

Wood biofilm as a food resource for stream detritivores

S. L. Eggert¹

Department of Entomology, University of Georgia, Athens, Georgia 30602

J. B. Wallace

Department of Entomology and Institute of Ecology, University of Georgia, Athens, Georgia 30602

Abstract

Published assimilation efficiencies indicate that leaf detritus is a more nutritious food for stream invertebrates than wood. Some studies, however, suggest that wood and wood biofilms (epixylon) may be an important but overlooked resource. We measured assimilation efficiencies of three detritivores for leaves and epixylon and compared attributes of grazed versus ungrazed wood epixylon to assess its use by detritivores. *Pycnopsyche gentilis* (Trichoptera), *Tipula abdominalis* (Diptera), and *Tallaperla* spp. (Plecoptera) assimilated epixylon more efficiently (26–36%) than leaf detritus (9–17%). Epixylon assimilation efficiencies were *T. abdominalis* > *Tallaperla* spp. > *P. gentilis*. Grazed wood had significantly lower microbial respiration rates, bacteria densities and biomass, fungal and chlorophyll *a* biomass, and biofilm ash-free dry mass than ungrazed wood, indicating that detritivores fed on epixylon. Detritivores ingested leaves at a higher rate (0.09–0.47 g g⁻¹ d⁻¹) than epixylon (0.04–0.07 g g⁻¹ d⁻¹). Assimilation rates, which incorporate both assimilation efficiency and ingestion rate, however, indicated that *Tallaperla* spp. and *T. abdominalis* were better able to use epixylon than leaves, whereas *P. gentilis* was more efficient at using leaves. Wood biofilm is readily ingested and assimilated by some stream detritivores and may serve as an important but overlooked food resource in stream food webs.

Stream invertebrates play a critical role in the transfer of energy to higher trophic levels of food webs through their consumption of autochthonous and allochthonous resources and the resultant alteration of organic matter particle size (Allan 1995). Invertebrate consumption and assimilation of food resources varies by food type and species (Waldbauer 1968; Slansky and Scriber 1982). The assimilation of leaf litter by stream detritivores ranges from 5% to 60% (e.g., Herbst 1982; Golladay et al. 1983; Hutchens et al. 1997). In contrast, wood is considered to be a poor-quality food resource (Anderson and Cummins 1979). In the only published study of wood assimilation by aquatic insects, Steedman and Anderson (1985) measured assimilation efficiencies of 4–7% for *Lara avara*, a slow-growing beetle species, fed alder and conifer wood.

Golladay and Sinsabaugh (1991) suggested that wood biofilms (epixylon) might be overlooked sites of metabolic activity in streams. Epilithon and epixylon consist of bacteria, fungi, detrital particles, algae, and exoenzymes embedded in a gelatinous matrix (e.g., Lock et al. 1984; Scholz and Boon 1993). Since leaves break down at a faster rate than wood in streams (Webster et al. 1999), wood serves as a long-lasting substrate for biofilm development. The physical stability and complex surfaces of wood explain why

microbial respiration (Tank et al. 1993), fungal biomass, total microbial biomass, algal biomass, exoenzyme activity (Sinsabaugh et al. 1991), and invertebrate density (Hax and Golladay 1993) are higher on wood than on leaves. Given the high microbial activity associated with wood biofilms, epixylon should serve as a high-quality food resource for invertebrates (Golladay and Sinsabaugh 1991; Hax and Golladay 1993; Ledger and Winterbourn 2000).

Objective 1 of this study was to estimate assimilation efficiencies of leaves and wood for three detritivores, *Tipula abdominalis* (Say), *Tallaperla* spp., and *Pycnopsyche gentilis* (MacLachlan) for use in trophic basis of production calculations (Benke and Wallace 1980). *T. abdominalis*, *P. gentilis*, and *Tallaperla* spp. make up 54–77% of the annual shredder production in Coweeta headwater streams (Wallace et al. 1999) and consume various amounts of leaf and wood detritus (Hall et al. 2000). We hypothesized that these taxa would assimilate leaves more efficiently than wood, and *T. abdominalis* would be able to utilize wood more efficiently than *Tallaperla* spp. or *P. gentilis* on the basis of previous studies documenting *T. abdominalis*' ability to efficiently derive nitrogen from complexes of proteins and lignins (e.g., Martin et al. 1980). Unexpectedly high assimilation efficiencies for wood measured during the assimilation study provided the impetus for a follow-up experiment examining insect feeding on wood biofilms (Objective 2). We hypothesized that the high assimilation efficiencies we observed for wood were a result of epixylon consumption. Previously, Bärlocher and Kendrick (1975) showed that *Gammarus pseudolimnaeus* assimilated 65–77% of fungal mycelium, a component of epixylon. We tested our hypothesis by examining differences in microbial biomass and respiration, biofilm ash-free dry mass (AFDM), and algal standing crops on grazed and ungrazed pieces of small wood with biofilm.

¹ Corresponding author (seggert@uga.edu).

Acknowledgments

Suggestions by Darold Batzer, Steve Golladay, Judy Meyer, Amy Rosemond, Cathy Gibson, and Sue Herbert improved this study. We thank Keller Suberkropp, Jennifer Tank, and Bob Sinsabaugh for discussions of epixylon assimilation. Comments by Alex Huryn, Everett Fee, and two anonymous reviewers improved earlier drafts of the manuscript.

The National Science Foundation (DEB-9207498, DEB-9629268, and DEB-0212315) supported this research.

Methods

Study site and organisms—Leaf litter and small wood (≤ 10 mm in diameter) were collected in January and June 2002 from a high-gradient, first-order stream draining Catchment 53 (C53) located within Coweeta Hydrologic Laboratory in the southern Appalachian Mountains in western North Carolina. The watershed is forested by northern red oak (*Quercus rubra*), hickory (*Carya* spp.), yellow poplar (*Liriodendron tulipifera*), and red maple (*Acer rubrum*). A dense understory of rhododendron (*Rhododendron maximum*) shades the stream year round. Allochthonous organic matter inputs make up $>90\%$ of the energy base of the stream (Webster et al. 1983). Fourth-instar *T. abdominalis* and *P. gentilis* and late-instar (5–7 mm body length) *Tallaperla* spp. were collected from C53.

Assimilation experiments—Assimilation efficiencies and ingestion rates of mixed leaf species and small wood were measured for 40–80 individuals each of *Tallaperla* spp., *T. abdominalis*, and *P. gentilis*. Individuals were randomly assigned to wood or leaf treatments and fed stream-conditioned leaves or wood for 1 week. Organisms were placed in individual containers with filtered stream water at 12.5°C and starved for 48 h before and after each experiment to allow complete gut clearance.

Disks were cut from leaves of four breakdown rate categories and fed to organisms according to the proportions of each breakdown category in previously measured leaf inputs to C53 (fast breakdown [dogwood] = 3%, medium breakdown [red maple] = 30%, slow breakdown [red oak] = 47%, very slow breakdown [rhododendron] = 20%) (Cuffney et al. 1990). Wood used in this study consisted of randomly collected stream-conditioned sticks ≤ 10 mm in diameter, with intact biofilms and in advanced states of decay. Sticks had little to no bark, a well-developed biofilm, and slightly softened texture. Since sticks were in advanced state of decay, we could not determine the tree species of origin. Sticks with accompanying biofilms were cut into $5 \times 10 \times 10$ mm pieces before being fed to insects. Leaf disks and wood pieces were blotted dry, and weighed to obtain initial wet mass before being fed to the insects. A portion of each piece of organic matter was saved for wet mass/AFDM conversions. Ten replicates containing only wood or leaf material in filtered stream water served as controls.

Feeding experiments were run 2–8 d and terminated before the complete consumption of organic matter. Feces were filtered onto 0.45- μm Gelman A/E glass-fiber filters. Filters, larvae, and uneaten organic material were dried at 60°C , weighed, ashed at 500°C , and reweighed to obtain AFDM. Final mass of organic matter was corrected for changes in mass measured in the controls.

Assimilation efficiencies and ingestion rates were calculated (Waldbauer 1968):

$$\text{Assimilation efficiency (\%)} = [(I - E)/I] \times 100 \quad (1)$$

where I = AFDM of food ingested, E = AFDM of fecal

material egested;

$$\begin{aligned} \text{Ingestion rate (g AFDM food g AFDM insect}^{-1} \text{ day}^{-1}) \\ = (I/M)/T \end{aligned} \quad (2)$$

where T = time in days, M = mean larval AFDM. Mean assimilation rates for each food type and taxon were calculated by multiplying assimilation efficiency by ingestion rate for each individual (Golladay et al. 1983). Differences in assimilation efficiencies, ingestion rates, and assimilation rates of leaf and wood diets were compared among taxa using one-way analysis of variance (ANOVA), or Kruskal–Wallis ANOVA on ranks.

Epixylon grazing experiment—Measurements of biofilm AFDM, bacteria and fungal biomass, microbial respiration, and chlorophyll *a* (chl *a*) concentrations on sticks grazed by the three detritivores were compared to those measured for ungrazed sticks to determine if shredders consumed significant quantities of epixylon.

Stream-conditioned sticks (200–250 mm in length, ≤ 10 mm in diameter), with intact biofilms and in advanced states of decay, were cut in half and placed in tubs of 12.5°C , aerated stream water. One-half of each stick was excluded from shredder consumption by enclosing it in a 1-mm mesh container. The other half was available for consumption by 5–21 individuals of each shredder taxon for 15 d. Eight control sticks were also cut in half and incubated as above, but were not subjected to shredder consumption.

Epixylic biofilm from a portion of each pair of grazed, ungrazed, and control sticks was removed with a razor blade and filtered onto glass-fiber filters. Filters were dried, weighed, ashed, and reweighed to obtain AFDM. The proportion of epixylic biofilm was expressed as g of AFDM of biofilm per unit stick surface area. Biofilm from an additional 50 ungrazed sticks was removed in a similar manner to calculate proportional AFDM of biofilm per unit AFDM of wood.

Bacterial counts were made for grazed, ungrazed, and control sticks preserved in 7% formalin. Bacterial cells were removed by sonicating samples for 10 min, stained with 0.01% acridine orange, filtered onto 0.22- μm Nuclepore black polycarbonate filters, and examined using an Olympus BHS epifluorescence microscope at $\times 1000$. Cocci and rod-shaped cells were counted in 15 fields per slide. Total cell density was calculated by dividing the sum of cocci and rods per sample by wood surface area. Diameters and lengths of 10 cells of each bacterial form were measured per slide for mean cell biovolume calculations. Cell biovolume was converted to biomass using a conversion factor of 2.2×10^{-13} g μm^{-3} C (Bratbak 1985) and expressed as total biomass per unit surface area of wood.

Fungal biomass of biofilm scraped from portions of the grazed, ungrazed, and control sticks was estimated using ergosterol extraction methods of Newell et al. (1988), K. Suberkropp (pers. comm.), and Tank (1996). Ergosterol extraction efficiencies were $97\% \pm 2.1\%$. Ergosterol was converted to fungal biomass using a conversion factor of

5.5 mg of ergosterol per gram of fungal biomass (Gessner and Chauvet 1993).

Microbial respiration was estimated as change in dissolved oxygen (DO) over time. Eighteen-hour incubations were run for pairs of ungrazed, grazed, and control sticks in opaque 1.9×18 cm polyvinyl chloride chambers. Filtered stream water at 12.5°C was used in all chambers. Micro-Winkler DO titrations were used to measure changes in DO. Final DO concentrations were adjusted for chamber volume, blanks, incubation time, and surface area of sticks to yield O_2 consumption ($\text{mg m}^{-2} \text{h}^{-1}$).

Chl *a*, an indicator of algal standing crop, was extracted for 24 h at 0°C from 2-cm portions of grazed, ungrazed, and control sticks using buffered 90% acetone. Samples were analyzed on a Turner model TD-700 fluorometer. Concentrations were expressed as chl *a* per unit surface area of wood.

Differences in mean biofilm, microbial biomass, respiration, and chl *a* concentrations between grazed and ungrazed sticks and each half of control sticks were examined using paired *t*-tests.

Gut analyses—Wood with epixylic biofilm was fed to *T. abdominalis* and *Tallaperla* spp. for 5 weeks for gut content analyses. At days 3 and 35, foregut contents dissected from 3–6 individuals were sonicated, vacuum-filtered onto membrane filters, and slide mounted. Foregut contents of individuals collected from C53 were treated similarly. The relative area of at least 100 food particles per individual was measured using a compound microscope ($\times 400$) equipped with a video camera and digitizing tablet. Differences in arcsine-transformed proportions of food type between dates were compared for each taxon using unpaired *t*-tests.

Results

Assimilation experiments—Assimilation efficiencies for leaves (9–17%) were not significantly different (ANOVA, $p > 0.05$) among the three taxa (Fig. 1a). Assimilation efficiencies of epixylon (26–36%) were higher than those observed for leaves. *T. abdominalis* and *Tallaperla* spp. assimilated wood biofilm more efficiently than *P. gentilis* (Fig. 1a).

P. gentilis ingested leaves at a rate of nearly half its mass per day (0.47 g of AFDM leaf g of AFDM per insect d^{-1}), which was significantly faster (Dunn's multiple comparison, $p < 0.05$) than that for *Tallaperla* spp. (0.09 g of AFDM leaf g of AFDM per insect d^{-1}), or *T. abdominalis* (0.13 g of AFDM leaf g of AFDM per insect d^{-1}) (Fig. 1b). *Tallaperla* spp., *T. abdominalis*, and *P. gentilis* consumed epixylon at similar rates (0.04 – 0.07 g of AFDM epixylon g of AFDM per insect d^{-1}) (ANOVA, $p > 0.05$). Epixylon ingestion rates were always slower than ingestion rates of leaves within a taxon (Fig. 1b).

P. gentilis assimilated leaves at significantly greater rates than did *Tallaperla* spp. or *T. abdominalis* (Fig. 1c). Mean assimilation rates were greatest for *P. gentilis* consuming leaves (6.6 g of AFDM leaf g of AFDM per insect d^{-1}) and *Tallaperla* spp. consuming epixylon (3.7 g of AFDM

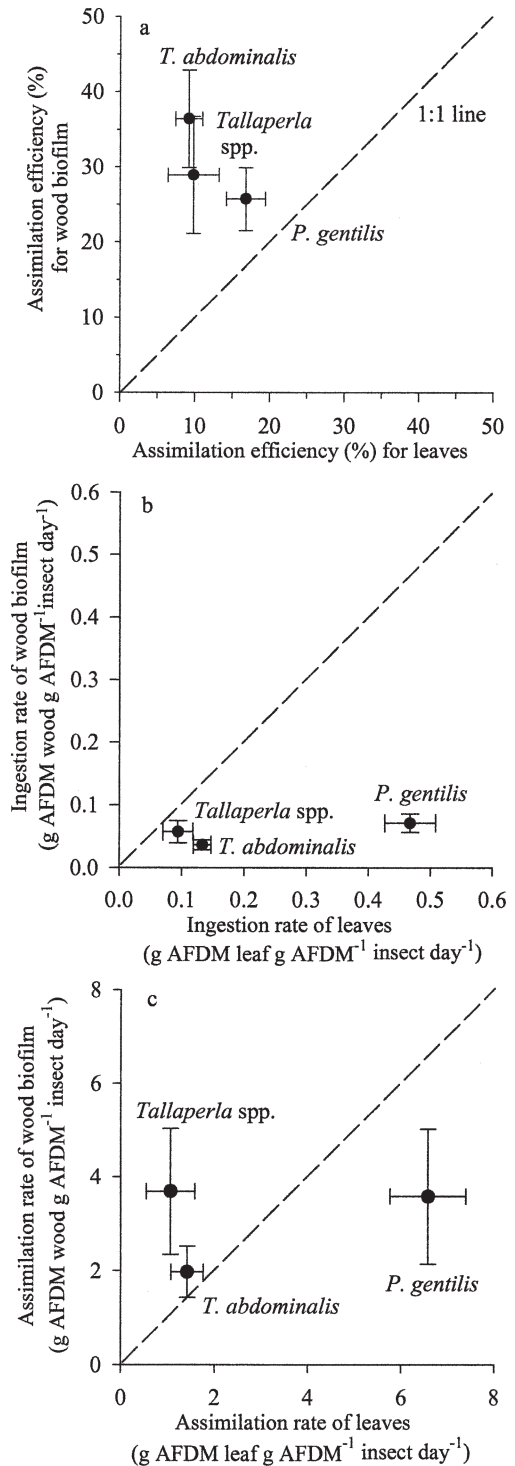


Fig. 1. (a) Assimilation efficiency, (b) ingestion rate, and (c) assimilation rate of epixylon and leaves for *Tipula abdominalis*, *Pycnopsyche gentilis*, and *Tallaperla* spp. All values represent mean \pm SE.

epixylon g of AFDM per insect d^{-1}). High leaf assimilation rates for *P. gentilis* resulted from both high assimilation efficiencies and very high ingestion rates of leaves. *T. abdominalis* assimilated leaves and epixylon at similar rates (Fig. 1c).

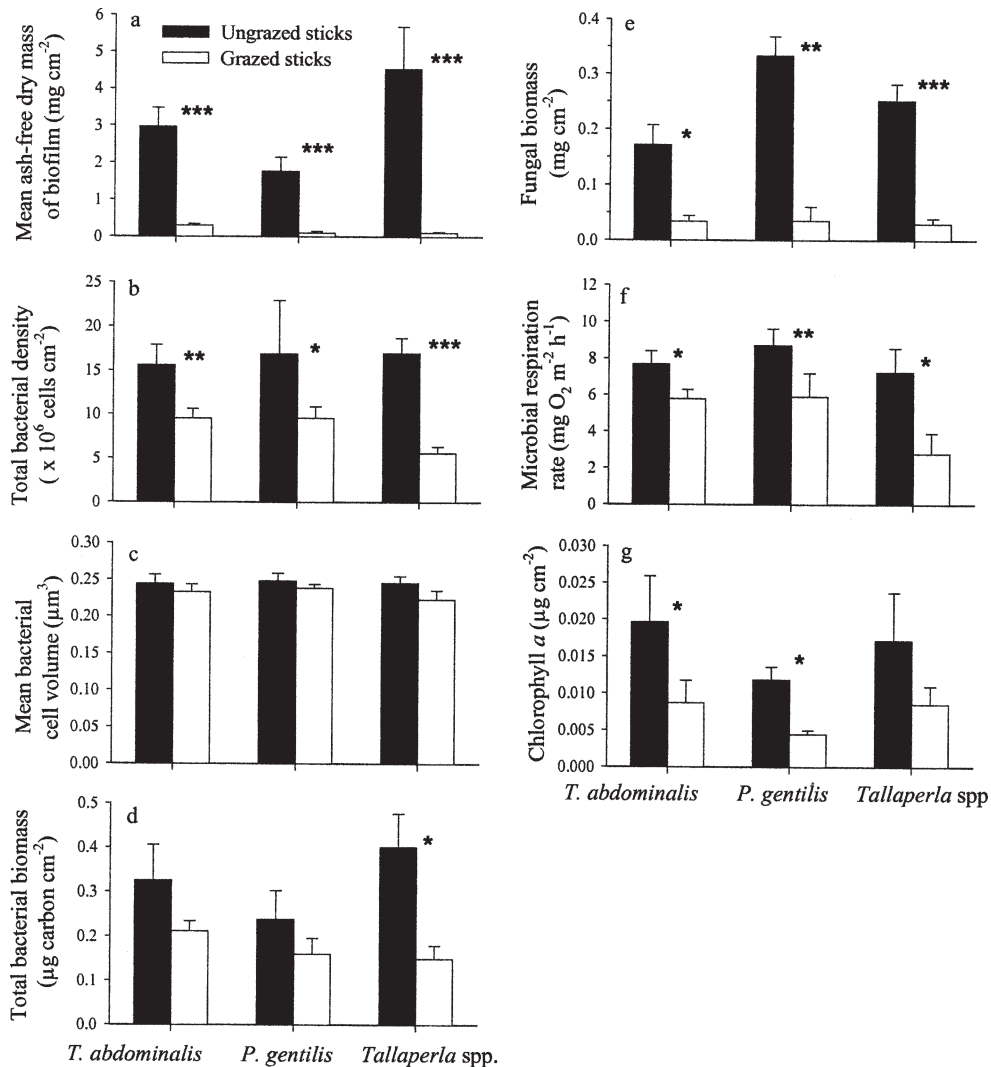


Fig. 2. (a) Ash-free dry mass of biofilm, (b) total bacterial cell density, (c) bacterial cell volume, (d) total bacterial biomass, (e) fungal biomass, (f) microbial respiration rate, and (g) chlorophyll *a* concentration of epixylon on ungrazed and grazed sticks for *Tipula abdominalis*, *Pycnopsyche gentilis*, and *Tallaperla* spp. All values represent mean \pm SE. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Epixylon grazing experiment—Visual differences between ungrazed and grazed wood were observed after only 7 d of feeding by *T. abdominalis*, *P. gentilis*, and *Tallaperla* spp. AFDM biomass of biofilm was significantly lower (paired *t*-test, $p < 0.001$) on wood grazed by the three detritivores than on ungrazed wood (Fig. 2a). There were no significant differences (paired *t*-test, $p > 0.05$) between paired halves of ungrazed control wood for AFDM biomass, or for any of the other parameters we measured in the grazing experiment. On the basis of an analysis of 50 random sticks collected from C53, we calculated that epixylic biofilm made up $5.6\% \pm 0.6\%$ of the total AFDM of small wood in C53.

Bacterial cell densities were 2–3 times lower on grazed than on ungrazed wood (Fig. 2b). We did not observe any significant difference in mean cell volume, indicating that the invertebrates were not selecting the large rod-shaped bacteria over the smaller cocci (Fig. 2c). Total bacterial biomass was significantly lower on wood consumed by

Tallaperla spp. (Fig. 2d). Fungal biomass was 5–10 times lower on grazed wood than on ungrazed wood (Fig. 2e). Microbial respiration rates for grazed wood were significantly lower than for ungrazed wood for all three taxa (Fig. 2f). Algal standing crops, measured as chl *a*, were significantly lower (paired *t*-test, $p < 0.05$) on wood grazed by *T. abdominalis* and *P. gentilis* (Fig. 2g).

Gut analyses—Typical *T. abdominalis* and *Tallaperla* spp. diets in headwater streams at Coweeta consist primarily of leaves and amorphous detritus (Fig. 3a,b). Guts of individuals that were fed only a diet of wood and epixylic biofilm contained significantly greater proportions of fungi and amorphous detritus after 3 d of feeding than after 35 d, indicating that invertebrates were selectively feeding on the biofilm layer (Table 1, Fig. 3c–f). Diatoms made up $<1\%$ of the gut contents after 3 and 25 d for both taxa. After 35 d of invertebrate grazing, little visible biofilm

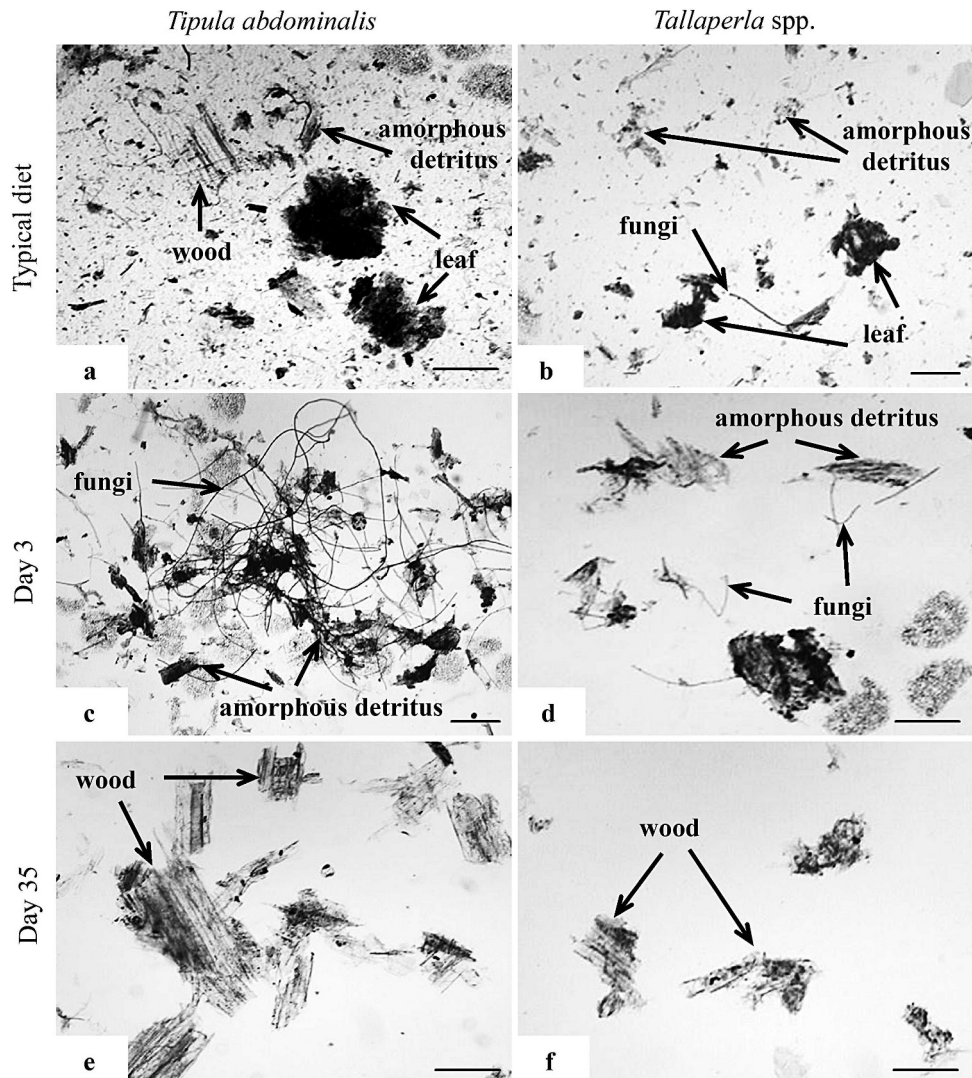


Fig. 3. Typical gut contents of (a) *Tipula abdominalis* and (b) *Tallaperla* spp. Gut contents of (c) *T. abdominalis* and (d) *Tallaperla* spp. 3 d after feeding on small wood. Gut contents of (e) *T. abdominalis* and (f) *Tallaperla* spp. 35 d after feeding on small wood. All scale bars: 0.2 mm.

remained on the wood pieces, and wood made up 92–99% of the diet of *T. abdominalis* and *Tallaperla* spp. (Table 1).

Discussion

We found that *P. gentilis* assimilated 17% of a mixed leaf diet. Hutchens et al. (1997) reported *P. gentilis* assimilation efficiencies of 7–11% for rhododendron leaves and higher rates (28–60%) for black birch and white oak leaves. Our assimilation values of 9% and 10% for *T. abdominalis* and *Tallaperla* spp., respectively, are the first reported leaf assimilation estimates for older instars of these taxa. The high assimilation efficiencies of epixylon (26–36%) by the three detritivores were unexpected. Steedman and Anderson (1985) reported assimilation efficiencies of 4–7% for *L. avara* fed wood, efficiencies that were much lower than what we found. Wood consumed by *L. avara* was highly grooved, indicating that individuals had ingested primarily wood (Steedman and Anderson 1985).

The detritivores in this study fed on the epixylic biofilm. We observed insects in the laboratory move from stick to stick, preferentially consuming the biofilm of all of the sticks before ingesting less palatable wood tissue. Our

Table 1. Mean (\pm SE) percentage composition of each food type in guts of *Tipula abdominalis* and *Tallaperla* spp. after 3 and 35 d of feeding on small wood. Sample number in parentheses. Significant differences between day 3 and 35 means for each taxon determined using unpaired *t*-test, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Food type	<i>Tipula abdominalis</i>		<i>Tallaperla</i> spp.	
	Day 3 (6)	Day 35 (3)	Day 3 (3)	Day 35 (3)
Wood	38.1 \pm 5.1***	98.6 \pm 0.2	56.7 \pm 7.1**	91.8 \pm 2.4
Amorphous detritus	50.3 \pm 5.4***	0.7 \pm 0.2	33.0 \pm 6.1*	6.7 \pm 3.1
Fungi	11.6 \pm 2.0*	0.7 \pm 0.2	10.3 \pm 1.2*	1.4 \pm 0.7

comparisons of ungrazed versus grazed wood showed that biofilm AFDM, bacterial abundance and biomass, fungal biomass, microbial respiration, and algal standing crop all declined significantly after detritivores fed on the biofilm-covered wood. The largest decline (95%) occurred for AFDM of epixylic biofilm. Our estimates of epixylic AFDM included microbes, periphyton, amorphous detritus, and the extracellular polysaccharide matrix. The microbial data suggest that declines in bacterial and fungal biomass could not entirely account for the 95% decline in epixylic AFDM on grazed wood. Other studies have suggested that extracellular polysaccharide and seston can be major components of epixylic biofilm (Golladay and Sinsabaugh 1991; Couch and Meyer 1992) and that they can be an important source of carbon for detritivores (e.g., Bärlocher and Murdoch 1989). Our gut data analyses suggest that the detritivores ingested and assimilated large portions of the amorphous detritus embedded in the polysaccharide matrix of the epixylon.

Estimates of algal standing crop on grazed and ungrazed wood were two orders of magnitude lower than other measures of epixylic chl *a* in fourth- and sixth-order streams in the U.S.A. (Golladay and Sinsabaugh 1991; Sinsabaugh et al. 1991; Couch and Meyer 1992) and in billabongs in southeastern Australia (Scholz and Boon 1993). We did not anticipate finding significant differences in chl *a* because dense shading in headwater streams at Coweeta limits periphyton colonization of epilithic substrates (Lowe et al. 1986). Despite the low periphyton standing crop, we observed significant declines in epixylic chl *a* content on wood grazed by two of the three detritivores.

Microbial biomass was dominated by fungal biomass (99%) on both grazed and ungrazed wood, a result also reported for wood and leaves (e.g., Couch and Meyer 1992; Findlay et al. 2002). Our values of fungal biomass and bacterial densities associated with ungrazed wood were similar to those of other studies (e.g., Golladay and Sinsabaugh 1991; Couch and Meyer 1992; Tank et al. 1998). The three detritivores in our study removed 50% of the total bacteria from wood surfaces, a value similar to the 58% reduction in bacterial density on leaves by copepods (Perlmutter and Meyer 1991), showing that these detritivores were effective at removing portions of the microbial community from the small wood.

Detritivore ingestion rates were 1.6–6.6× greater for leaves than wood biofilm, providing support for the idea that detritivores may compensate for lower-quality foods by consuming them at higher rates. However, food quality and palatability can affect consumption differentially (e.g., Waldbauer 1968; Iverson 1974; Golladay et al. 1983).

Assimilation rate, which may be the best way of interpreting an organism's ability to utilize food resources, takes into account physiological capabilities to assimilate a food type and ingestion rates. Our data showed that *Tallaperla* spp. and *T. abdominalis* utilized epixylic biofilms more efficiently than leaves, whereas *P. gentilis* was better able to use leaves. Studies of mouthpart morphology of shredders have described some shredders as having mouthparts consistent with that required to function as scrapers. Tank (1996) described the labrum and mandibles

of *Tallaperla* spp. as being “scoop-like” structures covered with setae, which allowed it to scrape biofilm components from wood surfaces. *Tipula sacra* collected from beaver ponds of Alberta, Canada ingest benthic algal particles by using its mandibles to scrape surfaces (Hall and Pritchard 1975). Setae on mouthparts also help to remove and “brush” periphyton into the mouth. Similar feeding mechanisms probably allow *T. abdominalis* and *P. gentilis* to behave like scrapers when food resources like leaf detritus are not available.

Differences in the physical structure of wood and leaf detritus may also influence assimilation rates and invertebrate utilization of these resources. Wood supports greater microbial biomass and respiration than leaves (Golladay and Sinsabaugh 1991; Tank et al. 1993; Findlay et al. 2002). Slowly decaying wood is a long-lasting carbon source, which can be recolonized by microbes after grazing by invertebrates (Golladay and Sinsabaugh 1991; Hax and Golladay 1993; Tank 1996). In contrast to wood, leaves fragment much more quickly than wood and are consumed in their entirety. The presence of wood with its highly assimilable epixylon can serve as an alternative food resource for detritivores after leaf detritus breaks down and becomes scarce in forested headwater streams. Small wood (≤ 10 mm in diameter) standing crop in C53 over a 7-yr period averaged $1,748 \pm 232$ g AFDM m^{-2} (Wallace et al. 2000). By combining average small wood standing crop estimates in C53 and our data that epixylic biofilm made up 5.6% of total AFDM, we calculate that wood biofilm standing crop averages 98 g m^{-2} AFDM in C53. Compared to a mean leaf detritus standing crop of 204 g m^{-2} AFDM for C53 (Wallace et al. 1999), epixylic biofilm is a substantial source of assimilable carbon in this forested headwater stream.

Our data showed that invertebrates ingest and assimilate epixylon, and that assimilation efficiencies of epixylic biofilm can be considerably higher than those for leaves for some detritivore species. Additionally, small woody debris with its associated biofilm may be an important food resource for detritivores in instances where leaf detritus is not available (e.g., late summer, or disturbed riparian habitats). This study lends support for maintaining small woody debris inputs along with inputs of leaf detritus to small forested streams to maximize benthic diversity and productivity.

References

- ALLAN, J. D. 1995. Stream ecology. Kluwer.
- ANDERSON, N. H., AND K. W. CUMMINS. 1979. Influence of diet on the life histories of aquatic insects. *J. Fish. Res. Board Can.* **36**: 335–342.
- BÄRLOCHER, F., AND B. KENDRICK. 1975. Assimilation efficiency of *Gammarus pseudolimnaeus* (Amphipoda) feeding on fungal mycelium or autumn-shed leaves. *Oikos* **26**: 55–59.
- , AND J. H. MURDOCH. 1989. Hyporheic biofilms— a potential food source for interstitial animals. *Hydrobiologia* **184**: 61–67.
- BENKE, A. C., AND J. B. WALLACE. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* **61**: 108–118.

- BRATBAK, G. 1985. Bacterial biovolume and biomass estimations. *Appl. Environ. Microbiol.* **49**: 1488–1493.
- COUCH, C. A., AND J. L. MEYER. 1992. Development and composition of the epixylic biofilm in a blackwater river. *Freshw. Biol.* **27**: 43–51.
- CUFFNEY, T. F., J. B. WALLACE, AND G. J. LUGTHART. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. *Freshw. Biol.* **23**: 281–299.
- FINDLAY, S., AND OTHERS. 2002. A cross-system comparison of bacterial and fungal biomass in detritus pools of headwater streams. *Microb. Ecol.* **43**: 55–66.
- GESSNER, M. O., AND E. CHAUVET. 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. *Appl. Environ. Microbiol.* **59**: 502–507.
- GOLLADAY, S. W., AND R. L. SINSABAUGH. 1991. Biofilm development on leaf and wood surfaces in a boreal river. *Freshw. Biol.* **25**: 437–450.
- , J. R. WEBSTER, AND E. F. BENFIELD. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: Leaf species and conditioning time. *Holarct. Ecol.* **6**: 157–162.
- HALL, H. A., AND G. PRITCHARD. 1975. The food of larvae of *Tipula sacra* Alexander in a series of abandoned beaver ponds (Diptera: Tipulidae). *J. Anim. Ecol.* **44**: 55–66.
- HALL, R. O., J. B. WALLACE, AND S. L. EGGERT. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* **81**: 3445–3463.
- HAX, C. L., AND S. W. GOLLADAY. 1993. Macroinvertebrate colonization and biofilm development on leaves and wood in a boreal river. *Freshw. Biol.* **29**: 79–87.
- HERBST, G. N. 1982. Effects of leaf type on the consumption rates of aquatic detritivores. *Hydrobiologia* **89**: 77–87.
- HUTCHENS, J. J., E. F. BENFIELD, AND J. R. WEBSTER. 1997. Diet and growth of a leaf-shredding caddisfly in southern Appalachian streams of contrasting disturbance history. *Hydrobiologia* **346**: 193–201.
- IVERSEN, T. M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. *Oikos* **25**: 278–282.
- LEDGER, M. E., AND M. J. WINTERBOURN. 2000. Growth of New Zealand stream insect larvae in relation to food type. *Arch. Hydrobiol.* **149**: 353–364.
- LOCK, M. A., R. R. WALLACE, J. W. COSTERTON, R. M. VENTULLO, AND S. E. CHARLTON. 1984. River epilithon: Toward a structural-functional model. *Oikos* **42**: 10–22.
- LOWE, R. L., S. W. GOLLADAY, AND J. R. WEBSTER. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. *J. N. Am. Benthol. Soc.* **5**: 221–229.
- MARTIN, M. M., J. S. MARTIN, J. J. KUKOR, AND R. W. MERRITT. 1980. The digestion of protein and carbohydrate by the stream detritivore, *Tipula abdominalis* (Diptera: Tipulidae). *Oecologia* **46**: 360–364.
- NEWELL, S. Y., T. L. ARSUFFI, AND R. D. FALLON. 1988. Fundamental procedures for determining ergosterol content of decaying plant material by liquid chromatography. *Appl. Environ. Microbiol.* **54**: 1876–1879.
- PERLMUTTER, D. G., AND J. L. MEYER. 1991. The impact of a stream-dwelling harpacticoid copepod upon detritally associated bacteria. *Ecology* **72**: 2170–2180.
- SCHOLZ, O., AND P. I. BOON. 1993. Biofilm development and extracellular enzyme activities on wood in billabongs of south-eastern Australia. *Freshw. Biol.* **30**: 359–368.
- SINSABAUGH, R. L., S. W. GOLLADAY, AND A. E. LINKINS. 1991. Comparison of epilithic and epixylic biofilm development in a boreal river. *Freshw. Biol.* **25**: 179–187.
- SLANSKY, F., AND J. M. SCRIBER. 1982. Selected bibliography and summary of quantitative food utilization by immature insects. *Bull. Entomol. Soc. Am.* **28**: 43–55.
- STEEDMAN, R. J., AND N. H. ANDERSON. 1985. Life history and ecological role of the xylophagous aquatic beetle, *Lara avara* LeConte (Dryopoidea: Elmidae). *Freshw. Biol.* **15**: 535–546.
- TANK, J. L. 1996. Microbial activity on wood in streams: Exploring abiotic and biotic factors affecting the structure and function of wood biofilms. Ph.D. thesis, Virginia Polytechnic Institute and State Univ.
- , J. R. WEBSTER, AND E. F. BENFIELD. 1993. Microbial respiration on decaying leaves and sticks in a southern Appalachian stream. *J. N. Am. Benthol. Soc.* **12**: 394–405.
- , ———, AND ———. 1998. Effect of leaf litter exclusion on microbial enzyme activity associated with wood biofilms in streams. *J. N. Am. Benthol. Soc.* **17**: 95–103.
- WALDBAUER, G. P. 1968. The consumption and utilization of food by insects. *Adv. Insect Physiol.* **5**: 229–282.
- WALLACE, J. B., S. L. EGGERT, J. L. MEYER, AND J. R. WEBSTER. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecol. Monogr.* **69**: 409–442.
- , J. R. WEBSTER, S. L. EGGERT, AND J. L. MEYER. 2000. Small wood dynamics in a headwater stream. *Verh. Int. Ver. Theoret. Angew. Limnol.* **27**: 1361–1365.
- WEBSTER, J. R., E. F. BENFIELD, T. P. EHRLMAN, M. A. SCHAEFFER, J. L. TANK, J. J. HUTCHENS, AND D. J. D'ANGELO. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshw. Biol.* **41**: 687–705.
- , M. E. GURTZ, J. J. HAINS, J. L. MEYER, W. T. SWANK, J. B. WAIDE, AND J. B. WALLACE. 1983. Stability of stream ecosystems, p. 355–395. *In* J. R. Barnes and G. W. Minshall [eds.], *Stream ecology*. Plenum.

Received: 19 April 2006

Accepted: 18 December 2006

Amended: 4 January 2007