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The Role of Aquatic Invertebrates in Processing of Wood Debris in Coniferous Forest Streams

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Abstract: A study of the wood-associated invertebrates was undertaken in seven streams of the Coast and Cascade Mountains of Oregon. The amount of wood debris was determined in terms of both weight and surface area. Standing crop of wood per unit area decreases with increasing stream order.

Invertebrates associated with wood were functionally categorized and their biomass on wood determined. Major xylophagous species were the caddisfly (*Heteroplectron californicum*), the elmid beetle (*Lara avara*) and the snail (*Oxytrema silicula*). Standing crop of these species is greater on wood in the Coast Range than in the Cascades, which is attributed to species composition of available wood debris. The density of *L. avara* was strongly correlated with the amount of wood available irrespective of stream size within a drainage. The standing crop of invertebrates was about two orders of magnitude greater on leaf debris than on wood.

A potential strategy for wood consumption, based on microbial conditioning, is presented. The data are used to develop a general scheme of wood processing by invertebrates in small stream ecosystems. Their impact is similar to that of invertebrates which process leaf litter in terrestrial and aquatic environments when the full decomposition cycle of wood debris is considered.

Introduction

The allochthonous inputs to streams in western coniferous forests include coniferous needles, deciduous leaves and woody material, ranging in size from small twigs and bark to large logs. The amount of fallen wood in these streams can be extremely large. Froehlich (1973) estimated that in one watershed of old-growth douglas fir *(Pseudotsuga menziesii)* the standing crop of wood debris (pieces larger than 10 cm diam) was more than 15 kg/m^2. The standing crop of small debris in the same stream was 1.08 kg/m^2 (Sedell *et al.*, 1974).

In view of the quantities of woody material in these streams, it is apparent that wood has a significant role in energy flow, nutrient dynamics, stream morphology and in shaping the biotic community of these lotic ecosystems. Although stream ecologists have emphasized the importance of allochthonous debris as the food base for stream invertebrates, most previous studies are based on leaf inputs (Hynes, 1970; Cummins *et al.*, 1973; Boling *et al.*, 1974). Current literature on aquatic invertebrate communities inhabiting logs or inundated trees has emphasized the exploitation of these sites as habitats for attachment or surfaces for grazing of periphyton (Claflin, 1968; Nilsen and Larimore, 1973; McLachlan, 1970) rather than as allochthonous energy and nutrient inputs to the aquatic system.

The present study is a preliminary investigation of the wood component in coniferous stream ecosystems of western Oregon and of the role of invertebrates in the biological processing or degradation of wood. The objectives were to survey the fauna associated with wood in streams and to determine some of the interactions between the fauna and the wood substrate. In order to develop generalizations on the invertebrate-wood interactions, we chose to compare large and small streams in two different areas rather than to investigate one site in detail.

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SITE DESCRIPTIONS

Seven streams, three in the Coast Range and four in the western slopes of the Cascade Range, were sampled for wood and associated invertebrates during July 1976. Physical and environmental data for the streams are provided in Tables 1 and 2. All of the streams studied, with the exception of Berry Creek, could be classified as draining dense coniferous forests, with a wet, mild climate in rugged mountainous terrain.

Streams in both the Coast and Cascade ranges have fairly comparable water chemistry. The *p*H ranges from 6.8-7.4. Total dissolved solids are between 35-45

TABLE 1.—Physical characteristics of the seven Oregon streams sampled for wood and associated invertebrates

Stream	Strahler stream order	Altitude (m)	Drainage area (km^2)	Gradient (%)
Coast Range				
Berry Creek	1-2	75	3.22	1.7
Flynn Creek	3	209	2.02	2.5
Five Rivers	6	40	295.00	1.4
Cascade Range				
Devil's Club Creek	1	835	0.05	35
Mack Creek	3	830	5.35	20
Lookout Creek	5	420	60.20	12
McKenzie River	7	410	1642.00	9

TABLE 1.—(continued)

	Discharge (m^3)			Stream width
	Summer	Winter	Annual mean	July
Coast Range				
Berry Creek	0.005	0.03	0.02	2.0
Flynn Creek	0.01	0.80	0.12	3.0
Five Rivers	1.05	38.0	16.90	18.8
Cascade Range				
Devil's Club Creek	<.001	0.15	.03	1.5
Mack Creek	0.10	2.2	0.60	7.0
Lookout Creek	0.23	20.0	3.77	12.5
McKenzie River	56.0	200.0	75.30	40.0

TABLE 2.—Environmental characteristics of streams in the Coast Range and western Cascade Range, Oregon

Parameters	Coast Range	Cascade Range
Geologic origin	Sedimentary Tyee sandstone	Volcanic Breccias and tuff
Streambed	Unconsolidated	Consolidated—armored
Substrate size	Sand and gravel	Boulders, rubble and boles
Degree days (°C/year)	3600	2700
Rainfall (cm)	250	220
Age of old-growth coniferous forest (years)	ca. 130	ca. 450
Dominant terrestrial vegetation	*Alnus rubra, Acer macrophyllum, Pseudotsuga menziesii, Rubus spectabilis*	*Pseudotsuga menziesii, Tsuga heterophylla, Acer circinatum, Thuja plicata, Acer macrophyllum*
Hydrologic pattern	Autumn-winter rains	Autumn-winter rains Spring snowmelt

mg/liter and total alkalinity is between 10-13 mg/liter for all the streams sampled. The Cascade Range streams had higher phosphates (150-200 $\mu g/l$ PO_4) than those of the Coast Range (40-60 $\mu g/l$ PO_4), and lower nitrates (< 10-50 $\mu g/l$ NO_3) than the Coastal streams (170-1200 $\mu g/l$ NO_3).

COAST RANGE STREAMS

Flynn Creek and Five Rivers lie 16 km and 35 km, respectively, from the Pacific Ocean on the W slope of the Coast Range. In its natural condition this area was densely forested with douglas-fir and red alder (*Alnus rubra*). Flynn Creek has remained in this state and is overgrown with salmonberry (*Rubus spectabilis*) and vine maple (*Acer circinatum*). Land adjacent to the sample site at Five Rivers has been logged and planted in pasture. A corridor of red alder and big-leaf maple (*Acer macrophyllum*), approximately 25 m wide, borders the stream.

The area has a maritime climate with warm, dry summers and cool, wet winters. Prolonged periods below -6 C or above 38 C are uncommon. Mean rainfall at the sampling areas is about 250 cm annually, with 70% falling between November and March (Hall and Lantz, 1969).

Berry Creek is on the eastern side of the Coast Range, approximately 85 km from the Pacific Ocean. A dense canopy of deciduous trees, primarily red alder and big-leaf maple, covers the stream. The area has topographically gentle terrain where the foothills form a boundary with the Willamette Valley. The hydrologic regime of Berry Creek is similar to the Coast Range but with only about 120 cm of rainfall. The study section of Berry Creek is a portion of the original streambed in which flow can be controlled by diverting excess water through a bypass channel. Controlled winter flows are between .014m^3/sec and .028 m^3/sec (Warren *et al.*, 1964).

CASCADE RANGE STREAMS

The four streams studied in the Cascade Range are located in or near the H. J. Andrews Experimental Forest about 65 km W of Eugene, Oregon. The forests surrounding each of the streams are a dense mixture of douglas-fir, western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). A shrubby corridor of vine maple and red alder borders the larger streams.

The basic climate of the area is also maritime, but with a greater temperature range than in the Coast Mountains. Temperature extremes range from near -18 C during unusually cold winters to over 38 C for brief periods almost every summer. Mean annual temperatures are around 9.5 C, with a January mean of 2 C and a July mean of nearly 20 C. Average annual precipitation for the period 1952-1975 was 239 cm. Precipitation is strongly seasonal with 72% occurring from November through March and only 7% from June through September. In general, permanent winter snowpacks can be expected above 1000-1200 m elevation; below these elevations snow cover is erratic (Rothacher *et al.*, 1967).

Streamflow of the three smaller streams is not well regulated. The hydrograph follows precipitation patterns very closely, with high flow during the winter months and an annual recession to low flow in late summer or early autumn. During most years, peak flows are 1500-2000 times higher than summer low flows.

The McKenzie River is well regulated because the porous lavas of the High Cascades store large quantities of snowmelt and release the water gradually. Discharge from these lavas cause relatively high streamflows in late summer, unlike the other streams studied.

METHODS

At each stream sampled, the study site consisted of a reach approximately 20 times the mean width. This reach was assumed to include all the major habitats found in

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nsisted of a reach approximately 20 times include all the major habitats found in

the stream (riffles, pools, debris dams and alcoves). Sites were selected at random within each reach and a band transect was established to sample the wood debris. Band transect lengths were related to stream size (1 m, Devil's Club Creek; 2 m, Berry and Flynn creeks; and 5 m for Mack and Lookout creeks and McKenzie and Five Rivers). Four to six samples were taken per stream.

WOOD DEBRIS ESTIMATES

Wood was either wet-weighed or measured for conversion to dry weight and surface area. Large branch and bole wood (> 10 cm diam) were measured in terms of diameter of the small and large end, and length. Measurements were converted to volume per piece and volume per area of stream according to the technique adopted by Lammel (1972) from Brown (1971) and Van Wagner (1968). Volume was further converted to weight and surface area. In each band transect, small wood debris (< 10 cm diam) was collected by hand and placed in buckets or sacks. Divers collected the wood debris from deep areas. The surface area of the small wood was derived from individual measurements of several hundred sticks and small twigs (< 10 cm diam) from Lookout Creek. This derived constant of 0.130 m^2/kg of wood was applied to wood from the other streams. Average diameter of this small debris appeared comparable from stream to stream. The surface area estimates are very conservative since each piece of wood debris is treated as a cylinder or truncated cone.

Adjustments were made on Five Rivers and the McKenzie River to exclude the central channel which was practically devoid of wood and could not be considered a faunal area. On Five Rivers, the faunal area comprised 40% of the total stream area. The faunal area comprised 15% of the total stream area of the McKenzie River and was restricted to a 2-3 m band at the river's edge. The entire streambed of the other streams was considered to be a faunal area.

INVERTEBRATE COLLECTIONS

Approximately 200 kg (dry weight) of small wood debris was examined in the field. The larger insects and snails were removed with forceps. After washing each stick in a tub of water, the resulting debris was retained by a 0.5-mm mesh, preserved in alcohol and sorted at the laboratory. The beetle, *Lara avara* (Elmidae), and the caddisfly, *Heteroplectron californicum* (Calamoceratidae), and other dominant groups were counted and weighed individually.

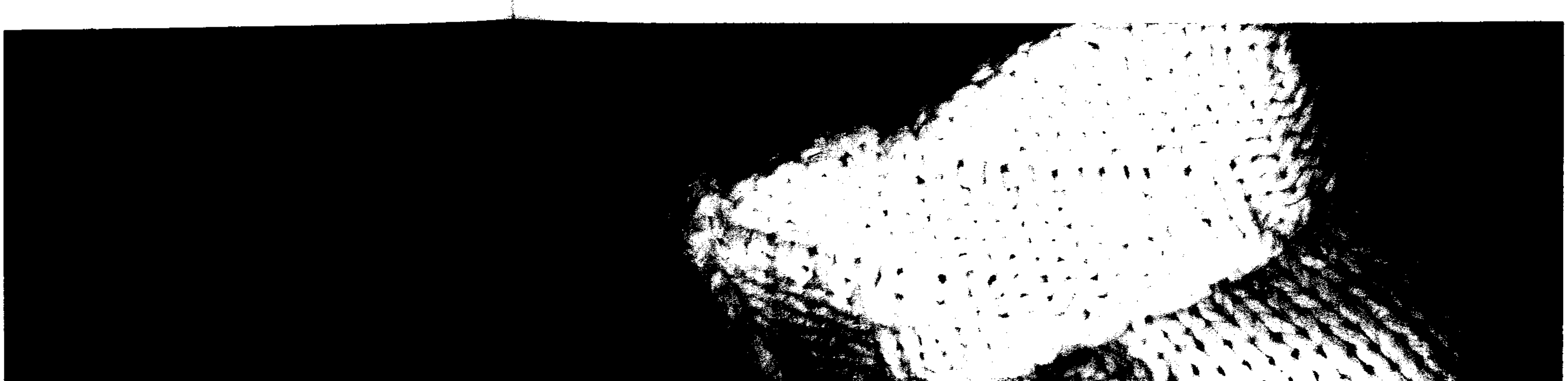
With the exception of the *Lara avara* larvae, the invertebrates were dried at 60 C for 24 hr and weighed. The *L. avara* were live-weighed (the larvae were used in other experiments) and dry weights were obtained from a regression equation ($Y = -1.18 + 1.04(X)$; X = wet weight; $R^2 = .87$; $n = 40$). Tissue weights of snails were obtained empirically, resulting in a value of 20% of dry weight including shell (D. McCullough, pers. comm.). Insect weights, except *L. avara*, were increased by 25% to adjust for weight loss in alcohol (Mackay and Kalff, 1969).

SOURCES OF SAMPLING ERROR

The estimates of invertebrate numbers and biomass are approximations which allow comparison between streams. These are underestimates because several factors resulted in losing or missing part of the population.

Some invertebrates were lost or escaped when the wood was picked up. This error was greatest in deep areas where diving was required and in fast water. It tended to be greatest for vagile species that use the substrate primarily as a resting site (*e.g.*, *Baetis* spp.) and for *Heteroplectron californicum*, which is easily dislodged.

Small twigs and other woody debris (less than 5 mm diam) were underrepresented in collections. This size class has a large surface-to-volume ratio and accumulates where it is impossible to distinguish the wood habitat from a core sample of benthos.



When picking out the wood and associated fauna, the individuals became dispersed and dislodged to such an extent that there was no way of determining their original location. Some *Heteroplectron californicum,* with their stick cases, were probably missed in this way.

No satisfactory technique was developed for sampling the very small material or, at the other end of the scale, logs larger than 40-cm diam. Attempts were made to examine the logs and to pick invertebrates under the water, but these were only qualitative collections. Considerable effort was required to remove logs, and the resultant disturbance caused losses of an unknown portion of the fauna. Where wood is lodged in debris jams, removal of key sticks caused a flushing action that washed away small wood and part of the fauna.

Visual examination of woody material was time-consuming, tedious and inaccurate. Locating individuals on this substrate was also greatly influenced by lighting conditions. Thus, counts on rainy days or those in dimly lit forested areas were low. Finding the insects on the wood substrate is difficult because species adapted for these habitats *(e.g.,* some stoneflies, mayflies and chironomids) were able to hide in cracks or beneath bark, while others, such as *Lara avara,* are cryptically colored, sessile and easily overlooked.

RESULTS AND DISCUSSION

QUANTITIES OF WOOD DEBRIS IN THE STREAMS

The quantities of wood found in the streams (Table 3) reflect both differences between the Coast Range and Cascade Range, as well as a small-to-large stream pattern of decreasing amounts of wood.

Coast Range streams contain little large branch or bole wood compared to the Cascade streams studied. This is probably due to two factors: (1) the coniferous trees of the former are about 130 years old and quite healthy, and (2) most of the wood coming into the stream is alder which is comparatively small in diameter and decomposes quickly. The forests in the Cascades are much older (ca. 450 years) with many trees badly affected with heartrot and more susceptible to windthrow. The conifer trees falling into the streams in the Cascades are typically over 50 cm in diam, while most of the alders and other trees in the Coastal streams are less than 25 cm in diam. The smaller the wood diameter is, the easier it is to be moved by the hydraulic properties of the stream.

TABLE 3.—Estimated quantities and surface areas of wood debris in seven Oregon streams

	Large branch and bole wood (>10 cm)			Small branch wood[1] (<10 cm)	
	Biomass of wood (kg/m²)	Surface area (m²/m²)	Surface to volume (m²/m³)	Biomass of wood (kg/m²)	Surface area (m²/m²)
Coast Range					
Berry Creek	2.43	0.06	20.25	0.30	0.04
Flynn Creek	0.97	0.05	37.06	0.86	0.11
Five Rivers	0.22	0.05	12.38	0.24	0.03
(adjusted)[2]	(0.55)	(0.12)	(12.38)	(0.60)	(0.08)
Cascade Range					
Devil's Club Creek	140.89	0.43	8.62	1.11	0.14
Mack Creek	28.50	0.16	9.94	0.61	0.08
Lookout Creek	11.65	0.04	5.37	0.08	0.01
McKenzie River	0.07	.003	19.28	0.08	0.01
(adjusted)[2]	(0.48)	(0.02)	(19.28)	(0.40)	(0.05)

[1] Surface:volume ratio of small branch wood measured only for Lookout Creek = 27.96

[2] Adjusted values for Five Rivers and McKenzie River include only the area of faunal activity

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(>10 cm)	Small branch wood[1] (<10 cm)	
Surface to 'olume (m^2/m^3)	Biomass of wood (kg/m^2)	Surface area (m^2/m^2)
20.25	0.30	0.04
37.06	0.86	0.11
12.38	0.24	0.03
(12.38)	(0.60)	(0.08)
8.62	1.11	0.14
9.94	0.61	0.08
5.37	0.08	0.01
19.28	0.08	0.01
(19.28)	(0.40)	(0.05)

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Debris dams and large accumulations of wood are less likely to form in large channels than in small streams, regardless of gradient. The larger streams deposit the bole wood on bends and flood terraces. Most of the debris in these larger streams functions as food or habitat for only 4-6 months of the year. In the smaller streams, the large boles are too big to be moved by the volume of water available unless the whole bed is sluiced out. They trap small debris and sediments and, essentially, shape and stabilize the system.

The proportion of small branch wood to bole wood is much higher in the Coast streams than in Cascade streams. The amount of bole wood, with its low surface-to-volume ratio, overwhelms the amount of small wood in the Cascade streams. The invertebrate studies were largely based on collections of branch wood.

LIFE HISTORY AND FEEDING BEHAVIOR

Previous fieldwork indicated that the elmid beetle *(Lara avara)*, the caddisfly (*Heteroplectron californicum*) and the snail (*Oxytrema silicula*) were species intimately associated with woody debris. Observations on their life history, behavior and laboratory rearing are given below as a basis for consideration of their functional role in degradation of wood.

Lara avara.—Despite 3 years of field collections of this large elmid beetle, the life cycle remains poorly known. Adults occur in July and August and are frequently found a few cm above the waterline on damp logs or wood. The number of larval instars is unknown and no discrete groupings are apparent from head-capsule measurements. Based on the relatively small increment of increase in head-capsule width at a moult, there appear to be more than five instars. Several size classes of larvae can be collected in all seasons of the year. The largest larvae are ca. 16 mm long and 18 mg dry wt. Pupae have not been discovered although numerous attempts have been made to locate them in wood and rotting logs both above and below the waterline.

The life cycle is believed to be 3 or more years. This estimate is based on the fact that several size classes of larvae occur simultaneously in the field and because the larvae feed on a nutrient-poor substrate where growth is slow. Additional supporting evidence for a very long life cycle comes from laboratory-rearing where moulting and growth rates are exceedingly low; one larva was kept for 2 years at 15 C without moulting.

The larvae occur on waterlogged wood or rootwads of many kinds. They typically gouge a superficial channel, or lodge in cracks, split ends or around knots. Less frequently, they are found under bark or in deep tunnels. After considerable field observation, we have found that a typical "*Lara* stick" is recognizable, based primarily on texture and evidence of gouging activity. The groove is usually in relatively soft wood only slightly deeper than the height of the body. To become suitable for colonization, different kinds of wood probably require varying conditioning times or amounts of decay. For example, the surface of alder decays rapidly compared with douglas fir and, thus, becomes colonized by *L. avara* sooner. However, the larvae are common on douglas-fir in streams, presumably on wood that has been submerged for an appropriate number of years or on pieces that were already in an advanced stage of decay when they fell into the stream. Sticks of willow *(Salix* spp.), cut and debarked by beaver, were devoid of larvae at the Five Rivers site except for the occasional specimen lodged in the split ends.

Although the larvae are very sluggish and may remain in the same groove for several months, drifting activity, as reported by Brusven (1970), was also observed. Presumably this behavior is important in dispersal and recolonization of other sites. Drifting is facilitated by air bladders in the body cavity that increase the buoyancy. Laboratory observations indicate that the larvae curl up and float in the water column when placed on unsuitable wood or if they are stressed by high temperature or low dissolved oxygen.

Larvae have been held at 15 C and long day-length (16 l: 8 d) in shallow dishes of water for several months. Under these conditions the larvae appear quite normal and chew grooves in stream-collected sticks to establish a typical feeding site. The larvae produced considerable feces (up to 10-30% of their body weight per day). However, on the basis of wet weight comparisons over 5 months, they did not increase in weight, so aspects of the rearing procedure need to be modified to provide suitable conditions for growth.

Heteroplectron californicum.—The larvae of this caddisfly are distinctive in that they hollow out twigs or pieces of wood for their portable cases. A few larvae have also been found in wood, 2 cm diam and 15 cm long, which obviously could not be transported. Although the larvae have been shown to be effective shredders of leaves in laboratory studies, their characteristic attachment to wood suggests that they also may be placed in the xylophagous category.

Winterbourn (1971) suggested that the life cycle of *Heteroplectron californicum* involved a rapid growth period during the summer because small larvae were collected in June or July and final instars were most abundant in August and September. However, our data indicate a 2-year life cycle without any periods of rapid growth (Anderson, 1976). Midwinter collections were composed of two main size classes: third instar larvae (mean dry weight, 0.94 mg) and fifth instar larvae ranging from 5-40 mg. As the emergence period of adults is relatively short, ranging from late May to mid-July, it seems likely that the overwintering final instars represent a cohort already in its 2nd year that would pupate in the spring, whereas the third instars would require the next season to complete development. Also, collections from late May to early July (during the adult emergence period) contained about 75% fourth instars and these would require another year to reach maturity.

Oxytrema silicula.—This snail is the most obvious invertebrate in western Oregon streams, being particularly abundant in the Coast Range and Willamette Valley. Benthos densities can exceed $3000/m^2$, resulting in a tissue biomass of 3-5 g/m^2. These snails occur on various substrates in both riffles and pools.

The life cycle of *Oxytrema silicula* extends over several years, so a range of size classes occurs in all seasons. Eggs are laid in the spring and early summer and newly emerged snails are abundant by July. There is a tendency for larger individuals to occur in larger streams. Where populations are extremely high, the mean size tends to be low.

Oxytrema silicula is an extreme trophic generalist. It is an important scraper of periphyton where primary production is high as well as a dominant consumer of fallen leaves. The rasping method of feeding results in obvious skeletonizing of deciduous leaves. Whether the leaves were eroded away at the surface or eaten completely through in isolated locations is not known. The characteristic mode of locomotion and feeding by snails explains their occurrence on flat or smooth surfaces such as rocks and leaves, and may also account for their presence on wood. We assume that they are primarily grazing periphyton on this substrate, but the rasping action of their radula also removes the superficial layers of wood.

FAUNAL SURVEY

Field observations and literature data were used to categorize the uses of wood debris by larvae of various insect groups (Table 4). The general nature of this classification reflects the lack of detailed knowledge of the natural history of these aquatic insects. The surface area and the large number of protective niches on wood afford considerable living space and concealment. Wood is used for oviposition, as a

TABLE 4.—Insects associated with wood in Oregon streams

Coleoptera	
Elmidae	
Lara avara: feeding (gouging), habitat	
Psephenidae	
Acneus: scraping	
Oedemeridae	Uncommon but restricted habitat
Ditylus: tunnelling	
Amphizoidae	
Amphizoa: habitat	
Diptera	
Tipulidae	
Lipsothrix: tunnelling	
Rhagionidae	
Atherix: habitat, feeding	
Simulidae	
Simulium: attachment	
Chironomidae	
Many genera (diverse associations ranging from microhabitat specificity to chance settling)	
Ephemeroptera	
Leptophlebiidae	
Paraleptophlebia: habitat, scraping (?)	
Heptageniidae	
Cinygma integrum: habitat, scraping (?)	
Ephemerellidae	
Ephemerella flavilinea (and other spp.): habitat, scraping (?)	
Plecoptera	
Peltoperlidae	
Peltoperla: habitat, shredding (?)	
Nemouridae	
Nemoura (s.l.): habitat, shredding (?)	
Pteronarcidae	
Pteronarcys, Pteronarcella: habitat, shredding (?)	
Chloroperlidae	
Alloperla: habitat, feeding	
Trichoptera	
Calamoceratidae	
Heteroplectron californicum: boring, gouging, pupating	
Lepidostomatidae	
Lepidostoma unicolor (log cabin case-maker): case construction, scraping and chewing, pupating	
L. quercina (and other chimney case-makers): scraping, attachment, penetrating for pupation	
Brachycentridae	
Brachycentrus: attachment, surface pupation	
Micrasema: scraping, penetration for pupation	
Limnephilidae	
Hydatophylax, Psychoglypha, Halesochila, Onocosmoecus, Cryptochia (wood case-makers): case-construction, shredding(?), surface and some penetration for pupation	
Neophylax, Dicosmoecus, Allocosmoecus (stone case-makers): surface pupation	
Glossosomatidae	
Glossosoma and *Anagapetus:* surface pupation	
Hydropsychidae	
Arctopsyche, Parapsyche, Hydropsyche: net and retreat attachments, some pupation	
Polycentrododidae	
Polycentropus: retreat site	
Philopotamidae	
Wormaldia, Dolophilodes: net attachments	
Rhyacophilidae	
Rhyacophila (esp. *acropedes*—group); habitat for predation (and detrital feeding?)	

nursery area for early instars, for resting, molting, pupation and emergence. Because of its unique capillary properties, it affords an ideal air-water interface with gradients of temperature and moisture.

Trichoptera.—The most conspicuous and diverse insects on wood were caddisfly larvae. They are relatively large and easily seen because of their cases and retreats. All major types of caddisflies, free-living, net spinners and case-makers, occur on wood debris.

Free-living larvae of *Rhyacophila* (especially the *acropedes* group) are common on wood surfaces. *Rhyacophila* spp. are generally considered to be predaceous but Mecom (1972) lists *R. acropedes* as a detritivore. It is probable that larvae of some of the rare species in this very diverse genus will be found that are specific to wood debris microhabitats.

Several genera of net-spinning larvae are associated with debris dams and submerged wood in lotic habitats. Exploitation of the habitat for net and retreat attachments is largely opportunistic, but there may also be a degree of specificity. For example, *Polycentropus halidus* is uncommon in these Oregon streams, but several of the larvae and their nets were found within pieces of decaying wood.

Among the case-making larvae, the uses of the wood substrate may be nonspecific, such as larval or pupal case-attachment, or they may be specific, for example, in selection of case material or in food intake. *Cryptochia* and *Pedomoecus,* obscure genera of western limnephilids, were collected during this survey; their rarity may be a reflection of microhabitat specificity. In the McKenzie River, the most abundant species collected on wood was *Brachycentrus americanus.* However, removal of woody debris would not greatly affect *B. americanus* as the larvae can attach their cases to stones just as well.

In addition to *Heteroplectron californicum,* other caddisflies intimately associated with wood debris include several *Lepidostoma* spp. and a number of genera of wood-cased limnephilids. Presumably because of their close association with this habitat, they also have the greatest impact in degradation. These species are presently included in the shredder functional feeding group. We suggest that, in addition to consuming leaves, all of these also feed to some degree on wood and the associated microflora.

Limnephilid genera that build wood or bark cases, such as *Hydatophylax, Psychoglypha, Onocosmoecus* and *Halesochila,* are among the largest insects found on wood in Oregon streams. In addition to their feeding activities, their case-building behavior has an impact on the particle size of woody debris. *Lepidostoma* spp. use small twigs and pieces of bark in case construction. Field observations indicate that larvae spend considerable time attached to wood, either feeding or resting. *Lepidostoma unicolor* larvae were observed to remove the bark of small twigs by chewing. Several species of *Lepidostoma,* including both wood-cased and sand-cased species, pupate within cracks in wood. In soft wood they may chew a hole for a pupation site.

Coleoptera.—Although several families of beetle larvae were collected on wood, none was common except *Lara avara.* The psephenid, oedemerid and amphizoid beetles were each represented by less than five individuals but they are included in Table 4 because they are not commonly collected and records of the larval habitat may lead to further investigation.

Diptera.—On a numerical basis, this order was the most abundant of the insects in the wood samples. Chironomid larvae were ubiquitous, but it is difficult to generalize about the role of this family because of the great variety of species and habits. The tubes of *Rheotanytarsus* were frequently abundant on wood although no more so than on adjacent rocks, so we do not ascribe any preference for the wood habitat as a surface for attachment. An undescribed species of *Brillia* (det. W. P. Coffman) was collected under the bark of recently fallen douglas-fir branches. The larvae were tunnelling in the live phloem and outer cortex of the wood. This species is a colonizer in the first stage of degradation, in contrast to other species of this genus that are known to bore into soft, waterlogged wood (Coffman, 1978).

Larvae of the tipulid, *Lipsothrix* spp. were common in Berry Creek. These slender, wormlike larvae occurred in tunnels in decayed alder wood that was so soft it could be broken apart by hand. Rogers and Byers (1956) provide detailed observations of *L. sylvia* in small Appalachian streams that demonstrate the restriction of this species to soft, waterlogged wood.

Ephemeroptera.—Although a number of mayfly species were collected on wood, most of these are considered chance associates (*e.g., Baetis* spp.) that are basically benthic species. Some taxa occurred with enough consistency to suggest a real association. In Devil's Club Creek, *Paraleptophlebia pallipes* is a characteristic species on wood, while in other sites *P. debilis* and *P. temporalis* occurred on wood as well as in leaf detritus of backwaters and marginal areas. Among the heptageneid mayflies, *Cinygma integrum* was largely restricted to wood substrates, where it apparently ingests periphyton and woody detritus by scraping. *Epeorus nitidus* is potentially another wood-associated species as it is found in the wood-choked first order streams. Several species of *Ephemerella* were common in the samples—especially from the larger streams—*E. flavilinea* appearing to be the most characteristic species of the wood habitat. Further study may well demonstrate some feeding specializations within this genus for exploiting the wood debris habitat. *Ameletus* spp. appeared to use wood preferentially as a site for emergence. This genus is somewhat unusual for mayflies in that larvae leave the water prior to moulting to the subimago.

Plecoptera.—The most common stoneflies in the collections were the detritivores, *Nemoura* and *Peltoperla*. Pteronarcids were less common but their large size made single individuals conspicuous. *Leuctra* spp. occurred on wood in small streams; their slender bodies are well-adapted for penetrating into the cracks and crevices. *Alloperla* spp. were also common on wood. These predators were presumably using this substrate as a source for prey.

QUANTITATIVE ESTIMATES OF WOOD-ASSOCIATED INVERTEBRATES

The results of the extensive sampling program for the seven streams are given in Table 5. The biomass of the dominant xylophagous insects (*Lara avara* and *Heteroplectron californicum*) is compared with that of the other wood-associated insects and snails. Invertebrate biomass is expressed both on a wood-weight and on a surface-area basis. The majority of organisms collected were from wood of intermediate size (ca. 1-10 cm diam).

The data indicate a greater standing crop of invertebrates on wood in streams of the Coast Range than in the Cascades. Although this could be attributed to differences

TABLE 5.—Biomass of invertebrates on small wood debris in seven Oregon streams, July 1976

	Invertebrate biomass/weight of wood (mg/kg)			
	Lara	*Heteroplectron*	Other insects	Gastropods
Coast Range				
Berry Creek	69.8	6.7	110.0	710.9
Flynn Creek	24.3	19.8	45.6	91.6
Five Rivers	19.8	0	23.2	72.9
Cascade Range				
Devil's Club Creek	12.9	0	14.8	0
Mack Creek	13.5	3.6	46.2	0.1
Lookout Creek	15.2	4.4	109.8	24.3
McKenzie River	19.3	0.1	62.0	36.4

TABLE 5.—(continued)

	Invertebrate biomass/surface area of wood (mg/m²)			
	Lara	*Hetero-plectron*	Other insects	Gastropods
Coast Range				
Berry Creek	538.7	51.9	848.9	5486.6
Flynn Creek	187.6	152.8	351.7	706.9
Five Rivers	152.7	0	179.4	562.9
Cascade Range				
Devil's Club Creek	100.0	0	113.9	0
Mack Creek	104.5	27.9	356.4	0.7
Lookout Creek	117.1	34.2	845.9	186.8
McKenzie River	148.7	0.9	478.3	280.6

in environmental factors (Table 2), we attribute the higher density of invertebrates in the Coast Range streams to the presence of more alder as a substrate and food source. The data for colonization rates on wood in Berry Creek support this contention (Table 9). The density of *Lara avara* is strongly correlated with the amount and species of wood available, irrespective of stream size within a drainage area. The density of *Heteroplectron californicum,* however, is more restricted by stream size. This species was essentially absent from large streams in both areas and also from the first-order Devil's Club Creek. Absence from the latter was unexplained, as the habitat of this species is known to include some very small streams (Anderson, 1976).

The data for "other insects" is more variable than for the xylophagous forms. This was expected because many of the individuals may only be chance associates (Nilsen and Larimore, 1973). In addition, limitations of the collecting techniques also increase the variability of these data. The biomass of the "other insect" group ranges from equal to that of the xylophagous group *(Lara* plus *Heteroplectron)* in Devil's Club Creek and the Coast Range streams, about 2.5-5.5 times greater in Mack Creek, Lookout Creek and the McKenzie River.

The snail, *Oxytrema silicula,* was the dominant invertebrate by biomass in the wood samples from Coast Range streams. In the Cascades, snails were abundant in McKenzie River and Lookout Creek but were largely absent at the altitude of Mack Creek and Devil's Club Creek. Since snails consume a wide variety of foods and have high biomass, their impact on the wood substrates may be greater than that of the wood-feeding insects.

The fauna of the experimental section of Berry Creek is atypical of a normal Coast Range stream because freshets are diverted through a bypass canal which prevents flushing by winter storms. As this site has not been flushed for over 15 years, a considerable amount of organic matter has accumulated. This lack of flushing may account for the high density of insects and the extraordinary biomass of snails. Most of the organic accumulation in Berry Creek is small twigs and fine particles not sampled as wood.

In addition to the xylophagous feeding group, some invertebrates obtain nutriment from the wood substrates by grazing or scraping the autotrophic epiphytes. McLachlan (1970) and Nilsen and Larimore (1973) suggest that the large numbers of chironomids responded to the development of algal films or mats, but they did not measure the quantity of periphyton. Table 6 compares standing crop of periphyton, measured by chlorophyll extraction, of wood with that on stream rocks in the four Cascade Range streams. In the densely shaded first-order stream, periphyton biomass is low on both substrates. In the other streams, the biomass on wood is considerably lower than on stream rocks. However, the amount of periphyton on wood appears adequate to support a low population of grazers. Periphyton ingested by snails, when they rasp the wood surface, probably contributes significantly to their nutrient intake because of the higher food quality. The feeding activity also exposes additional sites for microbes. This indirect role in the processing of wood in streams is little understood and is probably greatly underestimated.

COMPARISON OF WOODY DEBRIS FAUNA WITH LEAF-PACK FAUNA

Although there is a diverse fauna associated with wood, the biomass is low. Total invertebrate biomass (mg/kg of wood) ranged from about 28 in Devil's Club Creek to 897 in Berry Creek (Table 5). If the latter value is excluded as being exceptional due to lack of winter flushing, then the maximum biomass was 181 mg/kg for Flynn Creek.

The relative paucity of the wood fauna is strikingly illustrated by comparing the standing crop with that obtained in leaf detritus in Flynn and Mack creeks (Table 7). The leaf-pack method reported by Petersen and Cummins (1974) was used. The data for leaves are a composite mean of invertebrate biomass per gram leaf pack of alder, vine maple, big-leaf maple and douglas-fir leaves attached to bricks to simulate natural leaf accumulations. The packs were placed in the streams during November and sampled at about monthly intervals until May (Sedell *et al.*, 1975).

The standing crop of each group (shredders on leaves, gougers on wood, total insects and snails) is about two orders of magnitude greater on leaves than on wood. Underestimates of the wood fauna could account for some of the difference but even if the biomass on wood were doubled, the comparison would remain essentially unchanged. The seasonal difference in the comparison (leaf packs from November-May, wood sampling in July) undoubtedly contributes to some of the wide divergence in values. However, among the dominant components on both substrates, the snail biomass does not change greatly on a seasonal basis, and shredders such as *Lepidostoma unicolor, Hydatophylax hesperus* and *Onocosmoecus* sp. are approaching

TABLE 6.—Comparison of periphyton standing crop on wood[1] and mineral substrates[2] in four Cascade Range streams in the same drainage system

Stream	Strahler stream order	Wood surface g/m²	Mineral substrate g/m²
Devil's Club Creek	1	0.2	0.2
Mack Creek	3	0.7	1.5
Lookout Creek	5	0.4	5.5
McKenzie River	7	0.6	5.0

[1] Analysis of periphyton was from small sticks ca. 0.5-2.0 cm diameter and 10-25 cm long (Naiman and Gregory, pers. comm.)
[2] Lyford and Gregory (1975)

TABLE 7.—Comparison of standing crop of invertebrates in leaf packs and wood from a Coast Range and Cascade Range stream of similar size. The dominant processors on leaf packs are shredders, on wood are gougers

	Dominant processors mg/kg	Total insects mg/kg	Gastropods mg/kg	Total invertebrates mg/kg
Flynn Creek				
Leaf packs	6,020	9,010	7,950	16,960
Wood	44.1	89.7	91.6	181.3
Mack Creek				
Leaf packs	4,803	8,802	0	8,802
Wood	17.2	63.3	0.1	63.4

maximum weight during the summer (Anderson, 1976).

The difference in invertebrate biomass on leaves and wood is attributed primarily to differences in food quality. Although both are low in nitrogen compared with periphyton, seeds or fresh macrophytes (Table 8), the wood is so high in the refractory components (lignin and cellulose) compared with leaves, that it becomes available at a very slow rate. The greater surface area and penetrability of leaves results in microbial conditioning occurring within months, compared with years for wood. Conditioning is a key factor in the debris becoming available as food for the invertebrates.

IMPACT OF INVERTEBRATES ON WOOD DEGRADATION

Laboratory studies were undertaken to obtain preliminary estimates of the impact of invertebrates on degradation or reduction in particle size of wood debris. Larvae were held at 15.6 C in dechlorinated tap water in shallow dishes or pans. The quantity of feces produced is useful as an index of food consumption. For example, *Lara avara* larvae (N = 20) produced 0.15 ± 0.05 mg feces/mg body wt/day on stream-conditioned wood compared with 0.03 ± 0.01 mg/mg/day with wood sterilized with ethylene oxide, indicating a feeding response to the presence of a suitable microbial flora. However, even with high fecal production rates by *L. avara,* we have not demonstrated growth under laboratory conditions, possibly because the microbial flora changes after a period of time in the laboratory.

Fecal collections were also used as an index of food consumption by *Heteroplectron californicum* larvae supplied with various foods (Table 9). With the exception of the "twigs + *Quercus* leaves" series, the larvae were fourth or newly moulted fifth instars. Fecal production was about twice as high for larvae fed stream-conditioned wood (big-leaf maple) compared with those fed alder leaves. Wheat grains were readily consumed; the larvae chewed a hole in the husk and fed on the tissue within a few hours after the wheat was placed in water. The amount of feces produced on the wheat diet was the lowest for any of the diets. This may indicate both lowered consumption and higher assimilation efficiency of wheat grains. In all of the diets the larvae were observed attached to and chewing on cases of other larvae in

TABLE 8.—Nitrogen concentrations and carbon quality of selected particulate inputs to coniferous forest streams

	N (%)	C/N Ratio	Cellulose (%)	Lignin (%)	Total fiber (cellulose and lignin) (%)
Wood (douglas-fir)					
Twigs (with bark)	.20	235	40.2	34.4	70.6
Bark	.15	324	48.0	9.9	56.9
Wood	.04	1343	31.7	47.6	79.3
Leaves					
Red alder	2.03	23	9.0	9.5	18.5
Douglas-fir	.51	97	14.5	24.2	38.7
Big-leaf maple	.74	62	16.3	17.3	33.6
Vine maple	.56	77	14.7	8.5	23.2
Other					
Mosses[1]	0.8-1.2				
Algae[2]	6-10				
Flowers and fruit parts[3]	1-2				

[1] J. Lyford (pers. comm.)
[2] S. Gregory (pers. comm.)
[3] Cromack and Monk (1975)

the dish. Thus, wood was an ingested component in all trials. The larvae egested 1-2 times their body weight per day of fine particle feces with wood as food.

Field studies of invertebrate colonization were conducted by placing 46 wood sticks alder (14), douglas-fir (14) and hemlock (18)—in Berry Creek during April 1975. These were kiln-dried commercial grade 1″ × 1″ (2.5 cm × 2.5 cm) lumber, 0.92 m long, that were grooved with a saw blade 2 mm wide and 2.5 mm deep. The sticks were examined every 2-3 weeks for 56 weeks. The number of *Lara avara* larvae was recorded without removing them from the sticks.

Of the 232 *Lara avara* recorded between weeks 2 and 56, 44% were on alder, 38% on hemlock and only 18% on douglas-fir (Table 10). Half of the records are considered to be repeat counts of the same individuals at successive sampling intervals. For example, one larva remained in the same position for over 4 months. Larvae were recorded as "arrivals" when first counted and as "residents" when there was a larva on the same stick at two successive sampling dates. The number recorded as "arrivals" (Table 10) indicates that similar proportions of larvae initially landed on each type of wood. However, the "residency" index shows that the percent remaining on douglas-fir for 2 or more samples was less than half of that on hemlock or alder. That the grooved wood is attractive to drifting *L. avara* is apparent in that a similar amount of alder and douglas-fir branch material, placed in the stream at the same time as the sticks, only attracted six larvae compared with the 232 on the sticks. McLachlan (1970) demonstrated that submerged wood previously damaged by bark beetles was more readily colonized by mayflies than trees with solid bark.

After 15 months in the stream, alder showed a dramatic deterioration, whereas douglas-fir appeared unchanged and hemlock was intermediate (Fig. 1). The surface of the alder was abraded to the extent that the saw grooves were no longer apparent. The numbers of *Lara avara* alone were too low to have produced this change, based on laboratory studies of feeding rates. Field observation and collection indicated that the feeding activity of the entire invertebrate complex was involved, and that snails were the major component. The mean numbers of biomass of *Oxytrema silicula* per m^2 of wood in August 1976 were: alder, 91, 890 mg; hemlock, 121, 770 mg; and douglas-fir, 43, 279 mg. In contrast, the numbers and biomass of *L. avara* were: alder, 7, 45 mg; hemlock, 5, 35 mg; and douglas-fir, 3, 20 mg.

TABLE 9.—Fecal production by *Heteroplectron californicum* larvae on different food substrates at 15.6 C in the laboratory

Food	No. of larvae	Days	Total feces (mg)	Terminal wt. of larvae ($\bar{x}$)	Fecal production (mg/mg/day)
Stream wood (*Acer*)	9	13	354.15	1.49	2.15
Stream wood (*Acer*)	59	9	1323.15	2.27	1.10
Stream wood (*Acer*)	10	21	826.85	4.09	1.01
Alnus leaves	9	13	224.95	3.90	0.52
Alnus leaves	10	21	404.83	4.08	0.47
Wheat grains	10	20	363.50	4.92	0.37
Twigs + *Quercus* leaves	26	6	219.02	9.58	0.15

TABLE 10.—Colonization of three species of wood by *Lara avara* larvae in Berry Creek, Benton Co., Oregon, 1975-76

	Alnus rubra	*Tsuga heterophylla*	*Pseudotsuga menziesii*	Total
No. of larvae recorded (weeks 2-56)	101	89	42	232
No. counted only once (Arrivals)	49	36	31	116
No. recounted at next sampling interval (Residents)	52	53	11	116
"Residency" Index (Percent on each wood)	51%	60%	26%	

SYNTHESIS

ECOSYSTEM ROLE OF WOOD AND LEAF LITTER

Branch and bole wood in streams influences channel morphology by operating as a trap for organic material and a break in the channel gradient. Debris dams serve to retain materials in the stream long enough to be processed by both microbes and invertebrates. The wood dams also produce habitats such as pools, drop zones and madicolous areas (Hynes, 1970, p. 409), and by acting to dissipate the energy of running water, they decrease the amount of energy available to erode (Swanson *et al.*, 1976).

Woody debris and leaves, the two major allochthonous components entering a stream, operate in different ways in relation to quantity, quality and turnover time (Table 11). The leaves form a small pool of readily available organic material, while the wood forms a large pool of less available (slow turnover) organic matter compared to the leaves. The slowly processed wood also constitutes a long-term reserve of essential nutrients. The composition, metabolic structure and nutrient turnover time of the particulate organic pool effectively provides both a flexibility and stability within the system.

STRATEGIES OF WOOD-ASSOCIATED RESOURCE UTILIZATION

Invertebrate growth and survival require a source of fixed energy and nutrients, particularly nitrogen. These requirements present special problems to wood-consuming invertebrates since most of the carbon is tied up in wood fiber (lignin and

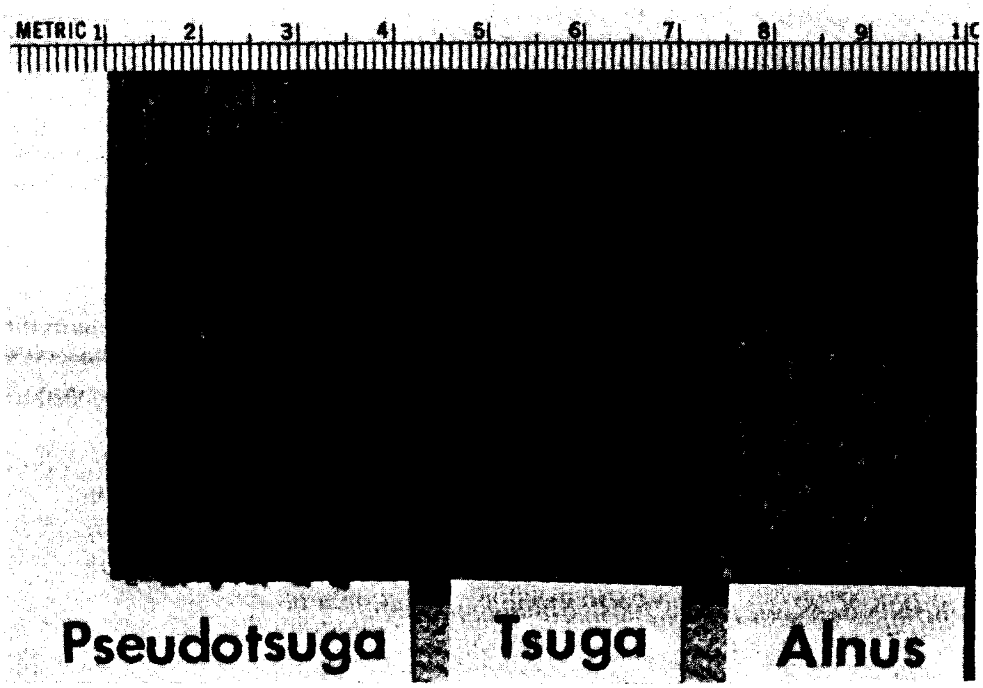

Fig. 1.—Appearance of grooved wood of douglas-fir (*Pseudotsuga*), hemlock (*Tsuga*) and alder (*Alnus*) after 15 months in Berry Creek. Note that the grooves in alder have almost disappeared

cellulose), and nitrogen concentrations are extremely low (Table 8). Two basic strategies may be involved in wood exploitation. One is the consumption of voluminous amounts of wood tissue to obtain enough digestible carbon and nitrogen from both the wood substrate and associated microbial flora to fill the energy and nutrient requirements of the organisms. This strategy is common to leaf-shredding invertebrates and appears to be employed by *Heteroplectron californicum* larvae which may consume up to 200% of their body weight per day of wood tissue in laboratory culture. A second strategy is cultivation and retention of a gut flora to furnish essential vitamins and amino acids and aid in the internal digestion of wood fiber (*e.g.,* termites). A final strategy would be some combination of the above mechanisms.

Despite the mechanism employed, strategies for wood exploitation are complicated in aquatic habitats by the waterlogged condition of the wood substrate. Microbial colonizaion of submerged sticks and twigs is primarily a "surface" phenomena (Savory, 1954), although some ascomycete and basidiomycete fungi which colonize wood prior to entry into the water survive and have been observed to produce fruiting bodies on submerged and waterlogged wood. In the terrestrial environment, fungal colonization occurs throughout the wood matrix. Thus, microbial-invertebrate interactions are possible for carpenter ants, beetles and termites which bore through the wood. In aquatic habitats, *Lara avara* produces only shallow gouges along the surface not much deeper than the larva itself. It is only in the later stages of decomposition, when the wood is soft and punky, that species such as *Lipsothrix* occur deep in the wood matrix.

In terrestrial habitats, wood consumption by invertebrates has been related to fixation of nitrogen in the gut and to other special microbial-invertebrate interactions. Nitrogenase activity by bacteria in the gut of termites (Breznak *et al.,* 1973; Benemann, 1973) and cellulase activity by protozoa (Mannesmann, 1972) and bacteria (French, 1975) have been demonstrated as strategies for fiber utilization.

In aquatic systems, Carpenter and Culliney (1975) demonstrated both nitrogen fixation and cellulase digestion by microflora of shipworms in the marine environment. Similar experiments have thus far yielded negative results with *Lara avara* larvae maintained in laboratory cultures for several weeks. Gut flora of laboratory-maintained specimens have also been placed in the selective media of Hino and Wilson (1958) for isolation of enteric nitrogen-fixing bacteria, and on cellulose media (Sigma MN-300). The results of these experiments have also been negative. M. J. Klug (pers. comm.) has found little evidence for a resident gut flora by microscopic examination. To what extent the result is a function of laboratory-rearing practices cannot be determined at this time.

TABLE 11.—Comparison of leaves and wood debris as components of small coniferous forest stream ecosystems

	Leaves	Wood debris
Standing crop (% of particulate organic matter)	<5	>60 (excluding boles)
Seasonality of inputs	Pulsed autumnal	Erratic
Impact on stream morphology	Minor	Major (stabilize and destabilize)
Carbon: nitrogen ratio	25-100:1	300-1000:1
Total fiber (%)	20-40	70-80
Degradation time	2-12 months	5-200 years
Microbial colonization pattern	Surface and Matrix	Primarily surface
Invertebrate component	High (mg/g)	Low (mg/kg)
Invertebrate utilization	Food, shelter	Shelter, substrate, oviposition, pupation, emergence, food (direct and indirect)

One alternative hypothesis to explain the feeding strategy of *Lara avara* is the consumption of a thin surface of partially degraded wood and microbial biomass, as a source of carbon and nitrogen, augmented by nonsymbiotic microbial fixation. Initially this strategy did not seem feasible, since *L. avara* spends over 2 years as a larva and consumes only 10-30% of its body weight/day on wood; only a small fraction of this diet is actual microbial biomass. Our preliminary studies on wood decomposition in water, however, lend some support for this hypothesis. Surfaces of fine wood debris in streams are colonized by both cellulose- and lignin-utilizing fungi within 6 months. Within 1 year, *Alnus* wood was softened to a depth of 0.5 mm. In addition, nitrogen fixation was also observed within 3 months by free-living bacteria on various wood substrates. Although the evidence is scant, *L. avara* with a straight tube gut and no current evidence of symbiotic gut flora (M. J. Klug, pers. comm.) may be able to grow with the activity of cellulase, lignase and nitrogenase on the surfaces of wood providing the digestible material. Use of wood as a food resource would decrease competition with most leaf-litter shredders. However, this strategy imposes a growth rate regulated by the rate of conversion of refractory carbon and nitrogen to a digestible resource by the enzymatic activity of free-living bacteria and fungi. The energetic cost of wood exploitation is a long life cycle and extremely low metabolic rate.

CONTRIBUTION OF INVERTEBRATES TO WOOD DEGRADATION

An estimate of the amount of wood processed by invertebrates can be obtained from the field data and fecal production values.

The *Lara avara* population would produce 0.6 g feces/kg wood/year assuming a density of four larvae/kg wood, mean weight of 6 mg and daily egestion rate of 10% body wt. For *Heteroplectron californicum,* fecal production approximates 9.6 g/kg wood/year, based on a density of 3-4 larvae/kg, mean weight of 15 mg and daily egestion rate of 50% body wt. *Oxytrema silicula* would produce 7.3 g feces/kg of wood, assuming 10 snails per kg wood, mean weight of 10 mg, and daily egestion rate of 10% body wt.

The resultant estimate of fecal production for the three major wood-processing invertebrates would be 17.5 g/kg of wood per year. Without snails, the total feces produced would be 10.2 g/kg of wood per year. Thus, a conservative estimate of the direct role of invertebrates in the processing of wood would be between 1-1.7% per year. The estimate is conservative because we have not included the amount of wood which went into xylophagous invertebrate production and respiration or into other associated invertebrates.

The time required for wood disappearance in fresh water has rarely been estimated. One measurement, by Hodkinson (1975), predicted a 57-year half life for 7.5-cm diam logs of *Populus balsamifera* found in a cold water beaver pond in Alberta, Canada. This is considerably longer than estimates by Gilson respirometry for fine twigs less than 1.0 cm in diam (B. Buckley, pers. comm.). Microbial degradation of these twigs, assuming an RQ of 1 and 50% carbon composition, was estimated at 18% per year or a 5.5-year disappearance time. Wood inhabited by xylophagous invertebrates is usually in excess of 2.0 cm in diam. Thus, disappearance time of this debris would be between the estimate of fine twigs and that of logs in the cold water pond, perhaps 10-20 years. With an estimate of 10-20 years, 1% consumption per year by invertebrates looks insignificant on an annual basis. However, the total direct role of invertebrates could be as much as 10-20%, considering the full decomposition cycle.

This approximation of wood degradation by invertebrates is in the same range as that found for litter in other terrestrial and aquatic environments. Petersen and

Cummins (1974) estimated 21% invertebrate leaf processing in a Michigan stream, and our own estimate (Sedell *et al.*, 1975) is 15% in Cascade streams. In terrestrial environments, Crossley and Witkamp (1964) estimate annual litter flux through soil arthropods at 15%, and Gist and Crossley (1975) at 10-20%.

The indirect role of feeding on senescent microflora, exposing more surface area and spreading fungal spores, would enhance the role that these invertebrates play in the processing of wood.

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LITERATURE CITED

ANDERSON, N. H. 1976. The distribution and biology of the Oregon Trichoptera. *Oreg. Agric. Exp. Stn. Tech. Bull. No. 134.* 152 p.

BENEMANN, J. R. 1973. Nitrogen fixation in termites. *Science,* **181**:164-165.

BOLING, R. H., JR., E. D. GOODMAN, J. O. ZIMMER, K. W. CUMMINS, S. R. REICE, R. C. PETERSEN AND J. A. VAN SICKLE. 1974. Toward a model of detritus processing in a woodland stream. *Ecology,* **56**:141-151.

BREZNAK, J. A., W. J. BRILL, J. W. MERTINS AND H. J. COPPEL. 1973. Nitrogen fixation in termites. *Nature,* **244**:577-580.

BROWN, J. K. 1971. A planar intersect method for sampling fuel volume and surface area. *For. Sci.,* **17**:96-102.

BRUSVEN, M. A. 1970. Drift periodicity of some riffle beetles (Coleoptera:Elmidae). *J. Kans. Entomol. Soc.,* **43**:364-371.

CARPENTER, E. J. AND J. L. CULLINEY. 1975. Nitrogen fixation in marine shipworms. *Science,* **187**:551-552.

CLAFLIN, T. O. 1968. Reservoir aufwuchs on inundated trees. *Trans. Am. Microsc. Soc.,* **87**: 97-104.

COFFMAN, W. P. 1978. Chironomidae, Chap. 22, p. 395-434. *In:* R. W. Merritt and K. W. Cummins (eds.). An introduction to the aquatic insects of North America. Kendall-Hunt, New York.

CROMACK, K. AND C. D. MONK. 1975. Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and a white pine watershed, p. 609-624. *In:* F. G. Howell, J. B. Gentry and M. H. Smith (eds.). Mineral cycling in southeastern ecosystems. Conf-740513. Natl. Tech. Inf. Service, Springfield, Va.

CROSSLEY, D. A., JR. 1970. Roles of microflora and fauna in soil systems, p. 30-35. *In:* Pesticides in the soil: Ecology, degradation and movement. Int. Symp. on Pesticides in the Soil, Feb. 25-27, 1970. Mich. State Univ. Press, East Lansing.

——— AND M. WITKAMP. 1964. Effects of pesticides on biota and breakdown of forest litter. VIII Int. Congr. Soil Sci. (Bucharest), **3**:87-91.

CUMMINS, K. W., R. C. PETERSEN, F. O. HOWARD, J. C. WUYCHECK AND V. I. HOLT. 1973. The utilization of leaf litter by stream detritivores. *Ecology,* **54**:336-345.

FRENCH, J. R. 1975. The role of termite hindgut bacteria in wood decomposition. *Mater. Org. (Berl.),* **10**:1-13.

FROEHLICH, H. A. 1973. Natural and man-caused slash in headwater streams. *Loggers Handb. 33.* 8 p.

GIST, C. S. AND D. A. CROSSLEY, JR. 1975. A model of mineral-element cycling for an invertebrate food web in a southeastern hardwood forest litter community, p. 84-86. *In:* F. G. Howell, J. B. Gentry and M. H. Smith (eds.). Mineral cycling in southeastern ecosystems. Conf-740513. Natl. Tech. Inf. Service, Springfield, Va.

HALL, J. D. AND R. L. LANTZ. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams, p. 355-376. *In:* T. G. Northcote (ed.). Symposium on salmon and trout in streams. Inst. Fish., Univ. British Columbia, Vancouver, British Columbia, Canada.

HINO, S. AND P. W. WILSON. 1958. Nitrogen fixation by a facultative bacillus. *J. Bacteriol.*, **75**:403-408.

HODKINSON, I. D. 1975. Dry weight loss and chemical changes in vascular plant litter of terrestrial origin, occurring in a beaver pond ecosystem. *J. Ecol.*, **63**:131-142.

HYNES, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ont. 555 p.

LAMMEL, R. F. 1972. Natural debris and logging residue within the stream environment. M.S. Thesis, Oregon State University, Corvallis. 49 p.

LYFORD, J. H., JR. AND S. V. GREGORY. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. Verh. Int. Ver. Limnol., **19**:1610-1616.

MACKAY, R. AND J. KALFF. 1969. Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. *Ecology*, **50**:101-109.

MANNESMANN, R. 1972. Comparison of twenty-one commercial wood species from North America in relation to feeding rates of the Formosan termite, *Coptotermes formosanus* Shiraki. *Mater. Org.* (*Berl.*), **8**:107-120.

MCLACHLAN, A. J. 1970. Submerged trees as a substrate for benthic fauna in the recently created Lake Kariba (Central Africa). *J. Appl. Ecol.*, **7**:253-266.

MECOM, J. O. 1972. Feeding habits of Trichoptera in a mountain stream. *Oikos*, **23**:401-407.

NILSEN, H. C. AND R. W. LARIMORE. 1973. Establishment of invertebrate communities on log substrates in the Kaskaskia River, Illinois. *Ecology*, **54**:366-374.

PETERSEN, R. C. AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. *Freshwater Biol.*, **4**:343-368.

ROGERS, J. S. AND G. W. BYERS. 1956. The ecological distribution, life history, and immature stages of *Lipsothrix sylvia* (Diptera:Tipulidae). *Occas. Pap. Mus. Zool. Univ. Mich. No. 572.* 14 p.

ROTHACHER, J., C. T. DYRNESS AND R. L. FREDRIKSEN. 1967. Hydrologic and related characteristics of three small watersheds in the Oregon Cascades. *U.S. For. Serv. Res. Note PNW.* 14 p.

SAVORY, J. G. 1954. Damage to wood caused by microorganisms. *J. Appl. Bacteriol.*, **17**:213-218.

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, p. 57-69. *In:* R. H. Waring and R. L. Edmonds (eds.). Integrated research in the coniferous forest biome. Coniferous For. Biome Bull. No. 5. University of Washington, Seattle.

———, ——— AND N. S. TRISKA. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. Verh. Int. Ver. Limnol., **19**:1617-1627.

SWANSON, F. J., G. W. LIENKAEMPER AND J. R. SEDELL. 1976. The history and physical effects of large organic debris in western Oregon streams. *U.S. For. Serv. Gen. Tech. Rep. PNW–56.* 15 p.

WAGNER, C. E. VAN. 1968. The line intersect method in forest fuel sampling. *For. Sci.*, **14**:20-26.

WARREN, C. E., J. H. WALES, G. E. DAVIS AND P. DOUDOROFF. 1964. Trout production in an experimental stream enriched with sucrose. *J. Wild. Manage.*, **28**:617-660.

WINTERBOURN, M. J. 1971. The life histories and trophic relationships of the Trichoptera of Marion Lake, British Columbia. *Can. J. Zool.*, **49**:623-635.

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