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Experimental studies of physical factors affecting seston transport in streams[1]

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Abstract

We conducted three series of experiments in laboratory and natural streams to evaluate effects of various physical factors on seston (particulate organic matter) retention, entrainment, and transport. Results of laboratory experiments showed that substrate characteristics were important in determining retention of all sizes of seston. Retention increased with roughness and substrate complexity. During simulated storms in laboratory streams, seston concentrations were not generally correlated with discharge. However, we found strong correlation between seston concentration and the rate of increase in discharge during rising hydrographs, and, after peak discharge, seston concentration dropped exponentially independent of discharge. Simulated storms conducted in a natural stream channel supported those findings. Results of these experiments and published field studies suggest that existing sediment transport models have little application to seston transport in small streams primarily because of limited availability of seston. During baseflow, seston transport depends on the rate of biological particle generation and retention characteristics of the streambed. Seston transport during storms depends on the rate of increase in discharge, streambed retention, and the availability of particulate organic material on the streambed.

Seston has been defined as particulate material suspended in water, including both living and nonliving particles (e.g. Hutchinson 1967). In this paper we use seston to refer more specifically to particulate organic matter in transport in streams. Organic matter is transported in streams as either dissolved organic matter (DOM) or seston. DOM-to-seston ratios (weight per volume) range from about 70 to 0.1 (Malcolm and Durum 1976; Moeller et al. 1979; Meybeck 1981; Schlesinger and Melack 1981). On average the two forms of organic matter are about equal in abundance. Meybeck (1981) estimated that 46% of the organic carbon transported from continents to oceans is sestonic.

In addition to being a major form of carbon transport between land and sea, seston is an integral component of stream organic and nutrient processes. Many stream organisms are adapted to feed on seston (e.g. Wallace and Merritt 1980; Lauritsen 1986), and transport of seston is an essential linkage along the continuum of stream ecosystems in a river system (Vannote et al. 1980).

Wotton (1984) suggested that two processes generate seston in streams: primary generation by breakdown of large particles, chiefly by insects (e.g. Wallace et al. 1982*b*), and secondary generation by aggregation from DOM (e.g Dahm 1981). Factors affecting the exchange of particles between the streambed and overlying water largely determine particle transport by streams. Initiation of motion occurs when water velocity is sufficient to produce a critical shear stress for particles on the streambed. Once moving, some particles may remain in contact with the streambed, and the mass of particles moving in this fashion is referred to as bedload. Smaller and lighter particles may be carried in the water column when gravitational forces acting on the particles are insufficient to counteract turbulent diffusion of particles away from the bed. These particles represent the suspended load. Transport of suspended material ceases once gravitational forces exceed upward, turbulent forces and the particles are deposited on the streambed. Similarly, bedload trans-

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port ceases when stream velocity is insufficient to produce the critical shear stress.

More extensive descriptions of entrainment and deposition processes have been published in a number of textbooks (e.g Morisawa 1968; Yalin 1977; Dunne and Leopold 1978; Dingman 1984); however, it is evident from this brief description that a variety of interacting physical factors is involved in determining particle transport. These factors include characteristics of the particles, such as size, shape, density, and fall velocity, and characteristics of the stream and its flow, including width, depth, slope, bed roughness, discharge, velocity, water temperature, and dissolved load. Numerous models have been developed to predict sediment particle transport in streams. However, there are several reasons why these models cannot be usefully applied to seston. One major assumption of most sediment transport models is that transport occurs in channels where particles in transport are similar to particles in the streambed (Einstein 1950). This is clearly not the case for most small, high-gradient streams; particles in transport are generally small and may contain a considerable organic fraction, whereas the bed is composed largely of cobbles, boulders, and large organic particles. A second assumption is unlimited availability of transportable solids (e.g. Bagnold 1966). Considerable evidence suggests that this assumption may at times be invalid (Allen 1977; Dunne and Leopold 1978). Depletion of transportable material becomes particularly evident in dealing with seston transport. Sediment transport models also usually assume that the particles are fairly large (>0.1 mm; e.g. Yang and Stall 1976), spherical, and of uniform high density. Recent studies have shown that the median size of particles carried in small streams is fairly small (often <0.1 mm; e.g Sedell et al. 1978; Gurtz et al. 1980; Wallace et al. 1982*a*). Also, the material is highly variable in shape and density, ranging from whole leaves with density near 1.0 g cm^{-3} to more or less spherical, inorganic particles with density >2.5 g cm^{-3}. Webster et al. (in press) found that average particle densities were generally <1.75 g cm^{-3} for several small streams at Coweeta Hydrologic Laboratory, North Carolina. Fisher et al. (1979) showed that the criteria for initiating motion of organic particles on a sandbed were similar to those for inorganic particles, although microbial adhesion may affect initial motion.

Bagnold (1966) formulated a theoretical model relating particle transport to stream power, and Sedell et al. (1978) first suggested that this relationship might be applied to seston transport. Stream power is the product of water density, gravitational acceleration, energy gradient, and discharge (Leopold et al. 1964). If other factors are constant, power is directly proportional to discharge. Some field studies have shown a direct relationship between seston concentration and stream power (or discharge) for either samples taken over a complete annual cycle (e.g. Fisher and Likens 1973; Meyer and Likens 1979; Webster and Patten 1979) or samples taken at short intervals during storms (Bilby and Likens 1979; Webster et al. 1983). However, Sedell et al. (1978) and Naiman and Sedell (1979*a*) found only weak relationships between seston concentration and stream power for streams throughout the United States, and Naiman (1982) also found low correlation between seston concentration and power in Canadian streams. In low-order southern Appalachian streams, highest baseflow concentrations of seston occur in summer when flows are generally low, while during high winter baseflows, seston concentrations are low (Webster and Golladay 1984). Also, seston concentrations are usually higher on the rising limb of a storm hydrograph than at equal discharges on the descending limb (e.g. Bilby and Likens 1979; Meyer and Likens 1979; Gurtz et al. 1980; Golladay et al. 1987). Thus, even though power may establish the potential for streams to transport particles, actual seston transport may be limited by other factors.

In this paper we report results of three series of experimental studies designed to evaluate effects of physical factors on seston transport in small streams. These physical factors included characteristics of the stream (discharge, velocity, bed roughness, and slope) and characteristics of the seston particles (size and availability). Two series of experiments were conducted in artificial streams, and the third series was done in a natural stream channel. Space for the artificial stream work was provided by the University Center for Environmental Studies, Virginia Polytechnic Institute and State University. Access to Guys Run was provided by the Virginia Commission of Game and Inland Fisheries.

Factors affecting retention of organic particles—artificial stream studies

This series of artificial stream experiments was designed to evaluate various factors that might affect retention of seston in streams. The general procedure was to add either fine particulate organic matter (FPOM, <1 mm) or large particulate organic matter (LPOM, whole leaves) to the upstream end of a laboratory channel for a short period (usually about 1 h) and to measure either the amount of material reaching the downstream end of the channel during this period (FPOM experiments) or retained in the stream at the end of the period (LPOM experiments). Results were expressed as retention efficiency (E_R), i.e. the percent of added material retained within the stream. Since the retention efficiency is a function of stream length, uptake length was calculated by assuming exponential uptake of seston from the water column:

$$C(x) = C_0\exp(-k_L x) \qquad (1)$$

where $C(x)$ is the concentration of seston at a distance x downstream, C_0 is the upstream concentration, and k_L is the uptake rate per unit length of stream. From Eq. 1, the uptake rate (k_L) was calculated as

$$k_L = \frac{\ln 100 - \ln(100 - E_R)}{d} \qquad (2)$$

where $d = 10$ m is the length of the artificial channels. Uptake length is the inverse of k_L and is the distance needed to retain 63.2% of the input. This parameter is equivalent to the mean drift distance used by Elliott (1971) for drifting insects and the average travel distance for leaves used by Young et al. (1978) and Speaker et al. (1984). Retention efficiency, uptake rate, and uptake length are related, since 10-m streams were used in all experiments, so statistical analyses were only performed on retention efficiency, though mean uptake lengths are also reported.

Methods—Artificial streams used in this study were straight, 10-m by 30.5-cm fiberglass channels (Frigid Units, Inc., Toledo, Ohio). The streams were located indoors and were filled with tapwater recirculated by electric pumps. Water depth ranged from 1 to 3 cm depending on substrate, gradient, and flow. Water velocities ranged from 13 to 73 cm s^{-1}. Wet whole leaves were added to the upstream ends of the channels by dropping individual leaves at intervals of 5, 10, or 15 s. The duration of whole-leaf deposition experiments ranged from 20 min to 10 h. Leaves passing the downstream end of the channel were collected and counted and, at the end of each experiment, leaves remaining in the channel were counted. In other experiments, FPOM was added to the upstream ends of the stream by gravity flow from a continuously mixed reservoir containing a measured concentration of FPOM. Addition rates were checked at the beginning and end of each experiment. All transported FPOM was collected in a net (mesh size appropriate to the particle size being used) placed at the downstream ends of the streams. After each experiment, material collected in the net was dried (24 h at 55°C, 24 h in desiccator) and weighed.

In the whole-leaf retention experiments we varied the following factors. We used white oak (*Quercus alba*) or dogwood (*Cornus florida*) leaves collected from trees just prior to abscission, and we used three stream gradients: 0.6, 1.2, and 1.9 cm m^{-1}. Discharge, which ranged from 0.8 to 2.2 liter s^{-1}, was measured by directing the flow from the head box into a 20-liter bucket and measuring the time to fill the bucket. Artificial turf and "pea" gravel (0.5–1.0-cm diam) substrates were used. Velocity in the channels was measured with rhodamine dye, and roughness (Manning's n) was calculated from Manning's equation:

$$V = (R^{2/3}S^{1/2})/n \qquad (3)$$

where V is velocity, R is hydraulic radius (cross-sectional area divided by wetted perimeter), S is gradient, and n is Manning's roughness coefficient (e.g. Dingman 1984).

Roughness coefficients for artificial turf and gravel were 0.017 and 0.026. In some experiments, 1–5 8-cm-diameter concrete hemispheres were placed in the stream channel to create obstructions to flow.

The following factors were varied in the FPOM retention experiments. Particles were made from either dogwood or white oak leaves. Leaves were ground in a Wiley mill, and particles were sieved into three size categories: 102–240, 240–560, and >560 μm. These particles were soaked in aerated tapwater for 1, 7, or 42 d before use in an experiment. The same three stream gradients were used as in the whole-leaf experiments. Discharge was varied from 0.7 to 2.5 liters s^{-1}. FPOM was added at rates of 1.2, 2.0, 3.7, and 6.0 g DW h^{-1}, which at the various discharges gave upstream concentrations ranging from 0.12 to 2.57 mg DW $liter^{-1}$. This range of FPOM concentrations is typical for small streams (e.g. Webster et al. 1979). Three different types of substrates were used: artificial turf, pea gravel, and smooth fiberglass (roughness coefficient of 0.008).

Streams were thoroughly cleaned between experiments and refilled with clean water. Thirty-five experiments were run using whole leaves, and 129 experiments were run with FPOM. Results were analyzed using a general linear models procedure (SAS Institute Inc. 1982). An $\alpha = 0.05$ level of significance was used in interpreting results. Arcsine-transformed retention efficiency was used as the dependent variable in all analyses.

Results—Retention efficiencies for the various whole-leaf experiments ranged from 1.3 to 99.0%. Initial statistical analysis showed that stream gradient did not significantly affect retention of whole leaves within the range of gradients used, so gradient was eliminated from further statistical analyses. Also, we found that the number of obstacles was not significant and in subsequent analyses used presence or absence of obstacles. Leaf species, discharge, and presence or absence of obstacles all significantly affected leaf retention efficiency ($P \leq 0.0001$), but substrate type (turf or gravel) was not a significant factor. However, there was significant statistical interaction between leaf species and obstacles. When the analysis was performed on the two leaf species independently to eliminate this interaction, substrate significantly ($P < 0.02$) affected retention of dogwood leaves but not oak leaves. In general, oak leaves were retained more efficiently than the smaller, softer dogwood leaves (Table 1). Gravel was more retentive than turf (significant only for dogwood leaves). The presence of obstacles greatly increased retention, and higher discharge reduced retention.

Table 1. Least-squares means of retention efficiencies in the whole-leaf retention experiments. Least-squares means correct for the unbalanced experimental design (SAS Institute 1982) and were calculated on arcsine-transformed data.

Variable	N	Mean retention efficiency (%)	Uptake length (m)
Leaf species			
Dogwood	15	47.1	15.7
Oak	20	82.6	5.7
Substrate			
Gravel	10	75.8	7.0
Artificial turf	25	55.7	12.3
Obstacles			
No obstacles	19	40.8	19.1
With obstacles	16	87.2	4.9
Discharge (liters s^{-1})			
2.0	26	35.0	23.2
1.7	2	32.1	25.8
1.3	3	97.4	2.7
0.8	2	91.5	4.1

Preliminary analysis of the FPOM experiments showed that leaf species, conditioning time, and addition rate had no significant effects on FPOM retention efficiency and these factors were eliminated in subsequent statistical analyses. The effect of gradient on retention of FPOM was inconsistent (Table 2). Gradient was not a significant factor on gravel and fiberglass substrates. Although retention on turf was significantly greater at gradients of 0.6 and 1.9% than at 1.2%, we doubt that the small differences in gradient had any real effect on retention. Experiments with turf at three different gradients were made in three different artificial streams, one for each gradient. Observed differences may have been due to

Table 2. Least-squares means of the retention efficiencies for the FPOM retention experiments. Least-squares means were calculated on arcsine-transformed data.

Variable	N	Mean retention efficiency (%)	Uptake length (m)
Gradient (%)			
0.6	41	66.6*	9.1
1.9	38	66.4*	9.2
1.2	50	49.8	14.5
Substrate			
Gravel	24	91.4*	4.1
Artificial turf	79	90.7*	4.2
Smooth fiberglass	26	4.6	212.4
Particle size (μm)			
>560	71	65.7*	9.3
240–560	46	64.4*	9.7
102–240	12	58.9	11.2

* No significant difference between means (t-test of least-squares means, $\alpha = 0.05$).

minor differences among streams, such as the number of joints in the turf or how firmly the turf was attached to the stream bottom.

Substrate type significantly affected retention of FPOM (Table 2). There was almost no retention of FPOM by the fiberglass, but the other two substrates were very efficient at retaining particles. Overall, there were no statistically significant differences in retention efficiencies between gravel and turf, but this result may have been due to a significant interaction between substrate and discharge. Figure 1 suggests decreased retention on gravel at high discharge, perhaps occurring when gravel particles began to move. Discharge had an overall significant effect on retention of FPOM (Fig. 1). However, when data from the different substrates were analyzed separately, the effect of discharge was not significant on the fiberglass, but increased discharge significantly reduced retention on turf ($r^2 = 0.64$, $N = 79$) and gravel ($r^2 = 0.50$, $N = 24$). FPOM size significantly affected retention on turf but not on gravel or fiberglass. In general, larger FPOM particles were retained more efficiently than smaller particles (Table 2). Perhaps larger particles were carried closer to the substrate and removed from transport by a combining action of the turf.

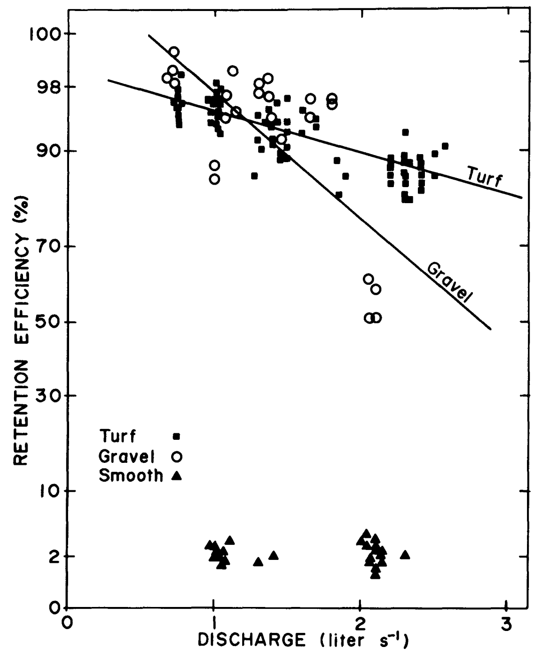

Fig. 1. Retention efficiency of FPOM as a function of discharge on three different substrates. For gravel substrate $r^2 = 0.50$, $N = 24$, and for turf $r^2 = 0.64$, $N = 79$. For smooth substrate, the correlation was not significant. Retention efficiencies were arcsine transformed for statistical analyses. Some points are masked in the figure.

Effect of benthic substrate on retention of seston during storms—artificial stream studies

Another set of experiments was run to evaluate effects of substrate characteristics on seston transport during periods of changing discharge ("storms"). The basic design was to place FPOM on the streambed, increase and decrease flow to stimulate a storm hydrograph, and measure seston export during the simulated storm. These experiments and others described below only simulate one aspect of storms—elevated discharge. Other factors, such as the impact of raindrops, addition of FPOM washed out of the canopy, and seston carried from upstream, were not studied.

Methods—The artificial channel used in these experiments was 33 m long, consisting of three parallel straight sections connected with two 180° bends. Channel width was 29.5 cm, and channel gradient was 0.5%. The channel was operated as a recirculating system in which tapwater was supplied from a head box and collected in a foot box. Baseflow was maintained at ca. 0.1 liter s^{-1}. Maximum discharge during simulated storms was 2.2 liters s^{-1}. Discharge at the downstream end of the channel was monitored continuously with a stilling well and water level recorder.

FPOM was prepared by grinding white oak leaves in a Wiley mill. The particles were sieved and only particles < 1 mm were used. Approximately 100 g (dry wt) of FPOM was soaked for 24 h and then sprinkled uniformly throughout the stream channel the day before each experiment. Except during "storms," the stream was kept at baseflow throughout this series of experiments. The stream was not cleaned between individual experiments.

Each simulated storm lasted about 1 h. Flow was increased from baseflow to peakflow over a period of about 20 min, held at peak for 15–20 min, and then decreased back to baseflow over about 20 min. Seston exported during the storm was collected with a 102-μm mesh net at the downstream end of the channel. Sampling intervals varied from 0.25 to 5 min depending on the time necessary to collect weighable samples. Approximately 25 samples were taken during each storm. Samples collected in the nets were filtered on preweighed glass-fiber filters, dried at 55° for 24 h, placed in a desiccator for at least 24 h, and weighed. Seston concentration was calculated by dividing transport by total discharge during the sample interval.

We used seven levels of substrate complexity (Table 3). For each level, an average roughness coefficient (Manning's n) was calculated using velocities measured with rhodamine dye (Table 3). The basic substrate was pea gravel (0.5–1.0-cm diam) spread uniformly in the stream to a depth of about 3 cm. The first modification of the basic substrate was to increase the substrate complexity by placing bricks (5.5 × 19.0 × 9.0 cm) alternately along the sides of the channel at 2-m intervals. The bricks were placed with the largest side down and the long axis perpendicular to the current. In the second modification, we tripled the number of bricks, so that they were spaced every 0.5 m. Additions of bricks resulted in substantial increases in bed roughness. The third change was to turn the bricks on edge so that the largest sides faced the current. It resulted in little change in roughness. We then scraped gravel out of the center of the stream, creating a central channel that meandered through the bricks. Because the smooth fiberglass bottom of the channel was exposed, there was a large decrease in roughness. In the next set of experiments, bricks were reduced to one every 2 m, and sticks and whole oak leaves were placed against each brick to simulate natural debris dams. The debris dams spanned the channel and caused significant pooling and a large increase in roughness. In the final set of experiments, bricks and debris dams were reduced to one every 6 m.

Table 3. Substrate arrangements used in the simulated storm experiments in artificial streams.

Substrate	Roughness coefficient	No. of replicate experiments
Uniform gravel	0.029	12
Uniform gravel with bricks every 2 m	0.047	3
Uniform gravel with bricks every 0.5 m	0.061	3
Uniform gravel with bricks on edge every 0.5 m	0.064	5
Bricks on edge every 0.5 m with gravel "channelized"	0.027	4
"Channelized" gravel with bricks and leaf packs every 2 m	0.146	3
"Channelized" gravel with bricks and leaf packs every 6 m	0.136	3

We ran a total of 33 experiments and used correlation to analyze results from each experiment for relationships among the following variables.

1. Seston concentration and discharge.
2. Seston concentration and discharge during the rising hydrograph.
3. Seston concentration and the rate of

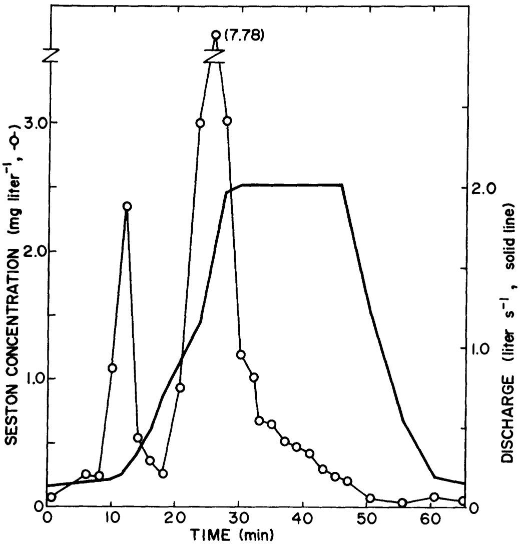

Fig. 2. Discharge and seston concentration during one of the simulated storms in the artificial stream.

change of discharge (ΔQ) during the rising hydrograph.

4. Seston concentration and time following the beginning of peak discharge.
5. Seston transport and the rate of change of discharge during the rising hydrograph.

Results—Figure 2 illustrates typical results of our simulated storms. Seston concentration increased greatly during the rising hydrograph, usually exhibiting one or more distinct peaks. Once peak discharge was reached, seston concentration immediately declined. Mean seston concentration during the simulated storms was inversely correlated with roughness ($r^2 = 0.63$, $N = 7$). That is, increased bed roughness and accompanying decreased water velocity resulted in less material being entrained during storms. However, within individual storms we found no general relationship between seston concentration and discharge. Seston concentration and discharge were significantly ($\alpha = 0.05$) correlated in only 6 of 33 storms, though in 14 of the 33 storms, there were significant ($\alpha = 0.05$) positive correlations between seston concentration and discharge during the rising hydrograph. This correlation was significant in 7 of the 16 storms with the lowest (0.027–0.029) roughness coefficients and 7 of the 17 storms with higher roughness.

We found a much more consistent relationship between seston concentration and the rate of change of discharge during the rising hydrograph. This relationship was significant ($\alpha = 0.05$) in only 18 of the 33 storms, but as roughness increased, the relationship became better defined. The correlation coefficient was significant in 5 of 19 storms with roughness coefficients <0.05 but significant in 13 of 14 storms with roughness coefficients >0.05. Slopes of regression lines relating seston concentration to the rate of change of discharge were also related to roughness. As roughness increased there was a significant decrease in slope ($r^2 = 0.69$, $N = 7$), indicating that with higher roughness, a unit of increase in discharge resulted in a lower seston concentration than did a similar increase in discharge under lower roughness conditions.

In 28 of the 33 storms there was a statistically significant correlation between the logarithm of the seston concentration during the falling hydrograph and time since the initial peak discharge. The only storms in which this relationship was not significant were five of the initial experiments on uniform gravel substrate. The rate of the exponential decrease in FPOM concentration varied from 0.071 to 0.133 min^{-1}, with a mean of 0.093 min^{-1}. There was no apparent relationship between this rate and roughness.

Effects of simulated storms on particulate transport—natural stream studies

Because we were concerned that our artificial stream studies might not be strictly applicable to natural streams, we used a technique for simulating storm flows in a natural stream channel. It involved diverting flow from a main channel into a smaller channel (Casey and Farr 1982). We then evaluated the effects of the simulated storm in the smaller channel on seston transport.

Methods—This series of experiments was conducted in Guys Run, a second-order stream in Rockbridge County, Virginia (Hornick et al. 1981). At the study site, the stream is divided by an island into a large and a small channel. The small channel is

50 m long, has an average channel width of 2.56 m, and some flow is present in this channel even during low flow periods. It has a fauna typical of small streams in the drainage.

Storms were simulated by damming the main channel with sandbags downstream of the mouth of the smaller channel to divert water into the smaller channel. Storms varied from 88 to 225 min. Discharge was monitored with a 46-cm (1.5 ft) H-flume and water level recorder at the downstream end of the smaller channel. Samples (1–4 liters) were taken at the flume and included both bedload and suspended load. The number of samples taken during a storm ranged from 28 to 85. Sampling frequency ranged from 0.1 to 1 min^{-1} with samples taken most frequently on the rising limb of the hydrograph. During warm periods, samples were filtered in the field, but at other times samples were chilled and filtered in the laboratory within 24 h. Samples were filtered with suction on preashed and tared Gelman AE glass-fiber filters. Filters were then oven-dried (55°C, ≥24 h), desiccated (≥24 h), weighed, ashed (550°C, 20 min), rewetted, dried, desiccated, and reweighed. Seston concentration was calculated as the ash-free dry weight divided by the volume of the sample.

During most storms, less frequent large-volume water samples were collected for particle size analysis (Gurtz et al. 1980). In the lab, these samples were filtered with suction through a series of stainless steel screens (25, 43, 105, and 280 μm). Material collected on each screen was resuspended and washed onto individual glass-fiber filters, which were treated as above. In addition, an aliquot of water that passed through the 25-μm screen was filtered through a glass-fiber filter. Median particle size was calculated by regressing the logarithm of cumulative percent of sample weight vs. the upper limit of the particle size class and then determining the 50% intersection of the regression line.

Samples of large particulate matter (LPM) transported during the storms were collected using a 1-mm mesh net positioned to strain all water passing over the flume. Material collected in the net over a timed interval was air-dried, weighed, subsampled, and ashed.

To evaluate the distance moved by leaves during storms, we placed painted and individually numbered dry white oak leaves in the stream channel before seven of the simulated storms. During the first two storms, the leaves were placed in grids with 20 cm between leaves. During the other five storms, leaves were placed in loose packs simulating the natural arrangement of leaves in the stream. Five packs were placed in the wetted stream channel at 10-m intervals, and five packs were placed in the dry channel adjacent to the stream at the same 10-m intervals. In the last storm, we used presoaked rather than dry leaves. After each storm, distances moved by individual leaves were recorded.

We collected data from 13 simulated storms between October 1980 and June 1982. Our primary means of data analysis from the storms was to compute correlations between particle concentrations and other variables. For all statistical tests we used an a priori significance level of $\alpha = 0.05$. However, because of the large number of correlations calculated (multiple testing), we discounted isolated high correlations and only considered trends that were significant ($\alpha = 0.05$) for more than half the simulated storms.

Results—We found significant ($\alpha = 0.05$) correlations between seston concentration and discharge in only 7 of the 13 simulated storms. In part, this lack of correlation resulted from a hysteritic effect—seston concentrations were higher on the rising limb of the hydrograph than at corresponding flows on the descending limb (Fig. 3). When the two limbs of the hydrograph were analyzed separately, seston concentration and discharge were significantly ($\alpha = 0.05$) correlated during the descending limb in 10 of 13 storms but were significantly correlated during the rising hydrograph in only 8 of 13 storms.

For rising hydrographs, we found high correlations (significant in 12 of 13 storms) between seston concentration and the rate of increase in discharge (ΔQ) (Fig. 4). Slopes of regression lines relating rising-hydrograph seston concentrations to ΔQ were

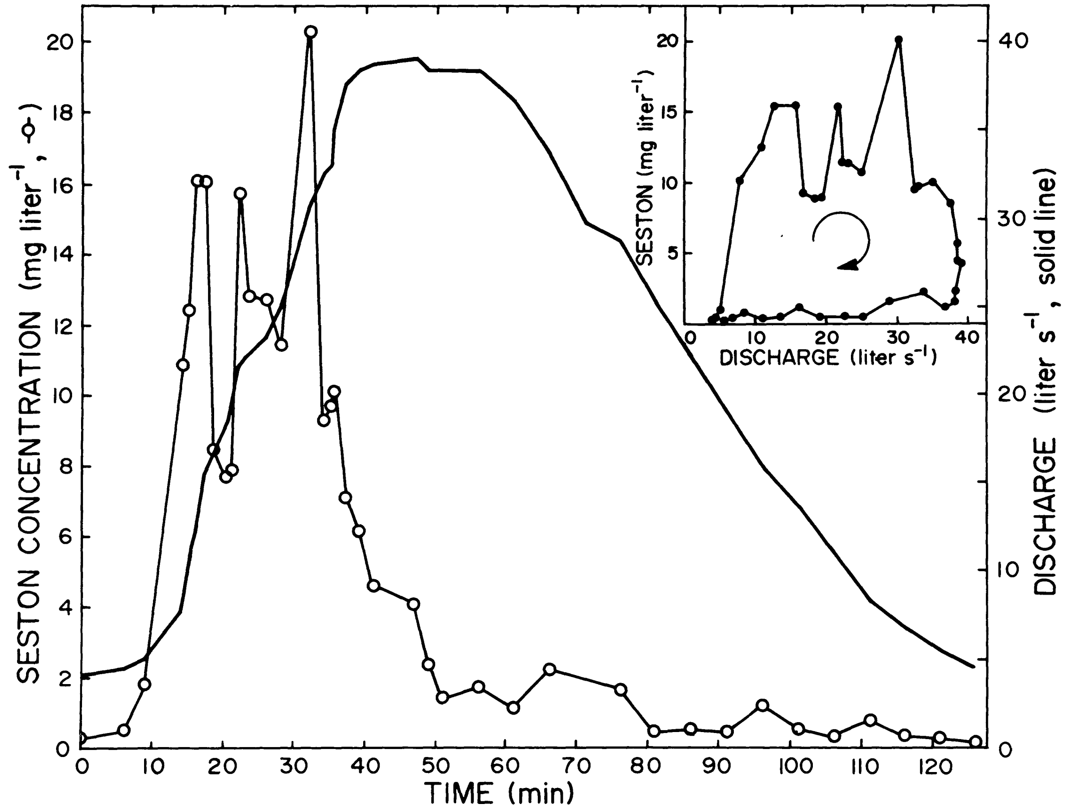

Fig. 3. Seston concentration and discharge during the April 1981 simulated storm in the natural stream channel. The inset shows hysteresis.

fairly consistent, and there were no evident seasonal trends.

Correlations between seston concentration and discharge during the descending hydrographs were significant for most storms, however, during each storm simulation, discharge was held at peak for 15–30 min, and during this period of constant discharge seston concentration dropped rapidly (Figs. 3, 5–7). The logarithm of seston concentration was significantly correlated ($\alpha = 0.05$) with time since the beginning of the descending hydrograph in 9 of 13 storms. However, correlations between ln (seston concentration) and time since the beginning of peak discharge were significant for all storms.

The inorganic, or ash, fraction of the particles transported during the storms behaved similarly to the organic fraction, as ash and seston concentrations were highly correlated ($P \leq 0.0001$ for all storms). Because ash and seston concentrations were so closely correlated, percent ash showed little variation, ranging from 63 to 78% for the various storms and varying little within individual storms (Fig. 5). Seston concentration and percent ash were significantly ($\alpha = 0.05$) correlated in 9 of 13 storms, but in eight of those cases the correlation was negative, that is, the percent ash was lower at higher particle concentrations. Few correlations between percent ash and discharge or ΔQ were significant. The one consistent relationship was a general, though small, increase in percent ash over the duration of 9 of 13 storms (Fig. 5).

Median particle size of seston increased greatly during the early part of each storm and then usually declined gradually (Fig. 6), though in some cases particle size remained high throughout the course of the storm. In

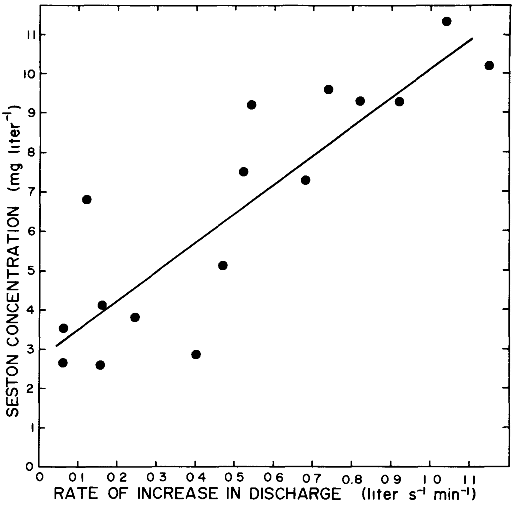

Fig. 4. Seston concentration as a function of the rate of increase in discharge during the rising hydrograph of the June 1982 simulated storm in the natural stream channel ($r^2 = 0.55$, $N = 16$).

all cases, the median particle size of the last sample was higher than that for samples taken before the storm. Median particle sizes calculated for ash and seston separately behaved similarly, though in all cases the median particle size of seston was larger (Fig. 6).

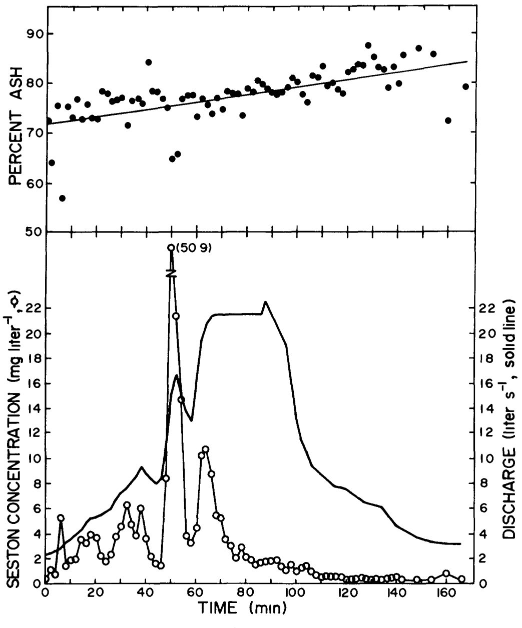

Fig. 5. Percent ash of total particulates, seston concentration, and discharge during the April 1982 simulated storm in the natural stream channel. For percent ash vs. time, $r^2 = 0.43$, $N = 76$.

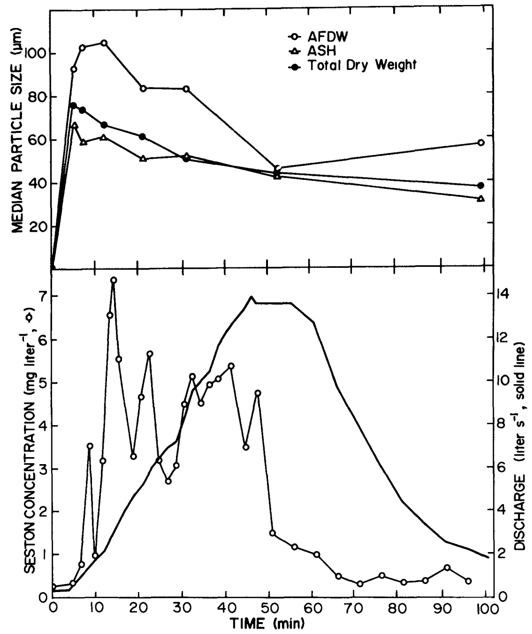

Fig. 6. Median seston particle size, seston concentration, and discharge during the January 1981 simulated storm in the natural stream channel.

Concentrations of LPM in transport increased more than an order of magnitude during all storms. In general, the behavior was similar to that of total particulates: concentration peaked during the rising hydrograph, in some cases corresponding to periods of rapidly increasing discharge, decreased rapidly once peak flow was reached, and further decreased during the falling hydrograph (Fig. 7). However, statistical analyses showed few significant relationships. LPM concentrations were significantly correlated ($\alpha = 0.05$) with discharge in only 3 of 10 storms and significantly correlated with ΔQ in another 3 of 10 storms. The lack of statistically significant relationships might be attributed to several factors. First, sample sizes were small—6–20 samples for the various storms including only 3–9 samples during the rising hydrograph. Second, the time periods over which LPM samples were collected (5–12 min during rising hydrograph, longer after

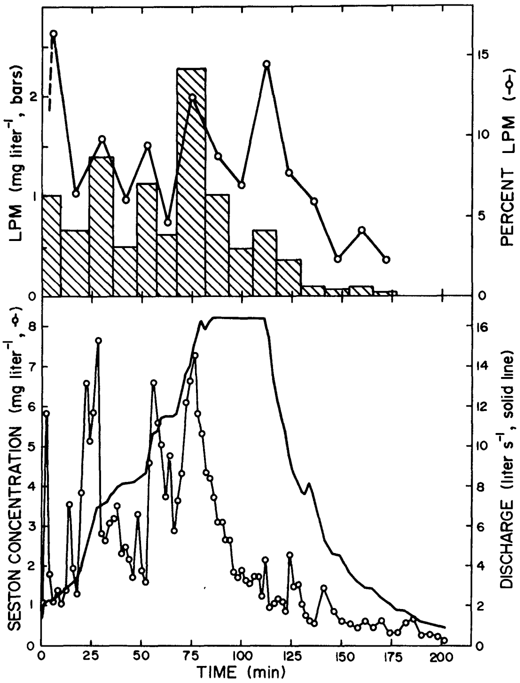

Fig. 7. Seston and LPM concentrations, discharge, and percent of total particulate matter that was LPM during the May 1982 simulated storm in the natural stream channel.

peak discharge) may have been too long, masking changes that occurred more rapidly. Third, we often observed that transport of LPM was highly irregular, perhaps related most closely to when individual accumulations of debris were entrained (Fisher and Likens 1973).

The concentration of organic matter in the LPM was consistently high and did not change during the storms. The percent ash ranged from 7.2% (±0.3 SE) in July 1981 to 26.9% (±4.5 SE) in February 1982.

LPM generally comprised a small fraction of total particulate material in transport during baseflows, but this percentage always increased during storms (Fig. 7). The average percent LPM during simulated storms ranged from 3.9 to 74.1%, and peak values on two occasions exceeded 100%, suggesting that grab samples used to estimate total particulate matter were less efficient than nets for catching LPM. It was especially true when large amounts of dry LPM were floating on top of the water.

Our experiments with marked leaves placed in the stream showed that the average distance moved by leaves ranged from 0.54 to 7.01 m (Table 4). The maximum distance traveled by an individual leaf per storm ranged from 7 to 26 m. There was a significant correlation between mean distance moved and peak discharge of the storm ($r^2 = 0.92$, $N = 7$). When discharge was low in the main stream, we could only create small storms, and leaves did not move far. When mainstream flow was high, larger simulated storms were possible and leaves moved greater distances. During three of five storms, the distance traveled by leaves placed in the stream was significantly greater (t-test, $\alpha = 0.05$) than the distance traveled by leaves placed on the stream margin (Table 4).

To evaluate the effect of antecedent conditions (time since last storm) on particle transport, we ran more than one simulated storm on three occasions. On 27 August 1981 and 2 October 1981, we followed particle concentrations during two consecutive

Table 4. Mean distances (±95% C.L.) traveled by leaves placed in the stream channel during simulated storms in the natural stream channel.

	Experimental setup	Peak discharge (liters s^{-1})	Mean distance traveled (m)		
			All leaves	Instream leaves	Margin leaves
22 Jul 81	9 grids, 280 total leaves	9.6	0.54±0.11	—	—
2 Oct 81	4 grids, 100 total leaves	8.8	0.62±0.29	—	—
6 Nov 81	5 packs of 10 leaves in stream, 5 packs of 10 leaves on stream margin	18.7	3.91±0.77	5.64±1.05*	2.14±0.86
11 Dec 81	Same as 6 Nov	15.0	1.91±0.48	2.73±0.63*	1.22±0.66
25 Feb 82	Same as 6 Nov	33.6	7.01±1.41	7.55±1.74*	6.48±2.26
11 Apr 82	Same as 6 Nov	21.6	2.61±0.57	3.80±0.93*	1.52±0.57
28 Jun 82	Same as 6 Nov, but presoaked leaves	17.7	3.26±0.75	3.81±1.03*	2.73±1.13

* Significant difference (t-test, $\alpha = 0.05$) between distances traveled by leaves placed in the stream and leaves placed on the stream margin.

storms; and on 18 June 1981, we ran a series of three consecutive storms. In each case the results were similar: both seston and ash concentrations were significantly (t-test, $\alpha = 0.05$) lower during the rising hydrographs of second and third storms (Fig. 8). Also, the slopes of lines relating seston concentration to ΔQ were lower during the second and third storms (Fig. 9).

Discussion

Streambed retention—Our experiments support the general conclusion that seston particles travel only short distances before being retained. A major factor contributing to short travel distances is the presence of streambed obstacles. In our artificial stream studies, average distance traveled by organic particles ranged from 2.7 to 25.8 m over rough substrates, but the distance traveled was much longer when the substrate was smooth (Tables 1, 2). During simulated storms in the natural stream channel, the greatest mean distance traveled by leaves was 7.5 m (Table 4). Speaker et al. (1984) also found short travel distances for leaves released into Oregon streams. Young et al. (1978) found much longer travel distances, but their study was conducted in a larger, third-order stream. These observations agree with a number of recent studies that suggest that streambed obstructions, particularly woody debris, not only reduce entrainment rates but also decrease distances traveled by seston by recapturing material from transport (e.g. Naiman and Sedell 1979*b*; Bilby and Likens 1980; Speaker et al. 1984). The FPOM used in our laboratory studies was prepared by grinding leaves and differed from natural stream FPOM in several ways. In particular, it was of much lower density. Therefore, the FPOM travel distances we observed were probably longer than would have been true for more natural material.

Our data suggest that seston retention is directly related to particle size, i.e. small seston particles travel farther (Table 2). This conclusion agrees with observations that coarse organic material is retained and degraded near where it enters a stream (e.g. Hall 1972; McDowell and Fisher 1976; Webster and Patten 1979; Mulholland 1981; Triska et al. 1982). Consequently most seston transport in small streams consists of very small particles (e.g. Sedell et al. 1978; Naiman and Sedall 1979a; Gurtz et al. 1980; Wallace et al. 1982*a*).

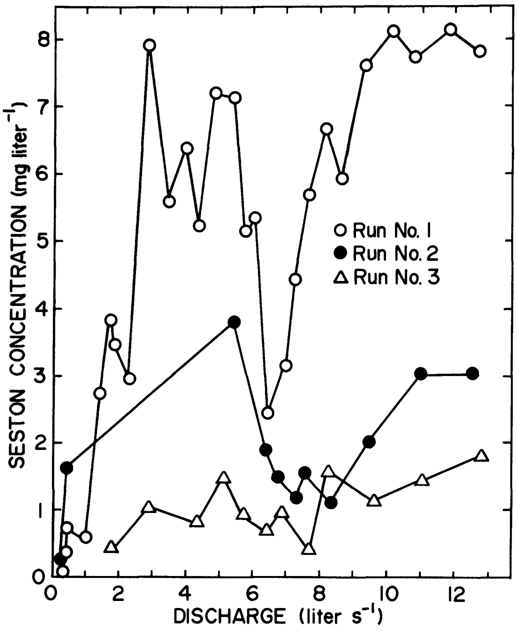

Fig. 8. Seston concentration and discharge during the rising hydrographs of three successive simulated storms in June 1981.

Seston concentration and discharge—We observed a hysteretic relationship between discharge and seston concentration in both artificial and natural stream channel experiments (e.g. Fig. 3). A similar pattern has been observed in many previously cited studies of real storms in small streams. Most material in the channels of small streams is larger and heavier than the streams are able to transport. During baseflow, materials small enough to be suspended, such as very fine grains of primarily inorganic material, or lighter, larger particles of organic material, are trapped by obstructions in the streambed. As streamflow increases during storms, some of this trapped material may become dislodged and entrained. Studies done at Hubbard Brook, New Hampshire, suggest that as discharge increases and the stream gets wider, protected pools, backwaters, and channel areas that are only wet during storms become exposed to currents (Fisher and Likens 1973; Bilby and Likens

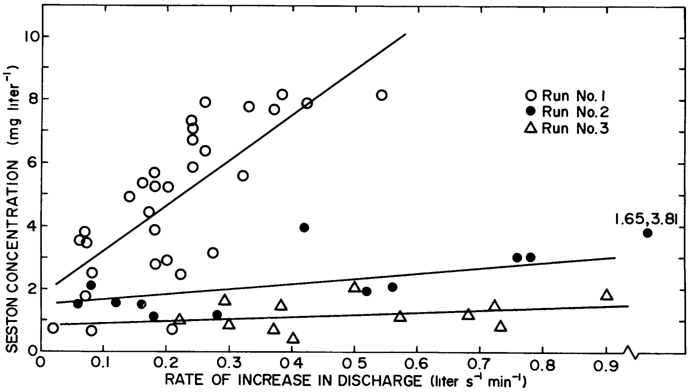

Fig. 9. Seston concentration vs. the rate of change in discharge during the rising hydrographs of three successive simulated storms in June 1981. Run No. 1, $r^2 = 0.54$, $N = 31$; run No. 2, $r^2 = 0.52$, $N = 12$; run No. 3, $r^2 = 0.09$, $N = 12$, correlation not significant.

1979; Meyer and Likens 1979). As these areas are inundated, transportable material generated or deposited since the last storm is entrained. A graph of seston concentration during a storm typically shows several concentration peaks during the rising hydrograph (e.g. Fig. 7). These peaks are correlated with periods of more rapid increase in flow. Thus the more rapidly discharge increases and the stream expands within its channel, the more rapidly transportable material is encountered. This mechanism for seston entrainment explains the observed correlations between seston concentration and the rate of increase in discharge (Fig. 4). It also implies that many factors affect the relationship between seston concentration and ΔQ, including the time since the last storm (Fig. 9), peak discharge of the previous storm, and the rate of particle generation since the last storm.

Particle availability—In small streams of the southern Appalachian region, baseflow seston concentrations are typically highest in summer, decrease in autumn to a winter minimum, and then rise in spring toward a summer peak (Gurtz et al. 1980; Wallace et al. 1982*a*; Webster and Golladay 1984). Similar patterns have been observed in other small streams draining deciduous forests (e.g. Wetzel and Manny 1977). This seasonal pattern of seston concentration is largely explained by effects of temperature on biological generation of particulate organic material (POM). However, other factors also affect seasonal patterns. In autumn, accumulations of new leaves act as filters, increasing seston retention, but this factor becomes less important as leaves break down and are washed out during winter storms. Another reason why baseflow seston concentrations are lowest in winter is because flow is highest at this time. Even if biological generation of POM were constant through the year, high flow would decrease the concentration due to dilution. Finally, winter storms may deplete benthic POM, decreasing material available for entrainment. Seston concentrations increase during storms at all times of year. However, increases are greatest during the first, early winter storms. For example, Wallace et al. (1982*a*) found an unusually large increase in seston concentration during a November storm. This example and considerable evidence from field studies discussed below support our experimental evidence (e.g. Fig. 8) that seston transport during storms depends largely on the availability of material.

Webster (1983) observed distinct seasonal relationships between CPOM concentration and discharge. The slope of the regression of CPOM concentration vs. discharge was greatest in late fall when recently fallen whole leaves were present in the stream and even small increases in discharge caused large increases in CPOM concentration. In winter after leaves had aggregated into stable packs, increases in discharge caused only small increases in CPOM concentration.

Once the leaves were well fragmented and decomposed in early summer, more particles were picked up by storms, and by late summer, effects of storms became even more pronounced. O'Hop and Wallace (1983) found a somewhat similar pattern for the transport of CPOM. A December storm increased CPOM transport to more than 20 g h^{-1}, but during a storm in March, peak CPOM transport was only about 3 g h^{-1}. The December storm was more intense, but peak flows were very similar. Dawson (1980) noted that transport of CPOM depended on the timing of the first fall–winter storm. If it occurred soon after macrophyte death and leaf fall, considerable amounts of CPOM were transported. However, if the first major storm occurred later, after much of the large material had fragmented, there was a much smaller fraction of CPOM in the seston and more smaller material.

Results of studies that included all organic particles or total particles (organic and inorganic) are consistent with these studies of CPOM. Wetzel and Manny (1977) observed maximum storm concentrations of seston in early winter and during high spring flows. Minimum seston concentrations occurred during the period of maximum leaf fall. In his study of the River Thames, Berrie (1972) found that fall storms washed out material that had accumulated during summer and that higher flows were necessary later in winter to produce similar quantities of seston. Nelson and Scott (1962) found that points on a graph of seston concentration vs. discharge in the Oconee River separated into two rather discrete groups, representing summer and winter samples. They suggested that differences between summer and winter could be attributed to differences in the amount of organic material available in the streambed. Fisher (1977) reported a similar winter–summer separation of the relationship between seston and discharge in the Fort River and related it to the accumulation of particulate organic material on the streambed. Also, in their calculations of particulate phosphorus transport, Meyer and Likens (1979) used different regression curves to relate winter and summer particle concentrations to discharge.

In addition to the seasonal patterns in availability of benthic POM, there may be a decrease in seston transport during a series of storms because of depletion of benthic POM. Our experimental attempt to demonstrate this pattern (Fig. 8) differed from what happens in natural streams in several ways. In our experiments we depleted material from only a short reach rather than from the entire stream network. On the other hand, during the falling hydrograph of a natural storm there would be deposition of material that had been entrained upstream. However, Bilby and Likens (1979) did observe a similar pattern of decreasing seston concentration in their study at Hubbard Brook.

In summary, our experiments and a variety of field studies suggest the patterns of seston transport in small streams cannot be predicted using models designed to predict sediment transport in rivers. Rather, patterns of seasonal and storm transport appear to be most affected by the amount of POM on the streambed and its retention by the physical structure of the streambed.

References

Allen, J. R. L. 1977. Changeable rivers: Some aspects of their mechanics and sedimentation, p. 15–45. *In* K. J. Gregory [ed.], River channel changes. Wiley.

Bagnold, R. A. 1966. An approach to the sediment transport problem of general physics. U.S. Geol. Surv. Prof. Pap. 422-I.

Berrie, A. D. 1972. The occurrence and composition of seston in the River Thames and the role of detritus as an energy source for secondary production in the river. Mem. Ist. Ital. Idrobiol. **29**(suppl.): 475–483.

Bilby, R. E., and G. E. Likens. 1979. Effect of hydrologic fluctuations on the transport of fine particulate organic carbon in a small stream. Limnol. Oceanogr. **24**: 69–75.

———, and ———. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology **61**: 1107–1113.

Casey, H., and I. S. Farr. 1982. The influence of within-stream disturbance on dissolved nutrient levels during spates. Hydrobiologia **92**: 447–462.

Dahm, C. N. 1981. Pathways and mechanisms for removal of dissolved organic carbon from leaf leachate in streams. Can. J. Fish. Aquat. Sci. **38**: 68–76.

Dawson, F. H. 1980. The origin, composition and downstream transport of plant material in a small chalk stream. Freshwater Biol. **10**: 419–435.

Dingman, S. L. 1984. Fluvial hydrology. Freeman.

DUNNE, T., AND L. B. LEOPOLD. 1978. Water in environmental planning. Freeman.

EINSTEIN, H. A. 1950. The bed-load function for sediment transportation in open channel flows. USDA Soil Conserv. Serv. Tech. Bull. 1026.

ELLIOTT, J. M. 1971. The distances travelled by drifting invertebrates in a lake district stream. Oecologia **6**: 350–379.

FISHER, J. S., J. C. PICKRAL, AND W. E. ODUM. 1979. Organic detritus particles: Initiation of motion criteria. Limnol. Oceanogr. **24**: 529–531.

FISHER, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Int. Rev. Gesamten Hydrobiol. **62**: 701–727.

———, AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. Ecol. Monogr. **43**: 421–439.

GOLLADAY, S. W., J. R. WEBSTER, AND E. F. BENFIELD. 1987. Changes in stream morphology and storm transport of seston following watershed disturbance. J. N. Am. Benthol. Soc. **6**: 1–11.

GURTZ, M. E., J. R. WEBSTER, AND J. B. WALLACE. 1980. Seston dynamics in southern Appalachian streams: Effects of clear-cutting. Can. J. Fish. Aquat. Sci. **37**: 624–631.

HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology **53**: 585–604.

HORNICK, L. E., J. R. WEBSTER, AND E. F. BENFIELD. 1981. Periphyton production in an Appalachian mountain trout stream. Am. Midl. Nat. **106**: 22–36.

HUTCHINSON, G. E. 1967. A treatise on limnology, v. 2. Wiley.

LAURITSEN, D. D. 1986. Filter feeding in *Corbicula fluminea* and its effect on seston removal. J. N. Am. Benthol. Soc. **5**: 165–172.

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

MCDOWELL, W. H., AND S. G. FISHER. 1976. Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. Ecology **57**: 561–569.

MALCOLM, R. L., AND W. H. DURUM. 1976. Organic carbon and nitrogen concentrations and annual organic carbon load of six selected rivers of the United States. U.S. Geol. Surv. Water-Supply Pap. 1817-F.

MEYBECK, M. 1981. River transport of organic carbon to the ocean, p. 219–269. *In* Carbon dioxide effects research and assessment program. Flux of organic carbon by rivers to the ocean. U. S. Dep. Energy CONF-8009140.

MEYER, J. L, AND G. E. LIKENS. 1979. Transport and transformation of phosphorus in a forest stream ecosystem. Ecology **60**: 1255–1269.

MOELLER, J. R., AND OTHERS. 1979. Transport of dissolved organic carbon in streams of differing physiographic characteristics. Org. Geochem. **1**: 139–150.

MORISAWA, M. 1968. Streams, their dynamics and morphology. McGraw-Hill.

MULHOLLAND, P. J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecol. Monogr. **51**: 307–322.

NAIMAN, R. J. 1982. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Can. J. Fish. Aquat. Sci. **39**: 1699–1718.

———, AND J. R. SEDELL. 1979*a*. Characterization of particulate organic matter transported by some Cascade mountain streams. J. Fish. Res. Bd. Can. **36**: 17–31.

———, AND ——— 1979*b*. Benthic organic matter as a function of stream order in Oregon. Arch. Hydrobiol. **87**: 404–422.

NELSON, D. J., AND D. C. SCOTT. 1962. Role of detritus in the productivity of a rock outcrop community in a Piedmont stream. Limnol. Oceanogr. **7**: 396–413.

O'HOP, J., AND J. B. WALLACE. 1983. Invertebrate drift, discharge, and sediment relations in a southern Appalachian headwater stream. Hydrobiologia **98**: 71–84.

SAS INSTITUTE, INC. 1982. SAS user's guide. SAS Inst. Inc.

SCHLESINGER, W. H., AND J. M. MELACK. 1981. Transport of organic carbon in the world's rivers. Tellus **33**: 172–187.

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. Int. Ver. Theor. Angew. Limnol. Verh. **20**: 1366–1375.

SPEAKER, R., K. MOORE, AND S. GREGORY. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Int. Ver. Theor. Angew. Limnol. Verh. **22**: 1835–1841.

TRISKA, F. J., J. R. SEDELL, AND S. V. GREGORY. 1982. Coniferous forest streams, p. 292–332. *In* R. L. Edmonds [ed.], Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**: 130–137.

WALLACE, J. B., AND R. W. MERRITT. 1980. Filter-feeding ecology of aquatic insects. Annu. Rev. Entomol. **25**: 103–132.

———, D. H. ROSS, AND J. L. MEYER. 1982*a*. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. Ecology **63**: 824–838.

———, J. R. WEBSTER, AND T. F. CUFFNEY. 1982*b*. Stream detritus dynamics: Regulation by invertebrate consumers. Oecologia **53**: 197–200.

WEBSTER, J. R. 1983. The role of benthic macroinvertebrates in detritus dynamics of streams: A computer simulation. Ecol. Monogr. **53**: 383–404.

———, E. F. BENFIELD, AND J. CAIRNS, JR. 1979. Model predictions of effects of impoundment on particulate organic matter transport in a river system, p. 339–358. *In* J. V. Ward and J. A. Stanford [eds.], The ecology of regulated streams. Plenum.

———, AND OTHERS. In press. Effects of watershed disturbance on stream seston characteristics. *In* W. T. Swank and D. A. Crossley, Jr. [eds.], Forest hydrology and ecology at Coweeta. Springer-Verlag.

———, AND S. W. GOLLADAY. 1984. Seston transport in streams at Coweeta Hydrologic Laboratory, North Carolina, U.S.A. Int. Ver. Theor. Angew. Limnol. Verh. **22**: 1911–1919.

———, AND OTHERS. 1983. Stability of stream ecosystems, p. 355–395. *In* J. R. Barnes and G. W. Minshall [eds.], Stream ecology. Plenum.

———, AND B. C. PATTEN. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecol. Monogr. **49**: 51–72.

WETZEL, R. G., AND B. A. MANNY. 1977. Seasonal changes in particulate and dissolved organic carbon and nitrogen in a hardwater stream. Arch. Hydrobiol. **80**: 20–39.

WOTTON, R. S. 1984. The importance of identifying the origins of microfine particles in aquatic systems. Oikos **43**: 217–221.

YALIN, M. S. 1977. Mechanics of sediment transport. Pergamon.

YANG, C. T., AND J. B. STALL. 1976. Applicability of unit stream power equation. ASCE J. Hydraul. Div. **102**(HY-5): 559–568.

YOUNG, S. A., W. P. KOVALAK, AND K. A. DEL SIGNORE. 1978. Distances travelled by autumn-shed leaves introduced into a woodland stream. Am. Midl. Nat. **100**: 217–222.

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