Ecology, 61(4), 1980, pp. 727–732

DETRITAL PROCESSING AND ASSOCIATED MACROINVERTEBRATES IN A COLORADO MOUNTAIN STREAM[1]

ROBERT A. SHORT,[2] STEVEN P. CANTON,[3] AND JAMES V. WARD
Department of Zoology and Entomology, Colorado State University, Fort Collins, Colorado 80523 USA

Abstract. Investigation of leaf litter processing in a Colorado mountain stream revealed that processing of alder (*Alnus tenuifolia*), willow (*Salix bebbiana*), and aspen (*Populus tremuloides*) occurred at rapid rates despite water temperatures at or near 0°C. Pine (*Pinus ponderosa*) was processed much more slowly. The loss rate coefficient (k) ranged from .0038 for pine to .0308 for alder. The high biomass of shredders per gram of leaf pack is a likely explanation for the rapid processing. Whereas a few large shredders per leaf pack are generally characteristic of eastern woodland streams, a large number of small-sized shredders (*Capnia* and *Zapada*) colonized leaf packs in the Colorado mountain stream. The numbers and biomass of collectors per leaf pack were directly related ($P <$ .01) to the ash-free dry mass of fine organic particles (75–1000 μm) indicating the importance of fine particulate organic matter in determining the suitability of leaf litter as habitat for fine particle-feeding detritivores.

Key words: collectors; Colorado; leaf litter; mountain stream; processing; shredders.

INTRODUCTION

Terrestrial leaf litter has been identified as a major component in the energetics of stream ecosystems and as a food source for stream macroinvertebrates (Anderson and Sedell 1979). Rates of leaf litter processing have been measured in a variety of stream types in North America (Petersen and Cummins 1974, Sedell et al. 1975, Benfield et al. 1977, Bärlocher et al. 1978). These and other studies have indicated that macroinvertebrates may play an important role in the processing of leaf material. Furthermore, leaf litter has been shown to be an important factor in the distribution of benthic macroinvertebrates in streams (Egglishaw 1964). The macroinvertebrates associated with leaf litter in Colorado mountain streams have proven to be different in several respects from those reported in other studies. Thus in October 1977 a study of leaf processing in a Colorado mountain stream was initiated to determine: (1) processing rates of four common species of leaves, (2) which macroinvertebrates colonize leaf litter, and (3) the importance of leaf litter as a source of or collecting system for fine particulate organic detritus, and as a habitat for fine particle-feeding detritivores.

DESCRIPTION OF STUDY AREA

Little Beaver Creek is located in north central Colorado in the South Platte River drainage system. It is a third-order stream with a watershed area of 4600 ha. The study site is located at an elevation of 2410 m where the stream emerges from a narrow valley heavily canopied with willows (*Salix* spp.) and alders (*Alnus tenuifolia*). Quaking aspen (*Populus tremuloides*) and ponderosa pine (*Pinus ponderosa*) are dominant tree species on the slopes surrounding the stream. Stream width varies from 2 to 10 m and the gradient is 8%. Substrate consists mainly of rubble in riffles with few pools present. The stream was completely ice covered (up to 30 cm thick) and at 0°C from mid-November through late March. Discharge was low (0.1 to 0.2 m^3/s) and relatively constant throughout this period but increased dramatically (15 m^3/s) with snowmelt in June. Nutrients are present in low concentrations (PO_4, 10–12 μg/l; NO_3, 22–29 μg/l); the water is soft (9.4–11.3 mg/l $CaCO_3$); and the pH is near neutral (7.0–7.1). Dissolved oxygen is always near 100% saturation.

MATERIALS AND METHOD

Leaf processing rates were studied with leaf pack samplers (Petersen and Cummins 1974). Leaves of willows (*Salix bebbiana*), alder (*Alnus tenuifolia*), aspen (*Populus tremuloides*) and needles of pine (*Pinus ponderosa*) were collected in September 1977, just prior to abscission for the deciduous species. Due to the large number of leaves needed, they were picked from more than one tree of each species, except for pine. The leaves were air-dried, oven-dried at 60°C for 48 h, weighed into 5-g packs and strung on monofilament line. A single leaf pack was lashed to each brick and placed in a riffle area of the stream on 15 October. Three leaf packs of each leaf type were removed from the stream in a downstream to upstream direction after 7, 14, 28, 56, 84, 112, and (except alder) 168 days. The initial position of the bricks was recorded so that none would be disturbed when sampling during ice cover. At the time of collection the brick was removed from

[1] Manuscript received 8 January 1979; revised 19 August 1979; accepted 27 September 1979.
[2] Present address: Aquatic Station, Southwest Texas University, San Marcos, Texas 78666 USA.
[3] Present address: Harner-White Ecological Consultants, 4901 East Dry Creek Road, Littleton, Colorado 80122 USA.

TABLE 1. Loss of mass (percent loss of initial mass ± SD) of leaf material due to leaching.

Leaf type	Temperature (°C)	24 h	48 h	72 h
Alder	1	25.3 ± 1.1	28.6 ± 4.6	28.9 ± 2.9
	5	26.0 ± 4.0	24.4 ± 2.0	27.7 ± 0.8
Aspen	1	24.7 ± 3.9	30.4 ± 8.8	34.8 ± 5.6
	5	19.6 ± 6.7	25.1 ± 3.7	27.2 ± 4.2
Willow	1	33.0 ± 4.1	39.6 ± 1.9	42.5 ± 4.4
	5	32.0 ± 3.4	41.3 ± 2.4	45.7 ± 1.9
Pine	1	4.8 ± 1.2	6.3 ± 1.2	7.9 ± 1.0
	5	5.7 ± 0.7	3.7 ± 0.9	4.9 ± 1.6

the stream; the leaf pack was cut free and placed in a plastic bag containing Kahle's fluid. Samples were processed within 4 h to minimize possible leaf material mass loss from the preservative, although this possible loss was not checked experimentally.

In the laboratory the leaf pack was thoroughly rinsed with tap water to remove accumulated sediment and particulate organic matter. Macroinvertebrates were separated from the material and stored in 80% ethanol for later analysis. The rinsings were retained from the samples collected at 28-d intervals and washed through a 1 000-μm and a 75-μm sieve. Inorganic and organic material retained by the 75-μm sieve was dried at 60°, the mass determined and combusted in a muffle furnace at 550° for 24 h to determine the ash-free dry mass of organic material (Petersen and Cummins 1974) present in the 75–1000 μm size range. The intact leaves were dried at 60° for 48 h and the mass determined (±0.1 g). Absolute loss of mass and percentage of the initial mass remaining were determined. Macroinvertebrates removed from the leaf packs were identified, enumerated and the mass determined after drying to constant mass at 60°. No attempt was made to correct for loss of mass due to preservation.

A laboratory study was conducted to determine loss of mass of leaf material attributable to leaching. Preweighed amounts (≈0.1 g) of each leaf type were placed separately into small jars containing 150 ml of stream water. These jars were placed into constant-temperature chambers maintained at 1° and 5°. Three jars of each leaf type from each temperature were removed at intervals of 24, 48, and 72 h. The leaf material remaining was dried at 60° for 48 h, and the mass and percent loss of mass determined.

RESULTS

Leaching

The greatest loss of mass due to leaching (72-h laboratory experiments) occurred in willow (44%) and the least in pine (6%), with alder (28%) and aspen (31%) intermediate (mean values from Table 1). The greatest

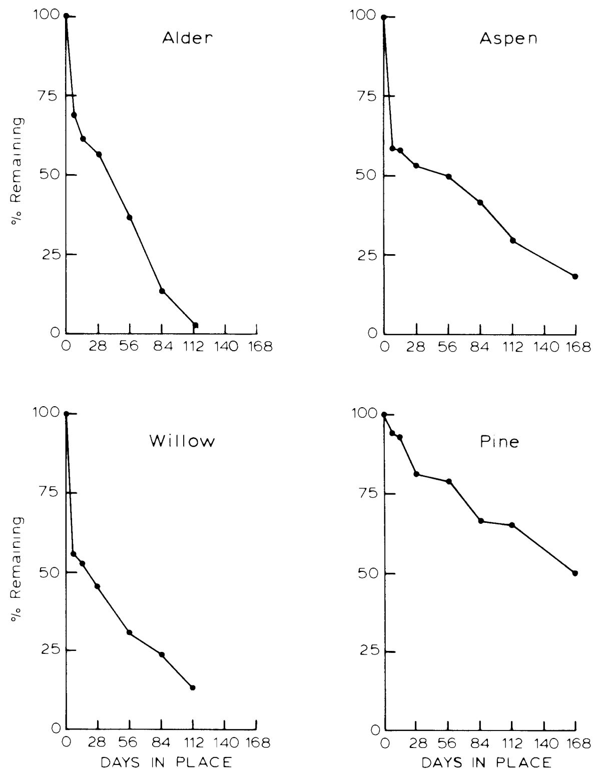

FIG. 1. Loss in mass of leaf packs in Little Beaver Creek, Colorado, 15 October 1977 through 1 April 1978.

loss of mass for each leaf type occurred within the first 24 h after immersion. Loss of mass increased with time except for alder at 5° and pine at 5°. These exceptions are probably the result of individual differences among leaves. The values obtained and the lack of temperature effects on leaching are similar to those reported by Petersen and Cummins (1974).

Leaf processing

The loss in mass of the leaf packs over time is shown in Fig. 1. Percent losses of mass obtained after 7 d in the stream were not significantly different from the 72-h laboratory leaching experiments, indicating that leaching was mainly responsible for the initial loss of mass. After leaching, alder demonstrated the most rapid processing, with willow the second fastest. Aspen was processed much more slowly and pine was by far the slowest. In studies of Oregon streams an alder (*Alnus rubra*) was one of the first leaves to be completely processed (Sedell et al. 1974, Sedell et al. 1975). Alder leaves have been shown to have a high concentration of nitrogen compared to other species (Triska et al. 1975) and to be readily consumed by stream detritivores (Wallace et al. 1970, Anderson and Grafius 1975). The more rapid processing of alder probably results from enhanced microbial degradation and increased shredder utilization. We found that alder was processed at such a rapid rate, despite water

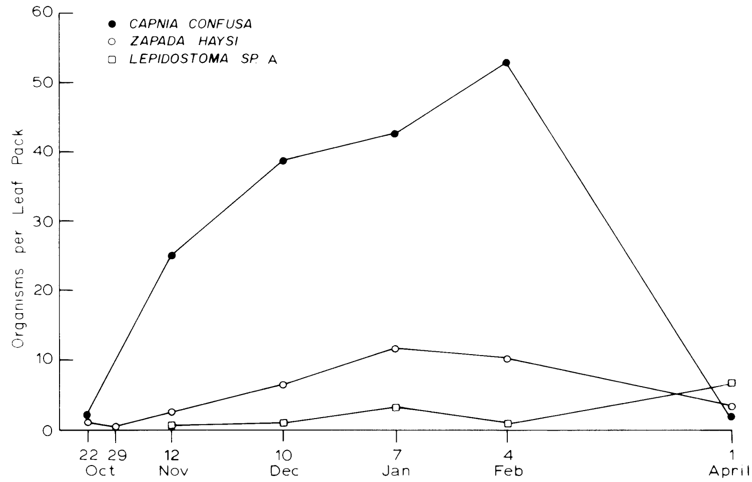

FIG. 2. Temporal occurrence and density of three shredder species in aspen leaf packs for Little Beaver Creek, Colorado, 15 October 1977 to 1 April 1978.

temperatures at or near 0°, that after 112 d in the stream little remained except the more resistant veins and midribs. Alder leaf packs were not collected after 112 d for this reason. Hart and Howmiller (1975) reported that alder was completely processed in 34 d in a California coastal stream at warmer temperatures (minimum temperature 9°). Willow was also processed rapidly in Little Beaver Creek, especially between 112 and 168 d. Only threads of monofilament remained on the bricks in the 168-d collections. Since the leaf packs had been completely processed on an unknown date between 112 and 168 d, the 168-d collections of willow were not included in the analysis.

Fall–winter leaf processing in streams has been assumed to follow an exponential decay model of the form $Y_t = Y_0 e^{-kt}$ where Y_t is the amount remaining after time t of the initial amount Y_0 (after leaching) and k is the loss rate or processing coefficient (Petersen and Cummins 1974). Following $\log_e$ transformation of the "percent remaining" data in Fig. 1, linear regression was used to estimate the processing coefficient for each leaf species after excluding the leaching loss. All equations were highly significant ($P < .01$) and the data fit the exponential model well. The processing coefficient values obtained in the present study are compared in Table 2 to those of the same or similar species used in other studies. Although direct comparisons with leaf processing rates measured in other studies are difficult to interpret due to differences in leaf pack construction, leaf pack size, and temperature, it is evident that leaf processing occurred at a rapid rate in Little Beaver Creek. Processing coefficients for the deciduous leaf species were approximately 1.7× greater in the Colorado mountain stream than those reported in other studies. If compared on a degree-day basis the difference would be even greater.

Macroinvertebrates

Generally the same macroinvertebrate taxa colonized the four leaf pack types (Table 3). Exceptions occurred when only a few individuals of a particular taxon were collected from certain pack types. The most abundant taxa collected were *Baetis* sp., *Ephemerella* spp., *Capnia confusa*, *Zapada* spp., *Heterlimnius corpulentus* and *Orthocladius* sp.

TABLE 2. Processing coefficients (k) for various species of leaves in streams

Species	k	Stream order	Season	Mean temperature (°C)	Reference
Alnus tenuifolia	.0308	3	Fall–spring	0°	Present study
Alnus rubra	.0168	3	. . .	4°	Sedell et al. 1975
Populus tremuloides	.0077	3	Fall–spring	0°	Present study
Populus tremuloides	.0046	. . .	Fall–spring	3–4°	Petersen and Cummins 1974
Salix bebbiana	.0135	3	Fall–spring	0°	Present study
Salix lucida	.0078	. . .	Fall–spring	3–4°	Petersen and Cummins 1974
Pinus ponderosa	.0038	3	Fall–spring	0°	Present study
Pinus resinosa	.0030	. . .	Fall–spring	—	Bärlocher et al. 1978

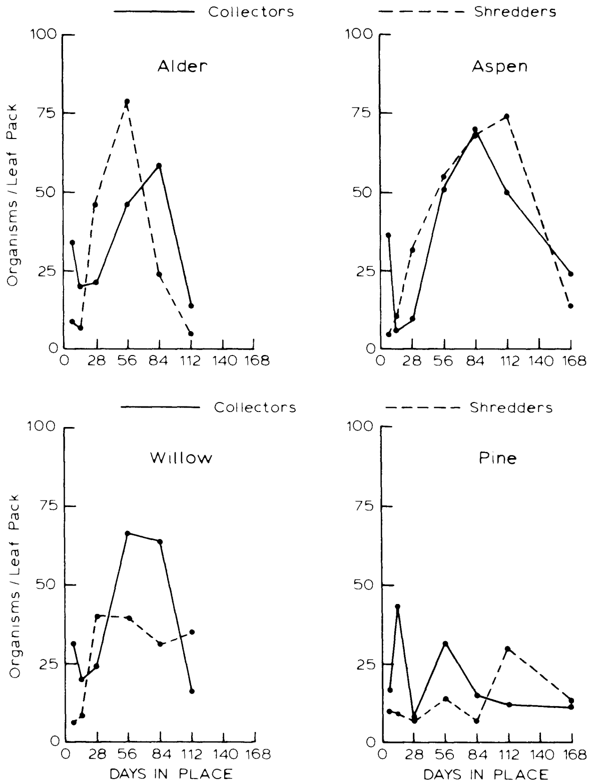

FIG. 3. Colonization of leaf packs in Little Beaver Creek, Colorado, according to functional group classification.

Macroinvertebrates were assigned to functional groups according to information contained in Merritt and Cummins (1978) and by inspection of gut contents. The dominant shredders were *Capnia confusa*, *Zapada cinctipes* and *Zapada haysi*. Two species of *Lepidostoma* were much less abundant. The densities of three shredder species on the aspen leaf packs shown in Fig. 2 are similar to the pattern found on the other deciduous leaves. Lower densities were found on the pine needle packs.

Other studies (Petersen and Cummins 1974, Benfield et al. 1977) indicate that a period of microbial conditioning is necessary before shredders colonize leaf litter in significant numbers. In our study, high densities of macroinvertebrates on leaf packs were obtained after 7 d in the stream (Fig. 3). Initially collectors exhibited the highest densities, mainly due to the presence of *Baetis*. After 28 d, the densities of shredders were higher than those of collectors except on pine. Highest shredder density occurred at 56 d for alder, 112 d for aspen, 28 d for willow and 112 d for pine. Higher shredder densities were not obtained after 112 d for the more slowly decomposing leaf packs (aspen and pine) due to the emergence of the winter stoneflies (Fig. 2). Maximal collector densities occurred at 84 d for alder, 112 d for aspen, 56 d for willow and 14 d for pine (Fig. 3).

TABLE 3. Macroinvertebrate taxa collected on leaf packs in Little Beaver Creek, Colorado. Functional group classification based on Merritt and Cummins (1978): S = shredder, C = collector, G = grazer, and P = predator.

Taxon	Functional group	Alder	Aspen	Willow	Pine
Ephemeroptera					
Ameletus sp.	C	+			
Baetis sp.	C	+	+	+	+
Cinygmula sp.	C/G	+	+	+	+
Epeorus longimanus	C/C		+	+	
Ephemerella grandis	C	+	+	+	+
Ephemerella infrequens	C	+	+	+	+
Paraleptophlebia sp.	C	+	+	+	
Rhithrogena sp.	C/G	+	+	+	+
Plecoptera					
Alloperla sp.	P	+	+	+	
Capnia confusa	S	+	+	+	+
Megarcys sp.	P	+	+	+	
Setvena sp.	P	+	+	+	+
Taenionema sp.	C	+	+	+	+
Zapada cinctipes	S	+	+	+	+
Zapada haysi	S	+	+	+	+
Coleoptera					
Heterlimnius corpulentus	C	+	+	+	+
Zaitzevia sp.	C				+
Trichoptera					
Arctopsyche sp.	C	+		+	
Brachycentrus sp.	C	+	+	+	+
Glossosoma sp.	C/G	+			
Hydropsyche sp.	C		+	+	+
Lepidostoma sp. A	S	+	+	+	+
Lepidostoma pluviale	S	+	+	+	+
Rhyacophila acropedes	C/P	+	+	+	+
Diptera					
Ablabesmyia sp.	P	+	+		
Atherix pachypus	P	+	+	+	+
Chelifera sp.	P		+	+	+
Orthocladius sp.	C	+	+	+	+
Palpomyia sp.	P		+		
Pericoma sp.	C		+	+	
Rheotanytarsus sp.	C		+	+	
Simulium sp.	C	+	+		+
Hydracarina	P	+			+
Oligochaeta					
Eiseniella tetraedra	?			+	
Total number of taxa		26	28	27	22

DISCUSSION

Detrital processing

Our results show that deciduous leaf packs are processed at a faster rate in Little Beaver Creek than in any stream previously studied using similar leaf species under a comparable temperature regime (Petersen and Cummins 1974, Sedell et al. 1975). We had anticipated a slower rate due to the low temperatures encountered. While increased physical fragmentation from swifter current is a possible explanation, Reice (1974, 1977) concluded that current velocity had no

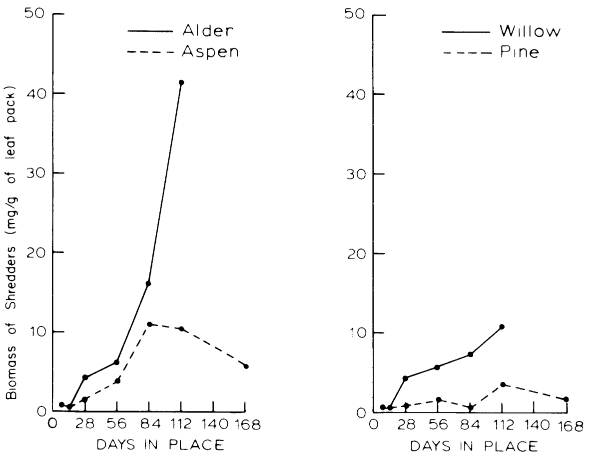

FIG. 4. Biomass of shredders (mg) per gram leaf pack for Little Beaver Creek, Colorado.

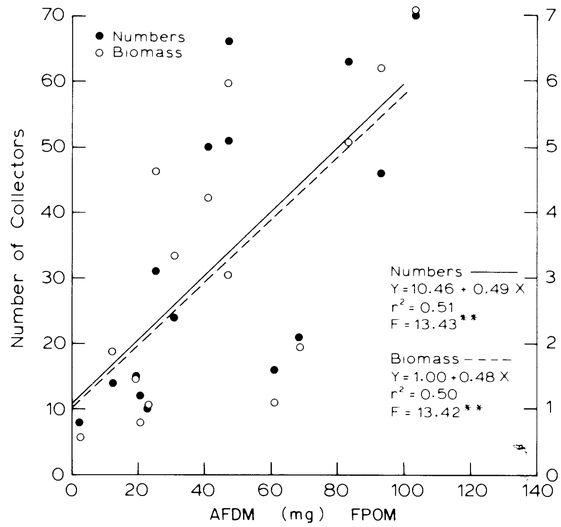

FIG. 5. Numbers and biomass (mg) of collectors per leaf pack as a function of ash-free dry mass (AFDM) in milligrams of fresh particulate organic matter (FPOM, 75 to 1000 μm).

significant effect on processing rate. Microbial metabolism of leaf tissue was not studied, but it is doubtful that it was responsible for the rapid processing, given the low temperature and nutrient levels. Increased colonization and utilization of the leaf material by shredders appears to be the most plausible explanation. It has been estimated that shredders account for about 25% of leaf pack processing in streams (Petersen and Cummins 1975). Biomass of shredders per gram leaf pack is shown in Fig. 4. The maximum value for alder is approximately seven times the highest value observed for a fast-decomposing leaf species in an Oregon stream (Sedell et al. 1975). This high value for alder may be somewhat exaggerated since it is a reflection of the rapid loss of mass exhibited by alder rather than an increase in the presence of shredders on a per leaf pack basis (Fig. 3). However, the decrease in leaf surface area may compensate for this. Even the more slowly processed leaf species (aspen and willow) had shredder biomass values greater than the fast species in Oregon. It is only for the coniferous species that the Oregon stream exhibited higher shredder biomass values. Since our coniferous species had a slower processing rate than the Oregon species and a lower shredder biomass value, this is additional evidence that shredder feeding activity is largely responsible for the high rates of processing found in Little Beaver Creek. While in eastern woodland streams the shredding process may result largely from a few large Tipulidae or Limnephilidae per leaf pack (Petersen and Cummins 1974), in this Colorado mountain stream a large number of small-sized shredders such as *Capnia* and *Zapada* are responsible. The method of feeding by *Capnia* and *Zapada* may also differ from the larger sized shredders. Whereas the large shredders actually bite off chunks of leaf material, smaller shredders may scrape the leaf surface, removing the cuticle, epidermis and mesophyll (Wallace et al. 1970). The scraping method produces the same result as obtained from the large shredders in that *Capnia* and *Nemoura* have been reported to skeletonize leaves (Brinck 1949) and thus decrease leaf weight.

Leaf packs as habitat for collectors

The microdistribution of stream benthos is a complex interaction of environmental factors such as current velocity, substrate size, and food availability (Minshall and Minshall 1977). Leaf litter in the stream offers a short-lived habitat for certain stream macroinvertebrates (Mackay and Kalff 1969). While shredders utilize leaf litter and associated microflora as a food source, other functional groups colonize leaf litter as well (Table 3). Fine particulate organic matter (FPOM) may accumulate in leaf packs from two potential sources; the leaf material in the pack itself as it is processed, and FPOM in transport which is filtered from the water mass by the leaf pack. FPOM entrapped within the leaf packs represents a potential food source for collectors which inhabit the leaf packs. Thus collector colonization of leaf packs may be a function of the amount of FPOM present. These data are plotted in Fig. 5 and indicate that numbers and biomass of collectors are directly related to the amount of FPOM (75–1000 μm) present in the leaf packs. There was no significant difference in the amount of FPOM present between leaf types for the entire sampling period (AOV, $P > .05$). Minshall and Minshall (1977) found that the abundance of two collector species was related to the amount of detritus present (all size categories included). Egglishaw (1964) reported that the presence of leaf material greatly affected the abundance of many macroinvertebrate species in a British stream. While quantity of FPOM present seems to be important for collector colonization, food quality of the FPOM is another major consideration. Ward and Cummins (1979) have found that different types of FPOM result in differential growth rates for a stream collector species. They determined that ground conditioned leaves produced the greatest growth, shredder feces was intermediate, and the least growth occurred when natural stream FPOM was used as a food source. This would indicate that the fresh leaves added to the stream during autumnal abscission represent an input of high quality food material not only to shredders (once the leaves have been properly conditioned), but also to collectors. Thus, collectors living in leaf packs may be in closer proximity to a higher quality food source than those found in the substratum. While the quantity of FPOM in the leaf packs may be small compared to that in the sediments, its presence during the fall and winter months coincides with the major growth period of many stream macroinvertebrates (Hynes 1961), which emphasizes its importance.

Results of several investigators (see references in Anderson and Sedell 1979) have shown that the leaf species [coarse particulate organic matter (CPOM) quality] has a great influence on leaf litter utilization by shredders. The data presented here show this is also the case for a Colorado mountain stream in that high-quality leaves such as alder are rapidly processed. A major finding of the present study is the important role FPOM has in determining the value of leaf packs as a habitat for collectors. Further investigation into the nutritive value and quantity of FPOM in leaf packs compared to sedimentary FPOM is needed to assess more clearly its importance in the stream ecosystem.

ACKNOWLEDGMENTS

Drs. Norman H. Anderson and Kenneth W. Cummins of Oregon State University, and Larry J. Gray, Arizona State University, offered valuable suggestions regarding the manuscript, as did two anonymous reviewers.

LITERATURE CITED

Anderson, N. H., and E. Grafius. 1975. Utilization and processing of allochthonous material by stream Trichoptera. Verhandlungen des Internationalen Vereins Limnologie **19**:3082–3088.

Anderson, N. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology **24**:351–377.

Bärlocher, F., B. Kendrick, and J. Michaelides. 1978. Colonization and conditioning of *Pinus resinosa* needles by aquatic hyphomycetes. Archiv für Hydrobiologie **81**:462–474.

Benfield, E. F., D. S. Jones, and M. F. Patterson. 1977. Leaf pack processing in a pastureland stream. Oikos **29**:99–103.

Brinck, P. 1949. Studies on Swedish stoneflies (Plecoptera). Supplementum XI, Opuscula Entomologica, Entomological Society of Lund, University of Lund, Lund, Sweden.

Egglishaw, H. J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. Journal of Animal Ecology **33**:463–476.

Hart, S. D., and R. P. Howmiller. 1975. Studies on the decomposition of allochthonous detritus in two southern California streams. Verhandlungen des Internationalen Vereins Limnologie **19**:1665–1674.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Archiv für Hydrobiologie **57**:344–388.

Mackay, R. J., and J. Kalff. 1969. Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. Ecology **50**:101–109.

Merritt, R. W., and K. W. Cummins. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa, USA.

Minshall, G. W., and J. N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (USA.) stream. Hydrobiologia **55**:231–249.

Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology **4**:343–368.

Reice, S. R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. Ecology **55**:1271–1282.

———. 1977. The role of animal associations and current velocity in sediment specific leaf litter decomposition. Oikos **29**:357–365.

Sedell, J. R., F. J. Triska, J. D. Hall, N. H. Anderson, and J. H. Lyford. 1974. Sources and fates of organic inputs in coniferous forest streams. Contribution 66, Coniferous Forest Biome, International Biological Program, Oregon State University, Corvallis, Oregon, USA.

Sedell, J. R., F. J. Triska, and N. S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates. Verhandlungen des Internationalen Vereins Limnologie **19**:1617–1627.

Triska, F. J., J. R. Sedell, and B. Buckley. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: II. Biochemical and nutrient changes. Verhandlungen des Internationalen Vereins Limnologie **19**:1628–1639.

Wallace, J. B., S. R. Woodall, and F. F. Sherberger. 1970. Breakdown of leaves by feeding of *Peltoperla maria* nymphs (Plecoptera: Peltoperlidae). Annals of the Entomological Society of America **63**:563–567.

Ward, G. M., and K. W. Cummins. 1979. Effects of food quality on growth rate and life history of a stream collector (*Paratendipes albimanus* (Meigen)). Ecology **60**:57–64.