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Patterns of exploitation by stream invertebrates of wood debris (xylophagy)

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With 2 figures and 2 tables in the text

The exploitation of wood debris by aquatic invertebrates has been investigated for about 10 years by our laboratory. The initial study (ANDERSON et al. 1978) developed a general scheme of wood processing by invertebrates, based on data from seven streams of the Coast and Cascade Mountains of Oregon. Of about 40 species associated with wood, the elmid beetle, *Lara avara* LECONTE, the calamoceratid caddisfly, *Heteroplectron californicum* MCLACHLAN, and the pleurocerid snail *Oxytrema (= Juga) silicula*[1] were considered to be the dominant processors associated with wood surfaces. Based on a survey in the western states, DUDLEY & ANDERSON (1982) listed 56 taxa of aquatic and semiaquatic invertebrates as "closely associated" with wood debris and 129 as facultative users of wood substrates. In contrast to the earlier study, the tunnelling and burrowing species received more attention. Diptera, especially Chironomidae and Tipulidae, were shown to be dominant borers, both in abundance and diversity.

This paper reports on continuing studies of aquatic insect-wood interactions, especially on long-term densities and rates of colonization. The patterns of exploitation by surface associates were monitored for five years on tethered sticks and branch wood at Berry Creek, near Corvallis, Oregon (see ANDERSON et al. 1978). Colonization by semi-aquatic and aquatic wood borers was also studied at Berry Creek. Alder posts were placed so that one end was submerged to the bottom of the stream and the other was above the waterline in contact with the bank.

We use a broad interpretation of xylophagy to include organisms whose feeding activities effect fragmentation of wood surfaces. The scrapers that utilize the aufwuchs film probably derive little nutrient from the wood. However, their guts contain wood (PEREIRA et al. 1982), and their feeding activity contributes to the mineralization of woody debris.

A general model of aquatic invertebrate-wood interactions

Wood quality or texture is important in determining the kinds of species that will colonize it. The species of wood, degree of waterlogging, and the soundness, or decay class, all affect wood quality. Texture is frequently related to the conditions of the wood when it entered the water so the extent of mycological invasion in the terrestrial habitat will have considerable influence on its attractiveness. Fig. 1 illustrates associations contrasting submerged wood that was sound when it fell into the water with a terrestrially-decayed stem that is partially submerged. In the former, decay only occurs on the surface as a thin layer (< 1 cm) stained and softened by fungal mycelia. This layer may be exploited by gougers and by shallow tunnellers, as well as surface scrapers. These functional groups will also occur on wood with deep decay. In addition, decayed wood may be colonized by more tunnelling species especially at the air-water interface. The many grooves, crevices and cracks in the well-conditioned wood offer refuge from predation and the abiotic environment. Other uses (oviposition, pupation, case-making and emergence) also will be greater on this type of wood than on the firm submerged pieces.

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[1] The name of this snail has been confused in our earlier work. In ANDERSON et al. (1978) it was listed as *Oxytrema silicula*, but in DUDLEY & ANDERSON (1982) as *Juga plicifera* (LEA). Dr. DWIGHT TAYLOR has recently informed us that the species in small streams is *Juga silicula* (GOULD). *J. plicifera* is a river-inhabiting species.

Wood associates on tethered alder wood

The initial phase of invertebrate colonization of new wood at Berry Creek was reported by Anderson et al. (1978) and population trends have since been monitored for four more years. Kiln-dried, 2.5 × 2.5 cm lumber, 0.92 m long, was grooved with a saw blade and tethered in the stream. Biomass of the dominant taxa on 14 alder sticks is compared with that on 20 alder branches (with bark) of a similar size (Table 1). The branches were considered representative of small wood that would fall naturally into a stream. Data are mean weights of invertebrates collected by washing the sticks with a back-pack sprayer in the field. Collections were made four times yearly from 1976 (year 2 of submergence) to 1980 (year 5).

The sticks and the branches supported a similar fauna in terms of both composition and biomass of fauna (Table 1). The branches had slightly lower populations until the bark began to break away and surface layers were conditioned by fungi; then biomass was similar to that on the sticks. By year 5 some sticks were breaking into small pieces and total surfaçe area had decreased by 60 %. However, at that time both the sticks and branches had the highest biomass of insects and snails for the four years (sticks, 883 mg · m^{-2}; branches, 903 mg · m^{-2}).

We attribute a substantial amount of the wood loss of the sticks to feeding activities of the taxa in Table 1, but cannot separate the feeding effects from losses by physical abrasion. The microbiota are responsible for biochemical degradation of the wood and both the macrobiota and scouring remove this softened layer.

Wood gougers account for only a small part of the wood-associated community, especially when *Juga* is considered along with the insects. Steedman (1983) has shown that washing or field picking is only about 50 % effective for collecting *Lara*, but even doubling its biomass would only raise it to 14 % of the biomass. The dominant insect was

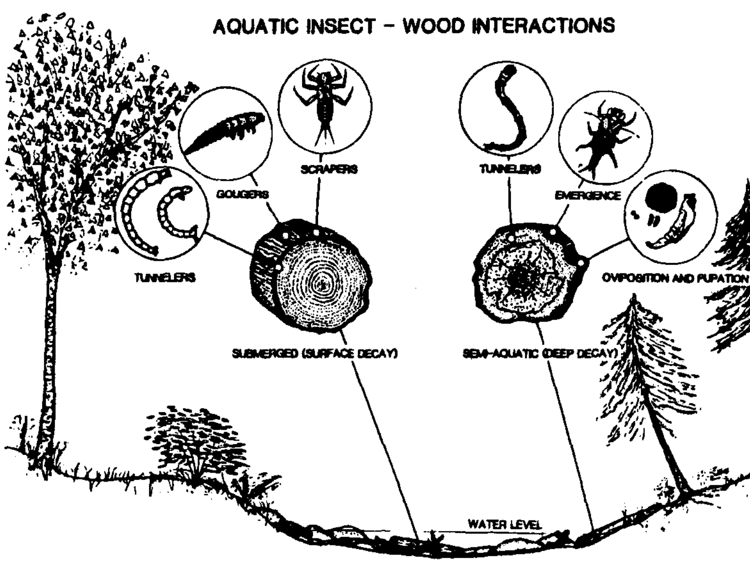

Fig. 1. A model of aquatic insect — wood interactions in a small stream.

Table 1. Mean biomass of dominant taxa on surfaces of alder submerged 2–5 years. Berry Creek, Oregon, 1976–1980.

	Functional group	Dry mass (mg · m^{-2})	
		Grooved sticks	Branch wood
Cinygma	Sc	60.0	54.8
Limnephilidae	Sh-G	40.2	39.4
Nemouridae	Sh	34.0	16.0
Lara	G	17.4	22.1
Heteroplectron	G-Sh	13.6	11.8
Epeorus	Sc	13.0	11.5
Chironomidae	Col	12.3	9.5
Baetis	Sc	8.5	12.8
Lepidostoma	Sh-G	7.5	6.3
Paraleptophlebia	Sh-Col	8.0	4.5
Total insects		227.3 (30 %)	207.8 (32 %)
Snails (*Juga*)		520.8 (70 %)	441.5 (68 %)
Total invertebrates		748.1	649.3

Sc = scraper; Sh = shredder; G = gouger; Col = collector.

Cinygma integrum Eaton, a xylophilous mayfly that ingests considerable amounts of fungi and wood fragments (Pereira & Anderson 1982). The limnephilid and lepidostomatid caddisflies may also be quite important as wood degraders; feeding, case-making and boring for pupation all effect particle-size reduction of the wood. The other taxa listed in Table 1 primarily use the wood as habitat. Nemourid stoneflies and *Paraleptophlebia* mayflies were often abundant as early instars. The Chironomidae collected by surface spraying are largely genera feeding on fine particulate organic matter.

The mean biomass of both insects and snails on the tethered sticks was much lower than that reported from natural wood debris by Anderson et al. (1978). They indicated that the Berry Creek fauna was atypical because a bypass canal prevents flushing by winter storms. The site had not been flushed for 15 years, which accounted for the high density of detritivorous insects and the extraordinary biomass of snails. The controlled flow does not explain the large difference in biomass between the tethered sticks and natural wood debris. The larger sample size of the earlier study included a wider range of woody substrates and there probably are substrate differences between the steam reaches where the two studies were conducted. However, we ascribe the major difference to time of sampling and to collecting techniques. Invertebrates on the tethered sticks were collected by non-destructive spraying in all seasons for four years. The wood debris sampling was done only once, in July 1976. *Juga* occurs in maximum abundance on wood in the summer, while in the winter they tend to be buried in the substrates. Destructive sampling, as was done for the debris collections, would collect a larger proportion of insects from cracks and crevices than would the spraying technique.

Colonization by wood-boring taxa

In November 1980, alder posts (6 cm dia. × 50 cm long) were positioned from bank to stream bottom (Fig. 2) to study the rate of colonization of new wood. Pupal exuviae of *Lipsothrix fenderi* Alexander (Tipulidae) and *Symposiocladius lignicola* (Kieffer) (Chironomidae) and mature larvae of *Austrolimnophila badia* Alexander (Tipulidae) were

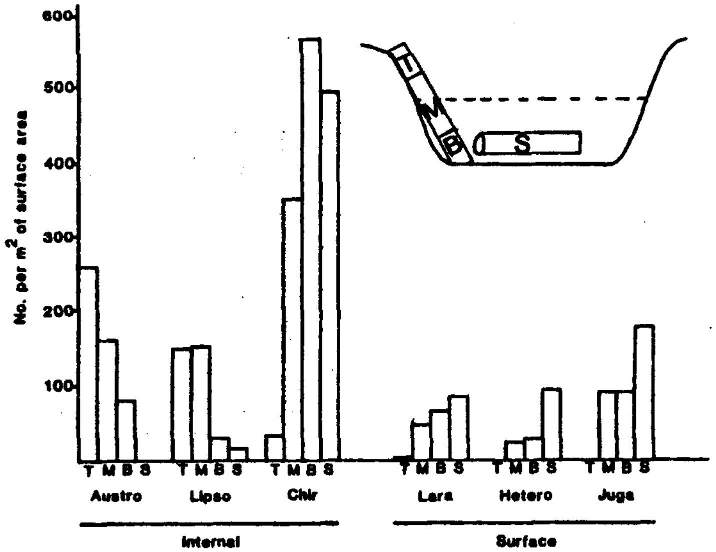

Fig. 2. Density of tunnelling and surface xylophages on alder posts 24—32 months after placement in Berry Creek. Data are means for collections from 10 leaning and 10 submerged posts in Oct., Mar. and June, except *Hetero(plectron)* and *Juga* only counted in Mar. and June. Abbreviations: *Austro(limnophila)*, *Lipso(thrix* spp.), Chir(onomidae). Insert indicates top, middle, bottom, and submerged treatment with respect to water level.

common when the first collections were taken in October 1982. *L. fenderi* has a minimum generation time of one year (Dudley 1982), so these posts had become suitable for oviposition and larval development within a year of being placed in the stream. Wood density (an index of decay) was not significantly different than the initial conditions, but a surface layer of fungal stained wood was evident.

Densities of internal and surface xylophages are compared for the top, middle, and bottom of leaning posts with those on submerged posts in Fig. 2. The sticks were cut into top (12.5 cm), middle (25 cm), and bottom (12.5 cm) and kept wetted in plastic bags. The sticks were washed once or twice weekly for several weeks to obtain larvae, pupae, exuviae and adults.

Differences in colonization patterns are evident from submerged to semiaquatic conditions (Fig. 2). The controlled flow prevents winter spates, but water level fluctuates on a seasonal basis. Density of the surface associates on different sections of the sticks is related to water level at the time of collections. The higher densities on submerged treatments compared with the bottom of learners is due to mud and fine organic matter accumulating around the latter. Distribution of the craneflies is partially related to availability of sites for oviposition. Females do not enter the water and dispersal by larvae is limited, so occurrence of larvae in bottom or submerged treatments indicates that the wood was partially exposed at the time of oviposition.

Cranefly distribution is partitioned along the moisture gradient with *Austrolimnophila* occurring primarily above the waterline, whereas *Lipsothrix* occurs at, and

slightly below, the water. Dudley (1982) has shown considerable spatial overlap between larvae of *L. fenderi* and *L. nigrilinea* (Doane), but the former extends higher above low-water level, and the latter tends to be in wood that is further submerged. We observed this trend but density of *L. nigrilinea* was only 20% of that of *L. fenderi*, so the two species are combined in Fig. 2.

The chironomids in Fig. 2 are distinct from the surface associates in Table 1. At least five genera of wood borers were represented. Based on collections to date, their relative abundance was: *Chaetocladius* > *Orthocladius* > *Limnophyes* > *Symposiocladius* > *Stenochironomus*. These genera were identified by Dr. D. Oliver, Ottawa, Canada, from pupae and adults obtained by washing the wood. *Brillia* larvae were collected from the initial washes, but no pupae or adults were obtained.

Fecal production rates

Fecal production is used as an index of wood degradation due to feeding activities because ingestion is difficult to measure. Data for *Lara* and *Heteroplectron* from Steedman (1983) and for *Lipsothrix* spp. from Dudley (1982) are summarized in Table 2 to compare potential feeding impacts by three types of xylophages.

Lara, an obligate xylophage, has a low feeding rate with no increase in rate between 4 and 18 °C. Relative consumption rates were very similar for 4—5th and 6—7th instar larvae. We estimate that the life cycle is 4—7 years, so a rapid feeding rate is not necessary. On wood of the same texture, *Heteroplectron*, which has a two-year life cycle, exhibited consumption rates that were 4—5 times higher than those of *Lara*. Feeding activity of *Heteroplectron* increased markedly with increased temperature. Though this species consumes large quantities of wood, it cannot complete development with well-conditioned wood as its total diet. In large-scale feeding trials (400—500 per treatment), larvae were less than half the weight at six months on a wood diet compared with those fed leaves + wood, and all had died on the former diet by nine months (R. W. Wisseman unpubl. data).

A strong relationship between wood texture and feeding rate exists for *Lipsothrix* (Table 2). Soft, well-rotted wood was consumed at over 200% body wt · day^{-1}. The effects of *Lipsothrix* activity on the mineralization of this recalcitrant material were further

Table 2. Fecal production rates of three xylophages under laboratory conditions.

	Wood type	Temp. (°C)	Larval wt. (mg)	Feces (% body wt. day^{-1})
Lara	Alder branch, 5 yrs in stream	4–18	1.5– 2	8–30 ($\bar{x}$ = 16.4)
	"	4–18	4 –10	9–19 ($\bar{x}$ = 14.4)
Heteroplectron	"	9	3.9	17
	"	13	3.9	65
	"	18	3.9	91
	"	5	9.5	28
	"	8	14.2	42–45
Lipsothrix	Firm alder	13	0.9– 1.2	88
	Med.-soft alder	13	0.9– 1.2	140
	Soft alder	13	0.9– 1.2	223

demonstrated in a laboratory stream. After 12 months exposure to *Lipsothrix* larvae, a 53 g piece of decayed alder was reduced to the point where only 5 g retained any structural integrity (DUDLEY 1982).

Discussion

TRISKA & CROMACK (1980) reviewed the role of wood debris in forest and stream ecosystems. They suggest that wood decomposition has been virtually ignored in ecological studies, partly because the extended period necessary for wood to decay makes it difficult to study nutrient recycling from such a process. By using small wood (< 10 cm dia.) and by selecting a fast-decaying species (alder), the time frame of processes that we studied can be measured in years, rather than decades or centuries.

Wood debris in small streams is exploited by a sizeable group of species, with diverse feeding habits and life-history patterns. Fungal conditioning of alder occurs within a year and the wood can then be exploited by burrowing forms, as well as scrapers and gougers. Based on the fecal production rates in Table 2 and field population estimates in Oregon Coast Range streams, the amount of wood processed per year ranged from $1.1\,g \cdot m^{-2}$ for *Lara* (STEEDMAN 1983) to $>20\,g \cdot m^{-2}$ for *Lipsothrix* spp. (DUDLEY 1982). When the entire community of surface associates and internal borers is considered, the macrobiota will contribute significantly to mineralization and nutrient recycling of woody debris in small streams.

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References

ANDERSON, N. H., SEDELL, J. R., ROBERTS, L. M. & TRISKA, F., 1978: The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. — *Amer. Midl. Nat.* 100: 64—82.

DUDLEY, T. L., 1982: Population and production ecology of *Lipsothrix* spp. (Diptera: Tipulidae). — M. S. Thesis, Oregon State Univ., Corvallis, 161 pp.

DUDLEY, T. & ANDERSON, N. H., 1982: A survey of invertebrates associated with wood debris in aquatic habitats. — *Melanderia* 39: 1—21.

PEREIRA, C. R. D. & ANDERSON, N. H., 1982: Observations on the life histories and feeding of *Cinygma integrum* EATON and *Ironodes nitidus* (EATON) (Ephemeroptera: Heptageniidae). — *Melanderia* 39: 35—45.

PEREIRA, C. R. D., ANDERSON, N. H. & DUDLEY, T., 1982: Gut content analysis of aquatic insects from wood substrates. — *Melanderia* 39: 23—33.

STEEDMAN, R. J., 1983: Life history and feeding role of the xylophagous aquatic beetle, *Lara avara* LECONTE (Dryopoidea: Elmidae). — M. S. Thesis, Oregon State Univ., Corvallis, 106 pp.

TRISKA, F. J. & CROMACK, K., 1980: The role of wood debris in forest and streams. — In: WARING, R. H. (ed.), *Forests: Fresh perspectives from ecosystems analysis*: 171—190. Proc 40th Ann. Biol. Colloquium, Oregon State Univ. Press, Corvallis.

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