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What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta

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SUMMARY

1. One of two things can happen to allochthonous material once it enters a stream: it can be broken down or it can be transported downstream. The efficiency with which allochthonous material is used is the result of these two opposing factors: breakdown and transport.

2. The present synthesis of new and published studies at Coweeta Hydrologic Laboratory compares biological use versus transport for four categories of particulate organic material: (1) large wood (logs); (2) small wood (sticks); (3) leaves; and (4) fine particulate organic matter (FPOM).

3. Over 8 years, logs showed no breakdown or movement.

4. The breakdown rate of sticks ($\leq$ 3 cm diameter) ranged from 0.00017 to 0.00103 day^{-1}, while their rate of transport, although varying considerably with discharge, ranged from 0 to 0.1 m day^{-1}.

5. Based on 40 published measurements, the average rate of leaf breakdown was 0.0098 day^{-1}. The leaf transport rate depended on stream size and discharge.

6. The average respiration rate of FPOM was 1.4 mg O_2 g $AFDM^{-1}$ day^{-1} over a temperature range of 6–22 °C, which implies a decomposition rate of 0.00104 day^{-1}. Transport distances of both corn pollen and glass beads, surrogates of natural FPOM, were short (< 10 m) except during high discharge.

7. Estimates of transport rate were substantially larger than the breakdown rates for sticks, leaves and FPOM. Thus, an organic particle on the stream bottom is more likely to be transported than broken down by biological processes, although estimates of turnover length suggest that sticks and leaves do not travel far. However, once these larger particles are converted to refractory FPOM, either by physical or biological processes, they may be transported long distances before being metabolized.

Keywords: breakdown, Coweeta, detritus, stream, transport

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Introduction

Many studies over the past 40 years have shown that substantial amounts of allochthonous detritus enter streams (e.g. Benfield, 1997). In small streams with extensive riparian forest, allochthonous input may be more than 1000 g m^{-2} $year^{-1}$ (e.g. Webster, Wallace & Benfield, 1995). In this paper, we have used data from new and previously published studies at the Coweeta Hydrologic Laboratory to synthesize the fate of particulate allochthonous material in streams. We divided allochthonous organic matter into four categories: (1) large wood (logs > 4 cm diameter); (2) sticks (wood < 4 cm diameter); (3) leaves; and (4) fine particulate organic matter (FPOM, particles between 0.45 μm and 1 mm in diameter). These categories cover most of the particulate allochthonous material in streams, but ignore leaf and wood fragments > 1 mm, and a variety of materials such as flowers, fruits and lichen fragments. Leaves of riparian trees are generally the largest component of allochthonous inputs and are often the major source of energy to heterotrophic organisms. Inputs of wood, especially logs, are difficult to measure because these are patchy in both time and space, but inputs of small wood may be as much as 425 g m^{-2} $year^{-1}$ (e.g. Smock, 1990). Log inputs may be as high as 880 g m^{-2} $year^{-1}$ in old growth coniferous forests, but are generally much lower (Harmon *et al.*, 1986). Because wood breaks down much more slowly than leaves, the standing crop of wood may greatly exceed that of leaves (e.g. Jones, 1997). Logs are important in the physical structure of streams except in areas without riparian trees and their surfaces may be important sites of biofilm development (e.g. Tank *et al.*, 1993). However, because of the small surface area exposed relative to their volume, logs break down slowly and generally make little direct contribution to energy flow in streams. Direct inputs of allochthonous FPOM have seldom been measured, although Golladay, Webster & Benfield (1987) found significant FPOM inputs during storms. Most FPOM is the result of the breakdown of larger particles, and considerable amounts of FPOM may consist of the faeces of grazers (e.g. Power, Matthews & Stewart, 1985) and detritvores (Wallace, Webster & Cuffney, 1982). The benthic accumulation of FPOM is usually lower than that of other forms of benthic organic matter, although it may exceed other types of benthic detritus in some streams (e.g. Jones, 1997).

Ultimately, one of two things can happen to allochthonous material once it enters a stream: it can be broken down or it can be transported downstream. Breakdown is the result of the combined action of physical, chemical and biological processes. The relative importance of these factors varies greatly with the type of detritus and the stream (Webster & Benfield, 1986). Although there have been few measurements of physical breakage, it is usually assumed to be unimportant except after detritus has been softened by microbial action (e.g. Suberkropp & Klug, 1980). Chemical leaching of dissolved material accounts for 10–30% of the initial weight loss from most leaf species, but it is likely that very little material is directly leached from wood, although we are not aware of any measurements of leaching from wood. Fungi, bacteria and animals play varying roles in the breakdown of detritus. Leaf material is generally attacked by fungi initially with bacteria playing a more important role later. Animals often consume leaf material only after it has been conditioned by microbes, but animal consumption may be very important in affecting the rate at which leaves break down (e.g. Wallace *et al.*, 1982). For the most part, animals do not seem to be prominent in the breakdown of woody detritus in freshwater, in contrast with marine and estuarine ecosystems (Maser & Sedell, 1994). Microbial degradation appears to be the major mechanism of FPOM breakdown. Rates of detrital breakdown vary greatly with the type of material, stream temperature and the availability of dissolved nutrients.

The transport of detrital particles is similarly variable, depending on the size and density of the particles, and on physical characteristics of the stream including depth, stream power and the abundance of retentive structures. Large logs that fall into small streams rarely move at all, whereas they may be moved a few metres in larger streams before accumulating in debris dams, while large rivers may transport logs all the way to the ocean. The distances travelled by small sticks similarly vary with steam size, and leaves generally move only a few metres before hitting obstructions and being retained (Webster *et al.*, 1994). Leaves often stay in a single spot until they are broken down, although they may be transported downstream another short distance during high flow. Transport of FPOM has been studied recently using one of two techniques: release of a

FPOM surrogate such as pollen (Miller & Georgian, 1992) or by using radio-labelled FPOM (Jones & Smock, 1991; Newbold, Cushing & Minshall, 1991; Cushing, Minshall & Newbold, 1993). Both techniques suggest that FPOM transport occurs in a series of saltations. Once particles are in the water column, they may be transported several hundred metres, depending on factors such as the size of the stream, characteristics of the substratum and the size and density of the particles. Once retained on the bottom of a stream, the residence time of a particle is highly variable. However, resuspension of a particle generally requires an increase in stream flow.

Breakdown and transport are processes which occur simultaneously in streams. When a detrital particle enters a stream, it is generally transported some distance before it is retained on an obstruction or settles on the stream bottom. There the particle begins to break down. During spates, it may be transported further downstream. These periods of transport may contribute to breakdown by directly causing physical breakage and by breaking up aggregations of detritus and exposing more surfaces to oxidative biological breakdown. The simultaneous process of breakdown and transport is referred to as stream spiralling (Webster & Patten, 1979).

Fisher & Likens (1973) suggested that the dynamics of benthic organic matter in a stream dominated by allochthonous inputs could be modelled as:

$$dX / dt = I - kX - k'X$$

where X is the standing crop of benthic organic matter (mass or energy per area) and dX/dt is the rate of change of X through time, I is the input of particulate material (litterfall, mass or energy per area per time), and k is the exponent in the negative exponential model, which has been commonly applied to particulate materials in streams (e.g. Petersen & Cummins, 1974). Other models may describe detrital breakdown in streams more exactly, but calculations of exponential rates of breakdown have been very useful for comparative studies (Webster & Benfield, 1986). The last term, k'X, expresses the exponential loss rate caused by transport, i.e. the rate at which the material is being transported downstream.

An analogous model for particle transport is:

$$dX / dx = k_x X$$

where X is the particulate material in transport, dX/dx is the change of X over distance and k_x is the exponential rate at which material is lost from the water column to the bottom per unit distance. k_x can be measured by releasing particles into the water column and measuring water column concentrations downstream. The inverse of k_x is the average transport distance and is designated as S_x. This model has been used for drifting insects (McLay, 1970; Elliott, 1971; Lancaster, Hildrew & Gjerlov, 1996), FPOM (Webster *et al.*, 1987; Miller & Georgian, 1992; Cushing *et al.*, 1993), leaves (Speaker, Moore & Gregory, 1984; Speaker *et al.*, 1988; Cummins *et al.*, 1989) and wood (Trotter, 1990; Covich & Crowl, 1990; Ehrman & Lamberti, 1992; Webster *et al.*, 1994). S_x is the average distance a particle is transported in the water column before it hits the bottom and is retained.

Particle movement has also been measured by releasing tagged particles (e.g. leaves and sticks), recording locations where the particles are subsequently found on the steam bottom and calculating the average distance travelled (e.g. Webster *et al.*, 1994). Theoretically, searching downstream for a sufficient distance to recover all released particles would give a value identical to S_x. If less distance is searched, the average travel distance underestimates S_x. However, incomplete recovery of particles should not affect the estimate of S_x as long as the probability of recovery does not change with distance.

The efficiency with which organic resources are used in a stream ecosystem is the result of these two opposing factors: breakdown and transport. The objective of this paper is to synthesize a variety of studies of streams at the Coweeta Hydrologic Laboratory to compare biological use versus transport for four categories of particulate organic material: large wood, small wood, leaves and FPOM. This synthesis is based on a number of previously published studies, two unpublished Master's theses and new studies of wood breakdown and transport. We have included descriptions of the methods and results of the unpublished research and summaries of the previously published information.

Site description

The Coweeta Hydrologic Laboratory, a research facility of the USDA Forest Service, is in the Nantahala Mountains in western North Carolina, U.S.A., in the Blue Ridge geological province. The 2185-ha laboratory area is drained by a dendritic network of streams.

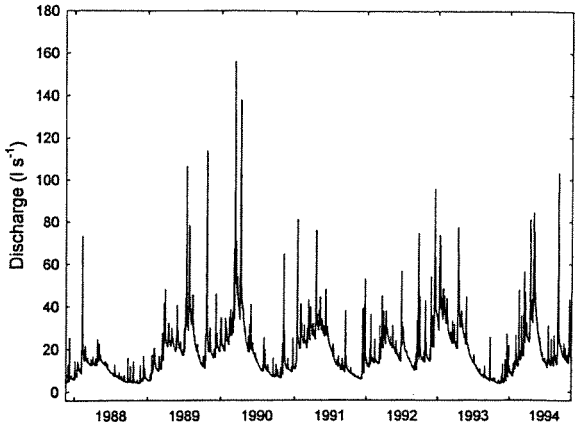

Fig. 1 Discharge in Cunningham Creek (C32) at Coweeta Hydrologic Laboratory between 1988 and 1994. The data were supplied by the U.S. Forest Service.

Two streams, Ball Creek and Shope Fork, join to form Coweeta Creek just upstream of the Coweeta Hydrologic Laboratory boundary. Downstream, Coweeta Creek continues for another 8 km before joining the Little Tennessee River. Coweeta Hydrologic Laboratory is 100% forested with the exception of a small administrative area, and the entire Coweeta Creek catchment is 94% forested, 3% pasture, and 3% residential and miscellaneous (Swank & Bolstad, 1993). The average monthly air temperature ranges from 3 to 22 °C, and annual rainfall varies from 180 cm at lower altitudes to 250 cm at higher altitudes (Swift, Cunningham & Douglass, 1988). Frequent, low-intensity rainstorms occur in all seasons, and the lowest baseflow generally occurs in summer and early autumn (Fig. 1). The entire Coweeta area was logged prior to acquisition by the Forest Service in 1927, and chestnut, *Castanea dentata* (Marsh.) Borkh., formerly dominant, was eliminated by the chestnut blight in the 1930s. Current forest vegetation of reference catchments is mainly deciduous, comprised primarily of oaks, *Quercus* L., hickories, *Carya* Nutt., red maple, *Acer rubrum* L., yellow poplar, *Liriodendron tulipifera* L., dogwood, *Cornus florida* L., and rhododendron, *Rhododendron maximum* L. (Swank & Crossley, 1988). Hemlock, *Tsuga canadensis* (L.) Carr., is also abundant along many streams, especially at higher altitudes.

The information reported in the present study is based on a variety of studies conducted in eleven different streams (Table 1). Most of these streams are small (first and second order), but some data from Ball Creek (third order) and Coweeta Creek (fifth order at its mouth) are included. Most of the small streams drain reference catchments, we have included some data from Hertzler Branch, which drains a catchment planted in white pine, *Pinus strobus* L. The drainage of Ball Creek includes some areas of experimentally logged catchments, and the Coweeta Creek drainage includes some agricultural and residential areas, especially in the valleys along the streams.

Coweeta streams have high gradients, ranging from 1 (Coweeta Creek) to 33 cm m^{-1} (Table 1). The stream substratum is typically cobble and gravel, but areas of bedrock and boulder are common, and considerable sand is present in most areas. Because of the relatively resistant crystalline bedrock, nutrient concentrations are very low in the streams. For streams draining reference catchments, NO_3-N < 0.004 mg L^{-1}, NH_4-N < 0.003 mg L^{-1} and PO_4-P < 0.002 mg L^{-1} (Swank & Waide, 1988). Because of heavy shading by riparian vegetation, primary production is very low in the small streams, and stream food webs are dependent on allochthonous energy sources (e.g. Wallace & Meyer, 1997; Webster *et al.*, 1997).

Materials and methods

Large wood

In July 1988, three logs from a single live yellow poplar tree were placed in Cunningham Creek (Wallace, Webster & Meyer, 1995a). The logs ranged from 20 to 32 cm in diameter and from 2.6 to 3.9 m in length. Just before placing each log in the stream, a 4-cm-wide slice was taken from the end of each log. This slice was measured, dried to constant weight (50 °C) and subsamples were take to obtain percent ash (500 °C). From this information, we were able to calculate the initial density of the logs in g ash free dry mass (AFDM) cm^{-3}. In June 1989 and October 1996, three samples were taken from a submerged portion of each log with a tree corer. Like the initial slices, these cores were measured, dried and ashed to determine density.

Small wood (sticks)

Yellow poplar sticks were collected primarily from the same tree that was used for the log addition study. Other sticks were collected from several saplings and all sticks were from live trees. The sticks were cut into

Table 1 Characteristics of the Coweeta streams used in the present study

Stream	Catchment number	Catchment area (ha)	Altitude (m above MSL)*	Stream gradient (cm m^{-1})	Mean annual discharge (L s^{-1})	Catchment and stream history	References
Bee Tree Branch	53	5.2	820	27	1.06	Reference, stream insecticide treatment 1980†	Wallace *et al.* (1995b)
Stillhouse Branch	54	5.5	841	33	1.45	Reference, stream insecticide treatment 1985–1988†	Wallace *et al.* (1995b)
Satellite Branch	55	7.5	810	20	1.72	Reference, leaf exclusion from stream from 1993 to present†	Wallace *et al.* (1997)
Grady Branch	18	12.5	726	20	3.77	Reference	Webster & Patten (1979), D'Angelo, Webster & Benfield (1991), Whiles & Wallace (1997)
Hertzler Branch	17	13.5	760	25	2.38	Clearcut 1942, white pine planted 1956	Webster & Patten (1979), D'Angelo *et al.* (1991), Whiles & Wallace (1997)
Hard Luck Creek (Upper Ball Creek)	27	38.8	1035	25	20.5	Reference	Huryn & Wallace (1987)
Cunningham Creek	32	42	914	3	–	Reference	Wallace *et al.* (1995a)
Big Hurricane Branch	7	58.7	724	19	18.5	Woodland grazing, clear cut 1977†	Webster *et al.* (1994)
Hugh White Creek	14	61.1	710	15	19.4	Reference	Webster *et al.* (1997)
Ball Creek (multiple sites)	–	199–723	685–922	4–17	85–279	Mostly forest	Tank, Webster & Benfield (1993), Schaeffer (1993)
Coweeta Creek (multiple sites)	–	1587–4350	650–685	≤ 2	600–1642	Mostly forest	Schaeffer (1993), Swank & Bolstad (1994)

*Altitude at gauging station or study sites; (MSL) mean sea level.
†Data from these streams came from studies made prior to disturbance or after recovery from disturbance.

705 35-cm lengths and then trimmed to 30 cm. The longer pieces were wet-weighed, their diameters were measured and they were tagged with numbered aluminium tags. Stick diameters ranged from 1.3 to 3.6 cm. The short pieces were dried to a constant weight (50 °C) and subsamples were taken to obtain percent ash (500 °C). The information from the short pieces was used to determine the initial AFDM of the longer pieces.

A total of 175 sticks was placed in a single area of Cunningham Creek on 22 July 1988. Random samples of between fifteen and twenty sticks were recovered in November 1988, June 1989, May 1990 and June 1991. In June 1992, we collected all the remaining sticks that could be found. Over the 5 years, we recovered 51% of the sticks. On each of the first three collection dates, and on five additional dates during that period, we noted the location of all sticks that they could find. We recorded the distance downstream from the initial release point to the nearest metre. Retrieved sticks were dried (50 °C) and weighed, and subsamples were taken to determine percent ash so that they could calculate AFDM remaining.

In Hertzler Branch, sticks of yellow poplar and white pine were prepared as above. Sticks of each species were collected from live trees. Sixty poplar sticks and 180 pine sticks were placed in Hertzler Branch on 22 November 1988. Nine pine and three poplar sticks were placed at each of 20 sites located at 5-m intervals along the stream. In June 1989, November 1989, June 1991 and June 1992, between five and nineteen poplar, and nineteen to twenty-eight pine sticks were collected and returned to the laboratory. On each of these dates and also in March 1989 and August 1990, we noted the location of each

stick found. In August 1993, we picked up all remaining sticks that we could find. A total of 69% of the pine and 75% of the poplar sticks were recovered. Retrieved sticks were treated as above.

Fine particulate organic matter

FPOM breakdown in Coweeta Creek was estimated by measuring respiration of benthic FPOM from seven sites located 1–13 km from the headwaters (Schaeffer, 1993). Approximately 1 L of FPOM slurry was collected at each site from a variety of patches using a hand vacuum pump with a 1-mm mesh over the intake port. Samples were put on ice and transported to the laboratory. The respiration rate of microbes on the FPOM was measured with a Gilson differential respirometer. Four, 5-mL subsamples of FPOM slurry from each site were placed in 15-mL Gilson flasks with a well containing 0.2 mL of potassium hydroxide to absorb carbon dioxide. FPOM that had been autoclaved for 30 min was used in controls. Measurements were made at the average stream water temperature for the seven sites on the day of collection, values that ranged from 6 to 22 °C over the year. Incubation time varied with temperature, ranging from 3 to 6 h. Samples were then filtered onto glass fibre filters, oven dried at 50 °C, weighed, ashed for 30 min at 550 °C, rewetted, dried and reweighed to obtain AFDM. Respiration rates were calculated (Umbreit, Burris & Stauffer, 1964) and expressed on an AFDM basis.

Ehrman (1994) measured transport distances of FPOM in ten streams, four at Coweeta, four in Montana and two in Indiana. In this study, we used only data from three reference streams at Coweeta, Bee Tree Branch, Satellite Branch and Hugh White Creek. Ehrman (1994) used corn pollen and glass beads as surrogates for natural FPOM, largely following the technique developed by Miller & Georgian (1992). Corn pollen (Polysciences, Inc., Warrington, PA, U.S.A.) has a diameter of about 87 μm (Miller & Georgian, 1992), which is very similar to the mean particle size of natural FPOM from Coweeta streams (Webster *et al.*, 1988). However, corn pollen has a density of 1.09 g cm^{-3} (Miller & Georgian, 1992) compared to natural FPOM density of 1.2 to 1.7 g cm^{-3} for Coweeta streams (Webster *et al.*, 1988). To study higher density particles, Ehrman (1994) used glass beads (Polysciences, Inc.) with a mean diameter of 78 μm and density of 2.48 g cm^{-1}.

Approximately 1 g of corn pollen, stained with basic fuchsin, and 2 g of glass beads were mixed with 4.0 L of water. An electric stirrer was used to keep the particles in suspension as the mixture was released into a well-mixed area of stream over a period of 3.0–3.5 min. Downstream from the release points, at between three and five stations spread over a 20–60-m reach, grab samples of water were taken every 30–60 s for 5–15 min in 500-mL Whirlpak bags. Samples were taken from a turbulent, well-mixed region of the thalweg. In the laboratory, sample volumes were measured and samples were filtered onto 0.45-μm gridded filters. These filters were examined under a dissection microscope at 60× magnification, and all corn pollen and glass beads were counted. Particle concentration was determined for each sample, integrated over time for each station and multiplied by stream discharge to determine the number of particles passing each downstream station. Possible dilution as a result of groundwater inflow was assessed immediately after each particle release by the release and downstream measurement of chloride (Webster & Ehrman, 1996). The rate of corn pollen or glass bead loss from the water column was determined by linear regression of ln(fraction in transport) versus distance from the release.

Results

Large wood

After 4–5 years, we observed that most of the bark had been lost from the upper surfaces of the logs, and after 8 years, there was some evidence of decay on the ends of the logs. However, none of the core samples showed any evidence of decay (e.g. dark colour, holes or texture change) beyond the first 5 mm and no significant decrease in wood density was seen. The initial wood density was 0.407 g AFDM cm^{-3} (SE = 0.003, n = 3). The mean density of the first set of cores (1989) was significantly higher than the initial density (mean = 0.438, SE = 0.005, n = 9; t-test, t = 3.4, P = 0.007). This initial increase in density was perhaps because these first cores contained relatively more bark than the initial slices. The density of the later cores (1996), taken after the bark was gone, was not different than the initial density (mean = 0.406, SE = 0.005, n = 9; t-test, t = 0.11, P = 0.9).

The logs did not move over the 8 years of the present study. Our observations of natural logs in similarly sized streams at Coweeta confirm the conclusion that streams of this size do not move relatively large logs.

Small wood (sticks)

The mean breakdown rate of poplar sticks in Cunningham Creek was 0.00050 day^{-1} (Table 2). Smaller sticks broke down significantly faster than larger sticks. In Hertzler Branch, poplar sticks broke down at 0.00103 day^{-1}, significantly faster than in Cunningham Creek. Pine sticks broke down significantly more slowly than poplar sticks. The differences in breakdown rates among pine sticks of different sizes were not statistically significant but followed the same trend (i.e. small sticks fastest and large sticks slowest) as the poplar sticks (Table 2) and red oak sticks from an earlier study (Golladay & Webster, 1988).

Distances sticks were transported averaged 7.4 cm day^{-1} in Cunningham Creek and less than 0.5 cm day^{-1} in the smaller Hertzler Branch (Table 3). The transport distances of poplar sticks in Cunningham Creek were significantly longer than in Hertzler Branch (*t*-test using mean transport distance during intervals as samples, $P = 0.02$). Transport distances of poplar and pine sticks in Hertzler Branch were not significantly different (paired *t*-test using mean transport distance during intervals as samples, $P = 0.52$). Most of the transport apparently occurred during storms (Fig. 1). In Hertzler Branch, transport distances were significantly related to peak flows (Table 3; linear regression: poplar, $r^2 = 0.87$, $P = 0.006$; pine, $r^2 = 0.80$, $P = 0.02$), but no significant relationship with flow was found in Cunningham Creek (linear regression: $r^2 = 0.08$, $P = 0.53$), perhaps because even relatively small storms were able to move the sticks.

Two other studies of stick transport in Coweeta streams have been published. Webster *et al.* (1994) studied stick transport in Hugh White Creek and Ball Creek. We conducted both long-term and short-term studies using large (length = 60 cm, diameter = 15 mm) and small (length = 30 cm, diameter = 6 mm) wooden dowels. In the long-term studies, they placed between twenty-five and 100 dowels at a site and located each dowel at monthly intervals over 7–12 months. Transport rates ranged from 0.6 to 23.5 cm day^{-1}. In each study, most dowel transport occurred during large storms. Also, longer transport rates were found at more downstream sites. Short-term studies consisted of releasing twenty-five small dowels at each of thirteen sites ranging from 883 to 5420 m downstream from the headwaters of Ball Creek–Coweeta Creek. After 5 min, the distance travelled by each dowel was recorded. Transport distances ranged from 0 to 41 m and increased exponentially downstream.

Wallace *et al.* (1995b) measured transport distances of sticks in Satellite Branch and Bee Tree Branch using 30-cm-long × 6-mm-diameter dowels. They released fifty dowels at each of three sites in each stream. At 3-month intervals for one year, and then after 3 and 4 years, they noted the location of all released dowels. Over the 4 years, dowels moved an average of 1.4 cm day^{-1} in Bee Tree Branch and 2.2 cm day^{-1} in Satellite Branch.

Table 2 Rates of stick breakdown in streams at Coweeta Hydrologic Laboratory. The Hugh White Creek data are from Golladay & Webster (1988). Breakdown rates followed by different letters within a comparison column were significantly different (analysis of covariance, ANCOVA, $\alpha = 0.05$)

Species	Diameter (mm)	Breakdown rate (day^{-1})	ANCOVA				
Cunningham Creek							
Yellow poplar	< 20	0.00062	A				
Yellow poplar	20–25	0.00042	B				
Yellow poplar	> 25	0.00040	B				
Yellow poplar	All	0.00050			A		
Hertzler Branch							
White pine	< 15	0.00028		A			
White pine	15–20	0.00024		A			
White pine	> 20	0.00017		A			
White pine	All	0.00027				A	
Yellow poplar	All	0.00103			B	B	
Hugh White Creek							
Red oak	< 10	0.00044					A
Red oak	10–30	0.00033					B
Red oak	> 30	0.00029					B

Leaves

We located forty published measurements of leaf breakdown for various leaf species done in first- and second-order, undisturbed Coweeta streams (Table 4). In all of these studies, senescent leaves were collected from trees in autumn, air dried, weighed, placed in large-mesh bags, and then placed in the streams in

Table 3 Mean transport distances of sticks placed in Cunningham Creek and Hertzler Branch. The flow data were provided by the USDA Forest Service, Coweeta Hydrologic Laboratory

Dates	Mean transport distance (m day^{-1})		Mean flow during the time period (L s^{-1})	Peak flow during the time period (L s^{-1})
	White pine	Yellow poplar		
Cunningham Creek				
July 1988–November 1988	–	0.091	5.7	16.8
November 1988–January 1989	–	0.0	7.3	17.3
January 1989–March 1989	–	0.072	17.5	48.1
March 1989–June 1989	–	0.072	22.7	40.7
June 1989–October 1989	–	0.114	28.2	113.5
October 1989–November 1989	–	0.103	20.6	46.1
November 1989–May 1990	–	0.065	31.8	155.8
Mean	–	0.074		
Hertzler Branch				
November 1988 – March 1989	0.0041	0.0062	1.5	13.4
March 1989–June 1989	0.0011	0.0	2.7	4.9
June 1989–November 1989	0.0060	0.0052	4.1	20.6
November 1989–August 1990	0.0152	0.0151	4.9	46.6
August 1990–June 1991	0.0010	0.0002	3.3	19.2
June 1991–June 1992	0.0015	0.0	2.1	10.4
Mean	0.0048	0.0044		

late autumn or early winter. Leaf bags were retrieved at intervals until most of the leaf material had disappeared. Retrieved leaves were washed to remove accumulated sediment, and then dried and weighed. Whole samples or subsamples were ashed to determine the AFDM remaining. For all leaves and studies, the average breakdown rate was 0.0098 day^{-1}. There was considerable variability around this number (range = 0.0016–0.0316 day^{-1}; standard deviation = 0.0067 day^{-1}). Most of the variability was caused by the different species studied. Using an analysis of variance (ANOVA) based on ranks (because of the lack of normality and unequal variances), we found significant differences among species ($P < 0.001$), but no differences among streams ($P = 0.27$). In Satellite Branch, breakdown rates of rhododendron and red maple were measured annually from 1985 through 1990. Breakdown rates for the two species were significantly different (ANOVA, $P = 0.001$), but differences among years were not significant ($P = 0.45$).

In two studies conducted at Coweeta, investigators measured transport distances using artificial leaves. Webster *et al.* (1994) used small rectangles of waterproof paper to simulate leaves and measure leaf transport distances. Approximately monthly for one year, twenty-five 'leaves' were released at each of 10 sites in Hugh White Creek. After 5 min, they recorded the distance travelled by each 'leaf'. Transport distances were shorter in summer than winter and were shorter at the downstream than upstream sites. They concluded that transport distances were related primarily to depth and the probability that a leaf in transport would contact an object on the stream bottom. For all sites and dates, the average transport distance was 156 cm.

Wallace *et al.* (1995b) measured the transport distances of artificial and natural leaves in Satellite Branch and Bee Tree Branch. For natural leaves, they used spray painted red maple leaves, and for artificial leaves, they used small triangles of coloured plastic transparency sheets. They released 100 natural and artificial leaves at each of three sites in each stream. At 3-month intervals for one year, and then after 3 and 4 years, they noted the location of all released leaves. Very few of the natural leaves were found after the first 158 days, but during that period, their transport rates were no different than those of artificial leaves. Over the 4-year study, artificial leaves moved an average of 10 m year^{-1} in Bee Tree Branch and 19 m year^{-1} in the slightly larger Satellite Branch.

Table 4 Breakdown rates of leaves in undisturbed first- and second-order steams at Coweeta Hydrologic Laboratory: (C) catchment

Stream; year	Breakdown rate (day^{-1})	Reference
Acer rubrum L.		
Hugh White Creek (C14)	0.0109	Golladay & Webster (1988)
Hugh White Creek (C14)	0.0094	Benfield *et al.* (1991)
Ball Creek (C27)	0.015	Paul & Meyer (1996)
Grady Branch (WS18)	0.0097	Whiles & Wallace (1997)
Satellite Branch (C55); 1985	0.0103	Cuffney, Wallace & Lugthart (1990)
Satellite Branch (C55); 1986	0.0108	Cuffney *et al.* (1990)
Satellite Branch (C55); 1987	0.0095	Cuffney *et al.* (1990)
Satellite Branch (C55); 1988	0.0080	Chung, Wallace & Grubaugh (1993)
Satellite Branch (C55); 1989	0.0075	Chung *et al.* (1993)
Satellite Branch (C55); 1990	0.0090	Chung *et al.* (1993)
Satellite Branch (C55); 1992	0.0160	Whiles & Wallace (1997)
Stillhouse Branch (C54); 1981	0.0138	Wallace *et al.* (1982)
Stillhouse Branch (C54); 1983	0.0141	Wallace, Vogel & Cuffney (1986)
Betula lenta L.		
Grady Branch (WS18)	0.0036	Meyer & Johnson (1983)
Cornus florida L.		
Big Hurricane Branch (C7)	0.0219	Webster & Waide (1982)
Hugh White Creek (C14)	0.0297	Golladay & Webster (1988)
Hugh White Creek (C14)	0.0160	Benfield *et al.* (1991)
Stillhouse Branch (C54); 1981	0.0169	Wallace *et al.* (1982)
Stillhouse Branch (C54); 1983	0.0316	Wallace *et al.* (1986)
Liriodendron tulipifera L.		
Hugh White Creek (C14)	0.0067	Benfield *et al.* (1991)
Ball Creek (C27)	0.016	Paul & Meyer (1996)
Pinus strobus L.		
Grady Branch (C18)	0.0054	Whiles & Wallace (1997)
Satellite Branch (C55); 1992	0.0056	Whiles & Wallace (1997)
Quercus alba L.		
Big Hurricane Branch (C7)	0.0064	Webster & Waide (1982)
Hugh White Creek (C14)	0.0056	Golladay & Webster (1988)
Stillhouse Branch (C54); 1981	0.0108	Wallace *et al.* (1982)
Stillhouse Branch (C54); 1983	0.0105	Wallace *et al.* (1986)
Rhododendron maximum L.		
Big Hurricane Branch (C7)	0.0037	Webster & Waide (1982)
Hugh White Creek (C14)	0.0047	Golladay & Webster (1988)
Hugh White Creek (C14)	0.0016	Benfield *et al.* (1991)
Ball Creek (C27)	0.007	Paul & Meyer (1996)
Satellite Branch (C55); 1985	0.0046	Cuffney *et al.* (1990)
Satellite Branch (C55); 1986	0.0046	Cuffney *et al.* (1990)
Satellite Branch (C55); 1987	0.0032	Cuffney *et al.* (1990)
Satellite Branch (C55); 1988	0.0060	Chung *et al.* (1993)
Satellite Branch (C55); 1989	0.0030	Chung *et al.* (1993)
Satellite Branch (C55); 1990	0.0055	Chung *et al.* (1993)
Stillhouse Branch (C54); 1981	0.0054	Wallace *et al.* (1982)
Stillhouse Branch (C54); 1983	0.0057	Wallace *et al.* (1986)
Robinia pseudoacacia L.		
Grady Branch (WS18)	0.0053	Meyer & Johnson (1983)

Fine particulate organic matter

The mean FPOM respiration rate for all sites was 0.072 μL O_2 mg $AFDM^{-1}$ h^{-1}. Respiration varied seasonally (Fig. 2) and increased with stream temperature at all seven sites (regression: $r^2 = 0.12$, $n = 218$, $P < 0.0001$, respiration log transformed). Respiration

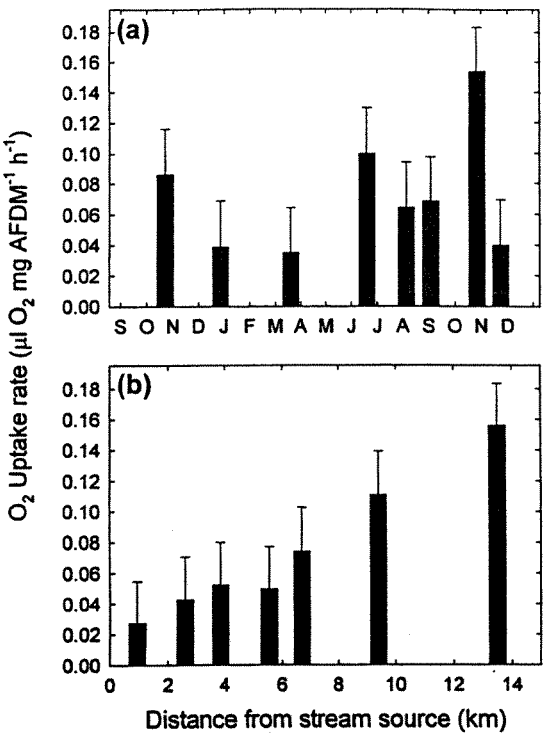

Fig. 2 Respiration of benthic FPOM from Ball Creek–Coweeta Creek at Coweeta Hydrologic Laboratory: (a) means of all sites at different dates; and (b) means of all dates at the different sites. The bars are least-square means with standard errors.

also increased downstream (Fig. 2), averaging 0.027 µL O_2 mg AFDM^{-1} h^{-1} at site 1 (least squares mean of non-transformed data) and 0.156 µL O_2 mg AFDM^{-1} h^{-1} at site 7. This trend was significant for the seven sites (regression of means versus distance: $r^2 = 0.96$, $n = 7$, $P < 0.001$), but was not significant for the four sites within Coweeta Hydrologic Laboratory (regression of means versus distance: $r^2 = 0.79$, $n = 4$, $P = 0.31$). Possible reasons for the increase in FPOM respiration at the sites downstream from Coweeta include higher nutrient concentrations (Swank & Bolstad, 1993), higher temperatures, and less canopy over the stream allowing higher algal production and more labile, algal-derived FPOM.

Based on an average temperature of 12 °C, the mean respiration rate was 2.4 µL O_2 mg AFDM^{-1} h^{-1} for all seven sites or 1.4 µL O_2 mg AFDM^{-1} h^{-1} for the upper four sites. These values are in the same range as those found for similar streams elsewhere in North America (Table 5). Using a respiratory quotient of 1.0, the mean FPOM respiration rate for the upper four sites converts to a decomposition rate of 0.00104 day^{-1}.

Transport distances for both pollen and glass beads were very short (< 10 m) except during high discharge (Table 6). Transport distances increased with

Table 5 Respiration rates reported for stream FPOM

Respiration rate (mg O_2 g AFDM^{-1} day^{-1})	Stream	Size	Reference
2.4	Coweeta Creek, NC; seven sites	0.45 µm to 1 mm	Present study
1.4	Coweeta Creek, NC; upper four sites	0.45 µm to 1 mm	Present study
2.4–9.6	Augusta Creek, MI	0.45–75 µm	Ward & Cummins (1979)
1.0–1.7	Augusta Creek, MI; used in lab study	75–250 µm	Ward & Cummins (1979)
2.6–5.0	*Tipula* faeces	–	Ward & Cummins (1979)
0.7–10.5	McKenzie River drainage, OR	All drifting particles	Naiman & Sedell (1979a)
1–7	Matamek and Moisie River drainages	0.5 µm to 1 mm	Naiman (1983)
1.4–10.6	Salmon River drainage, ID	50 µm to 1 mm	Bott *et al.* (1985)
0.2–2.5	McKenzie River drainage, OR	50 µm to 1 mm	Bott *et al.* (1985)
5.3	McCaughly Creek, MI	1–16 mm, leaf fragments	Petersen *et al.* (1989)
8.6	McCaughly Creek, MI	0.5 µm to 1 mm	Petersen *et al.* (1989)
9.9	McCaughly Creek, MI	0.5–75 µm	Petersen *et al.* (1989)
7.6	Wolf Creek, VA	0.45 µm to 1 mm	Schaeffer (1993)

discharge for both types of particles (pollen: $r^2 = 0.99$, $n = 6$, $P < 0.001$ for slope significantly different than zero; glass beads: $r^2 = 0.54$, $n = 7$, $P = 0.06$). We also regressed transport distances against a variety of other physical variables, including depth, velocity, shear velocity, Reynolds number, Froude number and stream power. Pollen transport distance was significantly related to depth ($r^2 = 0.78$, $n = 6$, $P = 0.02$), and the regression with Reynolds number was close to significant ($r^2 = 0.62$, $n = 6$, $P = 0.06$). The transport distance of glass beads was not related to any physical variable other than discharge ($P > 0.2$ for slope not equal zero for all regressions), whereas Ehrman (1994) found that gradient and shear velocity significantly affected transport distances in ten Coweeta streams that included a much broader range of these variables.

Sinking velocities of both pollen and glass beads were calculated from Stokes' Law using actual stream temperatures. Pollen sinking velocity averaged (± SE) 0.313 ± 0.01 mm s^{-1} and glass beads averaged 3.97 ± 0.12 mm s^{-1}. Webster *et al.* (1988) reported a sinking velocity for natural FPOM (43–105 μm) from Hugh White Creek of 1.19 mm s^{-1}. Even though natural FPOM is a mixture of organic and inorganic particles, with a density between that of pollen and glass beads, it behaves like less dense material because of its irregular shape. Thus, corn pollen is probably a better surrogate for natural FPOM than glass beads.

Our estimates of FPOM transport distances based on corn pollen fit well with results from previous studies (Table 7, Fig. 3). The longest transport distances have been found in the largest streams, which have no significant debris dams or other retention devices (Cushing *et al.*, 1993). However, Hall, Peredney & Meyer (1996) reported even longer particle transport distances for small (2-μm), low density bacterial particles.

Synthesis

Newbold (1992) pointed out that analysis of organic matter dynamics from the perspective of spiralling might provide insight to upstream–downstream linkages in streams. However, he further noted that such an analysis would require determining the rates of transport and transformation (i.e. breakdown) of various forms of organic matter. We are now in a position to attempt such an analysis with data from Coweeta streams.

The turnover length of organic carbon in a stream is the average distance downstream that a reduced (i.e. organic) atom of carbon is transported from the time it enters the stream from terrestrial sources or by autochthonous photosynthesis until its ultimate conversion to CO_2 by metabolic processes (Newbold *et al.*, 1982; Newbold, 1992). Thus, turnover length encompasses both transport and breakdown. Our use of turnover length for organic particles is slightly different than carbon turnover length as defined by Newbold *et al.* (1982), who calculated turnover length as particle velocity divided by carbon respiration rate. To apply this concept to various types of organic particles, we divided by breakdown rate instead, so that the particle turnover length represents the average distance a particle is transported before it is

Table 6 Pollen and glass bead transport lengths measured in three streams at Coweeta Hydrologic Laboratory. The r^2 values indicate the goodness of fit of the exponential model used to calculate transport lengths: (–) no significant uptake; $n = 4$ for most measurements

Date	Discharge (L s^{-1})	Pollen transport length (m)	r^2	Glass bead transport length (m)	r^2
Hugh White Creek					
September 1992	21.1	22.0	0.91	7.5	0.73
October 1992	18.5	–	0.11	6.4	0.99
November 1992	95.6	177.0	0.67	–	0.18
February 1993	30.8	–	0.00	27.8	0.91
August 1993	5.5	9.2	0.98	7.82	0.60
Bee Tree Branch					
November 1992	12.8	8.0	0.98	2.2	1.00
February 1993	6.7	3.5	0.96	9.0	0.44
Satellite Branch					
February 1993	4.6	7.1	0.76	5.8	0.48

Table 7 Transport distances of fine organic particles reported in various studies

Stream	Particle type	Transport distance (m)	Discharge ($L\ s^{-1}$)	Reference
Artificial channels	Ground leaves	4.1–14.5	0.7–2.5	Webster *et al.* (1987)
Dry Branch, NY	Corn pollen	133.0	198	Miller & Georgian (1992)
		122.1	140	
		189.6	178	
Buzzards Branch, VA	^{14}C tagged natural FPOM and ground leaves	11.9	17	Jones & Smock (1991)
		84.0	45	
Colliers Creek, VA		1.8	17	
		29.8	22	
Smiley Creek, ID	^{14}C tagged natural FPOM	800	700	Cushing *et al.* (1993)
		580	680	
Upper Salmon River, ID		630	250	
Hugh White Creek, NC	Bacteria	78	5.7	Hall *et al.* (1996)
		83	4.4	
Coweeta streams, NC	Corn pollen	3.5–177.0	2.0–95.6	Present study

metabolized, converted to dissolved organic material or (in the case of sticks and leaves) converted to FPOM.

Particles in streams do not move downstream continuously, but in a series of saltations consisting of a short time in the water column when the particle travels a 'transport distance' (S_w), followed by a longer time retained on the stream bed (turnover time as a result of transport, T_t) before the next downstream movement. The time a particle spends in the water column during one saltation is the product of S_w and the water velocity (V_w). During this time, the particle is also moving downward a net distance equal to the water depth (D) so that one can calculate a deposition velocity (V_{dep}) as:

$$D_{dep} = DV_w / S_w$$

(e.g. Newbold *et al.*, 1991). Multiplying this number by the water column concentration (C_w) gives the deposition flux (F) of particles from the water column to the stream bed:

$$F = C_w V_{dep}$$

and this flux divided by the benthic standing crop of particles is the turnover time as a result of transport (T_t). The inverse of this turnover time is the transport rate (k'). The time from the start of one saltation to the next is the turnover time plus the time in transport. The average downstream velocity of the particles (V_p) is then the distance travelled divided by the time:

$$V_p = S_w / [T_t + (S_w / V_w)]$$

(Cushing *et al.*, 1993). Finally, turnover length (S_p) is velocity divided by breakdown rate:

$$S_p = V_p / k$$

To synthesize the results presented in this paper, we calculated these parameters for a typical second order Coweeta stream (Table 8). They assumed a discharge of 20 $L\ s^{-1}$ and that the site was 1 km from the headwaters. This would be a stream similar in size

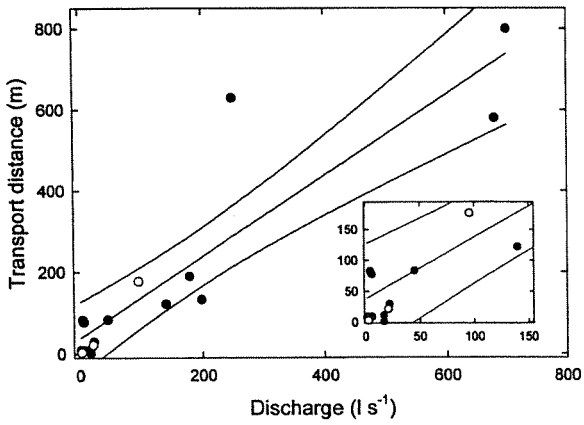

Fig. 3 Transport distances of fine organic particles. The open symbols represent data reported in the present paper, while solid symbols represent data from previously published studies (Table 6). The regression line is for previously published data only and is shown with 95% confidence limits ($r^2 = 0.81$, $n = 13$, $P < 0.001$ for slope greater than zero). The inset shows data points near the origin of the graph.

Table 8 Summary of the transport and breakdown of organic particles in a typical second-order Coweeta stream. This hypothetical stream reach is located 1000 m below the headwaters. It has a discharge of 20 L s^{-1}, an average depth of 10 cm and a velocity of 40 cm s^{-1} (Webster *et al.*, 1994; Wallace *et al.*, 1995a)

Factor	Sticks	Leaves	FPOM
Breakdown rate (k, day^{-1})	0.00050	0.0098	0.00104
Biological turnover time ($T_b = 1/k$, years)	5.5	0.28	2.6
Transport distance (S_w, m)	1.30[a]	1.56[a]	34.5[b]
Deposition velocity (V_{dep}, cm s^{-1})	3.08	2.56	0.116
Water column concentration (mg L^{-1})	–	0.07[c]	2.0[d]
Deposition flux (mg m^{-1} s^{-1})	0.20	1.79	2.32
Benthic standing crop (C_b, g m^{-2})[e]	306.0	228.5	156.5
Transport turnover time (T_t, h)	422	35.6	18.7
Transport rate (k', day^{-1})	0.057	0.674	1.28
Downstream velocity (V_p, m day^{-1})	0.074[f]	1.06	44.1
Particle turnover length (S_p, m)	148	108	42400

[a]Webster *et al.* (1994).
[b]Based on pollen in Fig. 2.
[c]Average of Satellite Branch (Wallace *et al.*, 1995b), Grady Branch (Webster & Patten, 1979) and Big Hurricane Branch (prelogging, Webster, 1977).
[d]Average of reference streams (Webster & Golladay, 1984).
[e]Average of Grady Branch and Hugh White Creek (Golladay, Webster & Benfield, 1989).
[f]Average for sticks in Cunningham Creek.

to Hugh White Creek, Cunningham Creek or Hard Luck Creek (Table 1). Breakdown rates are given in earlier sections of this paper. Biological turnover times (T_b), the inverse of breakdown rates, ranged from nearly 6 years for sticks to a few months for leaves. Our use of the term 'biological turnover time' for sticks and leaves is somewhat misleading since it is based on breakdown rates include any form of mass loss including leaching, physical abrasion, and biological processes of animal consumption and microbial decomposition. However, breakdown studies in Coweeta streams have suggested that biological processes certainly predominate (e.g. Wallace *et al.*, 1982).

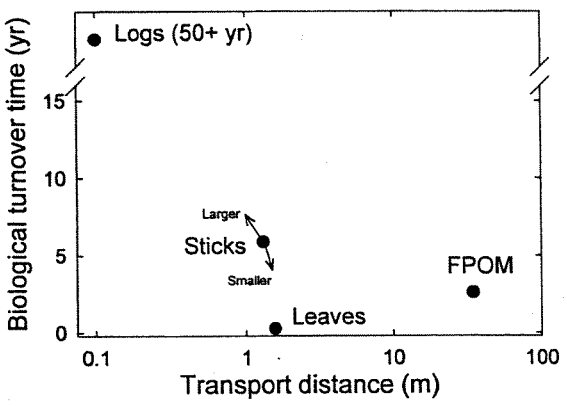

Fig. 4 Transport versus breakdown for organic particles in a typical Coweeta stream.

The transport distance for sticks in Table 8 was taken from the regression of small dowel transport distance versus distance from headwaters given by Webster *et al.* (1994). Their studies suggest that transport distances for larger sticks would be considerably shorter than the 1.3 m used in Table 8. The transport distance for leaves is the average of all measurements made by Webster *et al.* (1994). The FPOM transport distance was calculated from the regression of pollen transport length versus discharge for a stream with a discharge rate of 20 L s^{-1}.

Deposition velocities of sticks and leaves were very rapid (Table 8). However, this terminology is somewhat misleading for these large particles because the distance they are transported in small streams has little to do with the rate at which they sink through the water column, but is related to the probability that they are retained by an object such as a rock or log on the stream bottom instead. Cushing *et al.* (1993) reviewed the theoretical arguments that deposition velocity of small particles should be related to their sinking velocity in still water, as determined from laboratory experiments or calculated from Stokes' Law. Miller & Georgian (1992) found pollen deposition velocity to be very similar to calculated sinking velocity, but the deposition velocity of natural FPOM

measured by Cushing *et al.* (1993) was an order of magnitude below the sinking velocity they measured in the laboratory. Estimated pollen deposition velocity (Table 8) is about four times faster than sinking velocity calculated from Stokes' Law (0.313 mm s^{-1}), but almost identical to the sinking velocity, measured in the laboratory, of natural FPOM of a similar size collected from Hugh White Creek (1.19 mm s^{-1}; Webster *et al.*, 1988).

Deposition fluxes of leaves and FPOM were calculated from published water column concentrations and deposition velocities (Table 8). We do not have data for the 'concentration' of sticks in the water column. Although Wallace *et al.* (1995b) measured transport of wood in three Coweeta streams, the material that they collected consisted primarily of twigs, bark and wood fragments, and seldom included sticks as large as the ones we used to measure transport and breakdown (J. B. Wallace, personal communication). Therefore, the deposition flux for sticks in our study was calculated our measured downstream velocity of sticks in Cunningham Creek.

Deposition fluxes were used with benthic standing crops (Golladay, Webster & Benfield, 1989) to estimate transport turnover times and transport rates. Transport turnover times ranged from 18.7 h for FPOM to 422 h for sticks. Similar calculations have previously been made only for FPOM. Cushing *et al.* (1993) found an FPOM transport turnover time of 13 h, although they noted that the FPOM turnover time would be much longer if they included more deeply buried FPOM. Furthermore, their analyses suggested that surficial material should be divided into two pools, a rapid turnover pool and a slow turnover pool, with turnover times of 1.5–3 h and 17 days, respectively.

Our calculated transport rates were substantially larger than breakdown rates for all three types of particles (Table 8). This means that an organic particle on the stream bottom is more likely to leave that spot by transport than by biological processes. Our calculations of turnover lengths show that sticks and leaves are not transported very far. However, once these larger particles are converted to FPOM by either physical or biological processes, they are transported long distances before ultimately being metabolized. The distance travelled by FPOM is probably much greater than the 42 km indicated in Table 8 because turnover lengths get longer as particles travel downstream (Minshall *et al.*, 1983; Webster *et al.*, 1995; Webster *et al.*, 1997; Young & Huryn, 1997).

Figure 4 is an attempt to synthesize the information discussed above by comparing breakdown to transport graphically. We saw no transport or decomposition of logs, but to include logs in the figure, they used a transport distance of 0.1 m and a biological turnover time of 50 years. From our studies of sticks in Cunningham Creek, small sticks were found to break down more rapidly than large sticks, and Webster *et al.* (1994) found that transport distances of small sticks are greater than that of larger sticks. It is evident from Fig. 4 that, if only logs, sticks and leaves are considered, there is a trend with particle size. The larger organic particles, logs and large sticks are not transported far in streams of this size, and they breakdown slowly. Small sticks and leaves are more easily transported and breakdown rapidly. However, FPOM does not fit this trend. While these fine particles are easily transported, their biological breakdown rate (based on microbial respiration) is more similar to that of wood than leaves, i.e. on the order of years rather than months. Comparisons of the quality of detrital material may help explain Fig. 4.

The quality of detritus has often been related to microbial activity on particles by measuring respiratory activity. Odum & de la Cruz (1967), Fenchel (1970) and Hargrave (1972) demonstrated that microbial respiration on lake and marine detritus generally decreases with increasing particle size. However, no consistent relationship between respiration and particle size has been shown for streams. Naiman & Sedell (1979a) saw no significant relationship between respiration and particle size of suspended particles from two Oregon streams, but there was a significant positive correlation in two other streams, i.e. higher respiration on larger particles. They found significant negative relationships for benthic particles from the same four streams (Naiman & Sedell, 1979b), but pointed out that, because of small samples sizes, respiration rates of small particles were probably overestimated. Naiman (1983) measured FPOM respiration rates that were an order of magnitude higher than those of CPOM, but he noted that considerable algal biomass was associated with this detritus. Also, Bott *et al.* (1985) found higher respiration on FPOM than on CPOM from Idaho streams. Petersen, Cummins & Ward (1989) made an extensive study of respiration on particles in six size categories from

McCaughly Creek, Michigan. They found some of the highest respiration rates on the very smallest particles (0.5–75 μm), whereas leaf fragments (1–16 mm) had lower respiration rates than FPOM (from 0.5 μm to 1 mm). On average, the highest respiration rates were on whole leaves.

Other measures of detritus quality have been similarly inconsistent. Peters, Benfield & Webster (1989) examined seston in four size classes (10–500 μm) from a small stream in Virginia, and found highest glucose mineralization on the smallest particles, similar ATP content on all particles, and highest thymidine incorporation on intermediate-sized particles. They did not compare these fine particles with CPOM, but their FPOM mineralization rates were extremely low. Peters, Webster & Benfield (1987) measured microbial metabolism on FPOM from several small Coweeta streams using mineralization of ^{14}C glucose. While these measurements were only an index of the microbial metabolism on FPOM, rather than a direct measurement of the decomposition of the particle itself, their data suggest extremely low rates of microbial activity on FPOM compared to CPOM. Their data (1987) from Grady Branch suggest breakdown rates in the range of 0.000003–0.000005 day^{-1}, depending on the size of particle.

Sinsabaugh, Weiland & Linkins (1992) found similar levels of cellulase activity among various sizes of FPOM. Suberkropp & Klug (1980) found that FPOM generated by microbes in laboratory experiments was lower in cell wall material than the original leaves. In another laboratory study, Ward (1984) found that FPOM generated from leaves incubated in a laboratory chamber was lower in lignin than whole leaves, but the lignin content of stream-collected FPOM was higher than that of leaves. Earlier, Ward & Cummins (1979) compared the relative quality of leaves, FPOM generated by *Tipula* feeding on leaves and stream-collected FPOM by measuring ATP content, respiration and growth of the chironomid *Paratendipes albimanus* (Meigen) on each substrate. All these criteria indicated that the two types of FPOM represented lower-quality food than the whole leaves and that stream-collected FPOM was the poorest quality material. Furthermore, they concluded that stream-collected FPOM was too refractory to support chironomid development.

The major source of FPOM in small streams at Coweeta is from invertebrate feeding activities, primarily by generation of faeces, and previous studies have shown that removal of invertebrates results in an almost complete elimination of FPOM transport (Wallace *et al.*, 1982; Cuffney, Wallace & Webster, 1984). FPOM may also come from soil particles via bank erosion, aggregation of large molecular weight dissolved organic matter from soil or dust particles blown into the stream or washed off leaves by throughfall. In each case, FPOM is the refractory residue of previous biological activity. However, even though FPOM may be low quality material, it cannot be devoid of nutritional value since many invertebrate collector-gatherers and filter feeders use FPOM with its associated microflora as a food resource.

Our results confirm the findings of many others: sticks and leaves which fall into streams generally break down very close to the point where they enter the stream. However, this breakdown is very inefficient in that only a fraction of the organic carbon is actually converted to CO_2. Some of the material is lost as dissolved organic material, but the major product of breakdown is FPOM. Webster & Meyer (1997) found that streams, especially streams dominated by allochthonous inputs, are inefficient processors of organic matter, generally exporting considerably more material than is metabolized. This exported refractory material may then be transported great distances downstream to settle on the bottom of lakes, reservoirs or even oceans. An estimated 4×10^{14} g of organic carbon is carried by rivers to the ocean annually (Meybeck, 1981; Schlesinger & Melack, 1981), and of this, nearly half is particulate (Meybeck, 1981) and much is refractory (Ittekkot, 1988). While some of this refractory FPOM might be from erosion of soil organic matter (Sollins, Glassman & Dahm, 1985; Hedges *et al.*, 1986) (a product of the terrestrial breakdown of vascular plant material), we suggest that most of these particles are the remains of inefficient processing of allochthonous materials entering small streams throughout forested areas of the world.

Acknowledgments

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