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SOURCES AND FATES OF ORGANIC INPUTS IN CONIFEROUS FOREST STREAMS[1]

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ABSTRACT

A study of the quality and magnitude of particulate organic inputs was undertaken in two streams in the Oregon Cascades. Objectives included estimation of litterfall and lateral movement of organic debris into a stream, estimation of litter breakdown rates, and construction of a first-approximation organic material budget.

In this study, approximately 65% of the litterfall input consisted of Douglas-fir and hemlock needles, which fall throughout the year. Deciduous inputs occurred primarily mid-October through November and consisted principally of vine maple and bigleaf maple. Preliminary lateral movement data indicated that organic material entering watershed 10 from the bank was 1.5 times the litterfall. The total estimate of litter input is approximately 2.5 g m^{-2} day^{-1}. Both streams have the capacity to process all types of leaf litter within a year. Needles, the most refractory leaf litter, are processed by microbes and, once conditioned, are consumed readily by invertebrate shredders. Thus the large amounts of needle litter that enter the stream in late summer and fall constitute a food source usable by stream detritivores after deciduous litter has decomposed.

Leaf-pack experiments have revealed the danger of extrapolation of biological information from smaller to larger streams. Faster processing times for larger streams have been suggested by information on weight loss, invertebrate biomass, and leaf quality. Changes in litter quality were determined by increases in the percentage of lignin content. Increases in lignin composition were compared with decreases in non-cell-wall constituents to obtain an estimate of microbial activity.

Information on litterfall and lateral movement, in conjunction with previously collected data, led to a first-approximation particulate organic matter budget for watershed 10. When compared with a similar budget from a very different stream system, processing capabilities of the two streams were remarkably similar. In both streams almost 99% of the particulate organic material entered from terrestrial systems. About two-thirds of the organic inputs entering each stream were processed within the system, indicating the processing role of small forest streams.

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INTRODUCTION

The idea that most streams not significantly altered by man are predominantly heterotrophic has been well substantiated by stream biologists over the past few years. That is, the maintenance of stream community structure and function is dependent upon the import of organic matter from autotrophically dominated terrestrial communities. Woodland streams can be compared to soil litter communities and the benthic communities of lakes in that they are detritus based and dependent upon export of production from other systems.

Part of the work under way in Oregon under the Coniferous Biome program is designed to study the interrelations between the terrestrial and aquatic components of small watersheds. Under investigation in the stream ecosystem are the rates of production of aquatic plants, insects, and fish, along with the input of particulate organic material and the processing of it by microorganisms and invertebrates. The work reported in this paper represents a part of that research, with emphasis on the fate of the particulate organic material.

Some of the mechanisms involved in the degradation of vascular plant tissue in stream environments have been the subject of recent studies (Kaushik and Hynes 1971, Vannote 1970, Triska 1970, Cummins et al. 1972, 1973, Fisher and Likens 1972). The functional relationships among vascular plant tissue, dissolved organic matter, microbial organisms (fungi and bacteria), and animals have not been clearly defined, however.

The present study assessed the sources and magnitude of various particulate organic matter inputs and their fates in two Cascade Range streams. Three main objectives of this study were: (1) to estimate litterfall biomass and lateral movement of detritus into a stream running through an old-growth forest; (2) to estimate the rates of litter breakdown in two coniferous forest streams of different flow; and (3) to obtain a data base for construction of an organic material budget and for later systems modeling of energy or mineral cycling.

Study Area

The study was conducted in the H. J. Andrews Experimental Forest, a 6000-ha watershed in the western Cascades of Oregon. The drainage is characterized by steep topography, with about one-fifth of the study area consisting of more gentle slopes or benches. Elevation varies from 457 m to more than 1523 m. Mean forest air temperature varies from 2°C in January to 18°C during the summer months. Annual precipitation ranges from 225 cm at lower elevations to 350 cm at the highest ridges. Highest elevations are characterized by extensive snowpack during the winter, while rain predominates at lower elevations (Berntsen and Rothacher 1959). Mack Creek and the stream draining watershed 10 were the two streams in the drainage basin that were studied intensively.

Watershed 10 (WS 10) covers 10.1 ha and rises from 430 m at the outlet stream gaging station to 670 m at the highest point. The overall slope of the stream channel is 45%. Side slopes and headwall, however, range up to 90% because of the deep incision of the basin into the main ridge.

Stream discharge varies from around 0.23 liter/sec in the summer to about 140 liters/sec during winter freshets. The uppermost forks are intermittent during the summer months. Mean width of the stream channel ranges from 0.25 m in the upper reaches to 0.75-1.0 m at the base of the watershed.

Streambed morphology is best described as a "stairstep" series of small pools connected by free-fall zones or riffles running on bedrock. Pools are formed mainly by accumulations of organic debris. The substrate consists of loose rocks and gravel from weathered tuff and breccia material and bedrock of unweathered tuff and breccia.

Mack Creek is one of the three major streams that drain the entire Andrews Experimental Forest. The area being studied is between 700 m and 900 m in elevation and drains approximately 650 ha. The watershed slope in this area is 44%. Stream discharge at the study area is estimated between 100-140 liters/sec in late summer and 1500-1800 liters/sec during winter freshets. The stream morphology is a stairstep of gouged pools, free-fall zones, and fast water around large boulders. The substrate ranges from large boulders to fine silt. Unlike WS 10, Mack Creek has a well-developed armor layer on the bottom, which prevents all but the largest winter storms from moving large particles of sediment. Watershed 10 has no such layer and only the organic debris dams act as protection from streambed erosion during winter storms. In WS 10 even small winter storms cause extensive substrate movement in the pools.

Both streams have comparable water chemistry and temperature regimes ranging from 0°C to 15°C, with a mean of approximately 8°C. Water chemistry has been extensively investigated on WS 10 and preliminary results were reported by Fredriksen (1972). The streams are low in dissolved materials, carrying an average concentration of total dissolved solids of 40 mg/liter (Fredriksen 1971).

MATERIALS AND METHODS

Particulate organic material input and export was studied intensively on WS 10 only. The investigation to determine rates of litter breakdown was conducted on both WS 10 and Mack Creek. Litterfall input to the WS 10 stream system was sampled with eleven 1.0-m^2 litter traps placed randomly over the stream. The traps stand on angle iron legs about 0.5 m above the water. Traps are 15 cm deep and each has a removable muslin insert with a mesh opening of 500-800 µm. Litterfall was sampled monthly from March 1972 to March 1973. Litter was sorted into eight categories: cones, leaves, needles, twigs, wood, frass, bark, and fruit; it was dried at 50°C and weighed.

Since WS 10 is at the bottom of a deeply incised basin, organic material also enters by sliding down the bank slope and into the stream. This lateral movement across the forest floor is being sampled by 30 randomly placed, rectangular boxes (0.1 m high by 0.3 deep by 0.5 m wide) with aluminum tray inserts. Traps are placed on the forest floor adjacent to the streambed with the open end (0.5 m) oriented parallel to the stream and facing upslope. Lateral movement is collected monthly. Litter is sorted into categories as above, dried, and weighed.

To determine the rate of litter breakdown and the effect of streamflow on the rate of litter disappearance, a leaf-pack experiment was undertaken on two streams of different size. Four types of leaf litter, representing the predominant streamside vegetation and a range of decomposition rates, were used: conifer needles (*Pseudotsuga menziesii* and *Tsuga heterophylla*), vine maple (*Acer circinatum*), bigleaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). In addition, mixed leaf packs consisting of alternating leaves of bigleaf maple and red alder were placed in Mack Creek. Leaves or needles of each litter type were collected at abscission, air dried, and strung on monofilament line to produce a 5- to 15-g leaf pack. Leaf packs were oven-dried (50°C), weighed, tied to bricks, then placed in the stream. Packs were oriented upstream with the current holding the pack against the leading face of brick. Incubation in this manner allowed leaf packs to remain unconfined and completely accessible to all types of invertebrates. As a result, there was a great variation in weight loss due to physical abrasion, decomposition, and shredding by the insects. Nonetheless, this method was preferred over litterbags, since it more closely simulated natural leaf accumulations.

Three leaf packs of each type were collected monthly from each stream and returned to the laboratory for processing. Leaf packs were washed and insects and ancillary debris were removed by hand. Packs were then dried and reweighed to obtain weight loss information. Loss rates were estimated by fitting data to the exponential model $Y_t = Y_0 e^{-kt}$. Leaf packs were combined by leaf type and ground through a 40 mesh on a Wiley mill for chemical analysis. Kjeldahl nitrogen content was determined monthly for each leaf type. Phosphorus was determined monthly by digestion in nitric and perchloric acid and reduction with ammonium molybdate and sodium bisulfate for spectrophotometric analysis. Detritus quality was determined by the acid-detergent, lignin-cellulose method of Van Soest (1963).

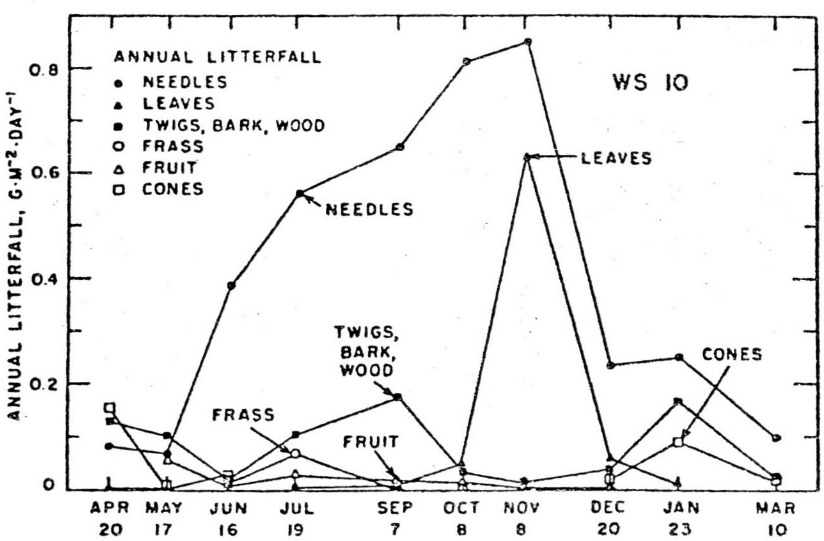

Figure 1. Annual litterfall into watershed 10 by litter type.

RESULTS AND DISCUSSION

Litter Input

Monthly collection of litterfall for a full year indicated a dominance by coniferous needles (Figure 1). Approximately 65% by weight consisted of litter from Douglas-fir and hemlock. Needle fall occurred to some extent throughout the year, but was particularly heavy from the conclusion of the rainy season in June until the return of autumn rains in November. As expected, major inputs of deciduous leaf material occurred from mid-October through November. Deciduous inputs consisted primarily of vine maple and bigleaf maple. Insect frass falling through the canopy during dry summer months constituted a significant energy input whose role remains to be clarified. Highly refractory material (twigs, bark, and wood) constituted 10% of the energy input. On a yearly basis, WS 10 averaged a daily input of 1 g m^{-2}. This value is low compared with the finding of Abee and Lavender (1972), who estimated 1.5 g m^{-2} day^{-1} for homogeneous reference stands of the same forest.

The first three months of lateral movement sampling (March-May) indicate that the amount of organic material entering the stream from the bank is approximately 1.5 times the litterfall. Thus approximately 2.5 g m^{-2} day^{-1} entered WS 10 in the form of litter. This value is in the low middle range of a series of values for input of large particulate detritus (>1 mm) from several eastern streams reported by Cummins et al. (1973).

Litter Breakdown

There were significant differences between streams and among species in the rate of disappearance of leaf material from the packs (Figure 2). All species broke down more rapidly in Mack Creek than in WS 10. In the single-species packs, coniferous needles disappeared most slowly and alder

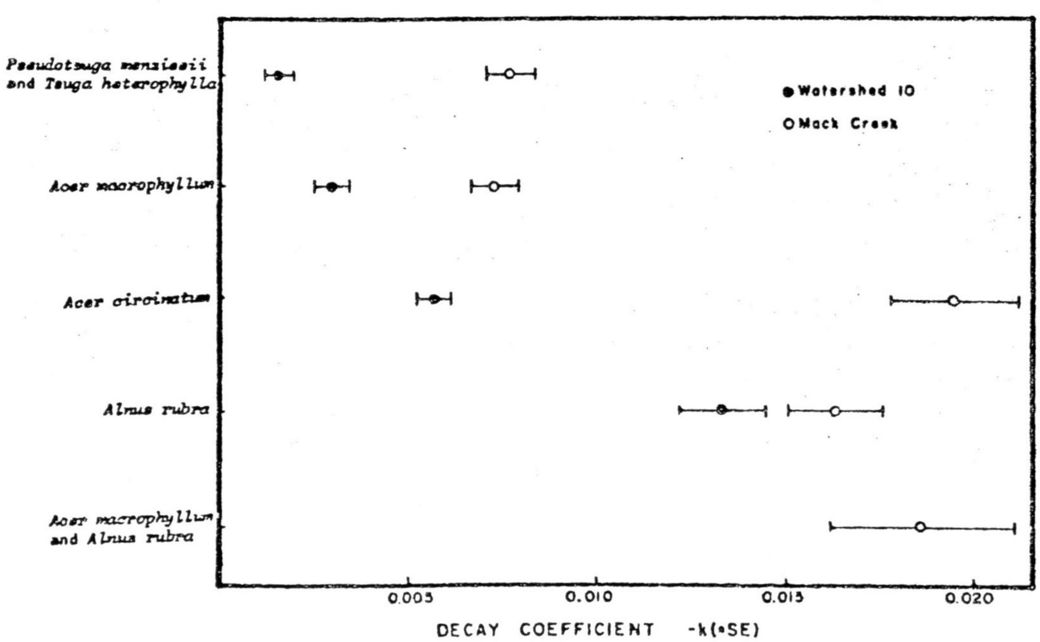

Figure 2. Decay coefficients (-k) and one standard error for five leaf-pack types in two Cascade streams.

and vine maple most rapidly. Mixed packs of leaf species that decomposed at different rates, fast for alder and slow for bigleaf maple, resulted in a decay coefficient higher than that of either species individually. This suggests that naturally occurring mixtures of leaves may decompose faster than monospecies leaf packs.

Linear trends of the data on weight loss of vine maple and conifer packs (Figure 3) indicated that regression analysis would be a valid technique for comparing weight losses from the leaf packs for both streams. All regression lines were highly significant ($P < 0.01$). Vine maple packs in Mack Creek lost 50% of their initial weight in 36 days as compared with 123 days in WS 10. Conifer packs in Mack Creek required 89 days to lose 50% of their weight as compared with an estimated 465 days in WS 10.

The differences in disappearance rates for the same leaf species between the two streams might be explained in part by the difference in the num-

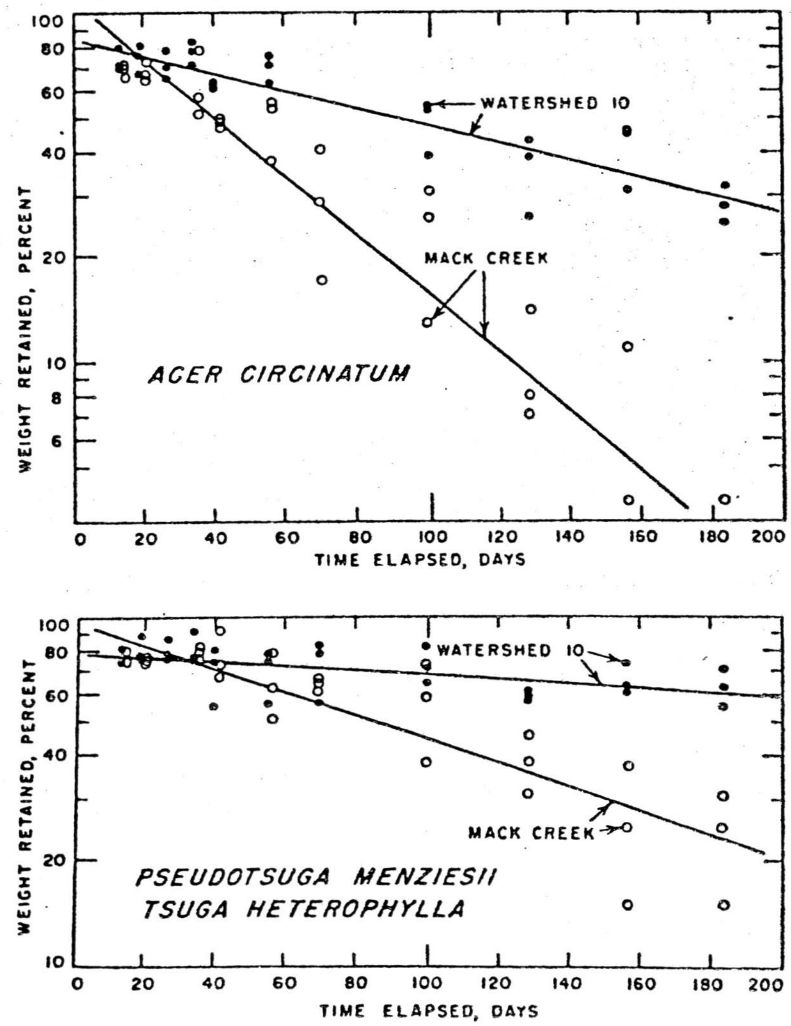

Figure 3. Disappearance rates by weight loss of vine maple (*Acer circinatum*) leaf packs, and Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs in Mack Creek and the watershed 10 stream.

ber of shredding invertebrates found in the two streams. There were greater numbers and biomass of invertebrates in Mack Creek compared with WS 10. The ratio of invertebrate biomass to leaf-pack biomass was also significantly greater in Mack Creek than in WS 10 (Figure 4). A large percentage of the invertebrate biomass on the conifer packs in WS 10 was composed of small snails. The two WS 10 ratios that rise above the Mack Creek ratios were due to large numbers of snails that appeared in the packs after 90 days' incubation.

The range of rates among leaf species is not surprising in that different leaf species become conditioned by microbial activity at different rates and, thus, more readily acceptable as food for shredding invertebrates (Triska 1970, Boling et al. 1974). Needle litter, generally considered highly refractory, was expected to be exported from the watershed prior to decomposition and to provide only a minor source of food energy for

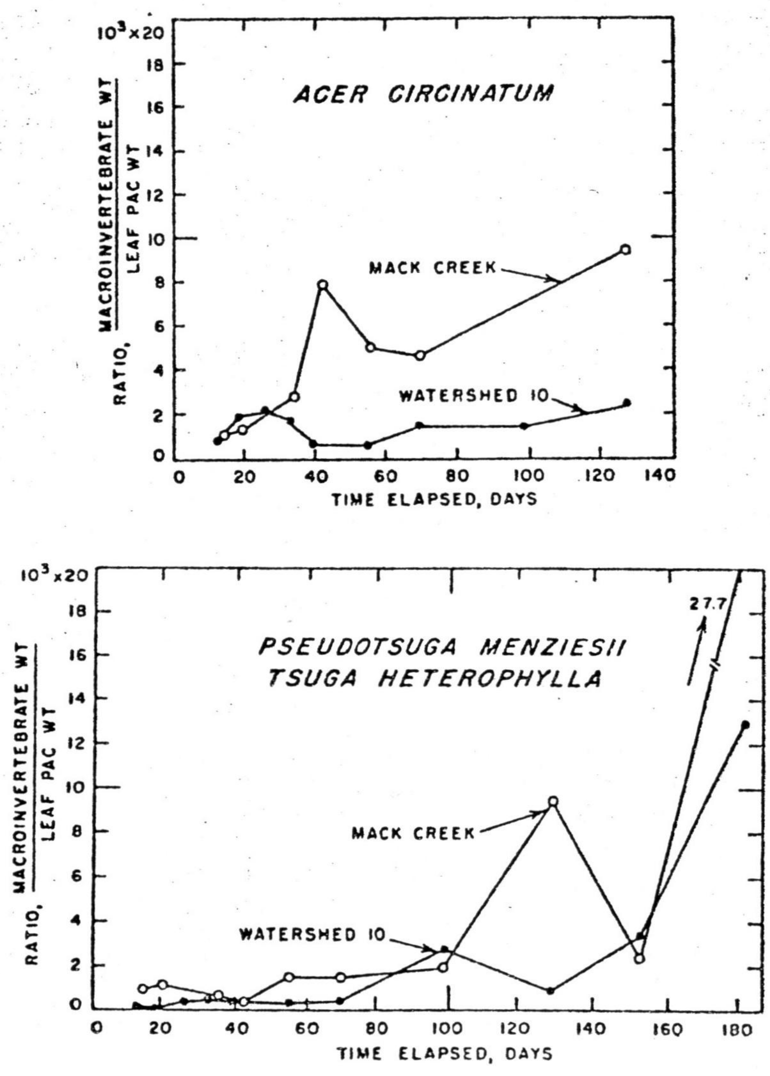

Figure 4. Ratio of macroinvertebrate biomass to mean leaf-pack weight for vine maple (*Acer circinatum*) leaf packs, and Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs in Mack Creek and the watershed 10 stream.

invertebrates. Conifer packs incubated in Mack Creek indicate, however, that after 140-180 days in the stream needle litter became palatable to shredding insects. After this conditioning, needle packs were heavily grazed by *Lepidostoma* sp. until they were entirely consumed. Prior to conditioning, needles were grazed minimally by insect detritivores.

A comparison of the decay coefficients in this study with other values reported in the literature shows that decay rates in Mack Creek for vine maple, alder, and the mixed pack are much higher than the fastest rates (k = 0.22) reported by investigators in Michigan (Boling et al. 1974). The slow decay rates of conifer and bigleaf maple from Mack Creek are in the middle range of their values. The decay rates of conifer needles and bigleaf maple in WS 10 are lower than in the lowest Michigan values. Approximate decay rates calculated for red maple, tulip poplar, and white oak in Tennessee (Thomas 1970) fall within the range of decay coefficients from Mack Creek.

The comparison of decay coefficients between Michigan and the Cascade streams is of great interest in that the water temperatures of the streams in these two regions were roughly the same. The temperatures of the Michigan streams ranged from 0.1° to 11°C with a mean temperature over the fall-winter season between 3° and 4°C (Robert Peterson, personal communication). The stream temperatures in the Andrews Forest ranged from 0.1° to 8°C, with a mean temperature also about 4°C. The decay rates from Tennessee were determined from a stream whose temperature ranged between 10° and 16°C.

Many of the problems in interpreting leaf-pack studies in forests have been discussed by other investigators, including Minderman (1968) and Anderson (1973). Leaf accumulations in streams are subject to breakdown processes analogous to those in the terrestrial litter. On land, abiotic fragmentation occurs from animal activity when the litter is wet. Leaf accumulations decomposing in streams are subject to freshets, which result in increased fragmentation and reduced animal consumption. As the water level drops and abiotic fragmentation diminishes, animal feeding increases. Conifer needles, being small and compact with a tight vein network, resist fragmentation more than vine maple or alder. Thus as Anderson (1973) points out, one would expect different leaf species to have various degrees of susceptibility to mechanical breakdown.

Since weight loss is a measure of leaf disappearance rather than decomposition, the biochemical parameter of lignin composition was used to obtain an additional index of microbial activity to help separate biotic from abiotic processes. Lignin was chosen since it is the leaf constituent most resistant to decomposition, and therefore increases in percentage of total composition as decomposition proceeds. Changes in lignin were compared with decreases in the most labile fraction, the non-cell-wall constituents. Alexander (1961), Peevy and Norman (1948), and Pinck et al. (1950) have indicated that changes in lignin composition may provide a good relative prediction of litter decomposition rates. In addition Cromack (1973), working in a wet hardwood forest and a white pine plantation, found that the rate of change of lignin content may be the best single criterion predicting leaf litter decay rates.

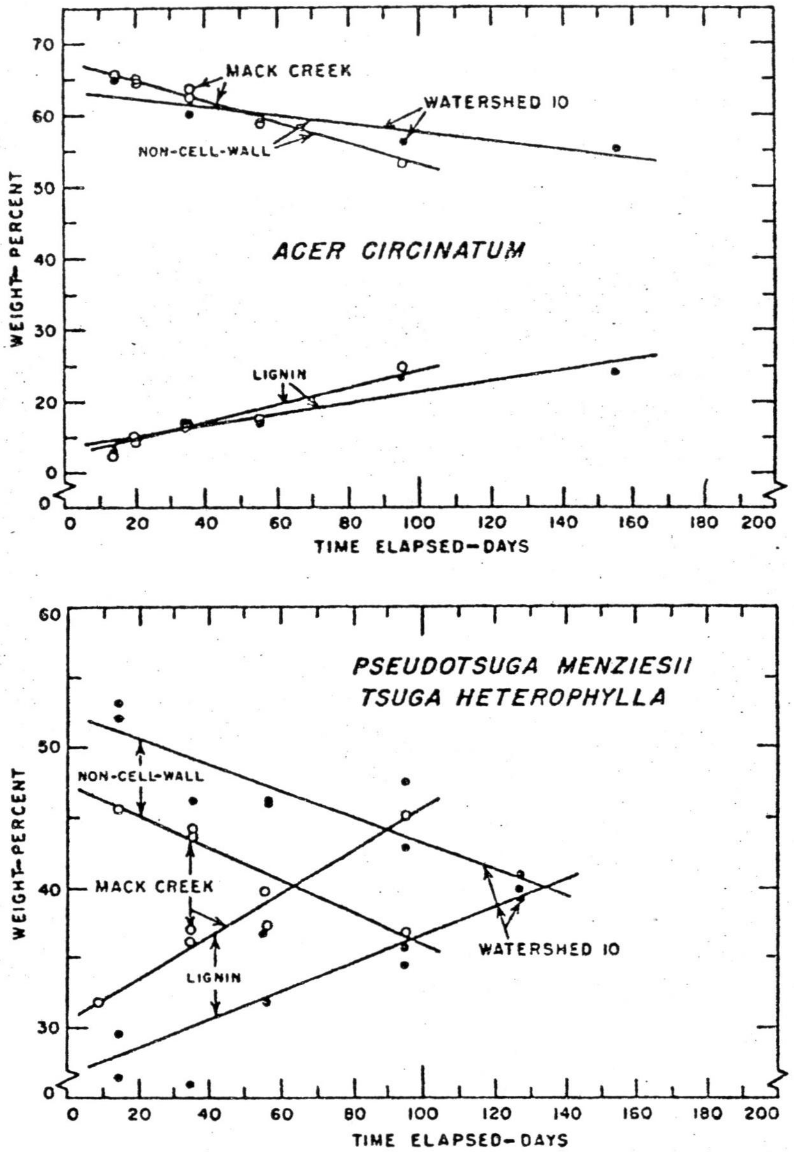

Figure 5. Percent changes of non-cell-wall constituents and lignin composition for vine maple (*Acer circinatum*) leaf packs, and Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) needle packs in Mack Creek and the watershed 10 stream.

In our study, increase in percentage of lignin and decrease in percentage of non-cell-wall constituents (NCWC) were consistent with the weight-loss data for conifer and vine maple packs (Figure 5). The NCWC consists of soluble carbohydrates, soluble protein, organic acids, nonprotein nitrogen, hemicellulose, and additional soluble organic material. The slower increase in percentage of lignin and the slower loss of NCWC in WS 10 than in Mack Creek indicated that decomposition was occurring at a slower rate in the smaller stream. Preliminary data on respiration rates of litter from the two streams also confirm greater microbial activity in Mack Creek.

Changes in litter quality may have proceeded at a slower rate in WS 10 because of fluctuating water levels that occasionally left leaf packs exposed to air. Although leaf packs remained wet continually, intermittent exposure to air could have altered bacterial and fungal communities. In Mack Creek all leaf packs were continually submerged.

The differences in processing rates of leaf litter material were also reflected in the chemical constituents of the litter. Throughout the experiment percentages of nitrogen and phosphorus for all leaf substrates were higher in Mack Creek than in WS 10.

Particulate Organic Budget for WS 10

The data gained from the lateral movement and decomposition study provided an opportunity to construct a first-approximation particulate organic matter budget (Figure 6). All values were measured independently rather than by difference; however, the results must be interpreted with caution because many of the estimates have been based on short-term sampling.

The stream bottom area was estimated at 300 m^2. Measurements of input were litterfall, lateral movement, throughfall, algal production, and moss production. Throughfall was estimated by G. C. Carroll (pers. commun.) at 0.1 g m^{-2} day^{-1} based on a three-day sample. Algal biomass was estimated at 0.33 g m^{-2} by chlorophyll extraction; turnover time was assumed to be 40 days. Moss production was estimated at 2.1 g m^{-2} yr^{-1} from Fisher (1970). Standing crop of detritus was calculated from 20 core samples, 15 cm in diameter. Macroinvertebrate biomass was based on an averaging of two different methods. The first was a single standing crop estimate (ten 15-cm cores), with production estimated at 3.5 times standing crop (Waters 1969). Standing crop was calculated by this method to be 1.3 g m^{-2}, with an annual production of 4.55 g m^{-2}. The second method used was year-round emergence data from WS 10 and indicated a standing crop of 2 g m^{-2}. This value was obtained by assuming emergence was one-fourth of the average standing crop. Annual production was calculated to be 7 g m^{-2}, using Waters' 3.5 turnover ratio. Respiration of detritus was based on 100 measurements of five size classes of detritus at 10°C. Caloric content was assumed at 16.7 x 10^3 J/g (4000 cal/g).

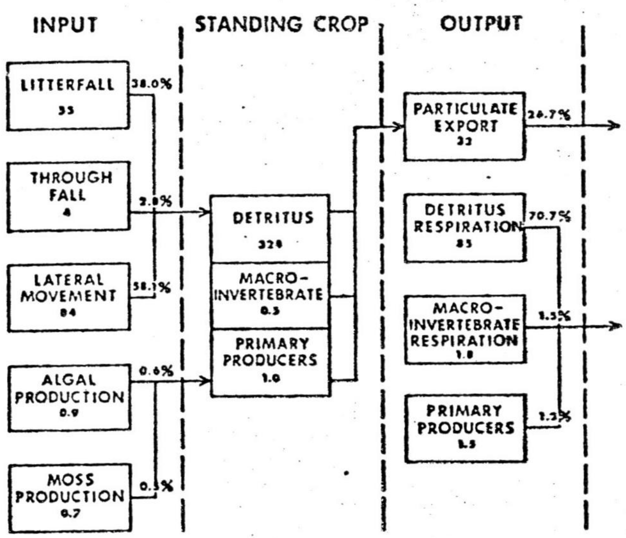

Figure 6. Annual flux of particulate material biomass (in kilograms per stream per year) in watershed 10 (1972-1973). The percentage value associated with each vector indicates the proportion of total input or output represented.

A net accumulation of 24.3 kg occurred in the water year 1972-1973. This water year was particularly dry, which could have resulted in less export and less microbial respiration. Detrital respiration accounted for about 70% of the loss of particulate organic matter, suggesting the need for more accurate assessment of this process.

The same general approach has previously been used by Fisher and Likens (1972) to construct an organic budget for a stream in New Hampshire. This stream has a relatively low gradient (14% streambed slope), receives the bulk of its litter input in the autumn, and has a fairly evenly distributed precipitation pattern of about 123 cm/yr. The Fisher and Likens organic budget assumed the stream was in steady state; that is, the inputs equaled the outputs. In addition, their largest component of the particulate organic output (microbial respiration) was obtained by difference. Watershed 10, as previously mentioned, is a high-gradient stream (45% slope), receives the bulk of its litter input over the summer and fall, and receives precipitation of 240 cm/yr, 90% of which falls in a six-month period between October and March. Nonetheless, for both systems, 99% percent of the particulate organic input is detritus or litter, and 1% or less is contributed by the primary producers. For both streams, about two-thirds of the detrital inputs were processed by organisms in the stream. Only about one-third of the detrital input was exported out of these small streams (Figure 7). Such data indicate small woodland streams are indeed significant biological processing units.

Reichle (1974) has compared some computed metabolic parameters of several different terrestrial ecosystems. The object of his comparison was to demonstrate consistent patterns that could be extrapolated between systems. One such ratio discussed by Reichle is ecosystem maintenance efficiency. This ratio represents the cost of production in an ecosystem and is defined as the ratio of autotrophic respiration to gross primary production. For purposes of comparison, one could assume that detrital input to a stream system is analogous to gross primary production in a terrestrial system. Both represent nearly all the gross energy input to their respective systems. Likewise, detrital respiration in streams could be substituted for autotrophic respiration in calculating an analogous ratio for stream ecosystems.

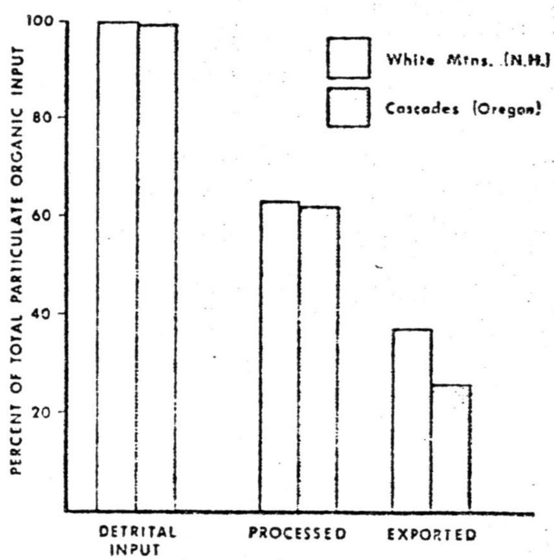

Figure 7. Comparison of particulate organic material input, processing, and export for two small mountain streams, Bear Brook in the White Mountains of New Hampshire, and watershed 10 in the Oregon Cascades.

For three terrestrial systems (coniferous forest, deciduous forest, and grassland) the maintenance efficiencies ranges from 0.53 to 0.62 (Reichle 1974). The corresponding values for the Oregon and New Hampshire streams were 0.59 and 0.63, respectively. These values suggest an unsuspected similarity between terrestrial and aquatic systems.

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