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The processing of conifer and hardwood leaves in two coniferous forest streams: I. Weight loss and associated invertebrates[1]

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With 4 figures and 2 tables in the text

Introduction

Over the past few years stream biologists have substantiated the idea of HYNES (1963) that most small streams are predominantly heterotrophic. The present status of our knowledge of stream ecosystem structure and function has been synthesized quite well by CUMMINS (1974). He divides the stream system into functional groups that comprise the biological communities. These groups are identified according to their roles in processing organic matter, which in small streams is derived largely from terrestrial inputs. The processing of the coarse particulate leaf litter by microbes and invertebrates is of prime interest and is fundamental to understanding detrital processing.

In terrestrial systems the presence of soil animals can be critical in the maintenance of decomposer systems (VAN DER DRIFT & WITKAMP 1959; MACFADYEN 1961, 1963; NICHOLSON et al. 1966; ANDERSEN 1973; AUSMUS & WITKAMP 1974). In stream systems the role of invertebrates in the breakdown of leaf detritus is significant (CUMMINS et al. 1973; PETERSON & CUMMINS, 1974; SEDELL et al. 1974).

The object of this study was to investigate differences in rates of breakdown of different leaf species common to the coniferous forest streams of western Oregon and to compare the rates of breakdown between a large and small stream. The role and possible differences of animal associations in the processing of leaf detritus was also investigated.

Study area description

The study was conducted in the H. J. Andrews Experimental Forest, a 6,000 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 1,523 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 snow pack during the winter, while rain predominates at lower elevations (BERNTSEN & ROTHACHER 1959). The dominant forest vegetation is Douglas-fir *(Pseudotsuga menziesii)* and western hemlock *(Tsuga heterophylla)*. Mack Creek and the stream draining Watershed 10 were the two streams in the drainage basin which were studied intensively.

Watershed 10 (WS-10) covers 10.1 hectares and rises from 430 m at the outlet stream gauging station to 670 m at the highest point. The average slope of the stream

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channel is 45 per cent. However, side slopes and headwall range up to 90 per cent due to deep incision of the basin into the main ridge. Stream discharge varies from around 0.23 l/sec in the summer to about 140 l/sec during winter freshets. The uppermost reaches are intermittent during the summer months. Mean width of the stream channel ranges from 0.4 m in the upper reaches to about 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 straems that drain the entire Andrews Experimental Forest. The study site is about 800 m in elevation and drains approximately 650 hectares. The stream gradient in this area is 25 per cent. Stream discharge at the study area is estimated between 100—140 l/sec in late summer to 1,500—1,800 l/sec during winter freshets. The stream morphology is a stairstep of gouged pools, free fall zones, and turbulent water around large boulders. The substrate ranges from large boulders to sand. Unlike WS-10, Mack Creek has a well embedded substrate which prevents all but the largest winter storms from moving large particles of sediment. Both streams have comparable water chemistry (Tab. 1) and temperature regimes ranging from 1—15° with a mean of approximately 8 °C.

Tab. 1. Summary of annual mean chemical data from Mack Creek and Watershed 10 in mg/l.

	Watershed 10	Mack Creek
NO_3	0.005	0.020
PO_4	0.20	0.15
Total alkalinity	10	11
Total dissolved solids	40	40
Si	5	6
pH	7.1	7.3

Materials and methods

To determine the rate of litter breakdown and the effect of stream size on the rate of litter disappearance, a leaf pack experiment was undertaken on two streams. Four types of leaf litter, representing the predominant streamside vegetation and a range of decomposition rates, were utilized: conifer needles *(Pseudotsuga menziesii* and *Tsuga heterophylla),* vine maple *(Acer circinatum),* bigleaf maple *(Acer macrophyllum),* and red alder *(Alnus rubra).* Leaves or needles of each litter type were collected at abscission, air dried, and strung on monofilament line to produce a 5 to 15-gram leaf pack. Leaf packs were oven dried (50 °C), weighed, tied to bricks, then placed in the stream. Packs were oriented upstream with current holding the pack against the leading face of the 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 litter bags, 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 removed by hand. Packs were then dried at 50 °C and reweighed to obtain weight loss information. Loss rates were estimated by fitting data to the exponential model $Y_t = Y_0e^{-kt}$. Lines were fitted by linear regression and logarithmic transforma-

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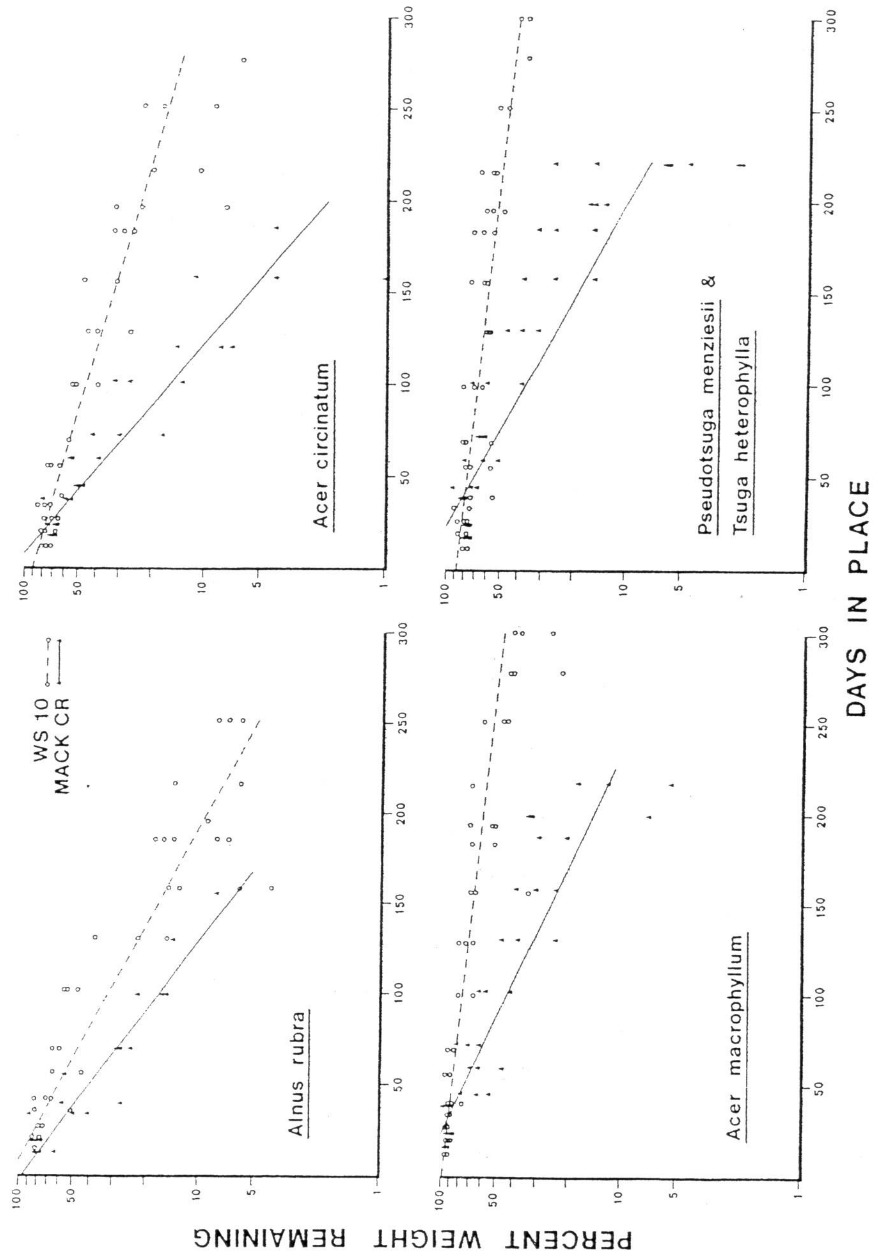

Fig. 1. A comparison of weight losses from four species of leaf litter between Mack Creek and Watershed 10. Regressions of $\log_e$ per cent leaves remaining in leaf packs against time.

tion. Leaf packs were combined by leaf type and ground through a 40 mesh screen on a Wiley mill for chemical analysis.

Invertebrates were preserved in 70 % ethyl alcohol, sorted into 36 taxa, dried, and weighed. These taxa were then assigned to a functional group. The functional group was recognized on the basis of particle size fractions eaten and method of feeding, shredder or large particle feeder and collector or fine particle feeder. While there are some inconsistencies that resulted from assigning broad taxa (families) to a functional group, in general the taxa found on the leaf packs could satisfactorily be assigned a group (e.g., Limnephilidae were in every case large particle feeders and not a mix of scraping types like *Neophylax* with *Hydatophylax*).

Results

Litter breakdown

There were significant differences between streams and among species in the rate of disappearance of leaf material from the packs (Fig. 1). All species disappeared more rapidly in Mack Creek than in WS-10. Conifer needles and bigleaf maple leaves disappeared most slowly and alder and vine maple most rapidly. Linear trends of the data on weight loss of vine maple and conifer packs (Fig. 1) 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 ($P < .01$). Vine maple packs in Mack Creek lost 50 % of their initial weight in 29 days as compared to 103 days in WS-10 (Tab. 2). Conifer packs in Mack Creek required 53 days to lose 50 % of their weight as compared to 277 days in WS-10.

Tab. 2. Processing coefficients for four leaf pack types and calculated time for 50 % and 90 % to be processed in Watershed 10 and Mack Creek. Time in days.

	Watershed 10				Mack Creek			
	k	50	90	$\%R_{365}$	k	50	90	$\%R_{365}$
Alnus rubra	.0124	56	186	1	.0168	41	137	<1
Acer circinatum	.0068	102	339	7	.0201	34	115	<1
Acer macrophyllum	.0024	289	960	40	.0108	64	213	2
Pseudotsuga menziesii and *Tsuga heterophylla*	.0025	277	921	34	.0131	53	176	1

Using the disappearance coefficient one can calculate the per cent of the leaf pack remaining after one year (Tab. 2). In Mack Creek, even for the slowest disappearing leaf used in the study, only 2 % of the leaf would be present after one year if it had remained in the pack. In Watershed 10, 40 % of the slowest disappearing leaf (bigleaf maple) still remains at the end of one year. Even a fast disappearing leaf such as vine maple would have 7 % of the pack remaining after one year.

Invertebrate colonization of leaf material

The differences in disappearance rates for the same leaf species between the two streams might be explained in part by the difference in the number of inı a 40 mesh screen on a

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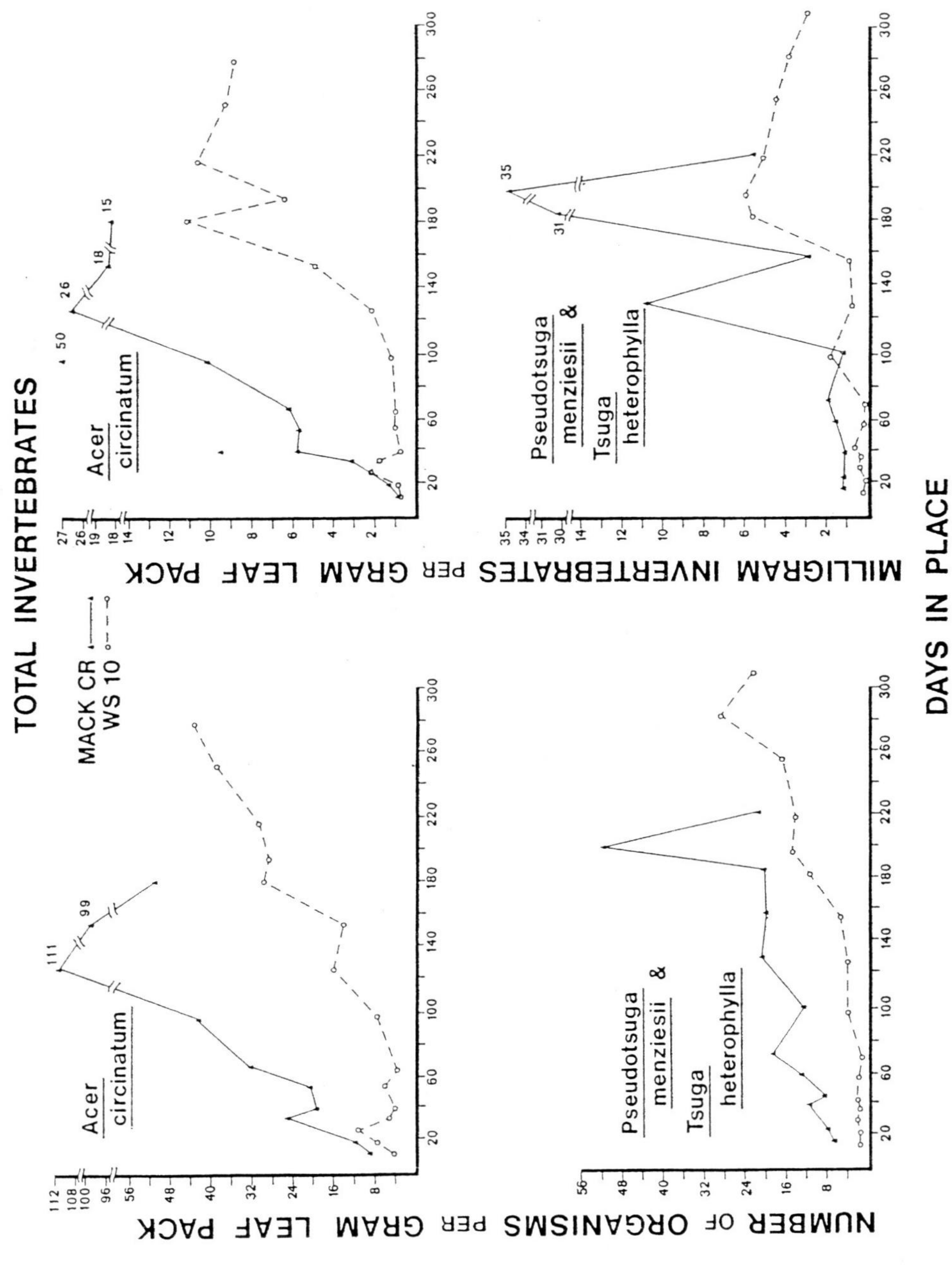


Fig. 2. Comparisons of total invertebrate numbers and biomass between (a) a fast decomposing leaf, *Acer circinatum*, and slow decomposing needles, *Pseudotsuga menziesii* and *Tsuga heterophylla*, and (b) Watershed 10 and Mack Creek. Points not on the line in the graph of invertebrate weight for *Acer* were a result of one large organism.

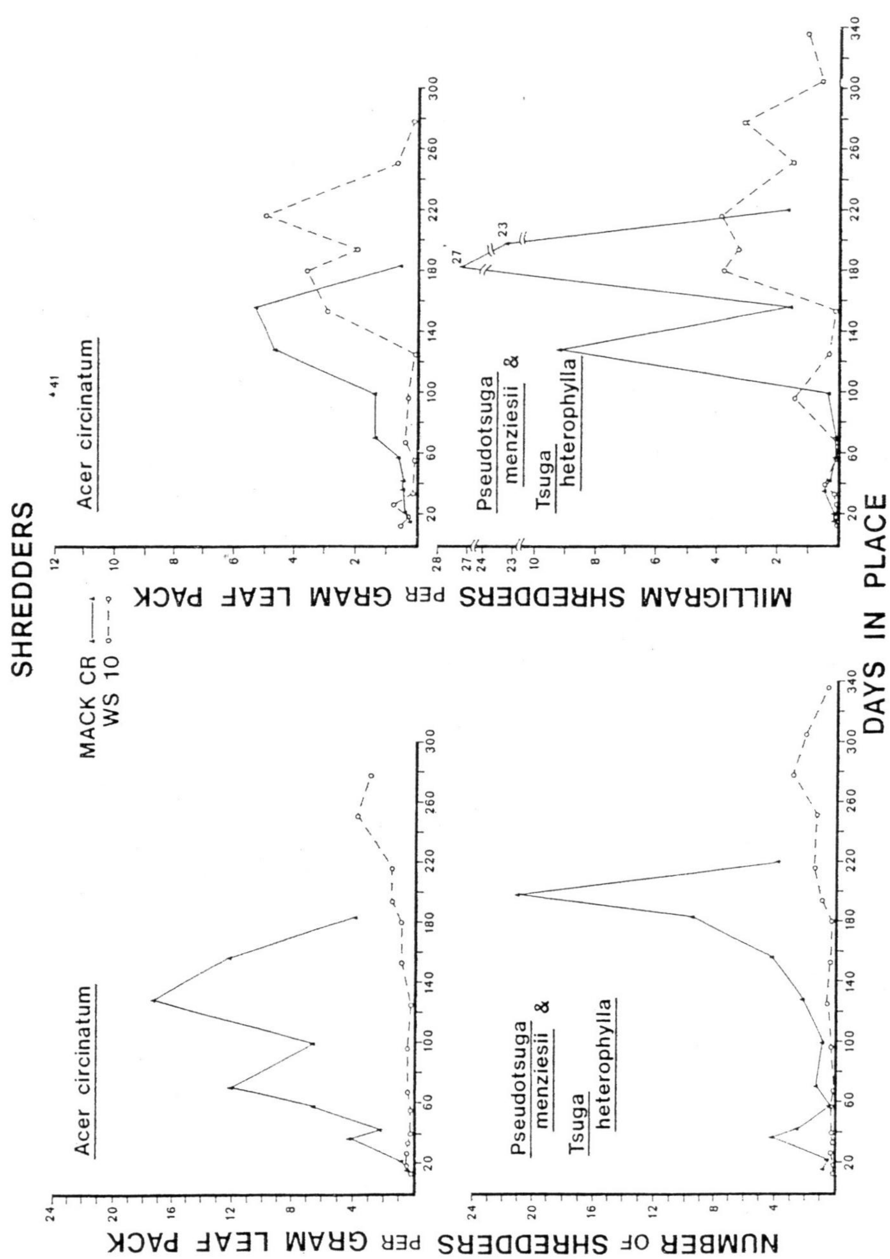
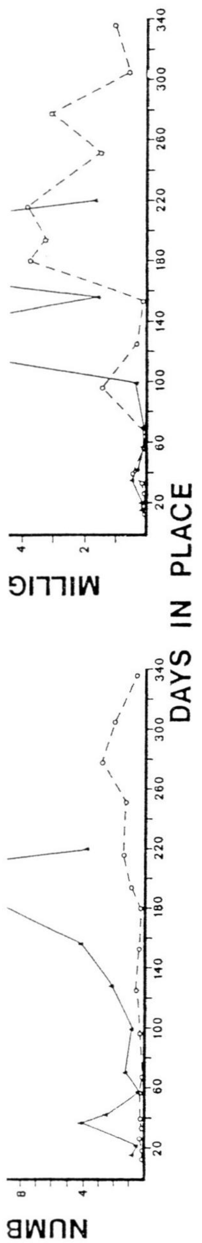


Fig. 3. Animal number and biomass of shredders (large particle feeders) are compared between: (a) two leaf types-conifer needles and vine maple leaves, and (b) two different streams. The point on the graph of shredder weight for *Acer* not on the line at 100 days represents the occurrence of one Pteronarcid.



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vertebrates found in the two streams. There were both greater numbers and biomass of total invertebrates per gram leaf pack in Mack Creek compared to WS-10 (Fig. 2). The quickly processed vine maple shows very little lag time between being put in the stream and being colonized by invertebrates. The mixed conifer pack in both streams lags for about 140 days before appreciable invasion of invertebrates. The lag time is longer for WS-10 than in Mack Creek.

Differences between the fast and slow disappearing leaves and between streams are more sharply defined when the shredders, or large particulate feeders, are analysed separately (Fig. 3). In Mack Creek the occurrence of shredder organisms, first on the vine maple packs and then on the mixed conifer packs, follows a predicted leaf conditioning pattern (Triska et al. 1975). The shredders in WS-10 do not exhibit as dramatic an appearance on the fast processing vine maple before showing up on the slow processing needles. Both leaf types in Mack Creek peaked in numbers per gram dry weight leaf pack and milligrams shredders per gram leaf pack before their respective leaf types in WS-10.

Numbers of shredders on *Acer circinatum* leaf packs in Mack Creek increased with time, reaching a peak in about 125 days. In WS-10, numbers of shredders did not start to increase before 130 days and at 250 days reached a peak that was one-fourth the number per gram leaf pack of the Mack Creek peak. The weight of shredders per gram leaf pack reached a peak more than 60 days before the numbers of shredders peaked in WS-10. This was due to small numbers of large Elmidae larvae.

The number of shredders in the Mack Creek conifer packs peaked between 180—200 days. The number of shredders per gram leaf pack in Mack Creek was an order of magnitude higher than the peak number was in WS-10.

The principle shredders in Mack Creek are *Lepidostoma,* particularly *Lepidostoma unicolor* in the late spring. *Lepidostoma* accounted for about 80 % of the number of shredders found on leaf and needle packs in Mack Creek and represented only about 40 % of the total weight. Limnephilidae represented about 14 % of the numbers and 30 % of the weight. Elmidae larvae were the other shredders present to any extent, representing 5 % of the numbers but about 25 % of the shredder biomass.

WS-10 shredders were primarily Elmidae larvae *(Lara),* Peltoperlids, and a few Tipulids. The largest numbers and weights were the beetle larvae and the Peltoperlids.

The fine particle feeders or collectors were the most numerous of all invertebrates on the two leaf pack types and for the two streams. Again, higher numbers and weights of collectors were found on both leaf types in Mack Creek with the peak numbers and weights preceding the peaks in WS-10.

Effect of invertebrates on leaf pack disappearance

The effect of invertebrates on the rate of disappearance of a leaf pack was dramatically demonstrated in Mack Creek. Conifer needles represent about 65 % of the litter inputs of these small streams. These needles are generally considered highly refractory; their role in the feeding of aquatic invertebrates was unknown and suspected to be minor because of export prior to decomposition. In fact, slow weight loss during the first 100 days was due primarily to microbial colonization and decomposition (Triska et al. 1975) since insect feeding appeared to be minimal. Yet, after about 100 days, the rate of weight loss increased dramatically as the needles were rapidly consumed by *Lepidostoma* (Fig. 4). During this period, mean insect weight increased rapidly. After conditioning of the needles, the invertebrates played the major role in the disappearance of the needle packs.

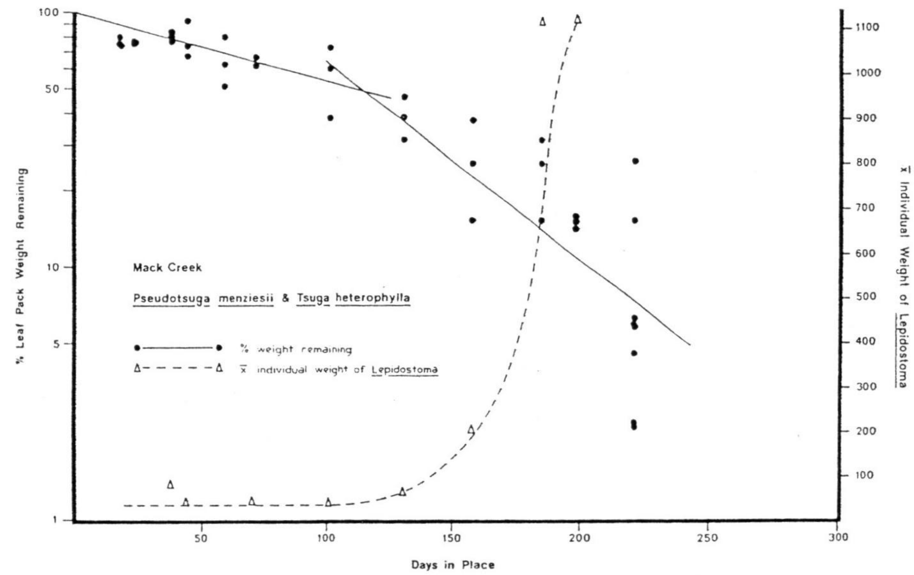

Fig. 4. Compared with Fig. 1, the rate of disappearance of conifer needle packs is more accurately represented by two regression lines: k = .0057 for the first 100 days, k = .0178 for the remaining time. The increase in the mean individual weight (μg) of the principle shredder, *Lepidostoma,* corresponds with the faster disappearance coefficient.

Discussion

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 and red alder leaf packs are much higher than the fastest rates (k = 0.22) reported by investigators in Michigan (Bolling, Peterson & Cummins 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 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

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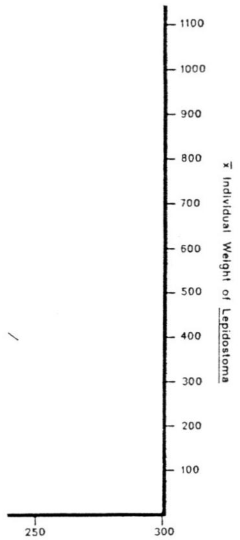

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streams ranged from 0.1—11 °C with a mean temperature over the fall—winter season between 3—4 °C (Peterson & Cummins 1974). The stream temperatures in the Andrews Forest ranged from 0.1—8 °C, with a mean temperature also about 4 °C. The decay rates from Tennessee were determined from a stream whose temperature ranged between 10—16 °C.

The range of disappearance rates among leaf species is not surprising, in that different leaf species have different chemical compositions (Triska et al. 1975). They become conditioned by microbial activity at different rates. Thus conditioned, they are more readily acceptable as food for shredding invertebrates (Triska 1970; Iverson 1973; Boling et al. 1975; Anderson & Grafius 1975). The idea that the leaf detritus fed upon by invertebrates must be microbially colonized is supported in this study by the existence of a period of time in which animals were not present in the leaf packs. There was a difference in the time when the two leaf species become acceptable to the same invertebrate community, and this is probably due to selection of those species most rapidly conditioned. Such a conditioning process would allow for a stepwise introduction of new food sources to the invertebrate community. This continuum from fast to slow decomposing leaves in the western coniferous forest supports the work of Peterson & Cummins (1974) working with eastern United States deciduous hardwoods.

Differences in the number of organisms per gram of leaf material between the two streams can be explained in large part by the different physical aspects of the streams. Watershed 10 is a small headwater stream, with tremendous amounts (17 kg/m^2) of natural organic debris (tree boles and large branches) in it. The substrate consists of loose rocks and gravel in the upper reaches and behind the organic debris dams. The water volume fluctuates rapidly and often during the winter rainy season. An average rainstorm can cause the stream to substantially move the loose substrate and carry a suspended load. This combination of water fluctuations and unstable substrates more than likely has prevented a large benthic invertebrate population from forming. The invertebrate community in this stream is to be found in the stable organic debris dams in the stream.

Mack Creek does not undergo such frequent and proportionally large increases in water volume as Watershed 10. The water velocity is higher and the substrate is not loose but packed tightly together around and between the large cobbles and boulders. Consequently, it is relatively stable during the period of high water caused by average winter storms and has a much richer variety of physical habitats than does the smaller stream.

The many factors controlling benthic invertebrates have been thoroughly discussed by Hynes (1970). The classic work of Percival & Whitehead (1929), who found fewer animals on loose stones than on embedded ones, appears to have been reaffirmed by this study.

Cummins et al. (1973) experimentally determined that invertebrates accounted for at least 20 % of the weight loss of leaf detritus in streams. Our study would indicate as great, if not a greater, role for invertebrates in detrital processing at least as far as conifer needles are concerned.

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Discussion

KOWALCZEWSKI: The influence of invertebrates on the rate of leaf disappearance is not observed in all environments. It was not observed in the studies performed by myself and MATHEWS on the leaf disappearance in the River Thames.

SEDELL: Very good observation. The Thames River is much larger than either of these two streams and possibly does not have an invertebrate community functioning as large particulate organic feeders.

GODSHALK: 1. Did you attempt to statistically correlate the numbers of biomass of consumers to the % leaf pack weight remaining directly? 2. Would you comment on the increased variability of the % weight remaining of the replicate leaf packs toward the end of the incubation period?

SEDELL: 1. No, but my guess is there would be a good inverse correlation. We will do that, however. 2. Variability of the % weight remaining increased in the later stages for a number of reasons. The biggest factor probably was the change in microhabitats of the leaf packs following spates.

KAUSHIK: Was any precaution taken to retain the animals on the leaf packs when the packs were removed?

SEDELL: Yes, a net was placed under the pack.