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Size distribution and lignin content of fine particulate organic matter (FPOM) from microbially processed leaves in an artificial stream

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With 2 figures and 2 tables in the text

Introduction

As one of the major functional attributes of stream ecosystems, the processing and decomposition of organic inputs has received considerable recent attention, in particular rates and mechanisms for processing of coarse particulate organic matter (CPOM) such as leaves, needles, and wood (Kaushik & Hynes 1968; Cummins 1974; Petersen & Cummins 1974; Sedell et al. 1974; Suberkropp & Klug 1976; Triska & Cromack 1979). Community processing of CPOM results in the leaching of dissolved organic matter (DOM), production of CO_2, consumer biomass, and fine particle organic matter (FPOM). This latter detrital fraction, defined as particles < 1 mm $\geq 0.45\,\mu$m diameter, occurs as a result of physical fragmentation, consumption and defecation by leaf shredding invertebrates, and by the metabolism of attached microbes.

One of the important microbial agents of leaf processing in stream environments is aquatic hyphomycete fungi (Suberkropp & Klug 1976). Many species of these fungi produce enzymes which degrade cellulose and hemicellulose, as well as pectic compounds that hold together individual leaf cells. With this enzymatic capability, aquatic hyphomycete fungi have the ability to completely skeletonize leaf litter, and in the process release mesophyll cells to become part of the FPOM pool (Suberkropp & Klug 1980).

Because FPOM represents a major dietary component of many stream insects, and because it is an energy and carbon source for microbiota, it is important to understand the sources and fates of FPOM as well as the chemical make-up of the particles. Fine detritus, newly derived from leaf litter, potentially represents a more utilizable food resource for detritivores than native detritus (Ward & Cummins 1979) and may in fact be of higher quality than the original leaf litter. Suberkropp & Klug (1980) demonstrated that FPOM sloughed from leaf litter following microbial processing contained less cellulose and hemicellulose than the original leaf litter. The lack of these compounds, for the most part not utilizable by detritivores, should allow such FPOM to be more nutritious for invertebrates.

With this in mind, the present work had three objectives: 1) to estimate from laboratory experiments the amount of leaf litter which could be expected to enter the FPOM pool during microbial processing; 2) to document the particle size distribution of microbially produced FPOM; 3) to determine the content of lignin present in microbially produced FPOM.

Methods

For a period of 21 weeks leaves of pignut hickory (*Carya glabra*) were incubated in a recirculating, plexiglass chamber (2.5 m × 30 cm × 21 cm) containing 70 l of stream water held at 10 °C ± 2 °C. At weekly intervals, after removing the leaf litter, water and all accumulated FPOM were passed through a series of sieves to size fraction the FPOM, after which leaf litter was returned to the chamber and fresh stream water added. Each time water was changed, fresh stream water from nearby Augusta Creek (Southwestern lower Michigan, U.S.A.) (Cummins et al. 1981) was first passed through a 53 μm sieve to remove large FPOM particles, and a 1 l subsample then filtered on to GF/F filters to determine a correction for the mass of particles $< 53\,\mu$m added to the

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chamber. Never did the FPOM added in fresh stream water equal 1 % of the weekly FPOM accumulation. Particle size frequency distributions were determined for 5 size ranges (1.0—0.5 mm, 0.5—0.25 mm; 0.25—0.125 mm, 0.125—0.053 mm; 0.053—0.00045 mm) but for lignin analyses (GOERING & VAN SOEST 1972) two size classes (1.0—0.5 mm and 0.5—0.25 mm) were combined.

Leaf weight loss was determined by harvesting 3 preweighed and numbered leaves at weekly intervals. However, after 10 weeks, leaves had softened to such an extent that the numbered tags stapled around the leaf midribs became detached. With the exception of the final point, the remaining weekly determinations of % leaf weight remaining were calculated by subtracting losses for each week (FPOM sloughing, CPOM fragmentation, and respiration) from the weight remaining for the previous week.

Respiration rates of the microbial community attached to leaves were determined weekly by placing approximately 10 g of leaves in closed 12 l plexiglass chambers (BOTT et al. 1979) and measuring O_2 loss overnight (YSI 54 ARC oxygen meter). Oxygen consumption values were converted to organic matter loss by assuming an RQ of 0.83.

Results and discussion

The first objective of this study was to determine the potential amount of FPOM which could be released from leaf litter under conditions of microbial processing alone. The experimental design allowed a partitioning of leaf weight losses among five categories. Losses were determined for initial 5 day leaching loss, fragmentation of particles >1 mm, losses to FPOM release, and weight loss due to microbial respiration. The summation of these losses over a 142 day period differed from actual weight loss by less than 1 %.

After 142 days processing at 10 °C, only 13 % of the original leaf material remained, and consisted mainly of veins and veinlets. Leaching losses accounted for 21 % of the original dry weight, CPOM fragmentation 4 %, FPOM sloughing 33 %, and mineralization 29 % (Table 1).

Production of FPOM was slow during the first seven weeks, as was total weight loss, however, weight loss rates increased greatly in the latter stages of processing when most of the FPOM was released. Peak FPOM release occurred during the 13th week of incubation, while relatively large amounts of release occurred between day 80—101, when 50 % of all FPOM accumulated (Fig. 1). To some extent the experimental conditions perhaps contributed to the weight loss pattern. The slow current speeds in the chamber ($\sim 3\,cm \cdot s^{-1}$) allowed tissue only partially loosened by microbial enzymatic activity to adhere to leaf surfaces longer than would have been the case if there had been more agitation. Had there been more agitation, weight loss rates would have been more constant as partially loosened FPOM would have been continually shaken off, eliminating any pulse in FPOM release. However, this pulsed pattern of FPOM release has been previously ob-

Table 1. Partitioning of weight losses from pignut hickory (*Carya glabra*) as a result of 142 days microbial/physical processing at 10 °C in an artificial stream.

	% of original dry weight
Weight remaining	13
Weight loss	87
Leaching	21
CPOM fragmentation	4
FPOM sloughing	33
Microbial respiration	29

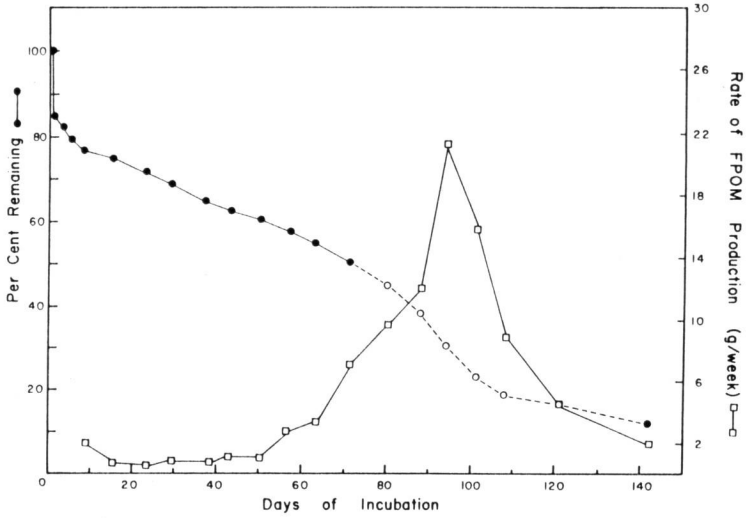

Fig. 1. Pattern of CPOM weight loss and FPOM production during microbial/physical processing of pignut hickory leaves (*Carya glabra*) in an artificial stream. Determinations of per cent leaf weight remaining from preweighed leaves are denoted by solid circles, while open circles denote calculations of per cent remaining based on summations of various sources of weight loss. See text for details.

served during an experiment reported by SUBERKROPP et al. (1975). Here leaves of green ash (*Fraxinus americana*) were incubated in large artificial stream channels (6000 l) (CUMMINS 1971) where stream size and current speed were similar to local first-order streams. After 60 days processing at 10 °C large quantities of FPOM were released from the leaves over a two day period, as the leaves seemingly "fell apart". So much FPOM was produced that the water became extremely turbid, and so much mass was lost from the leaf packs that further determinations of leaf weight loss rates were not possible.

In the present experiment the majority of the FPOM released was $< 53\,\mu m \geq 0.45\,\mu m$ in diameter. Overall 71 % of all FPOM was in this smallest size class. 12 % occurred in the next largest size class, $> 53\,\mu m < 125\,\mu m$, while approximately equal amounts were measured in each of the three larger size classes (Fig. 2). For a large majority of sample dates, the smallest size class dominated. The two largest size classes were dominant only during the first 3 weeks and again in the weeks following peak FPOM release.

In general FPOM particles collected in this study were not as clearly identifiable as were those reported by SUBERKROPP & KLUG (1980). They recovered FPOM particles from pignut hickory leaves clearly recognizable as mesophyll cells. During the early weeks of the present study, flakes resembling cuticle were observed under the light microscope as well as many amorphous masses of tissue. This latter particle type, by far the most dominant, appeared to be fragments of completely macerated tissue imbedded with fungal hyphae. Particles in the larger size ranges (< 1 mm ≥ 0.250 mm) often contained fragments of skeletonized leaves. These occurred either as transparent sheets containing venation or simply as pieces of the venation.

These observations of particle composition support results of the lignin analyses. Data from SUBERKROPP & KLUG (1980) indicated that fine particle detritus derived from

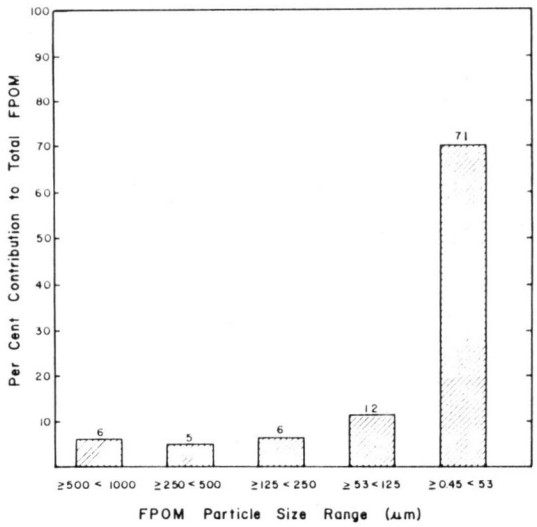

Fig. 2. Size distribution of FPOM generated during microbial/physical processing of pignut hickory leaves (*Carya glabra*) in an artificial stream.

Table 2. Lignin content of pignut hickory leaves and fine particulate detritus released as a result of the activity of attached microbes. Presented is the lignin content of leaves and FPOM from four periods during the leaf incubation and four particle size ranges.

Days of incubation	Leaves	Particle lignin content (% of AFDW)			
		1–0.250 mm	0.250–0.125 mm	0.125–0.053 mm	0.053–0.00045 mm
1– 50	10.7	17.4	–	10.1	7.5
50– 80	13.6	26.5	12.7	6.7	8.5
80–101	17.7	20.3	9.9	2.7	8.1
101–142	22.7	26.2	14.9	8.6	10.2

pignut hickory leaves contained less cellulose and hemicellulose than did the original leaf litter. For this study, a weighted average of particle size composition would support that observation, however, examination of the lignin content of FPOM, broken down by particle size, indicated that substantial differences in lignin content occurred in leaves and FPOM as well as between large and small particle sizes.

Particles >0.25 mm diameter contained a higher proportion of lignin than did leaves, while particles <0.125 mm contained much less lignin than either leaves or the larger particles (Table 2). The size fraction <0.25 ⩾ 0.125 mm was intermediate. The increased lignin content of larger FPOM sizes apparently occurred as a result of the fragmentation of partially skeletonized portions of leaves. Since the fragments retained the venation but had fewer mesophyll cells, lignin constituted a greater proportion of the organic matter. This would be consistent with the microscopic observations of particles discussed earlier.

Smaller FPOM contained much less lignin, and consisted mainly of macerated mesophyll cells. Although plant cells do contain lignin in cell walls, this detrital matter was not enriched with the lignified venation found in larger FPOM and in leaves.

These results have implications in several areas. First, the higher respiratory activity of small particle sediments has been attributed, in part, to a function of surface area (HARGRAVE 1972). No doubt that is true, but there may also be a substrate quality effect. In the present example, in addition to having greater surface area, smaller particles have a lower content of lignin. Given two particles of similar size and mass, the one with the smaller lignin content should exhibit a higher mass specific respiratory rate. Lignin, a substrate which supports only very low levels of microbial respiration in stream sediments, acts only to dilute the more easily metabolized compounds, thereby reducing particle respiration rates. Thus, if the more labile substances in larger particle sizes are diluted to a greater extent by lignin, this should reinforce surface area effects which produce higher respiratory rates in smaller particles.

Smaller mesophyll derived particles represent an input of relatively high quality detritus to a native FPOM pool that has a large percentage of low quality, recalcitrant lignin. Small size classes of native FPOM contain 30—35 % lignin (G. M. WARD unpubl. data), thus fragments of mesophyll tissue which contain only 8—10 % lignin, and likely a larger amount of more utilizable compounds, might be assimilated with greater efficiency by invertebrates as well as having the potential for rapid mineralization by microbes. By comparison, only particles from the completely skeletonized leaf would not represent a more nutritious detritus than native FPOM.

Because of the seasonal nature of leaf fall, the timing of mesophyll derived inputs of FPOM should also be pulsed. WARD & CUMMINS (1978, 1979), in describing the life history of the chironomid *Paratendipes albimanus*, noted a spurt in growth of I and II instar larvae during fall, following several months of growth inactivity during July, August and early September. Although no definite link between autumnal leaf fall, the generation of FPOM, and the stimulation of growth can be established, freshly produced detritus does seem to provide a relatively rich source of detrital food. Laboratory experiments with *P. albimanus* demonstrated that the summer lull in development could be broken by substituting ground leaves for native FPOM. It therefore is possible that if after months of microbial processing native FPOM may become too refractory to support insect development. If so, these fall inputs of FPOM from leaf litter represent an annual renewal of high quality detritus, necessary, in part, for completion of some insect life cycles.

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