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Processing of confined and naturally entrained leaf litter in a woodland stream ecosystem¹

Abstract—A comparison between stream community processing rates of naturally entrained leaf litter and leaves in packs or 1-mm-mesh bags demonstrated that packs served as a suitable analogue of processing in exposed sites (riffles) whereas bags did not. In riffles, leaves in bags were processed at rates characteristic of litter in depositional zones (pools and alcoves). A length-weight regression method for evaluating the range of microhabitat-related processing rates in stream communities appears suitable. Leaf litter nitrogen levels and increased processing rates by shredders reflected microbial conditioning. Shredders responded to high quality basswood (*Tilia americana*) leaves by increasing their density rather than growth per individual.

Particulate organic matter (POM or detritus) is a major energy source for small woodland streams (orders 1-3; Strahler 1957) (e.g. Fisher and Likens 1973; Cummins 1974; Sedell et al. 1975). POM represents about 50% of the total annual energy flux in headwater woodland streams. Coarse particulate organic matter (CPOM = >1-mm particle size) comprises up to 60% of POM during some seasons (e.g. Fisher and Likens 1973). Coarse wood may dominate CPOM in old growth forested streams. Changes in quantity of stream CPOM through time reflect the associated ecology, and differences in CPOM processing chronicle biotic differences between streams (e.g. Petersen and Cummins 1974; Cummins 1977).

Leaf litter, a dominant component of CPOM, lodges in accumulations, or packs, at the leading edge of obstructions such as cobbles, boulders, and wood debris, in erosional stream areas (riffles-debris jams), and settles out in depositional regions (pools and alcoves) (Cummins 1974; Cummins and Spengler 1978). Lit-

ter processing is fastest in primarily aerobic accumulations exposed to current, largely by biological action rather than by physical abrasion (Petersen and Cummins 1974). CPOM processing is the conversion of leaf litter to some other form, i.e. fine particulate organic matter (FPOM: <1 mm >0.45 μm), dissolved organic matter (DOM: <0.45 μm), animal biomass, and CO₂; microbial conversion to CO₂ is the major component of decomposition. Processing in habitats that are primarily anaerobic involves little or no utilization by aquatic hyphomycete fungi or CPOM shredders and occurs at much slower rates (Cummins 1973, 1974).

Leaf packs—leaves loosely fastened together and tethered in the stream—have been used as an analogue for aerobic leaf processing in streams (e.g. Petersen and Cummins 1974). Mesh bags have also been used in headwater streams to retain some of the small particles resulting from processing (e.g. Mathews and Kowalczewski 1969; Kaushik and Hynes 1971; Iversen 1975; Eidt and Meating 1978). We here compare the processing of loose, naturally entrained leaves with that of leaves confined in packs and mesh bags.

The experiment was done in a 58-m reach of a first-order woodland tributary of Augusta Creek (Kalamazoo Co., Mich.: Mahan and Cummins 1978) from 26 October 1977-3 January 1978. The study section had a 2-m mean width and 0.25-m mean depth and an average fall-winter discharge of 0.032 m³·s⁻¹; it was bounded by a road culvert upstream and Hamilton Lake at the lower end and was divided into two 29-m sections—a control reach upstream and an experimental reach below. Five gravel-cobble riffles constituted about 40% of the stream bottom, the remainder being fine sediment pool, alcove, and slow-flowing depositional habitats. The gradient was about 2%. Moderate amounts of wood debris (about 1

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Table 1. Correlation coefficients (r^2) resulting from regression of leaf dry weight on total leaf length (with petiole) for naturally entrained basswood leaves (n = number) recovered after five intervals from riffle and pool habitats.

Habitat	Interval and date									
	3 d 27 Oct		13 d 9 Nov		25 d 21 Nov		46 d 12 Dec		69 d 4 Jan	
	n	r^2	n	r^2	n	r^2	n	r^2	n	r^2
Riffle-debris jam	—	—	108	0.69	72	0.38	21	0.18	11	0.58
Pool-alcove	—	—	54	0.49	30	0.32	23	0.36	34	0.59
Combined total	106	0.79	162	0.69	102	0.38	45	0.36	45	0.65

kg·m⁻² dry wt) were the major retention structures for natural leaf litter.

The area is forested with ash (*Fraxinus* spp.), red maple (*Acer rubrum*), muscle wood (*Carpinus caroliniana*), and larch (*Larix laricina*). The riparian zone is dominated by shrubs such as dogwood (*Cornus* spp.), rose (*Rosa palustris*), black willow (*Salix nigra*), and *Viburnum lentago*.

There were only two basswood (*Tilia americana*) trees within 100 m of the stream bank along the study reach and these were stripped of all leaves before abscission to prevent any falling into the stream. Three kilograms (dry wt) of other leaves (especially *Cornus*), equal to about 40% of the basswood leaves, were removed from the riparian zone to help compensate for the introduced basswood and to produce total amounts in the normal range.

Seven kilograms (dry wt) of basswood leaves were introduced into the experimental section: 5.8 kg of loose leaves; 100 6-g packs, fastened two to a brick with elastic bands; and 100 18-cm², 1-mm-mesh fiber-glass screen bags, containing 6 g each, tethered to bricks by monofilament lines. A 4-cm-mesh weir was positioned at the downstream end of the study section to control any loss of basswood leaves.

Before introduction of the basswood leaves, sediment cores (30-cm diam, 10-cm depth) were taken in riffles to sample detrital (>0.45 μ m) and associated macroinvertebrate standing crops. Packs, bags, and loose leaves in riffles and pool-alcoves were sampled every 30–70 de-

gree-days (Southwood 1966), or from 10 to 30 days, for the 3 months of the experiment. At the end of the leaf processing study, additional cores were taken from the control and experimental zones for comparison with the original samples. Basswood leaves trapped on the downstream weir were reintroduced daily at the head of the experimental section during the first 20 days of the experiment and every 1–5 days thereafter; the weir was cleaned as needed. Except during the first 3 days and two major spates, the weir captured <1% per day (10–50 individual leaves) of the total amount of basswood introduced.

An initial (i.e. after 3 days of leaching and handling weight loss) length- (blade plus petiole) weight regression was used to estimate weight loss of loose basswood leaves. Leaves that had been in the stream a given length of time were collected, their length and weight measured, and initial weight estimated from the regression. This method worked well with basswood because the major vein and petiole are usually the last tissues processed. Measurements were facilitated by using outlines of a variety of basswood leaf sizes and shapes which were placed in pans of water over which the leaves to be measured were floated. As long as some of the leaf margin and petiole remained, the comparison with shapes provided a check on the integrity of the length of remaining midrib.

Dry weights were determined after at least 72 h at 50°C, ash-free dry wt (AFDW) after at least 6 h at 550°C. Macroinvertebrate biomass was determined

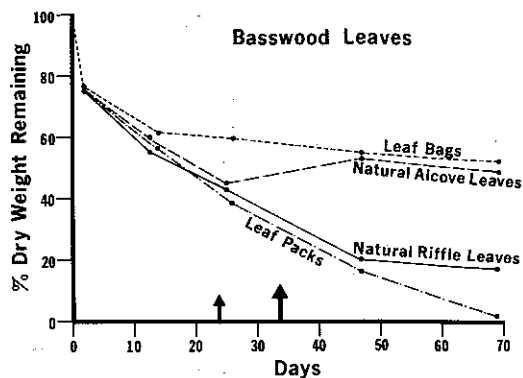


Fig. 1. Comparison of processing (% dry wt remaining) of basswood leaves in leaf packs (on bricks) in mesh bags and natural riffle (exposed) and depositional zone (alcove) accumulations over 70-day study period. (C.V. range, 20-50%; n for leaf packs and bags range, 10-44; n for natural leaves, 22-186.) Arrows indicate major spates.

by individual weighings. Invertebrate functional groups were classified according to Cummins (1973) and Merritt and Cummins (1978).

Examples of the length-dry weight relationship for basswood leaves are given in Table 1. The weight loss of a given leaf was determined as the difference between its processed weight and initial (3 day) weight estimated from its length. The general increase in variance of the

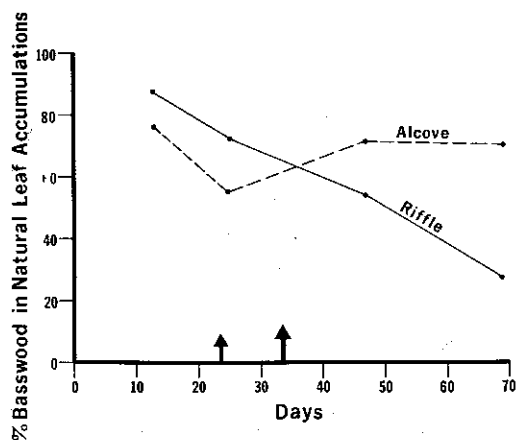


Fig. 2. Comparison of percentage of basswood (by dry wt) in natural litter accumulations between riffle (exposed) and alcove (depositional) sites. Arrows as in Fig. 1.

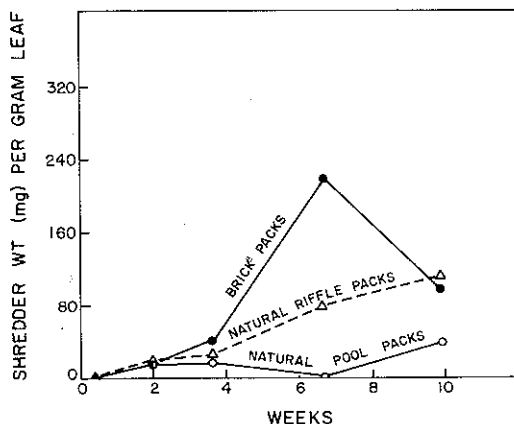


Fig. 3. Comparison of shredder biomass per unit leaf pack weight (dry wt basis) from basswood leaf packs and natural leaf accumulations (containing declining amounts of basswood) in riffle-debris jams and pool-alcove habitats. (Shredders dominated by *Tipula abdominalis*, *Pycnopsyche scabripennis*, and *Pycnopsyche guttifer*; C.V. range, 40-125%.)

regressions with time reflects the greater difficulty of accurate measurement of more processed leaves. However, the weight loss calculations only involved the use of the initial 3-day regression ($r^2 = 0.79$).

Processing rates of basswood brick packs and of loose leaves in exposed riffle sites were not significantly different (C.V. range, 20-50%), although these rates were significantly different from those of leaves in bags or in loose leaf pool-alcove accumulations (C.V. range, 20-40%). Thus leaf packs seem to constitute a suitable analogue for processing rates of natural litter accumulations, whereas leaves enclosed in mesh bags in riffles do not. The low rate of weight loss in mesh bags tracked that of loose leaves in depositional areas; both rates were probably strongly influenced by low oxygen or anaerobic conditions. Processing was primarily microbial, especially in the mesh bags. Except for the exposed surfaces of the uppermost leaves, litter from depositional areas was black, indicating reducing conditions. Processing of the outermost leaves in bags reflected the mesh pattern of the bag, also indicating

Table 2. Inputs of leaf litter to study reach. Based on 11 August–30 December data from 1975 and 1976. Litter classified as fast, medium, or slow according to processing rate (Petersen and Cummins 1974). Inputs measured with fall and bank traps. (Data after Mahan 1980.)

Processing rate	Input range (g·m ⁻¹ bank)	Σ input for period (%)
Fast	0.4–87.7	56.6
Medium	0.2–84.6	41.0
Slow	0–4.0	2.4

the importance of exposure to more aerobic conditions.

Two major spates that equaled (first) or exceeded (second) bankfull (indicated by arrows in Figs. 1 and 2), superimposed on a period of low, fairly stable flow (0.017–0.034 m³·s⁻¹), shifted loose leaves between erosional and depositional sites. In addition, leaves gradually shifted from erosional, rapid processing sites to depositional, slow processing locations during the first 3 weeks of the experiment. This had the apparent effect of increasing the weight loss of loose pool-alcove leaves (Fig. 1). The first major spate occurred the day before the second sample period. The second spate seemed to have less effect than the first on redistribution, resulting primarily in a shift of some alcove leaves to exposed sites. These shifts show as temporal changes in the percentage of basswood in natural riffle and pool-alcove packs (Fig. 2). The fourth sampling (66 days after 3-day controls) indicated that natural, riffle basswood leaves lost less weight than pack leaves. This was probably due to an increase in the relative proportion of leaves that had been recently transported from pool-alcoves to riffle-debris jams.

Shredder feeding has been estimated to account for 20–30% of leaf litter processing (Petersen and Cummins 1974). Shredder densities per unit weight of leaf litter were always higher in the basswood brick packs than in natural leaf accumulations, which showed a pattern of declining percentage of basswood (Fig. 3).

Shredder biomass per unit leaf pack weight peaked after 6 weeks in the bass-

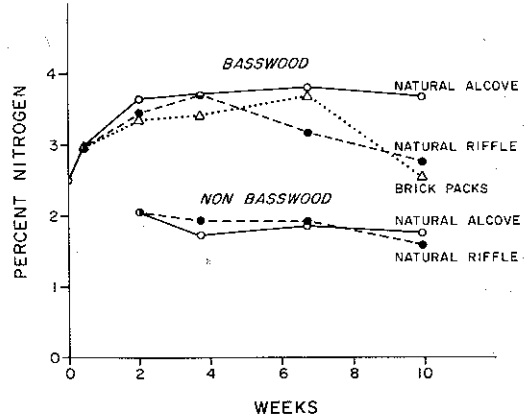


Fig. 4. Nitrogen content as a percentage of total dry weight of prepared basswood leaf packs and basswood and nonbasswood portions of natural riffle and alcove accumulations.

wood brick leaf packs but continued to increase until the last sampling in natural packs (Fig. 3). The continued increase in shredder biomass in natural packs reflected the gradual conditioning of leaf litter dominated by leaves with fast and medium processing rates (Table 2), as well as the inputs of new unconditioned litter during two spates (arrows, Fig. 1). Maximum conditioning of leaves with medium to fast processing rates and associated maximum shredder biomass at between 5–7 weeks has been reported previously (e.g. Cummins and Klug 1979). The decline in shredder biomass and the slight increase in numbers per unit weight of basswood in brick packs at 10 weeks (Fig. 3) reflected the replacement of the heavier shredders (e.g. *Tipula abdominalis* and *Pycnopsycha scabripennis*) with younger individuals and lighter species (e.g. *Pycnopsycha guttifer*). The reduced processing of pool-alcove basswood leaves was related to lower shredder biomass (Fig. 3) and indicates that, as in mesh bags, leaf weight loss was due largely to microbial decomposition.

The percentage of nitrogen, which probably reflects differences in food quality for shredders (Cummins and Klug 1979), was always higher for basswood than for the average of other leaves in the stream (Fig. 4). Loose leaves near the end

Table 3. Comparison of riffle standing crop detritus (30-cm diam, 10-cm depth cores) between control (no basswood leaves) and experimental (basswood added) sections of study reach before (24 October) and after (11 January) introduction (30 October) of basswood leaves. All values are means of two replicates.

Detrital particle size range	Control				Experimental			
	Before		After		Before		After	
	g AFDW · m ⁻²	%	g AFDW · m ⁻²	%	g AFDW · m ⁻²	%	g AFDW · m ⁻²	%
CPOM (>1 mm)	75.6	23.2	49.2	17.0	166.1	28.7	112.3	27.7
FPOM (<1 mm >0.45 μm)	250.2	76.8	239.3	83.0	413.6	71.3	293.1	72.3
Total POM (>0.45 μm)	325.8		288.5		579.7		405.4	

of the experiment had low (alcove) and declining (riffle) processing rates and reduced food quality, as indicated by declining nitrogen levels (Fig. 4). As discussed above, this too may have been the result of redistribution of lower quality alcove leaves that had been exposed to depleted oxygen conditions for varying periods, as well as of the general scarcity of basswood leaves that occupied less exposed sites and were less suitable substrates for continued microbial development.

The study reach normally contains leaf litter characterized by fast and medium processing rates (Table 2). Basswood processing at the study site was previously reported to be about $1.8\% \cdot d^{-1}$ (assuming a negative exponential function: Petersen and Cummins 1974), the fastest rate of any species tested in this first-order stream. However, other leaves in the study reach, with measured processing rates between 0.5 and $1.4\% \cdot d^{-1}$, undoubtedly lessened the impact of basswood leaves on the shredder populations. Shredder densities were at least 10 times higher in the experimental than in the control section, and shredders present upstream at the end of the study were concentrated in the few remaining litter accumulations. In addition, the quantity of CPOM (>1 mm) differed significantly between the control and experimental sections before and after introduction of basswood leaves, and the percentage of CPOM detritus was reduced only in the control section (Table 3). This indicates that changes in shredder populations in response to food quality might be pri-

marily adjustments in density through immigration and increased survival rather than in growth rate. Mundie et al. (1973) found general increases in density and biomass standing crop of macrobenthos, particularly collectors (FPOM-feeding detritivores), when they added hay, cereal grains, and leaves to stream substrates confined in trays. The implication is that food supplements of such high quality are significantly different from the natural detritus normally available (Anderson and Cummins 1979). The shredders apparently recognized the higher quality basswood leaves on the basis of density.

Basswood leaves naturally entrained and in leaf packs had similar processing rates in exposed sites, whereas rates in mesh bags were like the much slower processing typical of depositional pools and alcoves. The slow processing rates of leaves exposed to low oxygen conditions and less used by shredders were also indicated by the continued low weight loss of alcove (5.4%) and mesh-bag enclosed (9.0%) leaves over a 105-day period (4 January–14 April) after processing of brick packs and natural riffle leaves was essentially complete. Our results are further documentation that physical abrasion is subordinate to biological processing in headwater streams (Petersen and Cummins 1974). Packs can be used to estimate aerobic CPOM processing and confinement in mesh bags yields rates similar to those observed in depositional habitats. However, the length-weight method for unconfined leaves (rather than bags and packs) seems promising for

generally integrating community differences over the range of headwater stream habitats. The technique may be particularly useful because exotic leaves (e.g. eastern hickory in western streams: Cummins unpubl.) are processed by native stream biota at the predicted rates (Petersen and Cummins 1974). Such introduced leaves could serve as convenient markers in studies of CPOM processing in headwater streams.

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