The Use of Corn Pollen and Glass Beads to Estimate Fine Particulate Organic Matter Retention

by

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(ABSTRACT)

Corn pollen and glass beads were used as surrogates of natural fine particulate organic matter (FPOM). These particles were released into ten streams in three different physiographic regions, Appalachian Mountains, Rocky Mountains, and Central Plains, within the United States. Mean travel distance for corn pollen was 121 m and that for glass beads 40 m. Rates of deposition through the water column for both particles were 0.484 mm/sec and 0.643 mm/sec, respectively. This empirically derived deposition velocity was only a fraction of the still water fall velocity. Hydraulic parameters indicate that flow conditions at the streambed prevent establishment of a laminar sublayer. As a result, corn pollen and glass beads should be entrained and moved as bed- or suspended load. Gradient was the single best stream characteristic to explain variation in retention rates for both corn pollen and glass beads. Based on deposition velocities, estimates of benthic FPOM turnover times ranged from 20 hours to 8.3

days, rate of FPOM downstream movement was 1-24 m/d, and carbon turnover length was 1-24 km.

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"Never measure the height of a mountain, until you reach the top. Then you will see how low it was."

Dag Hammarskjöld

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Introduction

A unique feature of stream ecosystems is the unidirectional downstream transport of energy (i.e. organic material either in a dissolved or particulate form). Ultimately, estuaries and oceans "claim" any unused material. It has been the interest and task of stream ecologists, beginning with the energy budget approach of Odum (1957) and Teal (1957), to investigate and quantify the fate of organic matter. Since that time, inputs, outputs, storage, and biological processing of organic matter in stream systems have been quantified and described by numerous investigators (e.g. Bormann et al. 1969, Fisher and Likens 1973, Gurtz et al. 1980, Cushing and Wolf 1982, Minshall et al. 1983, and Cummins et al. 1983, 1988, and Webster et al. 1990).

In addition to budgetary analysis, downstream movement of organic carbon has been described by the spiralling concept (Newbold et al. 1982, Elwood et al. 1983). Spiralling directly measures connectivity between upstream and downstream reaches as turnover length, i.e. the distance traveled by carbon atoms in a reduced (i.e., organic) form. More efficient retention and biological consumption of transported organic carbon produces short turnover lengths. Material not retained is transported downstream and thereby made unavailable to stream organisms in upstream reaches.

Coarse particulate organic matter (CPOM) is retained efficiently in upper reaches of streams (e.g., Speaker et al. 1984, Webster et al. 1994), but it is fragmented into smaller, more readily transportable fine particulate organic matter (FPOM) via biological and physical processes. Downstream assemblages of organisms are adapted to "capitalize" on this inefficient upstream processing (Vannote et al. 1980). FPOM in transport represents a mobile energy resource available to organisms adapted to filtering the water column (Wallace and Merritt 1980), but this FPOM is unavailable to most stream organisms unless it is retained on the streambed. Because most organic particles in transport are between 0.45 μm and 1 mm in size (Sedell et al. 1978, Wallace et al. 1982, Webster et al. 1987, Minshall et al. 1983, 1992), it is important to understand the movement of these particles between the water column and streambed.

Particles sink through still water at a terminal velocity, or fall velocity (V_{fall}), defined by Stokes Law:

$$V_{fall}=2a^2g(\rho-\rho_o)/9\mu \qquad (1)$$

where *a* is particle diameter, g is the acceleration of gravity, ρ_o is density of water, ρ is particle density, and μ is dynamic viscosity of water (Vogel 1981). Deposition models for particles suspended in turbulent water have shown, for both lakes (Smith 1982) and flumes (Reynolds 1979, 1990; Graham 1990), that particle loss from suspension is a function only of still water V_{fall} and depth:

$$\frac{dP}{dt} = \frac{-V_{fall}}{z} \qquad (2)$$

where P is the concentration of suspended particles, t is time, and z is the depth of the mixed layer (Reynolds 1979). Equation (2) assumes a laminar sublayer whose depth exceeds particle size, and particles entering this layer are not resuspended. The solution to the differential equation above is:

$$P_t=P_o e^{-(Vfall)t} \qquad (3)$$

where P_o is the initial concentration of particles in suspension and P_t is the concentration of particles still in suspension some time t later (Reynolds 1990).

Reynolds (1990) empirically demonstrated particle (*Lycopodium* spores) loss from a flume to follow a negative exponential model:

$$P_d=P_o e^{-kd} \tag{4}$$

based on distance. Particles descend through the water at V_{fall} but at the same time are displaced longitudinally downstream due to water velocity. P_o is the initial number of particles released, P_d is the number of particles in transport some distance d downstream, and k (slope of the line) is the instantaneous rate of particle removal/retention (i.e., uptake rate). The negative reciprocal of this uptake rate, 1/k, is the uptake length (S_w) or average particle travel distance. It is the same variable used in calculating travel distances of CPOM (e.g. Speaker et al. 1984), FPOM (Webster et al. 1987), drifting insects (Elliot 1971), and nutrient uptake length (e.g. Newbold 1981, Stream Solute Workshop 1990).

Empirically, the effective sinking rate (Fisher 1979) or deposition velocity (V_{dep}) of particles can be calculated from the uptake length as:

$$V_{dep}=D(V_{wat})/(S_w) \tag{5}$$

where D is water depth and V_{wat} is stream water velocity. V_{dep} is the rate of particle descent through the water column as determined in the field but should be equivalent to V_{fall} as long as the assumptions from equation (2) are not violated.

In practice, few studies have examined fall and deposition velocities of FPOM in stream ecosystems. The study of FPOM retention in streams has lagged behind CPOM studies due to the lack of a suitable tracer. Exotic *Ginkgo* or painted native leaves, flagging tape, and wooden dowels are some of the natural or artificial analogs that have been used to empirically study CPOM retention (e.g. Speaker et al. 1984., Ehrman and Lamberti 1992). In natural systems, FPOM retention has been studied experimentally with radio-labelled particles (e.g. Newbold et al. 1991) and also with corn pollen (Miller and Georgian 1992).

In this study, corn pollen and glass beads were used as surrogates for FPOM to determine (1) longitudinal transport distances of FPOM, (2) vertical rates of FPOM deposition rates of FPOM through the water column, and (3) physical and hydraulic factors that affect (1) and (2).

Methods

Study Sites

I studied ten small streams from three different physiographic regions across the United States. These included four streams in the Appalachian Mountains of North Carolina, four streams in the Rocky Mountains of Montana, and two streams in the central lowlands of Indiana.

The four streams in western North Carolina were located at Coweeta Hydrologic Laboratory, a U.S. Forest Service and Biosphere Reserve unit in the Nantahala Mountains of the Blue Ridge Province. Two second-order streams drained similar sized watersheds, which have been paired for experimental manipulations. Hugh White Creek (HWC) drains Watershed 14 (WS 14), a reference watershed that has been free of disturbance since selective logging in the early 1920's and the chestnut blight of the 1930's. WS 14 covers 61 ha, faces northwest, and ranges in elevation from a maximum of 992 m to 707 m (Swank and Crossley 1988). The 100-m study reach ended just upstream from a 120° notch weir at the bottom of the watershed. A mixture of oak (*Quercus* spp.), hickory (*Carya* spp.), red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), and hemlock (*Tsuga canadensis*), among other mixed hardwoods, forms the riparian canopy along with a dense, evergreen understory of

Rhododendron.

Big Hurricane Branch (BHB) is a second-order stream draining WS 7, the experimental watershed counterpart to WS 14. WS 7 was commercially clearcut and cable logged in 1977. Previously, cattle grazed the basin from 1941-1952. Successional regrowth of the young riparian zone includes dense *Rhododendron* stands, black locust (*Robinia pseudoacacia*), tulip poplar, birch (*Betula* spp.), beech (*Fagus grandifolia*), and greenbrier (*Smilax* spp.). WS 7 encompasses 58 ha, faces south, and ranges in elevation from 1077 m down to 772 m at the 90° notch weir at the base of the watershed (Swank and Crossley 1988). As with WS 14, the study site was located just upstream from the weir.

Two first-order headwater streams drained smaller watersheds, which have also been paired for experimentation. Bee Tree Branch (BTB) drains WS 53, which encompasses 5.2 ha and extends to 829 m elevation, whereas Satellite Branch (SB) drains WS 55, which covers 7.5 ha and extends to 810 m elevation. Both watersheds support an oak-hickory overstory riparian canopy with *Rhododendron* forming the understory. H-flumes monitor streamflow on each watershed. Previously, the stream draining WS 53 was treated with methoxychlor insecticide (e.g. Wallace et al. 1991).

The four Montana streams are in or near Glacier National Park and are generally larger than the Coweeta streams. Yellowbay Creek lies at the northern boundary of the Flathead Indian Reservation and is a tributary to Flathead Lake. The study site was located ~500 m from the Flathead Lake Biological Station at Yellow Bay. Large moss-covered cobbles and small boulders dominate the substrate. Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) form the majority of the riparian woody vegetation. Howe Creek flows out of Howe Lake in Glacier National Park and is a tributary to Fish Creek. The 100-m study site (1073 m elevation) was upstream from the bridge on Glacier Route 7, which crosses the stream. Western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), and Douglas-fir dominate the upper riparian canopy whereas Rocky Mountain maple (*Acer glabrum*), alder (*Alnus* spp.), and herbaceous plants, such as devils walking stick, form the immediate streamside vegetation. Haystack Creek is an intermittent snowmelt stream which drains west off of Haystack Butte into MacDonald Creek. The study site (1097 m elevation) was just upstream of the culvert under Going to the Sun Highway and the confluence with MacDonald Creek. A large spate in the late 1960's has left this lower segment of Haystack underfit. Douglas-fir, black cottonwood (*Populus trichocarpa*), western red cedar, grand fir, Rocky Mountain maple, Engelman spruce (*Picea engelmanni*), birch, alder, and red-osier dogwood (*Cornus stolonifera*) comprise most of the riparian flora. Logan Creek, atop Logan Pass at 2024 m, is a bedrock stream covered with a thick, slippery aufwuchs. The stream is just above tree line, and the immediate riparian composition includes sub-alpine fir (*Abies lasiocarpa*), glacier lilies, heather, and willow (*Salix* spp.).

The two streams from just north of South Bend, Indiana, were located within ~2 km of one another and are tributaries of the St. Joseph River. Manion Creek flows through scattered farmland, residential areas, and woodlands before emptying into the St. Joseph River. The study site, about ~500 m upstream from the St. Joseph River (and immediately upstream from the bridge on Laurel Road just south of St. Patrick's park), is bordered by farmland, buffered by a thin strip of woodland on the north and a larger woodland on the south. Maple, basswood (*Tilia americana*), hickory, and various shrubs composed the riparian vegetation. St. Patrick's Creek is similar to Manion Creek in terms of surrounding upstream land use. The study site, located within St. Patrick's county park lies <200 m upstream from the St. Joseph River. Larger trees, primarily beech, maple, tulip poplar, and birch line the hilly floodplain. *Equisetum* was abundant along the moist banks.

The ten streams studied exhibited a wide range of physical and hydrologic characteristics (Table 1). Discharge in all streams was generally <150 L/sec except for the two in Indiana. Northern Indiana streams are typified by low summer discharge, augmented by periodic thunderstorms, and higher flow in winter and spring. Stream flow is also lowest in summer in the Coweeta streams. Precipitation, which is abundant at Coweeta, is highest in late winter and spring and lowest in the fall (Swift et al. 1988). The ratio of annual runoff to annual precipitation is 0.527. Streamflow in the Montana streams is highest in spring following snowmelt and steadily declines throughout the summer when the streams may become intermittent.

Particle Releases

Fine particle retention was studied from September 1992 through October 1993. Coweeta streams were studied throughout this period, but the Montana (June and July 1993) and Indiana streams (October 1993) were only studied once. I will refer to Coweeta streams first by name (HWC,BHB, BTB, or SB) and then by the month of release, so that a release of particles in HWC in the month of August will be referred to as simply HWC-August. Because the Montana and Indiana streams were only sampled once, I will refer to the stream by its proper name.

Commercially obtained corn pollen and glass beads

Table 1. Characteristics for the ten streams studied. Q=discharge, MSS=median substrate size, LWD=large woody debris, and Temp=stream temperature.

Stream	Q (L/sec)	MSS (mm)	Gradient (m/m)	LWD Surface Area (m^2)	LWD Volume (m^3)	Temp (°C)
HWC	11-133	10	0.1476	121.8	11.9	8-17
BHB	8-81	5	0.0735	56.4	2.5	9-17
BTB	7-13	.25	0.4780	56.0	3.6	10-12
SB	4.6	6	0.2710	60.4	4.1	10.0
Yellowbay Cr.	46.2	68	0.0956	59.9	2.6	8.0
Howe Cr.	114.8	70	0.0168	117.2	7.3	7.0
Haystack Cr.	86.4	95	0.0883	27.8	7.8	9.5
Logan Cr.	65.3	0	0.0803	0.0	0.0	10.5
Manion Cr.	243.0	10	0.0110	3.2	0.1	20.0
St. Patrick's Cr.	295.6	15	0.0386	157.2	12.6	13.0

(Polysciences Inc, Warrington, Pennsylvania) were used as surrogates of natural FPOM. Their efficacy as surrogates resulted from their similarity in size to natural particles and in their "ease" of recovery and identification. Both surrogates were similar in diameter to that of natural FPOM (78-183 μm) as determined for several streams at Coweeta Hydrologic Laboratory, NC (Webster et al. 1988). However, surrogate densities bracketed the natural density of FPOM (1.69 g/cm^3) as estimated by Kazmierczak et al.(1987).

Miller and Georgian (1992) estimated corn pollen diameter as ~87 μm and density as 1.092 g/cm^3. I measured thirty glass beads, listed as 50-100 μm (Polysciences), under a dissecting microscope with an ocular micrometer at 40x and estimated mean diameter as 78.3 ± 2.07 μm (± 1 SE, n=30). Glass bead density was assumed to be 2.48 g/cm^3 (Polysciences).

One vial of corn pollen (~1.0 g), stained with basic fuchsin, and ~2.0 g of glass beads were mixed with 4.0 L stream water in a container. A stirrer (automatic or manual) maintained particle suspension as the mixture was released into a well-mixed area of stream via tubing at the base of the container. Particles were released for 3-3.5 minutes.

Downstream from the release point, at 3-5 stations spread over a 20-60 m reach, grab samples of water were taken every 30-60 seconds for 5-15 minutes in 500-mL Whirlpak bags until particles were assumed to be cleared from the water column. Samples were taken from a turbulent, well mixed region of the thalweg. In larger streams, samples were taken at 0.6 depth, whereas the entire water column was sampled in smaller streams.

Samples were transported back to the lab where sample volume was measured prior to filtration onto 0.45-μm gridded filters. These filters were examined under a dissecting microscope at 60x magnification, and all corn pollen and glass beads were counted. Particle concentration was determined (#/vol) for each sample, integrated over time (seconds) for each station, and subsequently multiplied by stream discharge (L/sec) to determine number of particles passing each downstream station. Dilution was determined by chloride release (see below), but was not significant over the length of any of the reaches used. Due to leakage from some of the Whirlpak bags, particle concentration for these samples was overestimated. If volume loss was severe, a new volume for that sample was calculated as the mean volume of the remaining samples from that station. It was assumed particles would have settled to the bottom of the bag and water was lost from the top.

Based on equation (4), rate of corn pollen and glass bead loss from the water column was determined by linear regression of ln(fraction of particles still in transport) versus distance from release. Because the initial number of corn pollen and glass beads released could not be determined accurately, P_o was taken to be the number of particles from the first station downstream.

In addition to downstream movement, V_{fall} and V_{dep} were calculated for both corn pollen and glass beads for each release, based on equations (1) and (5), respectively. Water density and viscosity were corrected for stream temperature.

Chloride Releases

A conservative solute release, using chloride (delivered as NaCl), immediately followed each particle release. I selected a 100-m reach that included the shorter particle reach. This larger reach was delineated every 10 m with labeled flagging tape.

Two different chloride delivery systems were used. From September 1992 through January 1993, a battery-powered system maintained a constant head and delivery by pumping salt solution from a lower reservoir into an upper head box from which the solute emptied into the stream through valved tubing. For all subsequent releases a Mariotte bottle was used. Named for its 17th century creator, Edme Mariotte, the bottle allows for delivery of solute at a constant rate related to atmospheric pressure regardless of solute level in the reservoir (Mariotte 1718). Calibrated tips (Eppendorf 50-μL tips) connected to the spigot by rubber tubing allow variable release rates. In the lab, tips were cut to various aperture sized to yield various delivery rates of solute. A portable, chloride specific ion probe (Orion model 290A) was used to measure chloride in millivolts of resistance. The probe was calibrated with a series of chloride standards, 1, 1.5, 2, 3, 4, 5, 10, and 20 mg Cl/L, before and after the release. A log-log standard curve of Cl concentration vs millivolts was used for all releases, except for a linear standard curve for the Indiana streams, to convert from field mV readings into Cl concentration. The ambient levels of chloride were much higher in these Indiana streams than the more pristine mountain streams, and the standard curve was linear at these higher concentrations (10-100 mg/L).

Chloride ($\leq$144.4 g Cl/L) was released into a well-mixed zone at the upstream end at a rate sufficient to raise stream Cl levels approximately 5-10 fold over background. The desired release rate Q_{rel} was calculated as $Q_{rel}= Q*C_s/C_i$ where Q is stream discharge, C_s is target stream chloride concentration, and C_i is concentration of the release solution. For this equation, Q was determined from weir or flume readings at Coweeta and was estimated from cross-sectional area and velocity measurements in the field for the other streams (described below). Chloride release continued until the downstream chloride concentration had reached plateau, at which time several mid-stream grab samples were taken every 10-30 m for estimation of dilution from groundwater and tributary input. Probe readings and running time of release were continuously recorded by hand until background chloride concentrations were approached or re-established.

Ancillary Measurements

Discharge was estimated in one of three possible ways. For Coweeta streams, a V-notch weir (HWC and BHB) or H-flume (WS's 53 and 55) continuously measures stream flow. For all streams, discharge was calculated from the chloride release as

$$Q= (C_i-C_b)(Q_{rel})/((C_p-C_b)$$

where Q is discharge, C_i is concentration of chloride released, C_b is background chloride concentration, C_p is plateau chloride concentration, and Q_{rel} is release rate of chloride solution. A rough estimate of discharge was also be determined from the product of cross-sectional area and velocity for ungauged streams.

Every 10 m within the 100-m reach, wetted channel width, depth (every 30-50 cm), and thalweg velocity (if flow meter available) was measured. Mean depth was calculated as the mean of the average depth at each cross-section. Velocity was also calculated as Q/A where Q is discharge calculated from chloride dilution above and A is the cross-sectional area of the stream as determined from chloride travel time.

Median substrate particle size was estimated using the "big toe" procedure. At each step, walking upstream in a zig-zag pattern between banks, the particle stepped on was measured (intermediate axis) with a metric rule. Approximately 10-20 steps per 10 m were taken. All samples were ranked in size and the median diameter determined. For those particles less than 1-mm diameter, a size assignment was made based on a modified Wentworth classification (in Gordon et al. 1992). Sand was assumed to be 0.250 mm, silt 0.0156 mm, and clay 0.001 mm. Bedrock, which is not on the Wentworth scale, was designated as being 0 mm. A definite size can be assigned to particles, but bedrock is entire and not composed of particles with spaces between them. I assumed that the bedrock was essentially flat.

All large woody debris, that wood ≥ 1 m in length and

$\geq$ 10 cm in diameter, was measured. Wood that extended onto the bank or floodplain was included for it was considered "channel forming wood".

Gradient was measured with a transit (or hand held eye level for the Indiana streams) and stadia rod. Stream temperature was also recorded.

Hydraulic Characteristics

Unit stream power (Ω/w) is the power (Ω) available to do work in a stream. Ω is a product of discharge, stream water density, and gradient (Sedell et al. 1978). Dividing Ω by stream width (w) gives unit stream power.

U_*, shear velocity, is a measure of shear stress at the stream bed expressed in velocity units and can be estimated as $(gDG)^{1/2}$ where g is acceleration due to gravity, D is water depth, and G is stream gradient (Davis and Barmuta 1989).

Two dimensionless, yet descriptive parameters of mean motion of stream flow, Reynolds and Froude numbers, were also calculated. Reynolds number (Re) is the ratio of inertial forces to viscous forces and is UD/ν, where U is stream velocity, D is depth, and ν is kinematic viscosity. Froude number (Fr), the ratio of inertial to gravitational forces, is $U/(gD)^{1/2}$. Re describes flow as turbulent ($Re>2000$) or laminar ($Re<500$), whereas Froude number describes flow as critical ($Fr=1$), sub-($Fr<1$), or supercritical ($Fr>1$).

Roughness Reynolds number, Re_*, describes the microflow conditions near the bed surface and is related to Re. $Re_* = U_*(k_s)/\nu$, where k_s is a measure of the height to which substrate elements project into the overlying water column (Davis and Barmuta 1989).

Results

Particle Retention

Using the negative exponential model to calculate an uptake rate (k) of particles from the water column for each of the 17 releases, pollen uptake, or retention, from only 10 of these releases actually fit an exponential decline (i.e $r^2 \geq 0.750$). Furthermore, only 9 of these releases (HWC-September, HWC-August, BHB-February, BHB-August, BTB-November, BTB-February, Yellowbay Cr., Logan Cr., and St. Patrick's Cr.) showed a continual decrease in pollen concentration in a downstream direction. Pollen concentration was greater at one or more of the middle sites or at the bottom site than at upstream sites in the same release. This pattern is probably due to inadequate mixing of particles in the water column. SB-February (r^2=.758) fit the decay model with a slight increase in pollen abundance at the bottom site.

Pollen uptake rate ranged over two orders of magnitude (Table 2), not including two releases, HWC-October and HWC-February, which had no uptake of pollen (i.e, k>0) and were subsequently excluded from further analysis. Mean uptake rate of all releases was 0.0670 m^{-1} ± 0.0202 (± 1 SE, n=15), and mean pollen travel distance, S_w, was 120.79 m ± 53.8 (±

Table 2. Pollen travel distance (S_w), uptake rate (k_p), and r^2 of negative exponential model.

Stream	S_w (m)	k_p (1/m)	r^2
HWC-Sept 92	21.98	-0.04550	0.906
HWC-Oct 92	-	+0.00915	0.107
HWC-Nov 92	176.99	-0.00565	0.669
HWC-Feb 93	-	+0.00005	0.000
HWC-Aug 93	9.18	-0.10890	0.997
BHB-Jan 93	133.16	-0.00751	0.031
BHB-Feb 93	7.94	-0.12590	0.930
BHB-Aug 93	32.15	-0.03110	0.800
BTB-Nov 92	7.96	-0.12560	0.983
BTB-Feb 93	3.49	-0.28690	0.961
SB-Feb 93	7.11	-0.14060	0.758
Yellowbay Cr.	38.90	-0.02571	0.939
Howe Cr.	537.63	-0.00186	0.165
Haystack Cr.	724.64	-0.00138	0.012
Logan Cr.	27.58	-0.03626	0.978
Manion Cr.	61.24	-0.01633	0.328
St. Patrick's Cr.	21.87	-0.04572	0.903

1SE, n=15). Greatest retention per meter occurred in the Coweeta streams, particularly the small headwater streams in WS's 55 and 53. Comparable retention rates were also observed in two of the nine releases in the Coweeta second order streams, HWC-August and BHB-February. Howe and Haystack Creeks, two of the Montana streams, were the least retentive of pollen, followed by HWC-November and BHB-January.

Fewer glass bead releases fit the exponential decay model than the pollen releases. Only 6 of the 17 releases (HWC-October, HWC-February, BTB-November, Haystack Cr., Logan Cr., and St. Patrick's Cr.) produced an $r^2 \geq 0.750$, and these same releases were also the only ones, except for HWC-September ($r^2=0.73$), to show continual downstream decline in glass bead abundance. As with the pollen releases, those streams which yielded k's >0 (HWC-November, BHB-January, and Manion Cr.) were eliminated from further analysis.

Uptake rates of glass beads also varied over two orders of magnitude but were greater than pollen uptake rates (Table 3). Mean uptake rate of all releases for glass beads was 0.1050 m^{-1} ± 0.0310 (± 1 SE, n=14). Again, the Coweeta streams, especially the headwater streams of WS's 53 and 55 had the greatest retention, whereas Montana streams were the least retentive. Mean travel distance was 39.74 m ± 20.73 (±

Table 3. Glass bead travel distance (S_w), uptake rate (k_{gb}), and r^2 for negative exponential model.

Stream	S_w (m)	k_{gb} (1/m)	r^2
HWC-Sept 92	7.52	-0.13298	0.727
HWC-Oct 92	6.45	-0.15504	0.997
HWC-Nov 92	-	+0.00879	0.181
HWC-Feb 93	27.80	-0.03597	0.910
HWC-Aug 93	7.82	-0.12780	0.598
BHB-Jan 93	-	+0.03599	0.299
BHB-Feb 93	13.34	-0.07496	0.585
BHB-Aug 93	303.03	-0.00330	0.001
BTB-Nov 92	2.17	-0.46030	1.000
BTB-Feb 93	9.05	-0.11050	0.436
SB-Febr 93	5.85	-0.17100	0.476
Yellowbay Cr.	37.22	-0.02687	0.192
Howe Cr.	59.49	-0.01681	0.125
Haystack Cr.	40.16	-0.02949	0.998
Logan Cr.	24.59	-0.04067	0.747
Manion Cr.	-	+0.00760	0.182
St. Patrick's Cr.	11.86	-0.08435	0.908

1 SE, n=14). S_w for glass beads ranged between 2.17 and 303.03 m (Table 3). In order to determine which factors of these ten streams were potentially responsible for differences in retention (k), I used stepwise multiple regression with the ten following physical and hydraulic characters: LWD surface area and volume, depth, discharge, gradient, median substrate particle size, V_{shear}, Re, Fr, and Ω/w. Gradient and V_{shear} were the two variables that explained over 75% of the variation in pollen uptake rates (Stepwise regression, $p \leq 0.05$, Table 4). No other factors were significant at the 0.05 level. Gradient was positively associated with retention (k) whereas V_{shear} was inversely related to retention. Gradient was the only stream character significant ($p \leq 0.05$) in explaining the variation of glass bead uptake rates (Table 4). Again, gradient was positively related to retention.

Deposition Rates

Pollen fall velocity (V_{fall}) was 1.26 mm/sec ± 0.0350 (± 1 SE, n=15, Table 5). Variation is caused by differences in water viscosity at varying stream temperatures. Empirically determined deposition velocity (V_{dep}) ranged from 0.0640-1.80 mm/sec with a mean of 0.484 mm/sec ± 0.140 (± 1SE, n=15, Table 5). On average V_{dep} was only 39.27% ± 11.4 (± 1 SE,

Table 4. Partial and model R^2's and p values from stepwise multiple regression.

Variable	Partial R^2	Model R^2	p
Corn pollen			
Gradient	0.636	0.636	0.0004
V_{shear}	0.126	0.762	0.0268
Glass beads			
Gradient	0.547	0.547	0.0025

Table 5. Pollen deposition (V_{dep}) and fall (V_{fall}) velocities and V_{dep} as a percentage of V_{fall}.

Stream	V_{dep} (mm/sec)	V_{fall} (mm/sec)	V_{dep}/V_{fall} (%)
HWC-Sept 92	0.7475	1.3992	53.4
HWC-Oct 92	-	1.2498	-
HWC-Nov 92	0.1293	1.2319	10.5
HWC-Feb 93	-	1.1107	-
HWC-Aug 93	0.0762	1.4384	5.3
BHB-Jan 93	0.1589	1.1274	14.1
BHB-Feb 93	1.5147	1.1445	132.0
BHB-Aug 93	0.1026	1.4384	7.1
BTB-Nov 92	0.3165	1.2319	25.7
BTB-Feb 93	0.2413	1.1792	20.5
SB-Feb 93	0.1662	1.1792	14.1
Yellowbay Cr.	0.5811	1.1107	52.3
Howe Cr.	0.0640	1.0772	5.9
Haystack Cr.	0.0297	1.1616	5.6
Logan Cr.	0.8794	1.1965	73.5
Manion Cr.	0.4541	1.5593	29.1
St. Patrick's Cr.	1.7998	1.2866	140.0

n=15) of V_{fall}. BHB-February and St. Patrick's Creek had V_{dep}'s greater than V_{fall}. Both of these streams had very high velocities relative to their travel distances; St. Patrick's Creek had the highest velocity of all ten streams. These velocities may be overestimates due to problems associated with calculating chloride travel times. Typically, the other streams with shorter S_w's also had slower velocities. Glass bead fall velocity was much greater than pollen and was 15.76 mm/sec ± 0.405 (± 1 SE, n=14, Table 6). Again, variation is due only to changes in viscosity. Deposition velocities for glass beads were 0.643 mm/sec ± 0.167 (± 1 SE, n-14). Although glass bead V_{fall} was ~13 times greater than corn pollen V_{fall}, glass bead V_{dep} was only 1.3 times as large as that of pollen. Glass bead V_{dep} was only an average 5.61% ± 1.47 (± 1 SE, n=14) of V_{fall}. The highest such percentage was for St. Patrick's Creek at 20%. Deposition velocities exhibited a wide range of values and were not significantly different.

Hydraulics and Mean Motion Flow

Re and Fr describe the mean motion of stream flow (Davis and Barmuta 1989). All streams could be described as sub-critical for Fr<1 for all sites (Table 7). Because all streams had Re>500, none was laminar in nature, and most

Table 6. Glass bead deposition (V_{dep}) and fall (V_{fall}) velocities V_{dep} as a percentage of V_{fall}.

Stream	V_{dep} (mm/sec)	V_{fall} (mm/sec)	V_{dep}/V_{fall} (%)
HWC-Sept 92	2.1899	17.661	12.4
HWC-Oct 92	1.3046	15.867	8.2
HWC-Nov 92	-	15.644	-
HWC-Feb 93	0.2308	14.149	1.6
HWC-Aug 93	0.0895	18.125	0.5
BHB-Jan 93	-	14.356	-
BHB-Feb 93	0.9043	14.568	6.2
BHB-Aug 93	0.0108	18.125	0.6
BTB-Nov 92	1.1612	15.644	7.4
BTB-Feb 93	0.0928	14.998	0.6
SB-Feb 93	0.2021	14.998	1.4
Yellowbay Cr.	0.6076	14.149	4.3
Howe Cr.	0.5785	13.729	4.2
Haystack Cr.	0.6350	14.780	4.3
Logan Cr.	0.9866	15.210	6.5
Manion Cr.	-	19.536	-
St. Patrick's Cr.	0.0033	16.310	20.4

Table 7. Hydraulic characteristics for all ten streams. Velocity was determined by discharge/cross sectional area(based on chloride release), U*=shear velocity, k_s=maximum substrate size to maintain hydraulically smooth flow, Re=Reynolds number, Fr=Froude number, and Ω/w=unit stream power (kg $m^{-1}sec^{-1}$).

Stream	Velocity (cm/s)	U* (cm/s)	k_s (mm)	Re	Fr	Ω/w (kg m^{-1} sec^{-1})
HWC-Sept 92	25.9	30.3	0.0128	14787	0.328	169
HWC-Oct 92	37.8	28.2	0.0154	6803	0.208	141
HWC-Nov 92	23.7	37.4	0.0117	18252	0.244	442
HWC-Feb 93	9.5	31.3	0.0155	4630	0.116	137
HWC-Aug 93	3.1	18.0	0.0211	645	0.066	96
BHB-Jan 93	27.0	23.8	0.0201	15492	0.308	282
BHB-Feb 93	19.0	21.4	0.0220	8932	0.241	219
BHB-Aug 93	12.5	13.8	0.0275	3044	0.246	37
BTB-Nov 92	8.0	38.4	0.0114	2009	0.144	550
BTB-Feb 93	3.8	24.4	0.0188	642	0.080	253
SB-Feb 93	6.2	19.1	0.0240	904	0.143	91

Table 7 continued.

Stream	Velocity (cm/s)	U* (cm/s)	k_s (mm)	Re	Fr	Ω/w (kg m^{-1} sec^{-1})
Yellowbay Cr.	16.5	35.8	0.0136	16307	0.142	187
Howe Cr.	33.1	13.1	0.0382	24098	0.328	68
Haystack Cr.	27.6	26.0	0.0179	16219	0.316	190
Logan Cr.	32.8	24.1	0.0187	18816	0.385	171
Manion Cr.	29.8	10.0	0.0352	27675	0.311	107
St. Patrick's Cr.	39.5	19.0	0.0217	32722	0.400	426

could be described as turbulent (Re>2000). A few streams had Re in transition between laminar and turbulent (HWC-August, SB- and BTB-February).

Discussion

Particle Retention

Corn pollen and glass beads travel relatively short distances, on the order of 1-100 m, in these small streams before being lost from the water column (i.e., retained). Because of differences in density, pollen and glass beads should set upper and lower limits to actual expected transport distances of natural particles, which are an agglomeration of organic and inorganic material (Kazmierczak at al. 1987, Webster et al. 1988).

Retention rates and travel distances reported here lie within the range of values found in the small handful of studies that have measured FPOM travel distances directly either with natural FPOM or some other surrogate (Table 8). For these table values (not including the artificial streams), travel distance increases with discharge (regression, $r^2=.79$, $p=.0006$) and stream power (regression, $r^2=.78$, $p=.0007$).

An indirect measure of FPOM travel distance in another Appalachian Mountain stream similar in size to those I studied, was made by Newbold et al. (1983). These authors, who were studying phosphorus spiralling length in Walker Branch, reported the travel distance, s_i, of this nutrient

Table 8. Comparison of travel distances (S_w), discharge (Q), depth, and unit stream power (Ω/w) from five previous studies.

Study	Particle type	S_w (m)	Q (L/sec)	Depth (cm)	Ω/w (kg $m^{-1}sec^{-1}$)
Webster et al 1987	Ground leaves	4.1-14.5	0.7-2.5	1-3	
Jones and Smock 1991	^{14}C natural FPOM+ ground leaves	1.8-11.9	17	25-36	.17-.54
		30-84	22-45	25-36	.22-1.44
Miller and Georgian 1992	Corn pollen	122-190	148-220	13-15	40-60
Newbold et al. 1991	^{14}C natural FPOM	710	680	33	66
Cushing et al. 1993	^{14}C natural FPOM	630	250	34	56
		800	730		77
		580	710		75

with various particulates. The sum of s_i from all the different components studied, relative to the probability of a phosphorus atom entering that compartment, is the spiralling length for phosphorus. Phosphorus, attached to FPOM, traveled 51-141 m before being released back into the water column or taken up by organisms. This phosphorus s_i for the FPOM compartment can be considered a measure of FPOM travel alone, assuming that the rate of phosphorus release from the particles is much smaller than the rate of FPOM movement downstream.

For the streams I studied, neither stream power nor discharge was important compared to gradient and V_{shear} in explaining retention. Bagnold (1966) demonstrated a model for describing fine sediment transport as a function of stream power. This relationship with organic particles has been shown in a few studies (Fisher and Likens 1973, Webster 1983, Vadeboncoeur 1994) but has not been an adequate or useful predictor in several other studies (Sedell et al. 1978, Naiman and Sedell 1979, Minshall et al. 1983, 1992). The importance of discharge may be masked by the Indiana streams which had the highest discharge (~300 L/s) of all the streams, yet still had relatively high pollen retention. Pollen and glass beads traveled shortest distances in streams with the lowest discharges (BTB and SB) overall.

And in HWC, particles traveled less than 21 m (Q=11-44 L/sec) except in November 92 during a spate (Q=133 L/sec) in which pollen was carried 177 m. Considering just HWC, if the initial data point on HWC-October is eliminated (which then yields a negative and therefore useful k value), travel distance on that watershed increased with discharge (r^2=.963, p=0.0187). Q does have an effect on retention in this stream, but for all ten streams together, discharge was not related to retention (k).

Unit stream power or discharge is more an index of potential retention, but actual retention must be determined empirically (Minshall et al. 1992). This is also evident from studies in which wood has been removed or added (e.g. Trotter 1990) from a reach and retention studied before and after manipulation. Retention is significantly reduced or enhanced, yet discharge and unit power have not changed on this time scale.

Surprisingly, gradient was not only the most important factor in explaining variation of retention rate for both particle types, but it was also positively related to retention. Higher gradient is typically associated with more turbulent flow and higher velocity (as compared to a low gradient section of the same stream), and therefore retention should decrease and not increase. This paradox is resolved in recognizing that gradient is negatively (and significantly) related to depth, Re, and Fr for both types of particles (Corn pollen: depth, r=-.621, p=0.014; Re, r=-.683, p=0.005; Fr, r=-.672, p=0.006; Glass beads: depth, r=-.605, p=0.022; Re, r=-.631, p=0.016; Fr, r=-.612, p=0.020). The Coweeta streams, which were typically the most retentive, had the steepest gradients yet were also smallest in depth and discharge. In addition, pollen and glass bead uptake rate significantly decreased with depth considered alone (corn pollen, r^2=.453, p=.006; glass beads, r^2=.326, p=0.0330).

Besides gradient, V_{shear} was the only other significant factor explaining uptake rate (and only for pollen). This V_{shear} is only an approximation, as discussed above, and describes part of the micro-flow environment. Ideally, V_{shear} should be derived from field measured velocity profiles (Davis and Barmuta 1989). Although velocities near the bed should be lower than main channel flow due to frictional forces, particles at rest on the bed are subjected to shear forces, of which V_{shear} is a measure in terms of velocity units (V_{shear}, ideally derived from velocity profiles near the bed, is mathematically related to shear stress but has no "physical realization" per se, see Carling 1992). Ultimately, it is those forces acting on particles at the bed that will determine whether a particle remains in suspension or will settle and deposit. Thus, at least for corn pollen, the shear forces (i.e. V_{shear}) at the bed are an important factor in explaining overall retention.

My study focused on FPOM retention by estimating deposition rates of particles from the water column to the streambed, assuming that particles are not resuspended. Of course, entrainment of particles from the streambed to the water column is the complimentary half to the study of particle transport dynamics (e.g., Fisher et al. 1979, 1983). Graham (1990) asserted that "even the finest particles must deposit everywhere in a stream under all conditions of water velocity and turbulence. Further, the rate depends only on the concentration and Stokian sinking velocity of the particles." Particles will settle out but only form a deposit if not forcibly resuspended. Thus, it is not deposition but entrainment that is the limiting or defining factor. To precisely understand particle dynamics, micro-flow parameters, such as shear stress, should be known.

I did not empirically measure entrainment criteria for either corn pollen or glass beads, but I did indirectly evaluate the micro-flow environment via Re_* by approximating U_*. Re_* is critical for it describes the overall flow conditions at the bed, specifically whether a laminar sublayer is present. And a crucial condition for particle deposition rates to be a function of only V_{fall} and depth is the presence of a laminar sublayer of zero velocity through which particles sink and are not resuspended (Reynolds 1979, 1990, Smith 1982). Re_* describes the flow regime close to the bed as hydraulically smooth ($Re_* <3.5$), hydraulically rough ($Re_* >70$), or transitional between the two (Davis and Barmuta 89). Hydraulically smooth flow is a prerequisite for the existence of a laminar sublayer.

Re_* is a function of three variables, U_*, ν, and k_s as described above. However, I did not measure k_s which is a metric of bed roughness or substrate particle size. Initially, I estimated substrate particle size as an index of roughness, for particle retention has been shown to increase with bed roughness (Webster et al. 1987). Particle diameter, however, is not necessarily correlated with substrate roughness (Davis and Barmuta 1989). In the place of particle size, Davis and Barmuta advise using k_s, which they defined as the mean change in height of the stream bed measured at 5-mm intervals as described by Ziser (1985). Carling (1992) suggested measuring k_s, not from substrate profiles, but from velocity profiles. The latter would more fully integrate all of the bed roughness.

Therefore, to determine if hydraulically smooth flow is present (i.e. $Re_*=3.5$), I used U_* and temperature corrected ν to calculate the unknown k_s. For rocky bottom streams, k_s is no longer equal to particle size as it is for sand-bottomed streams (Carling 1992b), but I will assume, however, that k_s is equivalent to particle size for all cases. k_s, then, is the maximum allowable substrate size to still maintain hydraulically smooth flow. For any of the ten streams I studied to have this type of flow, the stream measured particle size must be $\leq k_s$.

k_s was determined for each of the streams to be equivalent to fine sand (k=0.01-0.04 mm, Table 7). The actual smallest median substrate particle size from any of the ten streams was in WS 53 and that was 0.25 mm, but all other median particle sizes were ≥5 mm. Thus, none of the streams had hydraulically smooth flow. The median particle size is so low on WS 53 because of the abundance of bedrock outcrops. k_s, however, may not be accurate for U_* is only an approximation and is probably too large by an order of magnitude. Generally, U_* is ~5 cm/s for rocky streams (Davis and Barmuta 1989, Carling 1992b). Decreasing U_* by a factor of ten subsequently raises k_s tenfold to 0.1-0.4 mm, yet k_s still does not exceed the smallest stream particle size if each release is looked at individually (Tables 1 and

7). I conclude that hydraulically smooth flow was absent and the laminar sublayer was at least disrupted and most likely annihilated in these streams.

The presence of hydraulically transitional or rough flow and the lack of a laminar sublayer suggests that pollen and glass beads were likely to be immediately entrained after they settled. Cushing et al. (1993) actually calculated the shear stress present at the bed in Idaho streams and determined it to be sufficient to entrain natural particles. I have no direct measure of entrainment of pollen or glass beads, only strong circumstantial evidence. In addition, I cannot say whether corn pollen and glass beads are moving as bed load or suspended load, although I would assume that because of the high density of glass beads they would travel as bed load.

Without a laminar sublayer, V_{fall} and V_{dep} uncouple and are no longer theoretically equal (Smith 1982, Reynolds 1979, Cushing et al. 1993). For both pollen and glass beads, V_{dep} is only a fraction of V_{fall}. This observation is consistent with other studies. Reynolds (1990) reported V_{dep} of *Lycopodium* spores as ~50-60% V_{fall}, and Cushing et al. (1993) showed V_{dep} of natural FPOM to be only 7-12% V_{fall}.

Glass beads, being more dense, seem to be affected more by shear forces and resuspension than pollen grains.

Although glass beads actually travel a third as far as pollen, the beads travel much further than predicted based on V_{fall} relative to pollen. Perhaps this difference can only be resolved with further microscale examination of the particles, as suggested by Brush and Brush (1972). These authors released fourteen types of pollen into recirculating chambers and determined that the travel distance of the different types did not correspond to expected travel based solely on pollen settling velocities.

Webster et al. (1988) reported natural FPOM (43-105 μm) V_{fall} as 1.19 (WS 14) and 1.46 (WS 7). These values are in the range of pollen V_{fall} and suggest that pollen may be a more accurate surrogate for FPOM than glass beads which have V_{fall} thirteen times greater. Based on density differences alone, natural FPOM should have a higher fall velocity, but corn pollen is much more spherical than the irregularly shaped and planar FPOM.

Comparison of pollen and glass bead retention

Overall, corn pollen and glass beads appear to be adequate surrogates for natural FPOM in that estimated travel distances are in agreement with other studies. However, I think the reduction of natural stream heterogeneity to average values plus technique problems limit resolution of retention comparisons among streams.

Flow conditions are described generally by discharge, velocity, Re, and Fr. However, no measure of flow heterogeneity, for example flow associated with lateral habitats and shallow slow water environments, was made. And it is here that particles are most likely to deposit and not be entrained.

Also, in terms of technique, S_w itself is time dependent. Particles were collected over 10-15 minutes with the assumption that most of the pollen and glass beads would be cleared from the water column in that time period, however, examination of many of the filters at the lower sampling sites indicate that the surrogate particles were still in transport. If samples were taken over a longer time period, more particles would pass out of the reach due to clearing of the water column as well as from resuspension.

I had assumed pollen travel would exceed glass bead travel for each release because of pollen's much lower density, yet the ratio of pollen S_w to glass bead S_w was not always >1. Ratios were not calculated for the releases which had k's>0. Most of the releases had ratios between 1-4. Howe and Haystack Creeks had ratios of 9 and 18, respectively, whereas BHB-February (0.60), BHB-August

(0.11), and BTB-February (0.39) had ratios less than unity. These last five releases, in addition to the five releases with k's>0, strongly indicate problems with technique.

Limitations in technique are also suggested from lack of fit to the negative exponential model and large variation among releases. For example, releases in HWC-September and HWC-October were similar in discharge (44 vs 36 L/sec) and identical in reach length and all other physical parameters, yet retention rates between the two streams were drastically different. For the September release k was -0.04550 and for October k was >0. I think that this degree of variability associated with each release precludes a confident and meaningful comparison of individual streams, such as HWC to BHB.

The discrepancy in travel ratios and k described above are probably a result of inadequate particle mixing throughout the water column over the 20-60-m study reaches. Besides incomplete mixing, the depth of sampling may be a potentially large source of error. If particles, especially the glass beads, move as bed load, i.e. within a few grain diameters of the bed (Morisawa 1968), samples taken higher in the water column would miss the majority of those particles.

Another procedural source of error resulted from counting particles on filters that had large amounts of natural particles. For the Coweeta streams only, natural seston collected in the sample bags sometimes obscured detection of pollen and glass beads on the filters. As a result, some individual samples were eliminated or particle abundance was underestimated. Corn pollen and glass beads were readily detected and counted from streams in Montana and Indiana. Lower seston concentrations resulted in filters fairly clear of natural particles.

Significance to Stream Ecology

The previous discussion has focused on the dynamics of individual particles and of a slug release of particles, but how does such a pollen and glass bead release relate to the continual downstream movement of FPOM.

Following the analysis of Cushing et al. (1993), I estimated a crude value of benthic FPOM turnover time. Concentration of FPOM in the water column (g/m^3) multiplied by V_{dep} (m/sec) gives the flux ($g\ m^{-2}\ sec^{-1}$) of particles to the bed. Turnover time is standing crop (g/m^2) divided by flux. To determine the range of turnover time, I selected the lowest (HWC-August) and highest (HWC-September) corn pollen V_{dep}'s from HWC. These are also the second lowest and highest of all corn pollen deposition velocities. Using a conservative summer concentration of FPOM from HWC of 3 g/m^3

(Golladay et al. 1987) and V_{dep} of .74 mm/sec produces a flux of 195 g m^{-2} d^{-1}. Given a HWC standing crop on the benthos of 166 g/m^2 (Golladay et al. 1989), turnover time of FPOM is 20 hrs. If V_{dep} from HWC-August (0.07) is used instead, turnover time is 8.3 days. In BHB, which has a slightly lower standing crop (113 g/m^3), turnover times for these same parameters above are 13 hours and 5.7 days, respectively (Golladay et al. 1989).

All of these turnover times were based on summer concentrations of FPOM, which are higher than concentrations in winter (Golladay et al. 1987). The lower the concentration, with all else equal, the longer the turnover time of FPOM in the benthos. Because a conservative summer concentration was used, turnover times reported above are a moderate estimate of turnover time. The turnover times are also in the same range as turnover times reported from other studies. Cushing et al. (1993) reported that 99% of their particles were resuspended within 24 hours (turnover time of 13 hours) and that the final 1% was resuspended within 17 days. This relatively quick turnover time is due to the low standing crop of only 0.8 g/m^2, which is only 0.5% of the HWC benthic FPOM standing crop. Newbold et al. (1983) calculated FPOM turnover time to be 7-99 days in Walker Branch. Standing crop of FPOM in this stream was 150 g/m^2, very close to those from HWC and BHB.

FPOM is an important energy source for many invertebrates, particularly collector-gatherers (Wallace and Merritt 1980), yet FPOM must reside long enough in the benthos to be used. Based on turnover of the benthic standing crop, organisms seemingly have a large supply of fresh organic matter. But it is not known what fraction of the corn pollen and glass beads became part of the buried FPOM pool and what fraction remained exposed primarily on the surface. Particles of FPOM on the surface may be a potentially rich source for microbes because of continual exposure to oxygen (Cushing et al. 1993) and are also more readily entrained than buried FPOM.

These measures of turnover time (T) indicate that the pool of exchangeable FPOM moves fairly quickly downstream. The rate, or velocity, of particle movement downstream (V_s) can be calculated as S_w/T (Newbold et al. 1982). With each movement, FPOM (i.e. corn pollen and glass beads) travels some distance S_w downstream, then temporarily resides in the benthic sediments for T amount of time before re-entering the water column. This saltatorial movement repeats itself downstream. V_s is 24 m/d and 1.1 m/d, respectively, for HWC-September and HWC-August. During summer low (HWC-August), particles move downstream very slowly. Even for the spate in HWC-November, V_s was 35 m/d.

Again, these velocities are similar to those from other small streams. FPOM V_s in Walker Branch ranged from 1.4-7.4 m/d (Newbold et al. 1983). Minshall et al. (1983) reported V_s for several different streams as: 0.2-5.2 m/d (Devil's and Mack Creek, Oregon), 32.3 m/d (Camp Creek, Idaho), 7.3 m/d (Augusta Creek, Michigan), and 1.9-7.7 m/d (White Clay Creek, Pennsylvania). V_s was 12 m/d in Camp Creek, Idaho (Minshall et al. 1992). These latter two studies include all organic particles and not just FPOM. Unfortunately, V_s could not be compared across biomes for the streams I studied because I do not have measures of FPOM stream concentrations or standing stocks.

In larger streams, rates of FPOM movement are much greater. FPOM moved downstream at ~1.2 km/d in Smiley Creek and the Salmon River (Cushing et al. 1993). Minshall et al. (1983, 1992) reported downstream increases in V_s (of total organics and not just FPOM). In the Salmon River drainage, V_s increases from 12 m/d at the upstream site to 17 km/d at the downstream site.

This acceleration of particle movement downstream indicates how linked upstream and downstream are in lotic ecosystems. A fragment of leaf generated in the headwaters can potentially be moved hundreds to thousands of meters downstream in a manner of days to weeks. Surely, this reveals the importance of retention of particles in streams. Retention of CPOM in streams is more efficient than for FPOM. Experimental releases of natural CPOM indicate that it travels ≤ 200 m (Young et al. 1978, Speaker et al. 1984, Speaker et al. 1988, Lamberti et al. 1991, Trotter 1990, Jones and Smock 1991, Prochazka et al. 1991, Ehrman and Lamberti 1992, Webster et al. 1994). The upper range of distances traveled are in streams with discharges 2-5 times that of the streams I studied. Direct comparison of retention between CPOM and FPOM within the same site always shows greater CPOM retention. Corn pollen and glass beads traveled 8-177 m in HWC and BHB, but CPOM traveled only ~5 m before being retained in these same streams (Webster et al. 1994). In two coastal plain streams, FPOM traveled 1.2-2.3 times further than CPOM at summer low flows and 5.4-6.8 times further at higher winter flows (Jones and Smock 1991). And in Walker Branch, s_i for CPOM was 0.4 m compared to s_i for FPOM, reported above, as 51-141 m (Newbold et al. 1983).

CPOM is likely to be physically retained by structures within the stream (Speaker et al. 1984, Ehrman and Lamberti 1992, Webster et al. 1994). Biological processing of these larger, more stationary particles generates smaller and more mobile FPOM, which is subsequently transported downstream more rapidly. Because of its small size, FPOM is not as likely to encounter obstructions or to be retained by them. This was evident in this study where physical macro-scale variable did not significantly affect FPOM retention.

In stream ecosystems, LWD, especially in accumulations of debris dams, has been shown to retard the downstream movement of CPOM (Bilby and Likens 1980, Bilby 1981, Speaker et al. 1984, Trotter 1990, Ehrman and Lamberti 1992, Webster et al. 1994). LWD, however, was not important in FPOM retention in this study. Perhaps, the length of the reaches (20-60 m) was too short, or the range of variables in the ten different streams masked the effect. Most likely, the lack of debris dams as such was the cause. Debris dams have been shown to greatly affect the transport and retention of FPOM in small streams. Debris dams filter the water column and can trap some FPOM, but less than 1% of the total organic matter in a low-gradient headwater stream was stored as FPOM (.15-1 mm) in the actual dam itself (Smock et al 1989). By removing debris accumulations, Bilby (1981) observed a six-fold increase in FPOM transport, particularly at higher streamflow. Debris dams dissipate energy and create depositional pools in which FPOM is sorted (Bilby and Likens 1980). Without debris dams, however, these pools, and the FPOM within, are easily eroded.

The majority of LWD in the ten streams studied was not accumulated as debris dams, and the debris dams present were comprised of only large pieces and not filled with a matrix of smaller sticks and organic material, which would effectively filter the water column. Manion and St. Patrick's Creeks are the best candidates to determine the role of wood in these streams, for they are similar in depth (9.35 cm vs 9.97), discharge (234 vs 310), velocity (.30 vs .33), and both are lower gradient (1.1 vs 3.9%). St. Patrick's Creek, however, has 157 m^2 of LWD surface area compared to 3.2 m^2 in Manion Creek. Pollen traveled only 22 m in woody St. Patrick's Creek and 61 m in Manion Creek. Glass beads traveled 12 m in St. Patrick's Creek, but no significant uptake of glass beads occurred in the 60-m reach of Manion Creek.

Particles could also be removed from the water column by active macroinvertebrate filtering and trapping by moss and aufwuchs. Invertebrate filtering of the water column, such as by black flies and hydropsychid nets, can be discounted because of their low abundance (based on visual examination). Webster (1983) estimated that collector-filterers ingested at most 4% of the FPOM in transport in a 1200-m headwater stream. However, high densities of collector-filterers have been shown to efficiently and rapidly remove phytoplankton (e.g. Maciolek and Tunzi 1968) and zooplankton (e.g. Voshell and Parker 1985) from lake outlets. But filterers were not nearly so abundant as this in the streams I studied. I would surmise that filterer contribution to particle removal in these ten streams is more like that reported by McCullough and Minshall (1979), i.e. filterers remove about 0.01% of the seston in the water column per m^2.

Two other unexamined sources of potential particle removal are in moss and the aufwuchs on rocks. Yellowbay Creek had an abundance of moss on the cobbles and could have effectively filtered pollen and beads from the water column. Moss has been shown to be important not so much as a resource itself but as a trapping substrate of organic material (Johnson 1978). Logan Creek's bedrock substrate was coated with a slimy and slippery aufwuchs assemblage. Particles, even in areas of high turbulence, could be trapped by the stickiness of the aufwuchs, just as fine sediments were trapped by epilithic periphyton (Graham 1990).

Carbon Turnover Length

This study has examined transport and retention of FPOM, but this in no way indicates how these particles are used by stream organisms. Carbon turnover length (S), however, is the distance organic carbon (FPOM in this study) travels before it is respired as CO_2. Essentially, S is a measure of the rate of carbon use within the stream ecosystem relative to its rate of movement downstream (Newbold et al. 1983). Turnover length is calculated as V_s/k_r where k_r is the rate coefficient of respiration (Newbold et al. 1982, Elwood et al. 1983). k_r was estimated to be 0.369 %/yr in Ball Creek, another stream at Coweeta (Schaeffer 1993). Using this k_r and V_s's of 24 m/d and 1.1 m/d, turnover lengths of FPOM are 23.7 km and 1.1 km, respectively. This indicates that FPOM travels great distances before its organic carbon is respired. These values are consistent with other calculated turnover lengths in small streams. Newbold et al. (1982) calculated turnover lengths in three streams: Bear Brook (2.9 km), Creeping Swamp (5.2 km), and Fort River (42.3 km). In the upper reaches of the four streams studied by Minshall et al. (1983) turnover lengths were: 1-5 km (Oregon), 11 km (Idaho), 10 km (Michigan), and 1-2.8 km (Pennsylvania).

As with V_s, turnover lengths also increase downstream. S increased from 4-1227 km in the Salmon River drainage (Minshall et al. 1992). Naiman et al. (1987) reported S of 8-15 km in first- to sixth-order streams and 426 km for a ninth-order stream. Richey et al. (1991) calculated S to be

4000 km in the Amazon, the largest river in the world. Because all of these studies used total carbon, turnover lengths will be larger than if only FPOM had been used (due to inclusion of dissolved organic carbon).

Small streams, such as the ones I studied, retain and use carbon (FPOM) much more efficiently than larger streams, based on the shorter turnover lengths. Yet these turnover lengths, as discussed with V_s, also reaffirm the longitudinal linkages between upstream and downstream.

Summary

In the ten small streams I studied, corn pollen, more so than glass beads, was an effective surrogate for natural FPOM, and its use indicates that FPOM traveled on average 121 m downstream and sank through the water column at 0.484 mm/sec. Corn pollen estimates of uptake length and deposition velocities were used to calculate benthic FPOM turnover time, rate of FPOM downstream movement, and FPOM turnover length. Based on these measures, FPOM is retained much more effectively in the upper reaches of streams such as the ten I studied, than in larger systems. But FPOM movement accelerates as the stream increases in size. FPOM links upstream and downstream together. Particles formed in the headwaters can be transported several kilometers downstream in only a matter of days to weeks. Thus, upstream reaches of streams can be an important source of organic carbon for downstream organisms.

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CURRICULUM VITAE
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1987-91	University of Notre Dame, B.S. in Biology
1991-present	VPI&SU, M.S. in Biology, Thesis topic: The use of corn pollen and glass beads to estimate fine particulate organic matter retention

Teaching Experience:

1991-94	Graduate Teaching Assistant; Freshwater Ecology, Field and Lab Ecology, Honors Biology, and General Biology, Dept. of Biology, VPI&SU.
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1990-91	Undergraduate research with Dr. Gary Lamberti at the University of Notre Dame. Examined particulate matter retention in a third-order stream.
1990	Research Technician for Dr. David Lodge at UNDERC. Used fluorometry to measure primary productivity of epiphytic, epipelic, and epilignic

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Papers Published:

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