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Woody Debris as a Source of Fine Particulate Organic Matter in Coniferous Forest Stream Ecosystems[1]

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The potential contribution of woody debris to fine particulate organic matter pools (0.45 μm ≤ FPOM < 1 mm) was investigated in a coniferous forest stream ecosystem in western Oregon. The amount of wetted surface area of both large (>10 cm) and fine woody debris (1–10 cm) was 0.018 and 0.069 $m^2 \cdot m^{-2}$ stream bed, respectively, during summer base flow. These values increase to 0.062 and 0.195 $m^2 \cdot m^{-2}$ stream bed during winter flows. Studies of vertical distribution indicated that most fine wood is concentrated within 0.3 m of the stream bottom, while large wood is more evenly distributed up to 0.7 m. Lignin concentrations of large wood, soil, and FPOM were very similar. Examination of FPOM samples with scanning electron microscopy revealed an abundance of wood-derived particles. Erosion rates of wood surfaces ranged between 0.5 and 11 $mm \cdot yr^{-1}$ depending on decay state of the log. Using conservative estimates of processing rates, woody debris could be a source for approximately 90 $g \cdot m^{-2} \cdot yr^{-1}$ of FPOM, but with slightly a less conservative estimate, wood processing could easily generate several times the FPOM that is contributed by leaf and needle litter.

L'apport des débris ligneux à la matière organique particulaire (0,45 μm ≤ MOP < 1 mm) a fait l'objet d'une étude portant sur un écosystème de cours d'eau de forêt de conifères de l'ouest de l'Orégon. La surface mouillée des débris ligneux grossiers (> 10 cm) et fins (1–10 cm) était, respectivement, de 0,018 et 0,069 m^2 par mètre carré de lit de cours d'eau au cours de l'écoulement de base d'été. Ces valeurs atteignaient 0,062 et 0,195 m^2 par mètre carré au cours des écoulements d'hiver. L'étude de la distribution verticale a montré que la plus grande partie des débris fins était concentrée à moins de 0,3 m du fond du cours d'eau tandis que les débris plus gros étaient distribués plus également à moins de 0,7 m. Les teneurs en lignine des gros débris de bois, du sol et de la MOP étaient très semblables. L'examen d'échantillons de MOP au microscope électronique à balayage a montré une grande abondance de particules ligneuses. Le taux d'érosion des surfaces ligneuses variait de 0,5 à 11 mm par an tout dépendant de l'état de décomposition de la bille. Des estimations prudentes des taux de transformation indiquent que les débris de bois pourraient être une source d'environ 90 $g \cdot m^{-2}$ par an de MOP. L'utilisation d'estimations légèrement moins conservatrices indique cependant que la transformation du bois pourrait facilement être la source d'une quantité de MOP équivalent à plusieurs fois celle produite par la litière de feuilles et d'aiguilles.

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Over the past several years the importance of woody debris in the ecology of small, high-gradient streams (Bilby and Likens 1980; Triska and Cromack 1980) and large, lowland rivers (Sedell and Froggatt 1984; Triska 1984; Wallace and Benke 1984) has become well recognized. Large woody debris (LWD, >10 cm) is important in shaping channel structure (Swanson and Lienkaemper 1978), in retention of inorganic sediment, leaves, and fine particulate organic matter (Bilby 1981; Speaker et al. 1984), and in the formation of habitat and food for fish and invertebrates (Hall and Baker 1977; Sedell and Triska 1977; Benke et al. 1985).

Wood debris is also an important component of organic matter budgets in stream ecosystems, particularly those in the Cascade Mountains of Oregon where accumulations are quite large. On a mass basis, loadings of all LWD lying within the channel (both submerged and emergent) range from 43 $kg \cdot m^{-2}$ in first-order channels to 28 $kg \cdot m^{-2}$ in third-order streams (Keller and Swanson 1979). Fine woody debris (FWD, 1–10 cm) is less abundant (0.61 $kg \cdot m^{-2}$; Triska and Cromack 1980) than LWD, but is a primary food source for xylophagous insects (Anderson et al. 1978, 1984) and has the potential to contribute substantially to energy flow and nutrient cycling as a result of its large nutrient pool and its intermediate availability between leaves and large wood (Triska and Cromack 1980).

Like leaf and needle litter, woody debris also has the potential to be a source of fine particulate organic matter (0.45 μm

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≤ FPOM < 1 mm). Cummins et al. (1983) speculated that FPOM generation from wood could be an important detrital process even in systems where wood is not overly abundant. However, the generalized view of coniferous forest stream structure and function given by Triska et al. (1982) did not include FPOM resulting from LWD processing. Production of FPOM from wood most likely results from a combination of microbial activity and physical abrasion from the current. Preliminary observations in Mack Creek revealed the presence of many logs that possessed relatively soft surface wood. The exposure of these wood surfaces to highly turbulent water during winter base flow periods, and particularly during storm flows, could produce FPOM through fragmentation.

The potential significance of large and fine woody debris as a source of FPOM is likely to be proportional to the quantity of submerged wood in a stream channel as well as the rate at which wood surfaces are fragmented. Previous estimates of woody debris standing crop in Cascade Mountain streams (e.g. Anderson et al. 1978; Keller and Swanson 1979) have included all wood within the channel, whether potentially in contact with the current or not. Thus, more precise measurements of submerged wood surface area are needed for calculations of FPOM production. The quantities of FPOM generated from wood will also be a function of the rate at which microbial decomposition softens the wood surfaces. Estimates of LWD processing rates are at best only speculative, and turnover rates are certainly measured in decades, if not centuries. Processing rates of FWD are known to be greater than those for LWD (Triska and Cromack 1980), and processing rates of FWD are faster for wood with high surface to volume ratio, such as chips and twigs (Triska and Cromack 1980). However, at present there are no estimates of FPOM production for either FWD or LWD. In this study we have sought to provide evidence that woody debris can be a significant source of FPOM to the Mack Creek system. To do this, we determined the quantities of woody debris submerged during summer and winter, estimated losses of wood from LWD surfaces, compared the lignin and cellulose content of woody debris, soil, and FPOM, and examined FPOM samples for the presence of wood-derived particles.

Study Site

All measurements and sample collections were conducted in Mack Creek, a third-order channel located at 830 m elevation in the H. J. Andrews Experimental Ecological Reserve in the Western Cascade Mountains of Oregon. Mack Creek is a high-gradient (10%), bedrock-constrained system that drains a 6.0-km^2 watershed. The channel morphology consists of stair-steps of pools, free-fall zones, and turbulent water around boulders (Triska et al. 1982). The surrounding forest is composed of massive, old-growth Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) that typically reach heights of 60 m. Leaf and needle litter inputs from riparian areas are approximately 360 $g \cdot m^{-2} \cdot yr^{-1}$ (S. V. Gregory, Oregon State University, Corvallis, OR, unpubl. data).

The most apparent physical feature of the Mack Creek stream channel is the large accumulations of woody debris. Because of the large diameter (often >0.5 m) and long length of Douglas-fir trees, a narrow channel width, and the steep side slopes, logs often fall with one end in contact with the streambed and the other extending many metres above the channel bottom. Additionally, storm flows often dislodge even large debris, repositioning the pieces in large accumulations or depositing them outside the active channel. As a result, relatively few logs are in contact with the stream bottom along their entire length, and much of the large woody debris is located above summer base flow.

At summer low flow, the average water depth in Mack Creek is <0.1 m, with many areas of stream bottom barely wetted. However, winter base flow is approximately 0.4 m higher than summer (George W. Lienkaemper, Forestry Sciences Laboratory, Corvallis, OR, pers. comm.) as a result of the seasonal concentration of precipitation during November–April. Because of the very shallow water depths and large size of the debris, few logs are completely submerged in summer, and large debris projects from the stream bottom to a point well above winter stage heights.

Materials and Methods

Surface area and mass of LWD was determined for all 100 logs present in a 220-m reach of Mack Creek where the average channel width was 10 m. Measurements of log diameter, length, and height above the stream bottom were conducted in July of 1985 at summer low flow in order to determine the minimum surface area that was wetted during the annual hydrologic cycle. Only logs located in the active channel were selected and measurements were restricted to the portion of each log situated below a 1.5-m height above summer base flow. The 1.5-m height was selected for being well above Mack Creek's winter discharge. The remaining portion of each log above the 1.5-m mark often continued many metres up the hillslope and would rarely be affected by stream flow. Surface areas were calculated for wetted portions of each log at summer base flow and at the projected winter flow. Surface area data were divided into 10-cm vertical increments to illustrate vertical distribution patterns of large woody debris. Mass was calculated from volume data using a density of 0.361 $g \cdot cm^{-3}$ (SD = 0.042, n = 8). Densities were determined empirically (Hg displacement) for randomly collected pieces of FWD and for samples from surfaces of LWD.

Surface area of FWD was determined by sampling ten 2-m-wide transects evenly spaced along a 100-m reach of Mack Creek. Within each transect, diameters and lengths of each piece of fine wood (approximately 1000) were measured and the vertical distribution was noted up to 0.7 m above summer base flow. Preliminary observations indicated that most of the fine wood located in the active channel was situated in this vertical region. Each piece was assumed to be either a rectangular solid or a right circular cylinder and the appropriate calculations for surface area and volume applied. Mass was calculated from volume estimates using a density of 0.395 $g \cdot cm^{-3}$ (SD = 0.126, n = 16).

One of the most likely sources of wood-derived FPOM is from the surfaces of microbially processed logs that are subjected to physical abrasion from stream flow. In order to document LWD processing, reductions in the cross-sectional area of several Douglas-fir logs influenced by stream current were observed over a period of several years. Five logs ranging in length from 3.7 to 5.1 m and in diameter from 24 to 70 cm were initially chosen for study. Each had fallen into the channel some years prior to the beginning of the study and already had the bark removed by natural processes. No accurate estimates could be made of the previous residence time of these logs in the channel, but they represented a wide range of decay, from soft, punky wood to very sound wood. For the purposes of this

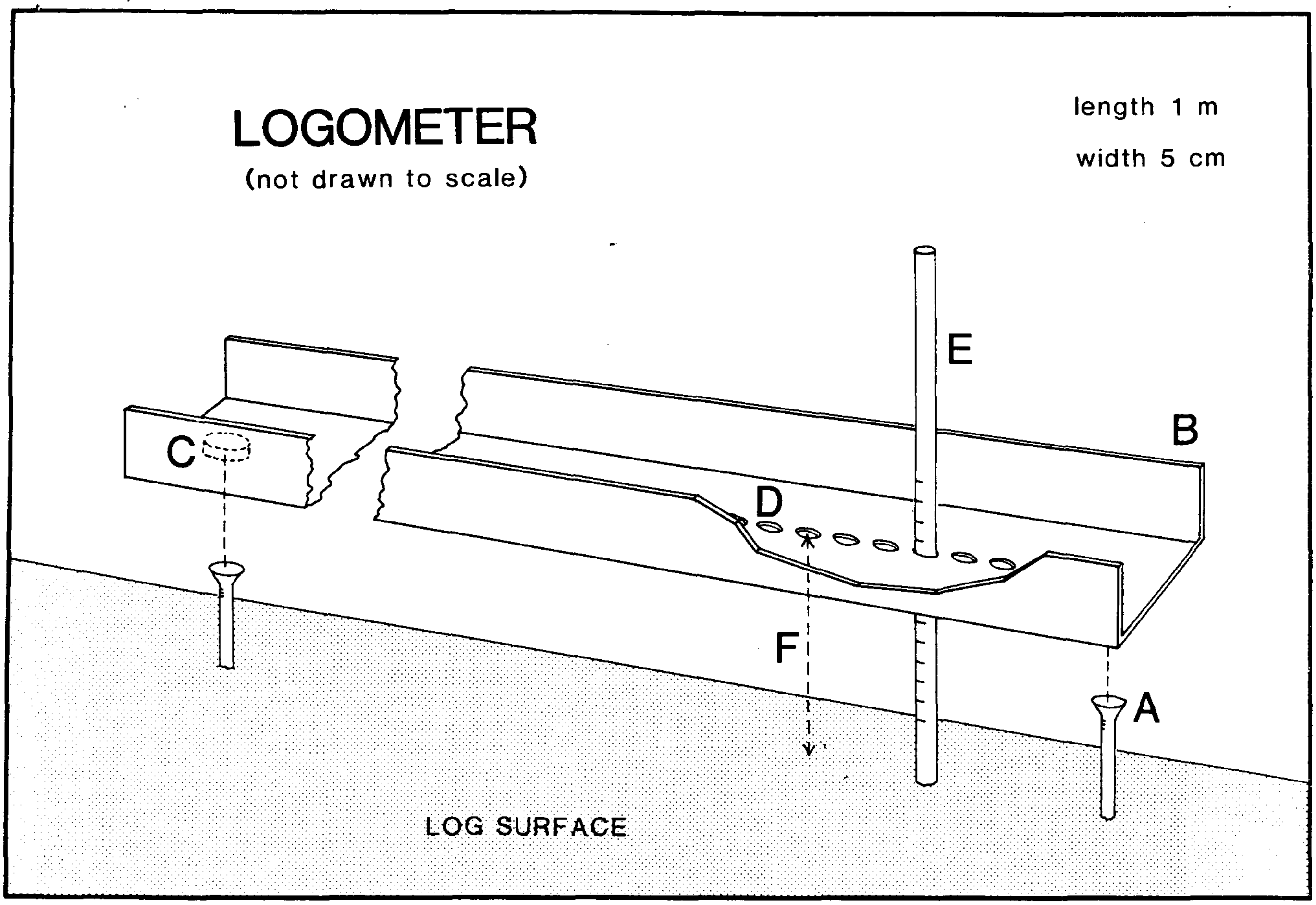

FIG. 1. Cut-away drawing of "logometer" used to determine surface wood loss from decomposing logs. Galvanized spikes (A) (18 cm) are driven into the study log at approximately 1-m intervals with the top 3–5 cm of each spike left exposed. The spikes serve as permanent reference points for positioning the logometer (B), with the spike heads fitting into receptacles (C) at either end of the instrument. This allows the logometer to be repositioned in exactly the same place each time the log is measured. The body of the logometer is constructed of 3-mm aluminum plate with holes (D) drilled through the bottom at 2-cm intervals. These holes serve as guides for a rod graduated in 1-mm increments (E) used to determine the distance (F) between the log surface and the bottom of the instrument. This distance is determined at each of the holes along a 2-m transect of the study log, and can be remeasured repeatedly and accurately over a long-term study period (years).

study, each log was reoriented perpendicular to the current to simulate naturally occurring logs that receive substantial stream flow. Over the winters of 1983 and 1984, four of the five logs were repositioned out of the active channel by storm flows and only one log remained in its original position throughout the entire experiment. Logs were first measured in August of 1982 and remeasured in October of that year. Logs that remained in the active channel were again measured in the fall of 1983 and 1984 and July of 1985. The study logs were monitored yearly by measuring changes in their surface profile using the "logometer" illustrated in Fig. 1. Galvanized spikes (18 cm) were driven into the logs as reference points and holdfasts for the instrument. Detailed measurements of changes in the surface profile of each log could be made by situating the logometer on the spikes. Any loss from the surface profile due to processing would be reflected in an increased distance from the instrument to the surface of the log. A 2-m transect of each log was measured for changes at 2-cm intervals, and it was determined that these measurements were reproducible to be <2 mm. The mean change in distance from the logometer to the surface of the log was calculated based on 92 points along the transect.

Surface scrapings were collected from the five study logs when they were originally placed in their new positions in August of 1982. Lignin and cellulose concentrations of the surface wood were determined as described below, and samples were obtained for [^{14}C]lignocellulose decomposition experiments as described in Aumen et al. (1983) according to the methods of Crawford (1981). Briefly, scrapings were homogenized and placed in incubation bottles with ^{14}C-labeled natural lignin and cellulose prepared from Douglas-fir. The microbial decomposition rates of lignin and cellulose on the wood scrapings were determined by monitoring the evolution of $^{14}CO_2$ over a 3-wk incubation period in the laboratory.

Collections of FPOM for lignin and cellulose determinations were obtained from a series of backwater and pool habitats in Mack Creek by wet-sieving sediment detritus through a series of standard sieves. Soil samples were likewise collected from the riparian zone immediately adjacent to the active channel. Surface wood scrapings approximately 1 mm thick were obtained from a series of downed Douglas-fir logs in Mack Creek using a standard carpentry plane as described by Aumen et al. (1983). Fine wood samples were collected from the belt transect studies described above. All samples were dried at 50°C and the wood scrapings and fine wood were ground to pass a 0.85-mm sieve (No. 20 mesh). Wood scrapings, fine wood,

TABLE 1. Seasonal comparison of the surface area and mass of submerged large (>10 cm in diameter) and fine wood (1–10 cm) in a 220-m reach of third-order Mack Creek. Winter flow is defined as a stage height 0.4 m above low summer flow. Estimates of large wood mass and surface area are from a single 220-m reach and thus, no error terms are available.

	Summer base flow		Winter base flow	
	Average	SD	Average	SD
Large wood surface ($m^2 \cdot m^{-2}$ stream bed)	0.018	—	0.062	—
Fine wood surface ($m^2 \cdot m^{-2}$ stream bed)	0.069	0.113	0.195	0.138
Total wood surface ($m^2 \cdot m^{-2}$ stream bed)	0.087	—	0.257	—
Large wood mass ($kg \cdot m^{-2}$)	0.871	—	10.975	—
Fine wood mass ($kg \cdot m^{-2}$)	0.212	0.284	1.03	0.868
Total wood mass ($kg \cdot m^{-2}$)	1.083	—	12.005	—

soil, and FPOM samples were analyzed for cellulose and acid-detergent lignin content after the method of Goering and van Soest (1970) as modified by Mould and Robbins (1981). Results were expressed as a percent of ash-free dry weight (AFDW) after correcting for insoluble ash and losses of acid-soluble ash.

Soil and FPOM samples for scanning electron microscopy (SEM) were preserved in 1.5% glutaraldehyde, fixed in 1% OsO_4, and dehydrated in a graded ethanol series. Samples were dried using a Denton Vacuum DCP-1 critical point dryer, coated with 10-nm-thick Au/Pd wire using a Technics Hummer V, and examined with a ETEC Autoscan SEM. The percentage of wood particles in FPOM samples was determined by examining at least 100 FPOM particles in each of three size classes (1.0–0.5 mm, 0.25–0.1, and 0.1–0.053 mm) with SEM at magnifications >300× and determining the percentage of recognizable wood fragments in the total number of particles examined.

Results

Vertical Distribution of Wood

The vertical distribution of LWD surface area is rather even (Fig. 2). There are, however, somewhat greater amounts at summer and winter base flow levels. During summer low flow, approximately 0.018 m^2 of LWD surface is submerged per square metre of stream bottom, but during winter, submerged surface area increases by 3.5 times to 0.062 $m^2 \cdot m^{-2}$ stream bottom (Table 1). Storm flows would, of course, result in even higher water levels and more submerged wood. With an increase of 20 cm above normal winter base flow, there would be an additional 40% increase in submerged surface area.

In contrast with LWD, FWD surface area is concentrated within 0.3 m of the stream bottom (Fig. 2). Approximately 0.069 m^2 of FWD is submerged per square metre of stream bottom during summer low flow, but at winter, base flow surface area increases by a factor of 2.8 to 0.195 $m^2 \cdot m^{-2}$ stream bottom (Table 1). The quantity submerged in summer represents 36% of the total fine wood surface area submerged at winter base flow, but with only a 10-cm rise in stage, more

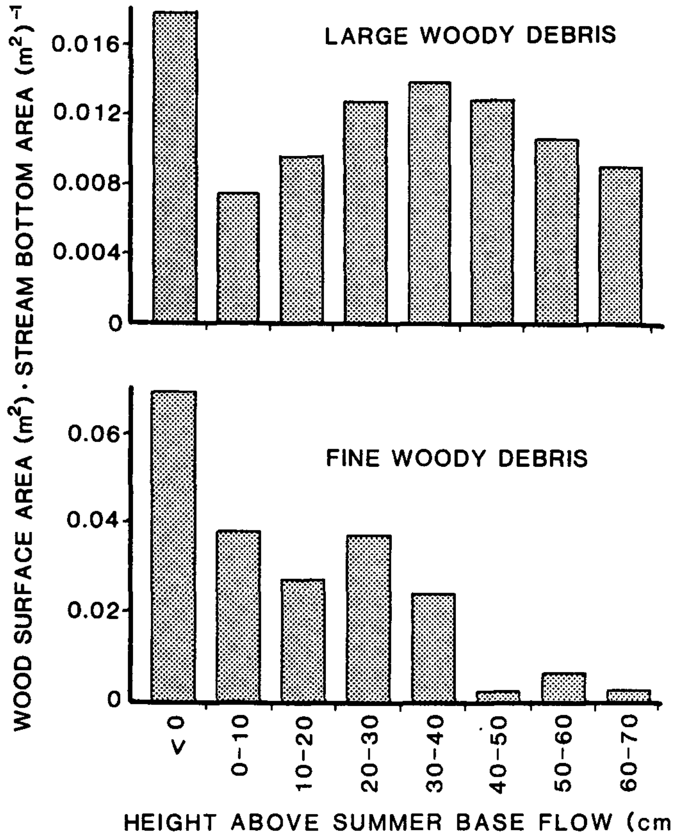

FIG. 2. Vertical distribution of large (>10 cm in diameter) and fine (1–10 cm) wood in Mack Creek. Arrows indicate typical summer and winter base flow levels.

than 50% is submerged. Above 0.4 m, quantities of fine wood surface area decline sharply (Fig. 2). Storm flows up to 0.7 m would therefore submerge little more fine wood than is wetted at winter base flow.

There is much more wetted surface area in FWD as compared with LWD (Table 1). During the summer, FWD surface area is 12 times larger than that of large wood (79% of the total submerged wood surface is FWD), although the relative difference declines to 3 times during winter. Further increases in stage height, such as occurs during storm flows, would make the difference even smaller.

Large and fine wood mass is more evenly distributed vertically than is surface area. Approximately 0.2 $kg \cdot m^{-2}$ is submerged during summer, but that increases by 5 times during winter (Table 1). Much of the fine wood submerged during summer is relatively small pieces with high surface to mass ratios, but wood located above the streambed near winter base flow heights tends to be larger. LWD mass submerged at winter flow is approximately 10 times that wetted at summer flow (Table 1).

Production of FPOM from Wood Surfaces

At the beginning of the experiment, log A was considerably more processed than log B and possessed a surface with much softer wood. Lignin values for the two logs were somewhat similar, with log A containing 30.6% lignin and log B containing 27.3% lignin; however, the surface wood of log A contained 33.9% cellulose, while log B contained 41.5% cellulose, similar to that of living Douglas-fir (Table 2). The dissimilarity in substrate composition may be explained by differ-

TABLE 2. Lignin and cellulose content (% of AFDW) of FPOM and potential sources of FPOM in an old-growth, conifer-dominated reach of Mack Creek.

Organic material	% lignin	SD	% cellulose	SD
Sound Douglas-fir bole wood	26.8	1.95	42.4	1.63
Fresh Douglas-fir chips[a]	30.0	—	48	—
Fresh Douglas-fir twigs[a]	33.0	—	40	—
Large woody debris (>10 cm)[b]	43.4	16.28	27.4	13.2
Douglas-fir needles[c]	24.5	—	14.5	—
Red alder (*Alnus rubra*)[c]	9.5	—	9.0	—
Vine maple (*Acer circinatum*)[c]	8.5	—	14.7	—
Fine woody debris	59.1	6.83	18.1	2.29
FPOM (0.01−1 mm)	44.7	5.16	13.2	2.92
Soil (0.1−1 mm)	43.4	8.19	10.9	3.74

[a]F. J. Triska, unpublished data.
[b]Average of 27 logs from a variety of age and decay classes.
[c]Triska et al. (1975).

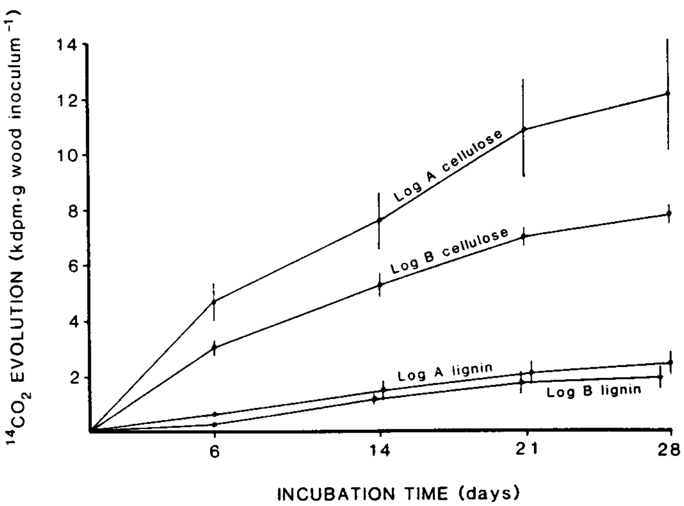

FIG. 3. Decomposition of [^{14}C]lignocelluloses in surface wood samples obtained from logs A and B (see text) in October of 1982. Bars indicate standard errors of the means.

ences in lignocellulose processing rates. Figure 3 illustrates that the two logs had similar rates of lignin decomposition, but that log A had a considerably faster rate of cellulose mineralization.

Logometer data demonstrated that measurable amounts of wood were lost from the surface profiles of logs A and B during the study period (Fig. 4). Log A, with its softer and more decomposed surface, exhibited the greater losses. Portions of the surface of log A lost up to 6.3 cm of wood in 1 yr. The average loss was 11.1 mm·yr^{-1}. While it is unknown if this wood was removed all as large pieces or as FPOM, it is clear that the wood surface experienced significant erosion.

In contrast, log B had relatively sound surface wood and exhibited a much lower processing rate (Fig. 4). Slight losses of wood occurred all along the surface profile, and after 3 yr the average loss at each point along the profile was 0.5 mm·yr^{-1}. The rate loss for this log was near the lower limits of detection with this technique; however, comparison with a control is possible. A third log was initially measured along with the others, but unlike the rest, never came into contact with the stream. The initial profile and one measured a year later were almost identical. It thus appears that processing does occur even in rather sound wood.

Average depth of wood loss for the two logs ranged from <1 to 11 mm·yr^{-1}. These values represent logs within different decay states. Based on this range, we have calculated the potential quantities of FPOM produced through woody debris processing. However, our calculations must be considered preliminary given the limited number of logs measured and the limited knowledge of FWD processing rates. Nevertheless, these calculations suggest that substantial inputs of woody FPOM are possible even with conservative estimates of wood surface erosion. For example, given 0.062 m^2 LWD surface·m^{-2} stream bottom (Table 2), and assuming that all woody debris is relatively sound, losing only 1 mm·yr^{-1} (all as FPOM), approximately 22 g·m^{-2}·yr^{-1} would be transferred to the FPOM pool. Assuming this same loss rate for fine wood, inputs would be approximately 77 g·m^{-2}·yr^{-1}. Together, losses from woody debris surfaces may at a minimum be 2 times the mean FPOM standing crop in Mack Creek (Naiman and Sedell 1979), and equivalent to approximately 50% of FPOM generated annually from leaf and needle litter inputs (assuming 25% leaching and 30% mineralization loss from leaves and needles, Ward 1984). However, the majority of woody debris exhibits a substantially greater degree of decomposition and would likely be processed at rates greater than for sound wood. Therefore, if we assume losses of 5 mm·yr^{-1}, approximately 100 g FPOM·m^{-2}·yr^{-1} would be generated from LWD processing and 375 g·m^{-2}·yr^{-1} from FWD. Together these values are greater than estimates of total litter fall (360 g·m^{-2}·yr^{-1}) and more than 10 times average FPOM standing crop (Naiman and Sedell 1979).

The data of Triska and Cromack (1980) may also be used to estimate quantities of FPOM generated from fine wood. A conservative estimate of FWD processing might be approximately 10%·yr^{-1}. Using this value, FWD processing would generate approximately 100 g FPOM·m^{-2}·yr^{-1} (based on FWD mass from Table 1). Although this estimate is lower than the 375 g·m^{-2}·yr^{-1} cited above for FWD processing, LWD and FWD together could still be a source for 200 g FPOM·m^{-2}·yr^{-1}. This amount is equivalent to quantities of FPOM generated from leaf and needle processing and still many times greater than mean annual FPOM standing crop.

Lignin and Cellulose Content of Particulate Detritus

Lignin is a major component of potential allochthonous inputs and various detrital size fractions in Mack Creek (Table 2). The lignin content of FPOM was approximately 43% AFDW, very similar to that of both soil particulate organic matter and

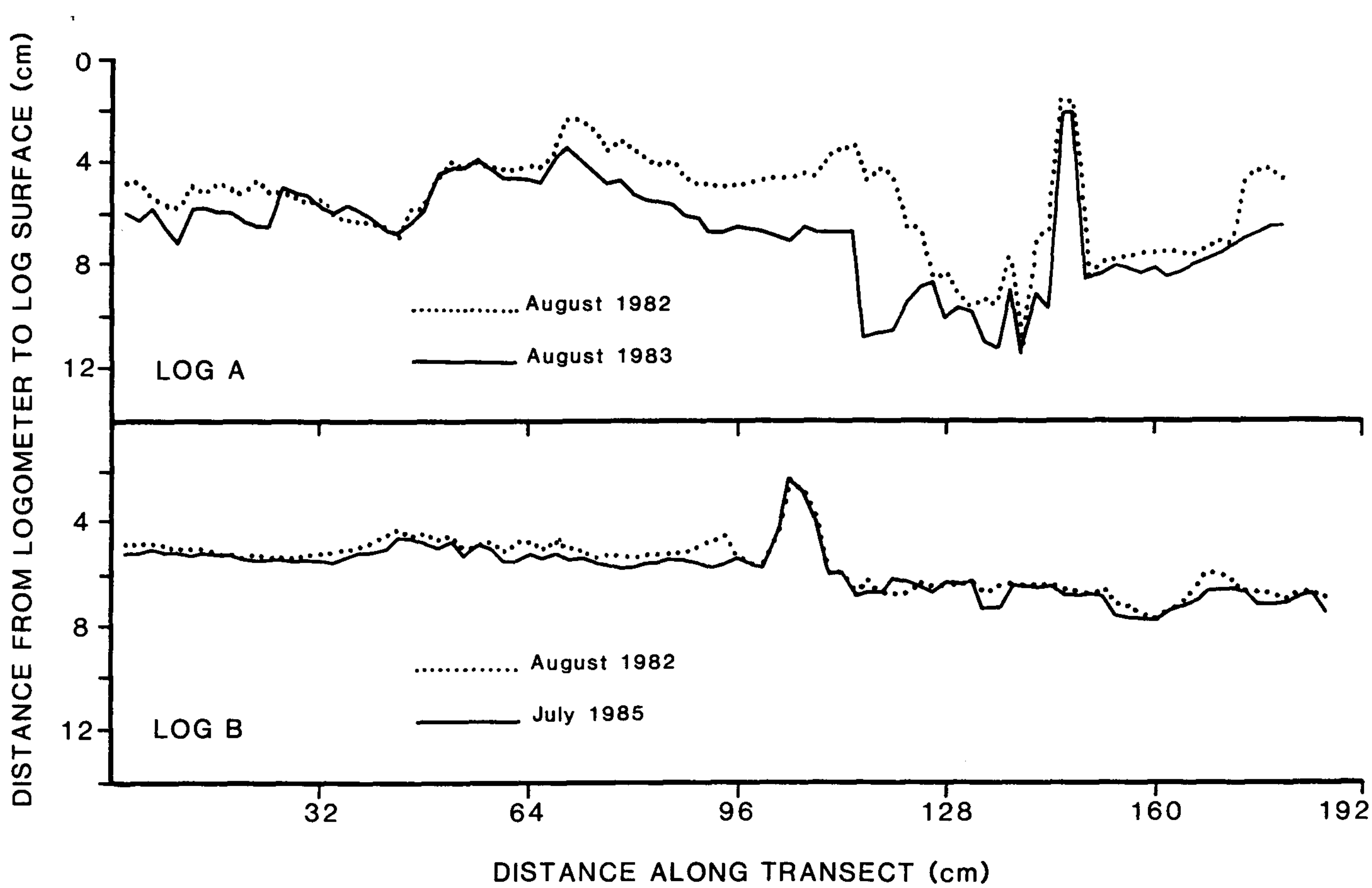

FIG. 4. Changes in the surface profile of two logs in Mack Creek as measured by the logometer. Log A was repositioned by high stream flows in the winter of 1983 and yielded data for only 1 yr. Log B was measured at yearly intervals, but only the first (1982) and last (1985) measurements are presented. Note exaggeration of the vertical scale.

the surfaces of LWD (Table 2). A survey of 27 logs in Mack Creek and its tributary Snag Creek revealed that the average lignin content of surface wood was 43.4% AFDW. A wide range of values was encountered, reflecting variations in both the diversity of decay states among separate pieces of debris as well as within individual logs. Some logs possessed low lignin concentrations (23–30% AFDW) similar to that of living wood, while at the other extreme, well-decayed logs contained up to 87% AFDW lignin. FWD contained almost 60% lignin (Table 2). These smaller sized pieces were primarily cones and twigs, as well as pieces of bark and chips of wood. The larger pieces were usually small branches. The lignin content of soil particulate organic matter was also 43% AFDW, very similar to that of LWD (Table 2).

By comparison, the lignin content of fresh allochthonous inputs is much less. The lignin content of Douglas-fir needles is 25% AFDW, and the content of vine maple (*Acer circinatum*) and red alder (*Alnus rubra*) leaves is near 10% AFDW (Table 2). In general, the lignin content of FWD is substantially greater than that of fresh chips and twigs, and the cellulose content is much reduced (Table 2). Although FPOM and soil were enriched in lignin as compared with leaves and needles, they contained substantially less cellulose than did fresh allochthonous inputs. This likely reflects the continued decomposition of the material once it reaches the FPOM size category.

SEM Observations of FPOM

Samples of FPOM and soil were examined under SEM to determine the extent to which wood particles could be observed. This analysis demonstrated that wood particles were most abundant in the 1–0.5 mm particle size range. However, they were recognizable even in sizes <0.01 mm. Approximately 35% of particles 1–0.5 mm were recognizable as wood, the remainder being insect and leaf parts plus many of unidentifiable origin. Particles 0.25–0.1 mm were 28% wood derived. Percentages of woody particles were less in smaller size classes. Samples from the 0.1–0.053 mm range yielded 15% of particles recognizable as wood. These must be considered conservative estimates, since only particles of obvious wood origin were counted as such.

Discussion

For stream systems where accumulations of coarse and fine woody debris are large, we believe that processing of this debris can produce a significant input to the FPOM pool. The abundance of submerged wood surface area and mass at Mack Creek makes it a site where wood processing could play a particularly significant role. We have based this conclusion not only on the large amounts of wood that were present in the stream, but also because degradation and erosion of wood surfaces were measurable on an annual basis, a high percentage of FPOM particles was clearly of wood origin when viewed with SEM, and the lignin and cellulose content of FPOM was similar to that of surface wood.

Large accumulations of both coarse and fine debris exist in Mack Creek, but much of it lies above winter base flow water levels. Our estimates of LWD mass were approximately one third of that previously reported for this stream (Anderson et al. 1978; Keller and Swanson 1979); however, ours included only that debris submerged during winter. Substantial amounts of LWD also exist above the winter base flow height, although above 0.4–0.7 m it may contribute little to the FPOM pool. Our estimates of FWD surface area are larger than those of Anderson et al. (1978); however, we included all forms of fine wood >1 cm in diameter, whereas they reported data only for small branch wood.

Even though the results of these studies demonstrate the abundance of wetted wood surface area, our values are undoubtedly underestimates. Surface area calculations assumed smooth surfaces and did not take into account the roughness inherent in natural wood. The surface area of the ends of logs also was not calculated. A more important consideration is that within the 220-m study reach there were no large debris dams. Debris dams serve as retention structures for all types of organic detritus and have been observed to trap massive amounts of both large and fine wood (Bilby and Likens 1980; Cummins 1980; Triska and Cromack 1980). Below our study site on Mack Creek, two such dams occur, each containing wood wetted as the stream flow percolates through the structure. Unfortunately, accumulations of wood associated with these debris dams (some as high as 5–8 m in Mack Creek) were not considered in this study because of the difficulty in measuring buried woody debris in such large structures.

Much of the data presented here are expressed per unit surface area of wood. Although the data could be expressed in units of mass, we believe that the production of FPOM from large wood is best expressed in relation to surface area. The vast majority of wood decomposition occurs in the outer few millimetres of surface (Triska and Cromack 1980; Aumen et al. 1983) and thus, the majority of the wood mass is not metabolically active and not subject to processes which generate FPOM.

The production rate of FPOM is related to the extent of previous microbial degradation and softening of the wood surface. The FPOM is generated when the surface tissue, softened by the differential mineralization of cellulose, becomes sufficiently weakened to be removed by mechanical abrasion from streamflow. Removal of the surface layers exposes the fresh wood substrate beneath, which then can be colonized and degraded to continue the cycle of FPOM production. All of our FPOM production data were derived from Douglas-fir logs. Compared with hardwoods, conifer wood is likely to be processed much slower. Thus, in streams where LWD from hardwoods is abundant, FPOM generation per square metre of wood surface could be greater than in streams where conifers dominate.

At present it is not clear whether LWD or FWD contributes more to the FPOM pool. Fine wood constitutes by far the majority of submerged surface area (Table 1) and in the terrestrial environment is more rapidly processed than coarse wood (Triska and Cromack 1980). However, the majority of FWD is located in more protected areas of the channel, whereas LWD is often oriented more perpendicular to the direction of streamflow and exposed to greater current velocities and to greater erosive forces.

Our calculations suggest that FPOM generated from wood has the potential to be greater than that generated from leaf and needle litter processing. Even if one assumes that all surface wood of all LWD is relatively sound, FPOM inputs could be approximately 50% of that generated from leaf and needle litter processing. However, the surfaces of most logs in Mack Creek are partially decomposed and thus subject to more rapid processing than sound wood. Assuming only a slightly less conservative processing rate, inputs to FPOM would be greater than total annual litter fall. The actual contribution from LWD remains to be determined, for these estimates are not weighted for logs of different decay state, for orientation of the logs (which may affect the erosive capabilities of the current), or for the fact that upstream and downstream sides of logs may be processed at different rates. Our estimates of FPOM production also include that proportion of wood volume lost to mineralization. At present we have no good estimates of mineralization rates, but existing evidence suggests that it is quite slow and is likely small in proportion to fragmentation rates. Turnover rates of large wood based on microbial respiration alone are calculated in terms of centuries. However, few logs older than 75–100 yr are ever observed in Mack Creek (Triska and Cromack 1980). We believe that the difference is due to fragmentation of LWD surfaces.

The production of FPOM from wood surfaces should be greater in winter months than in summer. Rising water levels associated with high winter rainfall increase greatly the amount of submerged woody debris subjected to the physical abrasion of current. The normal winter rise in water level of 0.4 m over summer base flow in Mack Creek increases wetted wood surface by 300%, and during storm flows would of course be even greater. Degradation of wood surfaces continues throughout the year on both submerged and exposed surfaces; however, microbial activity is greater during the summer months (Aumen et al. 1983). Temperatures are warmer, and for many logs exposed by the lower water levels, reductions in water saturation occur, which may enhance diffusion of oxygen through the wood stimulating microbial metabolism. This exposure likely enhances the erodability during winter. There is also likely to be some contribution to the FPOM pool from large wood located above winter base flow. Rotting of this wood, under essentially terrestrial conditions, would produce FPOM as a result of either wind action, rain, alternate freezing and thawing, or processes similar to dry raveling in soils.

An additional source of wood-derived FPOM may be lateral transport from soils in the riparian zone. Riparian soils near Mack Creek contain large amounts of buried wood, and woody debris exists in great abundance on adjacent slopes (Harmon et al. 1986). Therefore, any erosion inputs to the stream channel may contain particles derived from wood. No erosion data exist for Mack Creek, but does for Watershed 10, a second-order stream channel near Mack Creek. Based on data for surface erosion, soil creep, and root throw (Swanson et al. 1982) and from lateral movement of coarse particulate litter (Triska and Cromack 1980), we calculated that erosional inputs contributed 225 g soil organic matter$\cdot m^{-2} \cdot yr^{-1}$. This is somewhat higher than annual litterfall estimates of 151 $g \cdot m^{-2} \cdot yr^{-1}$ (Triska and Cromack 1980) and compares favorably with potential wood-derived FPOM inputs to Mack Creek. The extent to which wood-derived particles are present in soils is not known, but the average lignin content of soil is very near that of FPOM (Table 2). This source may also be important in streams where the quantities of wood in channel storage are small. The overall contribution of soil movement processes to wood-derived FPOM in streams is unknown at this time and warrants further study. Given the potential inputs of FPOM from soil and LWD processing, it appears that leaf and needle litter inputs can no longer be assumed to constitute the majority of organic matter inputs to a stream system. In many situations, to omit these inputs could result in a serious underestimate of carbon flux into the system.

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