.

TROTTER, E. H. 1990. Woody debris, forest-stream succession, and catchment geomorphology. Journal of the North American Benthological Society 9:141–156.

WALLACE, J. B., T. F. CUFFNEY, J. R. WEBSTER, G. J. LUGTHART, K. CHUNG, AND B. S. GOLDOWITZ. 1991. Five-year study of export of fine organic particles from headwater streams: effects of season, extreme discharges, and invertebrate manipulation. Limnology and Oceanography 36:670–682.

WALLACE, J. B., J. R. WEBSTER, AND T. F. CUFFNEY. 1982. Stream detritus dynamics: regulation by invertebrate consumers. Oecologia 53:197–200.

WEBSTER, J. R. 1977. Large particulate organic matter processing in stream ecosystems. Pages 505–526 *in* D. L. Correll (editor). Catchment research in eastern North America. Smithsonian Institute, Washington, D.C.

WEBSTER, J. R., E. F. BENFIELD, S. W. GOLLADAY, B. H. HILL, L. E. HORNICK, R. F. KAZMIERCZAK, AND W. E. PERRY. 1987. Experimental studies of physical factors affecting seston transport in streams. Limnology and Oceanography 32:848–863.

WEBSTER, J. R., S. W. GOLLADAY, E. F. BENFIELD, D. J. D'ANGELO, AND G. T. PETERS. 1990. Effects of forest disturbance on particulate organic matter budgets of small streams. Journal of the North American Benthological Society 9:120–140.

WEBSTER, J. R., S. W. GOLLADAY, E. F. BENFIELD, J. L. MEYER, W. T. SWANK, AND J. B. WALLACE. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. Pages 231–253 *in* P. J. Boon, P. Calow, and G. E. Petts (editors). River conservation and management. Wiley, Chichester.

WEBSTER, J. R., AND B. C. PATTEN. 1979. Effects of catchment perturbation on stream potassium and calcium dynamics. Ecological Monographs 49:51–72.

WEBSTER, J. R., AND W. T. SWANK. 1985. Within-stream factors affecting nutrient transport from forested and logged watersheds. Pages 18–41 *in* B. Blackman (editor). Proceedings of forestry and water quality: a mid-south symposium. University of Arkansas, Monticello.

WEBSTER, J. R., J. B. WAIDE. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. Freshwater Biology 12:331–344.

WINTERBOURN, M. J., J. S. ROUNICK, AND B. COWIE. 1981. Are New Zealand stream ecosystems really different? New Zealand Journal of Marine and Freshwater Research 15:321–328.

YOUNG, S. A., W. P. KOVALAK, AND K. A. DEL SIGNORE. 1978. Distances traveled by autumn-shed leaves introduced into a woodland stream. American Midland Naturalist 100:217–222.

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