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Lignin and cellulose content of benthic fine particulate organic matter (FPOM) in Oregon Cascade Mountain streams

G. MILTON WARD

Aquatic Biology Program, Department of Biology, University of Alabama, Tuscaloosa, Alabama 35487 USA

Abstract. Compared to leaf litter, benthic fine particulate organic matter (FPOM) is considered very refractory. FPOM exhibits high carbon to nitrogen ratios, low respiratory rates, and is a relatively poor food source for invertebrates. However, little more is known of the qualitative nature of benthic FPOM, the nature of FPOM processing, or the relationship between benthic FPOM chemical composition and sources of organic matter to a stream system. In this study, qualitative characteristics of benthic FPOM were compared at three sites in the Oregon Cascade Mountains that received either conifer litter, alder leaves, or herbaceous and algal inputs. FPOM from these streams contained approximately 45% lignin and 10-15% cellulose (ash-free dry weight). Lignin content of particles >1 mm was almost 60% whereas in those <0.01 mm it was 30-40%. Based on qualitative differences between known organic matter inputs to these streams, lignin content in FPOM at the conifer site was predicted to be greater than that at the alder site, and to be least at the open site. No seasonal or site related patterns in FPOM lignin or cellulose content were found regardless of the type of canopy cover or aerial allochthonous inputs. FPOM respiration rates were predicted to follow the reverse pattern, highest at the open site and lowest at the conifer site. Respiratory rates at the open site were usually greater than those at the forested sites; but rates were not consistently lowest at the conifer site. Similarities in FPOM lignin and cellulose content and respiration rates among sites suggest that the qualitative characteristics of FPOM are not necessarily regulated by the qualitative characteristics of canopy inputs alone. Additional and as yet unquantified inputs of high lignin-containing allochthonous FPOM, such as soil or wood, may override differences of leaf litter inputs among these three sites.

Key words: lignin, cellulose, FPOM, benthos, Oregon, detritus, respiration, ecosystem stability.

Fine particulate organic matter (FPOM) is a quantitatively important component of the detrital structure of stream ecosystems (Cummins et al. 1981, Minshall et al. 1983, Wallace et al. 1982). In forested headwater streams, FPOM (<1 mm≥0.45 m) can constitute approximately 3-87% of the total benthic POM (Cummins et al. 1981, Triska et al. 1982), depending on site characteristics and the abundance of large woody debris (or its inclusion in the calculations). FPOM also serves as a primary food source for many detritivores (Cummins and Klug 1979), as well as an energy and nutrient source for attached bacteria.

FPOM in woodland stream ecosystems is derived from a variety of sources. Much of the FPOM in woodland streams is presumed to result from community processing of leaf and needle litter inputs, but sources such as woody debris, riparian soil particles, flocculated dissolved organic matter, and autochthonous plant production may also contribute to FPOM. The relative importances of these sources, however, have not been studied.

The importance of riparian inputs to shredder populations (Molles 1982) and the role of canopy cover for fish community structure have been documented (Molles 1982, Wilzbach and Hall 1985), but little is known about the nature of qualitative or quantitative linkages between riparian vegetation inputs and benthic FPOM. One potential linkage is through the qualitative differences among litter types. Litter types are known to vary in processing rates, carbon to nitrogen ratios (C/N), percent lignin, lignin to nitrogen ratios, and respiration rates (Melillo et al. 1982, Petersen and Cummins 1974, Triska et al. 1975, Ward and Woods 1986), and litter quality is known to affect metabolic rates of associated microbes as well as growth of macroinvertebrates (Brunnell et al. 1977, Iversen 1974). One could predict that slowly processed litter such as Douglas-fir needles (which have a rather high percent lignin: 25%) would produce FPOM equally as slow to be processed, whereas the FPOM from leaves such as red alder (which contain much less lignin: 10%) and are processed very rapidly (Sedell et al. 1975, Triska et al. 1975) might also be decomposed rapidly. Therefore, qualitative characteristics of litter inputs might produce corresponding characteristics in the quality of benthic FPOM.

The removal of canopy cover from a stream may also have an influence on the qualitative character of benthic FPOM. Increased algal production which accompanies the removal of canopy cover will alter the proportions of allochthonous and autochthonous inputs. Increases in primary production should increase inputs of algal detritus, a far more labile type of FPOM than that from leaf litter.

To assess the interactions between riparian canopy inputs and benthic FPOM, qualitative characteristics of FPOM must first be determined. The few existing studies of these characteristics have suggested that benthic FPOM is rather refractory, as indicated by the high C/N ratios, low respiratory rates, and low microbial biomass (ATP) (Naiman and Sedell 1979, Ward and Cummins 1979). In addition, feeding studies have shown that FPOM is nutritionally poor for stream invertebrates (Benke and Wallace 1980, Fuller and Mackay 1981, Ward and Cummins 1979). In contrast, the FPOM freshly generated during litter processing is similar in lignin and fiber content to that of the original leaf (Suberkropp and Klug 1980, Ward 1984, Ward and Woods 1986) and therefore should be more labile than resident FPOM. Freshly generated FPOM could be important in supporting macroinvertebrate growth and benthic microbial metabolism.

Questions regarding linkages between organic matter inputs and FPOM pools were addressed in this study by comparing qualitative characteristics of benthic FPOM among sites receiving either coniferous (Douglas-fir), deciduous (red alder), or herbaceous + algal inputs. Given the wide differences in lignin content and processing rates among these potential inputs, it was hypothesized that benthic FPOM at the open-canopied site would have lower percent lignin, higher respiratory activity, and greater amounts of algal detritus than FPOM in streams flowing in forested watersheds. FPOM in the conifer watershed would have the highest percent lignin, lowest respiratory rate, and least algal detritus. Percent lignin was chosen for study because of the large initial differences among conifer, alder, and algal detritus, and because it is a measure of a major refractory compound that could influence sys-

TABLE 1. Sample site characteristics. All sites were located in or near the H. J. Andrews Experimental Forest on the west slope of the Oregon Cascade Mountains. Further descriptions can be found in Triska et al. (1982) and Wilzbach and Hall (1985).

Site	Stream Order	Width (m)	Elevation (m)	Temperature (°C)	Light[a] (%)	Stand Age (y)	Allochthonous Inputs (g AFDW m^{-2} y^{-1})	Riparian Vegetation
Grasshopper Creek	3	6	915	4–15	100	5	92	herbs and shrubs
Quartz Creek	3	4	515	4–15	8	35	459	red alder
Mack Creek	3	3	760	4–15	5	450	369	Douglas-fir and western hemlock

[a] Percent of full sunlight penetrating canopy, measured at water surface.

tem metabolic rates. Detritus respiration was used as a direct measure of microbial utilization of detritus. Phaeophytin in benthic FPOM provided a measure of autochthonously produced FPOM.

Study Sites

All study sites are in the McKenzie River drainage in or near the H. J. Andrews Experimental Forest (HJAEF) on the west slope of the Oregon Cascade Mountains. The intensively studied sites, Mack Creek, Quartz Creek, and Grasshopper Creek, are 3rd-order streams having similar slope, parent material, temperature regime, and discharge, but differing in the composition of riparian vegetation (Table 1). At one time all three streams flowed through dense stands of old-growth Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). However, the old-growth timber at Grasshopper Creek was clear-cut in 1977, and the site was without canopy during the present study. Herbs such as fireweed (*Epilobium angustifolium*), colts-foot (*Petasites frigidus*), devil's club (*Oplopanax horridum*), and shrubs such as willow (*Salix sitchensis*) dominated the riparian vegetation. The Quartz Creek watershed was clear-cut in 1947 and the stream channel was dominated by a closed canopy of red alder (*Alnus rubra*). Old-growth vegetation at Mack Creek remains intact.

Methods

Detrital collections at Mack, Quartz, and Grasshopper Creeks were made during the summers of 1982 and 1983, and in fall 1982 and spring 1983. Three stream reaches separated by at least 50 m were selected at each site. Samples of detritus from depositional areas were removed from stream sediments with a small scoop and sieved wet through a series of seven screens and nitex nets: 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.053 mm, 0.037 mm, 0.01 mm. Water that passed through the 0.01 mm net was subsampled and particles concentrated by centrifugation. To initially confirm that this method removed all particles >0.45 μm, supernatant water was drawn through GF/F filters, and the filters dried and changes in weight determined. Quantitative estimates of FPOM standing crops at these sites were reported by Speaker (1985). Qualitative samples of FPOM were also collected at six other sites in the McKenzie River watershed for comparison of lignin and cellulose content of FPOM among stream orders. In these samples, particles 0.053–1 mm diameter were retained as a single size range.

Following size separation in the field, samples were transported on ice to the lab where fresh detritus was removed from each fraction for chlorophyll *a*, phaeophytin, and respiratory measurements. FPOM respiration rates were obtained by placing approximately 50 mg dry weight (DW) of each particle size into 30 ml serum vials containing 1 ml of filtered stream water. Vials were stoppered and incubated in the dark at the same temperature as the stream when samples were collected. Temperature differences among sites were 2°C or less on any one date. Sample vials were shaken at 15 min intervals by hand. After 1 hr of acclimation, and at hourly intervals thereafter for 3 hr, 0.25 ml of headspace gas was analyzed for CO_2 by gas chromatography (H-P 5830 equipped with Porapak Q column). Respiratory rates (μg C g $AFDW^{-1}$ hr^{-1}) were determined through CO_2 accumulation rates in headspace gas. In the vast majority of cases linearity in CO_2 production rates was maintained throughout the incubations, and all reported data were calculated from linear portions of the CO_2 curves. For FPOM >0.01 mm, filtered stream water was used as a control, and for particles <0.01 mm, filtered stream water + millipore filter were used.

Samples for chlorophyll *a* and phaeophytin analyses were weighed wet, frozen, ground, and extracted with basic 90% acetone. Extracts were filtered through GF/F filters and analyzed by the monochromatic method (Wetzel and Likens 1979). A separate set of samples was weighed wet, weighed dry, and ashed for calculation of a wet weight: AFDW ratio.

Acid-detergent lignin and cellulose determinations followed the method of Goering and Van Soest (1970), as modified by Mould and Robbins (1981). Subsamples of dried material from each particle size were analyzed. Results were corrected for acid-soluble and insoluble ash content.

Results and Discussion

Organic matter inputs

The land use histories of the Mack Creek, Quartz Creek, and Grasshopper Creek watersheds have resulted in very different ripar-

TABLE 2. (A) Litter inputs to Mack Creek (Conifer), Quartz Creek (Alder), and Grasshopper Creek (Open) and (B) Composition of litter inputs to three nearby streams with similar riparian vegetation.

A. Source	Conifer $g\ m^{-2}\ y^{-1}$ (%)	Alder $g\ m^{-2}\ y^{-1}$ (%)	Open $g\ m^{-2}\ y^{-1}$ (%)
Herbaceous litter	17 (5)	39 (8)	66 (72)
Tree and shrub litter	352 (95)	420 (92)	26 (28)
Total litter inputs	369	459	92

B. Source	Conifer (WS 2)[a] $g\ m^{-2}\ y^{-1}$ (%)	Alder (B301)[a] $g\ m^{-2}\ y^{-1}$ (%)	Open (WS 10)[a] $g\ m^{-2}\ y^{-1}$ (%)
Needles	90 (37)	8 (2)	1 (2)
Leaves	64 (26)	332 (73)	25 (60)
CTBW[b]	76 (31)	96 (21)	15 (36)
Miscellaneous	16 (6)	21 (4)	1 (2)
Total Inputs	246	457	42

[a] Three 2nd order sites in HJAEF: WS 2—Watershed 2; B301—unnamed tributary to Blue River near WS 10; WS 10—Watershed 10.
[b] Cones, twigs, bark, and wood.

ian vegetation structures at each site. Differences in species composition have produced both qualitative and quantitative differences in allochthonous organic matter inputs to stream channel systems (Table 2A). Allochthonous inputs were greatest at Quartz Creek and least at Grasshopper Creek. Inputs to Mack Creek consisted primarily of tree and shrub litter, and very little herbaceous litter (5%). Allochthonous inputs to Quartz Creek were primarily alder leaves with little herb input. In contrast, 70% of allochthonous inputs to Grasshopper Creek (open site) were herbaceous (Table 2A).

Data from a previous study of nearby watersheds differing in riparian vegetation are useful in further demonstrating qualitative differences in allochthonous inputs (Table 2B). Almost 70% of inputs from old-growth Douglas-fir and western hemlock forest consisted of needles and woody plant parts (cones, twigs, bark, and wood), whereas leaves were the most abundant input at alder-dominated sites. An open canopied stream also had high percentages of leaf litter input (Table 2B), but, as shown above, inputs in such streams are primarily herbaceous.

Qualitative differences have also been observed in the percent of lignin initially present in inputs (Table 3). Douglas-fir needles, the major input source at Mack Creek, contain relatively high initial amounts of lignin (24%) and cellulose (15%), and wood chips, twigs, and bark are 31–48% lignin. The dominant litter type at Quartz Creek, red alder, contains only 10% lignin and 9% cellulose. Herbaceous litter inputs, most abundant at Grasshopper Creek, also contain much less lignin than conifer litter, but an amount similar to that of alder litter. Algal detritus, of course, would contain no lignin.

Removal of the canopy at Grasshopper Creek reduced the amounts of allochthonous inputs, but increased the quantity of autochthonous detritus. Algal production was greatest at this open site (75 $g\ C\ m^{-2}\ y^{-1}$), 2× that at the alder site, and 4× that at the conifer site (Ward et al. 1982). Mean concentrations of chlorophyll *a* in benthic FPOM were highest at the open site (60 $\mu g/g$ AFDW), 2× to 3× greater than those at either of the two forested sites (Table 4). Average chlorophyll *a* concentrations in FPOM at the conifer site (21 $\mu g/g$ AFDW) and the alder site (29 $\mu g/g$ AFDW) were similar. Only at the open site were there differences related to particle size, particles <0.01 mm containing an average 102 $\mu g/g$ AFDW chlorophyll *a*, whereas larger particles contained 60% of that amount or less (Table 4).

Chlorophyll *a* degradation products such as phaeophytin can be used as a measure of algal detritus in benthic FPOM. Phaeophytin in benthic FPOM was highest (201 $\mu g/g$ AFDW) at the open site and lowest at the conifer site (69

TABLE 3. Percent lignin and cellulose in organic matter inputs to Mack, Quartz, and Grasshopper Creeks. Values are ash-free dry weight except where dry weight (DW) noted.

Source	% Lignin	% Cellulose	Reference
Red alder leaves	9.5	9.0	Triska et al. 1975
Douglas-fir needles	24.2	14.5	Triska et al. 1975
Vine maple leaves	8.5	14.7	Triska et al. 1975
Big leaf maple leaves	17.3	16.3	Triska et al. 1975
Fireweed (DW)	5.4	10.9	S. V. Gregory (unpublished)
Sweet coltsfoot (DW)	11.3	21.3	S. V. Gregory (unpublished)
Devil's club (DW)	7.1	16.3	S. V. Gregory (unpublished)
Douglas-fir wood chips (DW)	31.0	47.0	F. J. Triska (unpublished)
Doulgas-fir twigs (DW)	40.0	34.0	F. J. Triska (unpublished)
Douglas-fir bark (DW)	48.0	10.0	F. J. Triska (unpublished)
Soil organic matter			
>1 mm diameter	62.5	11.7	This study
0.053–1 mm	45.3	12.3	This study

μg/g AFDW) (Table 4). However, unlike chlorophyll *a*, the average phaeophytin concentration at the alder site (139 μg/g AFDW) was clearly intermediate between that of the open and conifer sites. At the conifer and open sites phaeophytin concentrations were greatest in FPOM <0.01 mm, and generally seemed to be higher in smaller particles (Table 4).

Clearly, the absence of canopy and the associated autochthonous production at the open site led to higher concentrations of chlorophyll *a* and phaeophytin in FPOM. However, substantial amounts of phaeophytin also occurred at the alder site where algal production was much lower (Ward et al. 1982). The higher average phaeophytin content in FPOM at the open site was contributed mostly by particles <0.01 mm. At the alder site, some larger particles actually contained more phaeophytin than did FPOM on average at the open site (Table 4). A substantial portion of the phaeophytin in these larger particle sizes may have been derived from non-algal sources, such as fragments of moss or leaves.

Lignin and cellulose in benthic FPOM

The lignin and cellulose data set consisted of triplicate samples for eight particle size ranges at three sites on four dates. Initially, $\log_{10}$ transformed data for percent lignin and cellulose were analyzed using two-way ANOVA. Multiple comparison tests (Tukey's w-procedure) were used to determine differences among sites and particle sizes (Sokal and Rohlf 1981).

Benthic FPOM in all streams examined contained relatively large amounts of lignin (about 45%) and moderate to low amounts of cellulose (about 13%). Table 5 and corresponding statistical analysis in Table 6 show that detritus particles can be separated into three groups on the basis of percent lignin and cellulose. The

TABLE 4. Chlorophyll *a* and phaeophytin content (μg/g AFDW) of FPOM at conifer, deciduous, and open canopied sites. Values are means of samples from three seasons (±1 SE).

Particle Size (mm)	Chlorophyll *a*	Phaeophytin
	Mack Creek	
0.053–1	15±10.0	37±12.3
0.037–0.053	13±13.0	64±21.5
0.01–0.037	26±12.6	75±6.0
<0.01	30±2.0	98±86.0
Average	21±8.2	69±25.3
	Quartz Creek	
0.053–1	37±5.5	175±65.1
0.037–0.053	26±4.0	142±14.0
0.01–0.037	24±9.5	238±115.5
<0.01	30±42.0	73±98.2
Average	29±5.7	157±68.7
	Grasshopper Creek	
0.053–1	31±15.9	60±18.9
0.037–0.053	60±23.4	127±65.6
0.01–0.037	48±32.2	199±49.2
<0.01	102±115.8	417±203.3
Average	60±30.2	201±154.9

TABLE 5. Percent lignin and cellulose (% AFDW) in FPOM at Cascade Mountain stream sites which varied in the type of riparian vegetation. Data are grand means (±1 SE) of triplicate samples collected on each of 4 dates.

Particle Size Range (mm)	Mack Creek (Conifer)		Quartz Creek (Alder)		Grasshopper Creek (Open)	
	Lignin	Cellulose	Lignin	Cellulose	Lignin	Cellulose
>1	58.1±8.66	17.5±1.65	59.3±7.85	17.9±1.23	59.9±6.85	18.9±3.84
0.01–1	43.6±2.83	13.7±1.36	45.6±4.00	12.4±1.68	45.0±3.86	13.7±2.04
<0.01	39.2±13.81	7.5±0.72	27.0±13.69	3.8±2.68	29.5±11.36	4.0±2.68
Mean percent	44.9±6.06	13.6±1.25	45.0±9.31	12.4±1.62	45.0±8.76	13.5±2.11

smallest particles examined (<0.01 mm) contained the least lignin (32%). Particles 0.01–1 mm formed an intermediate group with similar percent lignin among the five particle size ranges examined ($p>0.05$). Particles >1 mm, which included small pieces of wood, bark, cones, twigs, needles, etc., consistently had a higher percent lignin (60%) than particles <1 mm. Statistically, however, percent lignin in particles >1 mm did not differ significantly from FPOM 0.25–1 mm ($p>0.05$), although particles >1 mm were different from particles <0.25 mm ($p<0.05$). Similar patterns were observed on each sample date at each of the three study sites.

The percent cellulose in FPOM showed a similar trend. Particles <0.01 mm contained the least cellulose (5%), while the average for particles >1 mm was approximately 18% (Table 5). Particles <0.01 mm contained significantly less cellulose ($p<0.05$) than all larger particles, but the percent cellulose in the five particle sizes between 0.1 mm and 1 mm were not significantly different (Table 6, $p>0.05$). Particles >1 mm were consistently higher in percent cellulose; however, they differed significantly only from particles <0.037 mm.

A comparison of percent lignin in FPOM at different seasons revealed no distinct patterns common to all three sites. FPOM at the conifer site had the highest percent lignin during the summers of 1982 and 1983 (Tukey's w-procedure, $p<0.05$), but at the open site, percent lignin was highest in the spring. No seasonal differences in percent lignin in FPOM from the alder site were observed ($p>0.05$).

A similar statistical comparison of the three sites also revealed no trends. Contrary to the original predictions, percent lignin was not consistently higher at the conifer site, and only during one season was the predicted trend among the open, alder, and conifer sites observed. On two sample dates the open site had the greatest percent lignin in FPOM.

Compared to leaf litter and algal inputs at these sites, the benthic FPOM was relatively high in lignin and low in cellulose (cf. Tables 3 and 5). Together, lignin and cellulose constituted approximately 75% of AFDW in particles >1 mm, over 50% in particles 0.01–1 mm, and

TABLE 6. Statistical analysis of % lignin and % cellulose for seven particle sizes of benthic FPOM in three streams with either conifer, alder, or open canopy. Within each site particle size ranges with the same letter were not significantly different (Tukey's w-procedure, $p>0.05$).

Particle Size (mm)	% Lignin			% Cellulose		
	Conifer	Alder	Open	Conifer	Alder	Open
0.5–1.0	a	b	c	c	c	c
0.25–0.5	ab	b	bc	bc	bc	bc
0.125–0.25	b	bc	bc	bc	bc	bc
0.053–0.125	ab	c	bc	bc	bc	bc
0.037–0.053	ab	bc	bc	bc	bc	bc
0.01–0.037	ab	bc	b	b	b	b
<0.01	ab	a	a	a	a	a

30–50% in particles <0.01 mm. If this material originally entered the stream system as leaf or needle litter it has subsequently undergone a significant amount of decomposition to reach its present state. This observation is true for the entire particle size spectrum examined here. All particle sizes, large and small, had a much larger percent lignin than did the allochthonous inputs.

It was also evident that benthic FPOM did not have higher percent lignin in smaller particle sizes. According to processing patterns suggested by Odum and de la Cruz (1967) and Boling et al. (1975), smaller particle sizes have undergone the greatest amount of processing and decomposition, and presumably should contain the largest amount of refractory compounds (e.g., Nedwell 1984, Suberkropp et al. 1976, Triska et al. 1975). Experimental observations of this process are usually restricted to single types of organic matter, confined in such a way as to prevent mixing with other detritus. Benthic FPOM is, of course, a heterogeneous mixture of particles derived from a variety of sources, and processing patterns of each input type are likely obscured by the coexistence of several types, each in a variety of decomposition states.

Another interesting observation was that despite the qualitative differences in riparian vegetation inputs, the concentrations of lignin and cellulose in FPOM were very similar at all three sites. At least two possible mechanisms could explain this observation: 1) FPOM processing results in a common base level decomposition state in which all inputs, regardless of source or initial composition, reach the same concentration of lignin and cellulose; 2) the streams have in common a major input other than riparian vegetation. No studies either support or refute the first hypothesis; however, even if true, dilution of the resident benthic FPOM pool with relatively unprocessed FPOM should be observable following litterfall. Dilution of lignin in benthic FPOM at either the alder or conifer site was not observed in this study, despite the quantitatively large FPOM input relative to standing crop of benthic FPOM. Maybe freshly generated FPOM, particularly algal detritus, is decomposed so rapidly that it was not measurable by the methods used.

It is also possible that FPOM inputs to the streams come from sources other than leaf litter and algae. Quantities of soil FPOM inputs to the stream channel in Watershed 10 (HJAEF) reported by Swanson et al. (1982; also see Sollins et al. 1985) approximate those from leaf litter at the site, and Ward and Aumen (1986) suggested that inputs from processing of woody debris could also be quite large in these Cascade Mountain streams, perhaps even larger than that from leaf litter. Both of these FPOM sources are about 45% lignin. Large amounts of coarse woody debris from the former old-growth Douglas-fir and hemlock forests remain in channel storage at all three study sites. Substantial inputs from either soil or wood could override any qualitative effects (dilutions) on FPOM caused by inputs of litter or algal detritus. FPOM inputs from these two sources have yet to be quantified. Thus it may be only fortuitous, but values for the average percent lignin of stream FPOM (45%) and soil FPOM (43%) were very similar (cf. Tables 3 and 5).

FPOM particles <0.01 mm, with their lower percent lignin and cellulose, may have a separate origin. The low percent cellulose (3%) suggests that these particles are well-degraded, but this premise is contradicted by the high respiratory rates (see below). More likely, this size range contains particles that initially contain small amounts of both lignin and cellulose, as described by Bowen (1984) who suggested that amorphous FPOM (particulate matter without definite structure) is generated through flocculation of dissolved organic matter. Observations of FPOM with scanning electron microscopy (SEM) support the idea that much of the FPOM <0.01 mm is amorphous in nature, although many other particle types are also present (see below).

Respiration of benthic FPOM

The FPOM respiration data set was similar to that for percent lignin and cellulose. Carbon dioxide production rates were obtained in triplicate for seven particle sizes on four dates at the open, alder, and conifer sites. Respiration rate data were analyzed by two-way ANOVA using Tukey's multiple comparison test to determine differences among sites and among particle sizes.

Given the differences in the types of organic matter inputs to the three sites (needles/wood

TABLE 7. Seasonal measurements of FPOM respiratory rates (μg C g $AFDW^{-1}$ h^{-1}) at three sites in the Oregon Cascade Mountains that received either coniferous, deciduous, or herbaceous/algal inputs. In most cases each value is a mean (±1 SD) of triplicate determinations. Approximate water temperature: Summer 1982—13°C at the open site, 14°C at alder site, and 15°C at the conifer site; Fall 1982 and Spring 1983—4°C at all sites; Summer 1983—15°C at all sites.

Particle Size Range (mm)	Summer 1982 Mean ±1 SD	Fall 1982 Mean ±1 SD	Spring 1983 Mean ±1 SD	Summer 1983 Mean ±1 SD
		Mack Creek (Conifer site)		
0.5–1.0	103±18.8	28±8.3	25±11.3	208±44.9
0.25–0.5	76±20.3	24±6.7	24±8.3	153±34.5
0.125–0.25	58±7.9	21±4.5	20±2.5	110±18.4
0.053–0.125	79±23.7	30±6.8	25±6.8	126±74.1
0.037–0.053	66±14.4	41±4.5	20±12.2	190±68.6
0.01–0.037	135±46.7	50±7.6	48±14.2	308±119.5
<0.01	717±59.1	290±108.2	45±18.8	338±38.3
		Quartz Creek (Alder site)		
0.5–1.0	114±21.2	63±24.2	23±16.1	56±22.0
0.25–0.5	99±21.3	68±20.6	9±6.6	54±5.4
0.125–0.25	114±89.2	86±67.5	11±7.0	40±7.1
0.053–0.125	74±14.6	113±38.5	11±1.3	31±4.9
0.037–0.053	61±17.9	102±6.2	11±3.4	44±11.0
0.01–0.037	60±16.5	57±29.1	8±6.3	63±4.2
<0.01	738±92.0	165±159.2	nd[a] —	254[b] —
		Grasshopper Creek (Open site)		
0.5–1.0	208±141.3	101±69.3	63±38.9	363±141.4
0.25–0.5	149;±40.0	78±27.5	47±14.2	225±112.4
0.125–0.25	169±42.2	95±26.8	56±30.9	124±16.2
0.053–0.125	124±25.4	100±22.9	39±11.7	81±21.9
0.037–0.053	169±15.4	103±24.7	59±13.4	94±12.8
0.01–0.037	186±33.9	186±70.6	155±36.6	84±16.5
<0.01	1479[b] —	671±201.4	50±43.3	165±114.1

[a] No data available.
[b] Only one determination.

versus alder leaves versus algae), and their potentially different rates of decomposition, respiratory rates of FPOM were expected to be highest at the open site, lowest at the conifer site, and intermediate at the alder site. Except in summer 1983, respiratory rates of benthic FPOM at the open site were indeed higher (often 2×) than those at the two forested sites (Table 7). Statistical analyses of seasonal data revealed significant ($p<0.05$) differences among the sites, with the following results:

Summer 1982	open > alder > conifer
Fall 1982	open > alder > conifer
Spring 1983	open > conifer > alder
Summer 1983	conifer > open > alder

In summer and fall 1982, FPOM respiratory rates were as predicted, greatest at the open site and least at the conifer site, but in spring 1983, rates at the alder site were significantly lower than those at the conifer site. The pattern shifted yet again in the summer of 1983 when the respiratory rates at the conifer site were significantly higher than those at the open site, and rates at the alder site were least. FPOM respiratory rates at the conifer site were significantly greater than rates the previous summer in all particles except the <0.01 mm size class, which, in contrast to 1982 results, was not the fraction with the highest rate. As stream water temperatures differed by only 1°C, this inconsistency in respiration rate implies that detrital quality in 1983 differed from that of the previous summer.

In general, FPOM <0.01 mm had the highest respiration rate (Table 7). Carbon dioxide pro-

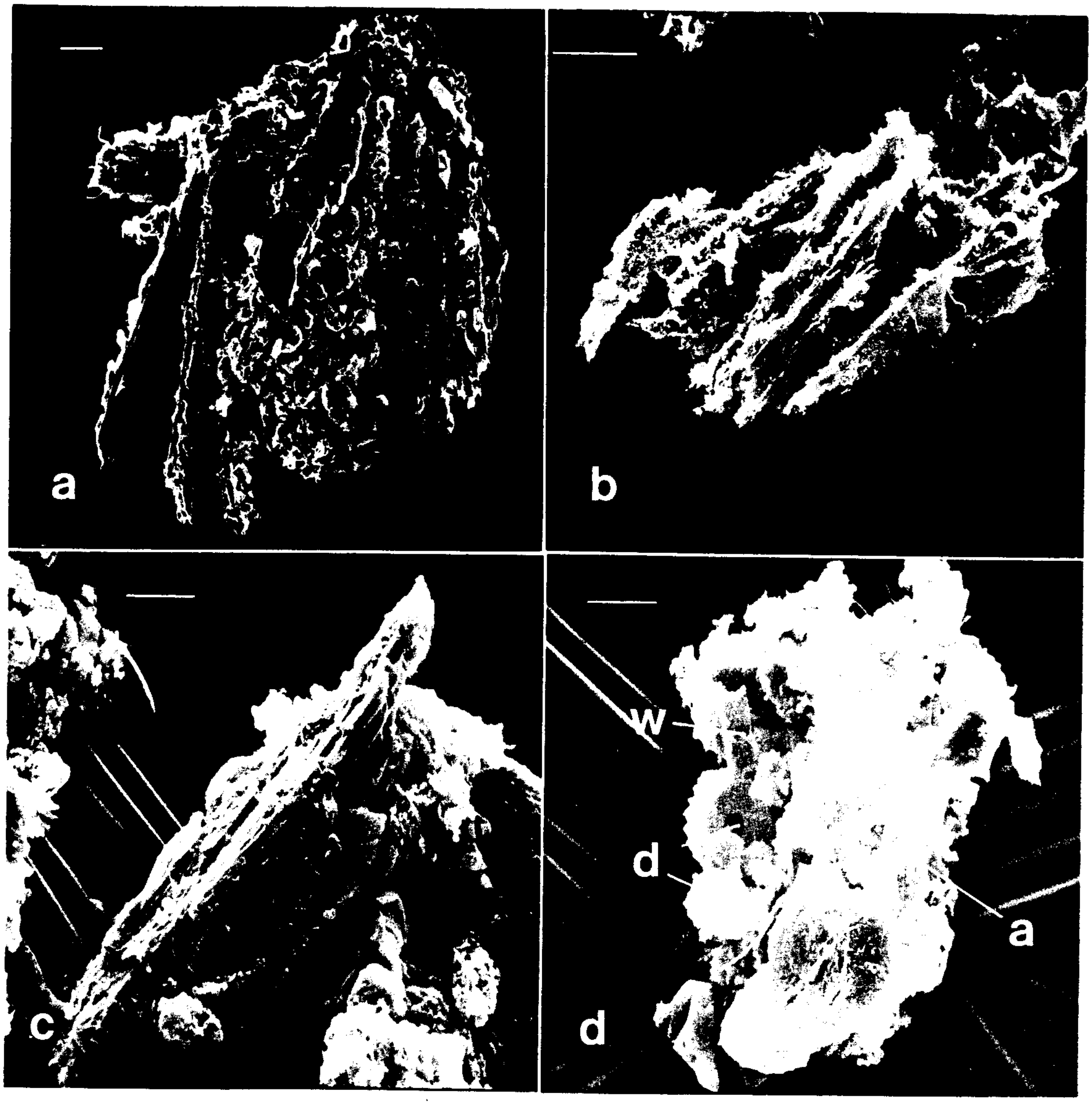

FIG. 1. Scanning electron micrographs of four benthic FPOM particles from Mack Creek, summer 1982. a–c, wood fragments from successively smaller particle sizes. (a) 0.5–1 mm, bar = 100 μm; (b) 0.1–0.25 mm, bar = 50 μm; (c) <0.01 mm, bar = 5 μm; (d) commonly observed "aggregate" detrital particle, bar = 5 μm, with various types of source material coded: a = amorphous; d = diatom; w = wood.

duction by this size of particle was often 5×, and occasionally as much as 10×, greater than particles >0.01 mm in size. In contrast to the results of Hargrave (1972) and Naiman and Sedell (1979), no statistically significant differences in respiratory rates were seen among particle size ranges between 0.01 mm and 1 mm (Table 7).

The higher respiratory activity of the <0.01 mm size range could have resulted from either a denser microbial flora on the particles and/or the activity of unattached bacteria collected on the millipore filter used to concentrate particles for respiration determinations. However, SEM (>2000×) rarely revealed the presence of unattached bacteria. Increased respiratory rates could also have been the result of the presence of moribund algal tissue. Although the <0.01 size fraction contained larger amounts of phaeophytin, the correlation between phaeophytin and respiratory activity was not significant. Another explanation is that a substantial

TABLE 8. Average lignin and cellulose content (% AFDW) of FPOM (0.053–1 mm) from sites of different stream order in the McKenzie River watershed, Oregon.

Site	Order	Width (m)	% Lignin ±1 SD	% Cellulose ±1 SD	Riparian Vegetation
Devil's Club Creek	1	0.5	57.2±1.32	16.8±2.12	Douglas-fir and western hemlock
Shorter Creek	1	1	44.0±1.72	14.7±2.27	Douglas-fir and western hemlock
Watershed 2	1	1	50.9±3.61	17.4±3.27	Douglas-fir and western hemlock
Snag Creek	2	2	45.7±1.36	13.2±3.14	Douglas-fir and western hemlock
Mack Creek	3	3	44.9±3.78	14.4±0.38	Douglas-fir and western hemlock
Quartz Creek	3	4	45.0±4.85	13.0±1.65	alder
Lookout Creek	4	12	41.5±0.25	15.5±4.67	conifer/open
Lookout Creek	5	24	43.7 —	18.9 —	open/conifer
McKenzie River	7	40	45.7 —	19.2 —	open/conifer

portion of the benthic FPOM pool consisted of "secondary FPOM": invertebrate fecal material and/or particles derived from flocculation of dissolved organic matter (Wotton 1984). Similar types of particles have been observed in lakes (Buscemi and Puffer 1975, Canfield and Bachman 1978, Paerl 1973) and in oceans (Riley 1970). Qualitative differences inherent in such particles, as a result of different source material (Bowen 1984), may have led to higher observed microbial activity.

FPOM particles clearly of secondary origin were often observed by SEM; they occurred primarily in the <0.053 mm size ranges, and were most prominent in the 0.01 mm and <0.01 mm sizes, particularly at the open site. Figure 1 illustrates FPOM seen with SEM. Wood-derived particles (Figs. 1a, b) were abundant at all sites, but more so at Mack Creek, and mostly in particle sizes >0.053 mm. Woody FPOM was not restricted to larger particles, but was also seen in sizes <0.01 mm (Fig. 1c). "Secondary" FPOM particles appeared to be aggregates, formed by the adherence or aggregation of smaller particles. An example in Figure 1d is composed of fragments of diatom frustules, pieces of wood, and what appear to be mineral particles and amorphous detritus. Such particles did not appear to be heavily colonized by microbes, but may still have been responsible for the much higher respiratory rates observed in the <0.01 mm particles at the three study sites.

Comparison of FPOM lignin and cellulose content among stream orders

Organic matter inputs of leaf litter are higher in narrow stream channels than in wider, open channels where the influence of the riparian zone is less and in-stream primary production is higher. If the quality of FPOM reflects the type, and therefore the quality, of organic inputs, then any gradation in FPOM quality should be correlated with stream order. To see if FPOM quality does indeed reflect input quality, the lignin and cellulose content of benthic FPOM was determined for nine sites over seven stream orders within the McKenzie River drainage.

With the exception of Devil's Club Creek and Watershed 2, two small streams with large accumulations of coarse woody debris, FPOM from all other streams contained approximately 40–45% lignin and 13–19% cellulose (Table 8). These data suggest that the proportion of lignin in benthic FPOM is rather constant and does not reflect inputs from either autochthonous production or leaf litter. However, these inputs are not the only ones possible. Higher order streams receive substantial quantities of seston imported from headwater reaches (Fisher 1977), and over time, headwater-derived inputs relatively rich in lignin could be dispersed throughout the lower part of the drainage. Alternatively, locally derived soil inputs, either from slow bank erosion or from flood plain erosion during high water, would produce FPOM of similar lignin content to that found in headwater FPOM. Similarities in FPOM lignin and cellulose content as well as in respiration rates (Naiman and Sedell 1980) suggest that longitudinal differences in FPOM quality are only weakly correlated with stream order. Perhaps additional, and as yet unquantified, inputs of high lignin-containing allochthonous FPOM such as soil or wood override differences in leaf litter input along the river continuum. Similarities in lignin and cellulose content with that of soil particulate organic matter suggest that stream FPOM may be only an extension of the riparian soil system.

Regardless of the source, lignin-rich FPOM has metabolic implications for the entire system. Naiman and Sedell (1980) noted that mass specific respiration rates of FPOM in the McKenzie River watershed did not change with increasing stream order, in spite of the much higher inputs of algal material at the higher order sites. While the decomposition rates of algal material are much faster than for many other particulate sources, inputs of refractory detritus (from hydrologic transport or local erosion) may attenuate potential metabolic fluctuations in the sediments of larger order streams brought about by seasonal fluctuations in primary production and subsequent decomposition of that material. Wetzel (1983) suggested this idea for lakes where a relatively refractory dissolved organic matter pool, derived from macrophytes and surrounding watersheds, provides a large energy source that is only slowly processed. Refractory DOM would be in relatively constant supply and might provide metabolic stability to the system during periods when the other energy sources are in short supply. This idea may apply to streams in that refactory FPOM provides a long-term energy source, which affords metabolic stability to both headwater and downstream reaches. Downstream reaches may therefore be dependent on upstream reaches, not just for the quantity of organic matter transported into them, but for the quality of these inputs as well.

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