

Effects of leaf type on the consumption rates of aquatic detritivores

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Abstract

Silver maple (*Acer saccharinum*) and cottonwood (*Populus deltoides*) leaves were incubated in cages excluding (controls) or containing (experimental) detritivores for periods of up to 123 days. Experimental cages contained either the crane fly larvae *Tipula abdominalis*, the amphipod *Gammarus pseudolimnaeus* or the caddisfly *Pycnopsyche guttifer*. Differences in daily consumption between leaf types and among species were compared.

In control cages 20–23% of initial leaf weight was lost by leaching and 8–10% by microbial processes. *T. abdominalis* and *P. guttifer* consumed more silver maple than cottonwood during feeding intervals; no significant differences were observed for *G. pseudolimnaeus*. Invertebrate consumption of cottonwood leaves significantly increased with time; no significant differences in consumption of silver maple leaves with time were observed. Potential factors influencing the observed feeding pattern between leaf species are discussed.

Introduction

The importance of allochthonous detritus as an energy source to lotic communities has long been recognized (Teal 1957; Nelson & Scott 1962; Minshall 1967; Tilly 1968; Fisher & Likens 1973). In recent years, the focus of numerous stream investigations has been the fate of allochthonous materials, principally leaves, entering streams (Kaushik & Hynes 1971; Petersen & Cummins 1974; Anderson & Sedell 1979; Cummins & Klug 1979).

Most estimates of microbial or macroinvertebrate consumption rates in streams, have been derived indirectly (Tilly 1968; Fisher & Likens 1973) or through laboratory observations (Cummins *et al.* 1973; Anderson & Grafius 1975); direct measurements *in situ* have been complicated by the inability to separate the effects of micro and macroconsumers (Iversen 1975). The interrelation-

ships of multiple factors, including temperature (Heiman & Knight 1975; Sweeney & Schnack 1977), food availability (Anderson & Lehmkuhl 1968), food quality and chemical composition (Bärlocher & Kendrick 1973; Mackay & Kalff 1973; Ward & Cummins 1979), life history stages (Howard 1976) and presence of competitors or predators (Cummins *et al.* 1973; Stein & Magnuson 1976) further complicate accurate determinations of consumption rates.

For almost 20 years terrestrial ecologists have used bags of different mesh sizes in attempting to estimate the relative contributions of macroinvertebrates and microconsumers (Witkamp & Olson 1963; Heath *et al.* 1966; Harding & Stuttard 1974; Crossley 1977). More recently these techniques have been applied to stream ecosystems (Mathews & Kowalczewski 1969; Hart & Howmiller 1975; Iversen 1975). Previous mesh bag studies have characteristically allowed the differential coloniza-

tion of invertebrates. In the current study a different approach was attempted; cages were incubated with predetermined numbers of consumer organisms and other animals were excluded. As a result, potential problems of predation, differential immigration and emigration were reduced. Additionally, by enclosing the experimental system within cages, the potential effects of current variation upon leaf decomposition were lessened.

The principal objective of this study is to accurately determine (in the field) the effect of leaf type on invertebrate consumption. Consumption is here defined as the mass of food material (leaves) lost as a result of the feeding activities of consumer organisms. Long term direct measurements (>30 days) *in situ* are undertaken in order to integrate potential effects of temperature and life history stages that can bias measurements of shorter duration (1–2 days).

Preliminary laboratory feeding experiments and literature values for invertebrate feeding preferences suggest that the leaf species chosen for study (*Acer saccharinum*, silver maple and *Populus deltoides*, cottonwood) encompass the range of leaf palatabilities available among major tree species in the lowland forest through which Roxbury Creek (the study site) flows. Therefore, consumption estimates derived in this study will provide an estimate of the significance of leaf type on overall invertebrate consumption. Comparison of leaf weight losses in cages either containing invertebrate consumers (experimental) or excluding them (controls) will also enable to estimation of the proportion of leaf material processed by the microflora (bacteria and fungi).

Background

Roxbury Creek is a small first order stream which arises in northwestern Dane County (T9 N, R6 E, S13) and enters the Wisconsin River (fifth or sixth order stream) just west of Sauk City, Wisconsin, U.S.A. It flows for approximately 11 km, intermittently in the upper 9.7 km and permanently only in the lower 1.3 km, where it is fed by numerous springs. The lower portion of the permanent stream, where Roxbury Creek enters a lowland forest (Mazomanie Wildlife Area), was chosen for study. Detailed descriptions of the area

have already been reported (Mendelson 1972; Herbst 1979).

Within the study area, Roxbury Creek is a shallow, low gradient stream, which consists of a series of runs and pools with irregular meanders. Depths in the runs vary from 10–40 cm. while pools attain maximum depths of 1.5 m. Current velocity is generally less than 30 cm/s, although velocities of up to 52 cm/s have been recorded during flooding (Mendelson 1972). Average stream width is approximately 3 m.

Owing to the presence of springs, the major portion of lower Roxbury Creek remains ice free during the winter. Water temperature varies annually between 0° and 19 °C. Water temperatures begin to fall in late August, and irregularly decrease until about the middle of December. From then until the middle of February water temperatures generally remain below 4 °C. Water temperature begins to increase from mid February to mid March and rapidly rises in the spring and summer months.

Roxbury Creek is a hard water stream (specific conductance of 540 Mmhos), having a high alkalinity (290–320 ppm CaCO₃) and a slightly basic pH (7.8). Specific chemical data are found in Poff & Threinen (1962).

Roxbury Creek flows through a typical mid-western American lowland forest. Dominant tree species include silver maple (*Acer saccharinum*), American elm (*Ulmus americana*), cottonwood (*Populus deltoides*) and green ash (*Fraxinus pennsylvanica*). Together they comprise 85% of trees present (based on 40 1/40 acre circular quadrat measurements). The forest surrounding the stream is a 'mature' lowland forest as indicated by species composition and size of the trees (Ware 1955). Pioneer species such as cottonwood and river birch (*Betula nigra*) comprise less than 15% of the trees and are all mature. In contrast, 'climax' species such as silver maple and American elm comprise greater than 75% of the trees present, are younger and exhibit new reproduction.

The invertebrate fauna of Roxbury Creek is rich, with over 145 taxa having been collected (Mendelson 1975; Herbst 1979). All major aquatic insect groups except stoneflies (Order Plecoptera) are represented. During the fall and winter the invertebrate fauna is numerically dominated by *Micropsecta* (fam. Chironomidae, tribe Tanytarsini) and by *Brillia* and *Cricotopus* (fam. Chi-

ronomidae, subfamily Orthocladinae).

During the early autumn, large detritivores include the crane fly larvae, *Tipula abdominalis*; the amphipod, *Gammarus pseudolimnaeus*; and the aquatic isopod, *Asellus racovitzai*. They are less abundant than chironomids but owing to their relatively large sizes comprise approximately 20 times more biomass and represent between 85 and 95% of total community biomass during early autumn. All three species are known to ingest leaf detritus (Minshall 1967; Vannote 1970; Kaushik & Hynes 1971; Cummins *et al.* 1973; and Bärlocher & Kendrick 1975a); however, *A. racovitzai* appears to feed primarily on fine particles. (Herbst 1979).

The limnephilid caddisflies *Pycnopsyche guttifer* and *Platycentropus radiatus* appear in November samples and grow rapidly through the winter period. A third limnephilid, *Hydatophylax argus*, is also present but is not abundant. Both *Pycnopsyche* and *Platycentropus* are known to consume large amounts of leaf detritus (Cummins 1964, Mackey & Kalff 1973; Wiggins 1978). *Hydatophylax* primarily consumes wood and bark (Anderson *et al.* 1978, personal observation).

The aforementioned information indicates that four taxa (*Tipula*, *Gammarus*, *Pycnopsyche* and *Platycentropus*) are the principal processors of large particle leaf material during the autumn and winter months in Roxbury Creek; the first three taxa are the object of further study in this paper.

Detailed life history information for *Pycnopsyche guttifer* can be found in Cummins (1964) and Howard (1976); studies on other closely related species can be found in Mackay & Kalff (1973). *Gammarus pseudolimnaeus* has been studied in Ontario (Hynes & Harper 1972) and most recently in southern Wisconsin (Miller 1978). Detailed life history information for *Tipula abdominalis* is lacking, although feeding and general life history observations have been made (Rogers 1933; Vannote 1970; Cummins *et al.* 1973); the ecology of *Tipula sacra* in abandoned beaver ponds has also been studied (Pritchard & Hall 1971; Hall & Pritchard 1975).

Methods

Determinations of leaf consumption were made *in situ* using cages filled with preweighed leaves and

known numbers of leaf consuming invertebrates. Cubical cages (10 cm × 10 cm × 10 cm) were constructed of sheet metal, open on the upstream and downstream sides. The open ends were covered by 200 μm Nitex mesh secured to a lip surrounding the openings with rubber bands and Duco cement. Each cage was secured flush to the stream bottom with metal rods which passed through a pair of perforated metal tabs spot welded to the cage bottom. In the stream, cages were oriented with the mesh sides at 45° angles to the current in order to minimize clogging of the Nitex mesh with leaves or other debris.

Leaves that were to be incubated in cages were picked from a single silver maple (*Acer saccharinum*) or from a clump of cottonwood (*Populus deltoides*) shortly before abscission. They were dried for 1 week at 60 °C and weighed, then placed in cages. A known weight of 5 ± 0.1 g of dry leaves was placed in each cage.

Consumption of two leaf species, silver maple and cottonwood, by three invertebrates is considered over three time intervals. Consumer invertebrates were the crane fly, *Tipula abdominalis*; the amphipod *Gammarus pseudolimnaeus*; and the caddisfly, *Pycnopsyche guttifer*. Only a single initial density for each species was utilized (Table 1). In the field, freshly collected invertebrates of the appropriate taxon and number were added to the cages just prior to placement in Roxbury Creek. All invertebrates were collected with a D-frame net; care was exercised in handling animals and an attempt was made within each taxon to choose invertebrates of a uniform size. All cages were placed between 12 and 14 October 1977; however, owing to the late hatching of *Pycnopsyche* larvae (November), these larvae were placed in already-incubating cages in early December.

Removals of experimental cages correspond to the times thought to be required for 'full conditioning' (31 days), onset of winter water temperatures (69 days), and the end of the 90 day 'processing period' (123 days) (Petersen & Cummins 1974). Removal of control cages after 6 days incubation is sufficient to include the time required for complete leaching loss (Kaushik & Hynes 1971; Petersen & Cummins 1974).

Since cages were removed from the stream at periods when the ambient air temperature was well below freezing, the remaining leaf material and

Table 1. Experimental design for cage consumption experiments October 1977 – February 1978.

Leaf type	Consumer species	Number of cages	Initial cage density	Incubation (days)	Number removed at the end of each period
<i>Acer</i>	Control	25	0	6, 31, 69, 123	5*
<i>Acer</i>	<i>Tipula</i>	15	5	31, 69, 123	5
<i>Acer</i>	<i>Gammarus</i>	15	25	31, 69, 123	5
<i>Acer</i>	<i>Pycnopsyche</i>	10	2	123**	10
<i>Populus</i>	Control	25	0	6, 31, 69, 123	5*
<i>Populus</i>	<i>Tipula</i>	15	5	31, 69, 123	5
<i>Populus</i>	<i>Gammarus</i>	15	25	31, 69, 123	5
<i>Populus</i>	<i>Pycnopsyche</i>	10	2	123**	10

* During the final period 10 control cages were removed.

** Animals were added at day 56.

organisms were frozen in the field. In the laboratory the cages were opened and the contents emptied into gallon jars and washed in distilled water. Remaining leaf material was removed, dried at 80 °C for a minimum of 48 h and weighed. Invertebrates were also gently washed, dried and weighed on a Cahn electrobalance. The remaining fine particles and any invertebrate 'contaminants', e.g. chironomids, microcrustaceans, were filtered through 200 μm mesh and preserved in 70% ethanol. Washings from 2–5 cages of a single leaf type for a single interval were combined; however, control cages were kept separate from experimental cages. Random subsamples of these specimens were selected and identified.

The number of animals surviving to the end of the interval was made by inference since all invertebrates were quickly frozen at removal; vitality was judged from the general appearance of an individual, i.e., size, color, turgidity and presence of appendages.

Invertebrate processing was expressed as mg dry wt. consumed/individual/day within feeding intervals. Each time interval was considered sequentially using the following formula:

$$C_{ij} = \frac{W_o - W_f - \bar{W}_L - \sum_1^{j-1} \bar{C}_i}{(N_{fij} + N_{fi(j-1)})/2} \quad (1)$$

where:

C = consumption
i = species
j = interval

W_o = initial dry wt. of leaves

W_f = final dry wt. of leaves

\bar{W}_L = mean non-consumption losses from control cages

\bar{C}_i = mean consumption of species i

N_f = final number of experimental animals/cage determined from all cages of the same leaf type

N_f = final number of experimental animals/cage.

The above formula results in consumption estimates per feeding interval in which the mean consumption and invertebrate survivorship of the j-1 interval is used as input for determination of the consumption within the j interval. This analysis minimizes the influence of consumption of animals which have died within the interval being considered and accounts for losses from other than invertebrate feeding (control cage losses). During the first interval the initial invertebrate densities are used for the $\bar{N}_{fi(j-1)}$ term.

In a similar manner the Consumptive Index (Waldbauer 1968) was calculated using the following formula:

$$K_{ij} = \frac{C_{ij}}{(\bar{B}_{i(j-1)} + B_{ij})/2} \quad (2)$$

where:

K = consumptive index

C = consumption determined from equation (1)

- \bar{B} = mean individual dry weight calculated from all cages containing the same leaf type and determined at the end of an incubation period
- B = mean individual dry weight calculated from a single cage and determined at the end of an incubation period.

For the first interval, the mean dry weights determined from October 1977 quantitative samples (Herbst 1979) serve as the $\bar{B}_{i(j-1)}$ term.

Consumption rates were compared between leaf types and among the three large particle consumers during each interval. These rates were then compared to known literature values.

Results

Decomposition in the absence of macroinvertebrates

Weight losses of silver maple and cottonwood leaves in control cages were initially very rapid; however, after 69 days of incubation loss rates approached 0 (Fig. 1 and 2). After 123 days, silver maple had lost 35% of its initial weight while cottonwood had lost 32%. Weight gains during the final interval for both cottonwood and silver maple leaves were insignificant (Dunn's Multiple Comparison Test; $p > 0.05$). Assuming that leaching of soluble organic materials is complete after 6 days and accounts for all weight loss during this period, between 23 and 24% of the initial leaf weight of both leaf species is lost by leaching. The remaining 8 and 10% of the weight loss over the 123 day period is thought to be due to microbial processes. Very little difference in the processing rates of silver maple and cottonwood leaves in control cages was found; the only significant difference occurred at 31 days of incubation (Mann-Whitney U test; $p < 0.01$).

Colonization

Several invertebrate taxa penetrated the Nitex mesh and colonized the cages. These included the cyclopoid copepod *Cyclops vernalis*; tubificid worms, the net spinning caddisflies *Cheumatopsyche* and *Hydropsyche*; dance fly larvae (Empididae); ostracods; and chironomids; all but the chironomids are represented by only a few individuals. Observed densities of chironomids were

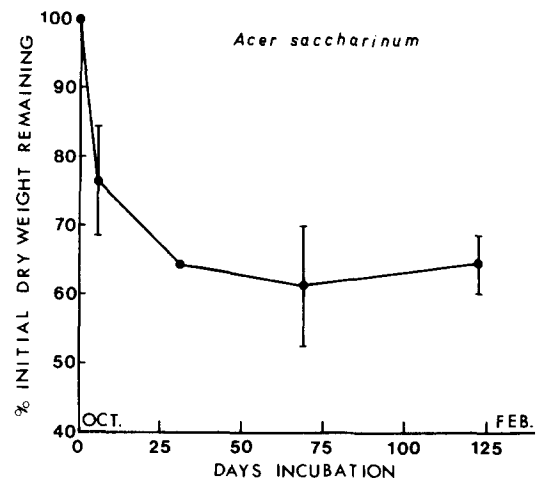


Fig. 1. Percentage of initial dry weight remaining in control cages containing *Acer saccharinum* (silver maple) leaves during 1977-1978. Error bars represent 95% confidence limits.

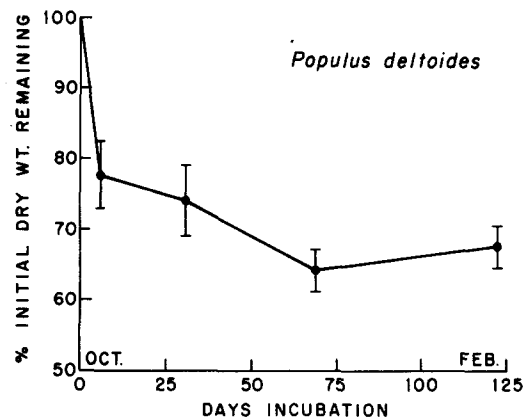


Fig. 2. Percentage of initial dry weight remaining in control cages containing *Populus deltoides* (cottonwood) leaves during 1977-1978. Error bars represent 95% confidence limits.

variable (Table 2) (coefficient of variation between 37 and 82%). No differences in colonization were observed between cages containing maple and cottonwood leaves (Mann-Whitney U tests; $p > 0.05$). Colonization increased with time ($r^2 = 0.99$ for silver maple cages; $r^2 = 0.98$ for cottonwood cages) (Fig. 3).

The chironomids colonizing the cages were small (1-2 mm) and were principally orthoclads (*Corynoneura* and *Orthocladus*). This is consistent with the known principal components of chironomid drift in Roxbury Creek (Mendelson 1972). Both genera are characterized as collector-gatherers and are thought to feed upon diatoms, filamentous algae

Table 2. Chironomid colonization of stream cages during the fall-winter of 1977-1978.

Leaf species	Time incubated (days)	Number of samples	Mean number of chironomids	Standard deviation
<i>Acer</i>	6	3	8	1.4
<i>Acer</i>	31	6	34	26.7
<i>Acer</i>	69	7	100	37.0
<i>Acer</i>	123	7	203	101.3
<i>Populus</i>	6	3	7	3.2
<i>Populus</i>	31	3	37	30.0
<i>Populus</i>	69	7	72	50.8
<i>Populus</i>	123	4	170	80.8

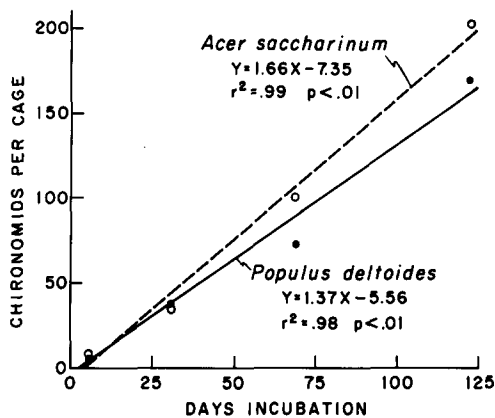


Fig. 3. Chironomid density in cages containing *Acer saccharinum* (silver maple) and *Populus deltoides* (cottonwood) compared to length of incubation during the autumn and winter of 1977-1978.

and fine particle detritus (Merritt & Cummins 1978). Mean dry weight of chironomids during the last sample period ($N = 25$) was 0.11 ± 0.05 mg.

Even assuming maximum density (203 chironomids per cage) and 100% feeding upon whole leaf material chironomid consumption is negligible. Assuming an assimilation efficiency of 10% (Ward & Cummins 1979) the quantity of leaf material necessary for a mean individual weight of 0.11 mg for 203 chironomids (maximum density) is only 220 mg per cage. This represents only 4% of initial dry weight. Since cage densities reached 203 individuals only during the final sampling interval and since the chironomids were most probably not directly feeding upon the leaf material, chironomid consumption is undoubtedly much less than 4% of the initial leaf dry weight. Consequently, the effects of chironomid consumption is not considered further

in calculations of consumption for *Tipula*, *Gammarus* and *Pycnopsyche*.

Comparative consumption of silver maple and cottonwood

Experimental cages containing *Tipula* or *Gammarus* were removed after 31, 69 and 123 day incubation periods. This corresponds to sequential feeding intervals of 31, 38 and 54 days. A single 54 day feeding interval was utilized for *Pycnopsyche*, since they were placed in the experimental cages in December. Initial density of *Tipula* was equal to one *Tipula* per gram of leaf; the density of *Gammarus* was equal to 5 per gram of leaf; and the density of *Pycnopsyche* was equal to 0.4 per gram of leaf (Tables 3 and 4).

The results from the experimental silver maple cages indicate no significant differences in consumption among feeding intervals for both *Tipula* and *Gammarus* (Kruskal Wallis Test; $p > 0.05$). In contrast, cages containing cottonwood leaves exhibit increased consumption during the final interval for both *Tipula* and *Gammarus* (Kruskal Wallis Test; $p < 0.05$). Similarly, the Consumptive Index for *Tipula* and *Gammarus* consumption of cottonwood is greatest during the final interval (Kruskal Wallis Tests; $p < 0.05$).

Comparison of maple and cottonwood consumption indicates that for *Tipula*, the consumption rate of maple exceeds the consumption rate of cottonwood after 31 days (Man-Whitney U Test; $p < 0.05$) and 69 days incubation (Mann-Whitney U Test; $p < 0.10$). There is no significant difference in consumption between maple and cottonwood incubated for 123 days. There are also no differences

Table 3. Consumption, Consumptive Index and mean survivorship for invertebrates incubated in cages containing silver maple leaves (*Acer saccharinum*). Each of three successive feeding intervals are reported: Interval 1 = Oct. - Nov.; Interval 2 = Nov. - Dec; Interval 3 = Dec. - Feb.

Consumer	Interval number	Length of feeding interval (days)	Number of cages	Mean consumption mg. dry wt./ animal/day	Mean consumptive Index mg./dry wt./ mg. animal/day	Mean % surviving
<i>Tipula</i>	1	31	5	3.30	0.189	52
	2	38	5	3.91	0.097	84
	3	54	4	1.63	0.031	65
<i>Gammarus</i>	1	31	3	.37	0.059	100
	2	38	5	.05	0.002	75
	3	54	5	.89	0.107	20
<i>Pycnopsyche</i>	3	54	9	21.40	2.36	72

Table 4. Consumption, Consumptive Index, and mean survivorship for invertebrates incubated in cages containing cottonwood leaves (*Populus deltoides*). Each of three successive feeding intervals are reported: Interval 1 = Oct. - Nov.; Interval 2 = Nov. - Dec; Interval 3 = Dec. - Feb.

Consumer	Interval number	Length of feeding interval (days)	Number of cages	Consumption mg. dry wt./ animal/day	Consumptive Index mg./dry wt./ mg. animal/day	Mean % survival
<i>Tipula</i>	1	31	5	0.22	-0.013	80
	2	38	5	0.64	0.040	84
	3	54	5	3.46	0.108	56
<i>Gammarus</i>	1	31	5	0.55	0.093	87
	2	38	4	-0.12	0.008	42
	3	54	5	2.09	0.595	27
<i>Pycnopsyche</i>	3	54	10	12.17	2.05	90

between *Gammarus* consumption of maple and cottonwood for all intervals.

The consumption rate of both maple and cottonwood by *Pycnopsyche* is significantly greater than for both *Tipula* and *Gammarus* (Kruskal Wallis Test; $p < 0.05$). Over the observed feeding interval *Pycnopsyche* consumption of maple exceeded consumption of cottonwood (Mann-Whitney U Test; $p < 0.01$).

Discussion

The consumption per animal and Consumption Index (consumption per biomass of animal) for both *Tipula* and *Gammarus* fall within the range of values of other workers (Table 5). Unfortunately, differences in methodologies, food sources and temperatures among studies makes comparisons difficult. Consumption rates and Consumptive In-

dex values determined in this study for *Pycnopsyche* are higher than reported in most studies of Trichoptera. However, in preliminary feeding trials reported by Anderson & Grafius (1975) *Lepidostoma unicolor* consumed more than 3 times its body weight per day. In my laboratory experiments *Pycnopsyche* feeding rates have been estimated to be 2-4 times that of *Tipula* and *Gammarus* (Herbst 1980). Consumption of small leaf discs (~1 cm²) by *Pycnopsyche* in these experiments resulted in 9-18% of animal wt being consumed per 24 hour feeding trial. However, leaf discs were often almost completely consumed before the end of the experiment, thus resulting in artificially low values.

In this study consumption was defined broadly as consumer induced leaf weight loss. As a result it includes both assimilated and non-assimilated leaf material. In either case the material consumed is removed from the large particle organic matter pool. Since *Pycnopsyche* is a 'sloppy' eater this

Table 5. Comparisons of consumption and Consumptive Index results of this and other studies. Unless otherwise indicated, consumption is expressed as mg. dry wt./ind./day and consumptive index as mg. dry wt./mg. ind. dry wt./day. 1 = weighted mean of 3 feeding intervals, present study; 2 = consumption/h; 3 = includes ranges for different instars; 4 = estimated from regression equation.

Taxa	Food type	Feeding time (days)	t °C.	Method	Consumption	Consumptive Index	References
<i>Tipula</i>							
<i>T. abdominalis</i>	Silver maple	123	0.1-10	Gravimetric	2.73 ¹	0.091	Present study
<i>T. abdominalis</i>	Cottonwood	123	0.1-10	Gravimetric	1.66 ¹	0.056	Present study
<i>T. abdominalis</i>	Mixed leaves	365	-	Gravimetric	1.15	0.041	Vannote (1970)
<i>T. spp.</i>	Hickory	106	0.1-20	Gravimetric	3.5	0.157	Cummins <i>et al.</i> (1973)
<i>T. spp.</i>	Hickory	51	0.1-20	Gravimetric	4.1	0.187	Cummins <i>et al.</i> (1973)
<i>T. spp.</i>	Hickory	-	11	Gravimetric	-	0.088	Cummins <i>et al.</i> (1973)
<i>T. spp.</i>	Oak	-	9	Gravimetric	-	0.030	Cummins <i>et al.</i> (1973)
<i>T. spp.</i>	Hickory	-	10	Gravimetric	-	0.187	Cummins <i>et al.</i> (1973)
<i>Pycnopsyche</i>							
<i>P. guttifer</i>	Silver maple	54	0.1-5	Gravimetric	21.40	2.36	Present study
<i>P. guttifer</i>	Cottonwood	54	0.1-5	Gravimetric	12.17	2.05	Present study
<i>P. guttifer</i>	Hickory	75	0.1-20	Gravimetric	2.18	0.332	Cummins <i>et al.</i> (1973)
<i>P. guttifer</i>	Silver maple	2.5	12	Tracer	-	2.34	Howard (1976)
<i>P. lepida</i>	Elm, alder with fungus, bact. and sterile	0.04	4-5	Tracer	0.25-1.49 ²	-	Sedell (1971)
<i>P. lepida</i>	Hickory	110	0.1-20	Gravimetric	1.30	0.005	Cummins <i>et al.</i> (1973)
<i>P. lepida</i>	Hickory	64	0.1-20	Gravimetric	1.62	0.002	Cummins <i>et al.</i> (1973)
<i>P. gentilis</i>	Ironwood	1	-	Gravimetric	0.04-0.50 ³	0.280-0.643	Mackay & Kalff (1973)
<i>P. gentilis</i>	Sugar maple	1	-	Gravimetric	0.02-10.89	0.326-1.130	Mackay & Kalff (1973)
<i>P. gentilis</i>	Red maple	1	-	Gravimetric	0.06-15.27	0.320-1.008	Mackay & Kalff (1973)
<i>P. gentilis</i>	Beech	1	-	Gravimetric	0.01-0.03	0.025-0.040	Mackay & Kalff (1973)
<i>P. gentilis</i>	Mixed leaves with fungi and bacteria	1	-	Gravimetric	20.45	1.30	Mackay & Kalff (1973)
<i>P. lucenta</i>	Ironwood	1	-	Gravimetric	0.03-0.38	0.500-0.636	Mackay & Kalff (1973)
<i>P. lucenta</i>	Sugar maple	1	-	Gravimetric	0.02-8.96	0.218-0.717	Mackay & Kalff (1973)
<i>P. lucenta</i>	Red maple	1	-	Gravimetric	0.04-10.47	0.290-0.808	Mackay & Kalff (1973)
<i>P. lucenta</i>	Beech	1	-	Gravimetric	0.002-0.017	0.015-0.030	Mackay & Kalff (1973)
<i>P. lucenta</i>	mixed leaves with fungi and bacteria	1	-	Gravimetric	9.40	0.728	Mackay & Kalff (1973)
<i>Gammarus</i>							
<i>G. pseudolimnaeus</i>	Silver maple	123	0.1-10	Gravimetric	0.49 ¹	0.062	Present study
<i>G. pseudolimnaeus</i>	Cottonwood	123	0.1-10	Gravimetric	1.02 ¹	0.282	Present study
<i>G. pseudolimnaeus</i>	Ash, maple and elm	1	17	Gravimetric	0.68-0.71	-	Bärlocher & Kendrick (1973)
<i>G. pseudolimnaeus</i>	Red pine	2	17	Gravimetric	0.015-1.56	-	Bärlocher <i>et al.</i> (1978)
<i>G. minus</i>	Elm with fungi and bact.	0.04	20-22	Tracer	0.09-0.76 ²	-	Sedell (1971)
Other aquatic taxa							
<i>Pteronarcys scotti</i>	Mixed leaves	-	10, 15	Gravimetric	-	0.291	McDiffet (1970)
<i>Lepidistoma unicolor</i>	Douglas fir	3	11	Gravimetric	-	1.53	Anderson & Grafius (1975)
<i>Lepidistoma quercina</i>	Alder	3	11	Gravimetric	-	1.57 ⁴	Anderson & Grafius (1975)
<i>Neophylax concinnus</i>	Algae and detritus	0.04	4-5	Tracer	-	1.20	Sedell (1971)
<i>Asellus</i>							
<i>A. racovitzai</i>	Silver maple	51	0.1-7.0	Gravimetric	0.08	0.029	Herbst (1979)
<i>A. aquaticus</i>	Alder	3-18	10	Gravimetric	0.23	0.21	Prus (1971)

extra consumption is not unexpected. It is also likely that the introduction of medium sized *Pycnopsyche* larvae (4.3 mg each; N = 17) into cages in which leaves have incubated for approximately 10 weeks may provide optimum conditions for consumption, thus accounting for the high values in this study.

The significance of leaf conditioning

Food type strongly influences invertebrate feeding in both aquatic and terrestrial ecosystems (Heath *et al.* 1966; Kaushik & Hynes 1971; Wood 1971; Anderson 1973; Bärlocher & Kendrick 1973; Mackay & Kalff 1973; Petersen & Cummins 1974; Sedell *et al.* 1975; and others). The development of fungal and bacterial growth on leaves after an appropriate 'conditioning period' has been demonstrated to enhance invertebrate feeding (Sedell 1971; Bärlocher & Kendrick 1973; Mackay & Kalff 1973) and invertebrates have been thought to 'view' leaves and associated microflora as 'peanut butter and crackers' (Cummins 1974). 'Fast' decomposing leaf species were thought quickly to develop fungal and bacterial colonies and become suitable food before 'slow' species (Petersen & Cummins 1974; Suberkropp & Klug 1976). Over-conditioning of leaf detritus is also thought to exist (Cummins 1974; Anderson & Sedell 1979). Consequently, according to these theories, highest animal consumption should occur at some intermediate time period between 'unconditioned' and 'senescent'.

The results of the consumption experiments in this study do not provide complete support to the aforementioned theories. Although consumption of cottonwood by *Tipula* and *Gammarus* clearly increases during the final feeding interval (beginning at day 69), suggesting the effects of conditioning, silver maple consumption does not significantly change with time. At the same time, silver maple is clearly a suitable food item; consumption rates of maple exceed those of cottonwood for *Pycnopsyche* and for *Tipula* (during the first two feeding intervals). Additionally, decomposition rates of silver maple leaf packs have been shown to be higher than for cottonwood leaf packs (Herbst 1980). The apparent lack of effect of conditioning time upon consumption rates of silver maple may be a consequence of the small sample size and inherent statistical difficulties. However, it may

also be due to the nature of leaf conditioning.

Although similar in organic, caloric and protein content, cottonwood leaves differ from silver maple by having a relatively thick and waxy cuticle (Herbst 1979). This cuticle may provide a physical obstacle to invertebrate feeding, until it gradually disappears as a result of weathering. Conversely, silver maple, lacking this cuticle may be immediately suitable as a food source. High consumption rates for unconditioned *Alnus* leaves by the caddisfly larva *Lepidostoma quercina* have been previously reported (Anderson & Grafius 1975). In addition, Sedell (1971) observed no significant differences in the amount of microbial treated and 'sterile' leaves consumed by *Pycnopsyche lepida*.

Conditioning is a combination of physical and microbial processes which result in increased palatability to invertebrate consumers. This increased palatability may simply result from the increased softening of the leaf over time. Therefore, silver maple leaves being initially soft are immediately consumed, while cottonwood leaves with a heavier cuticle must be worked on by physical as well as microbial processes. Evidence supporting this possibility is advanced by Bärlocher & Kendrick (1975b) who demonstrated that changes in the leaf surface that increased palatability to *Gammarus* could be caused by microbial excretions, or hot HCl, as well as by fungi. Presumably, the microbial excretions or acid soften or destroy the leaf cuticle thereby facilitating invertebrate feeding. Edwards & Heath (1975) also suggested that weathering (conditioning) makes beach leaves more palatable by reducing polyphenol content and by softening leaf tissues. Feeny (1970) reports that leaf toughness is an important factor in reducing summer feeding of lepidopteran larvae.

Chemical factors may also influence the differing responses of invertebrate detritivores to silver maple and cottonwood leaves. For example, the presence of polyphenols is known to affect leaf palatability and decomposition rates (Feeny 1970; Edwards & Heath 1975; Suberkropp *et al.* 1976). As polyphenols leach out of detritus in terrestrial systems invertebrate consumption increases (Heath & Arnold 1966; King & Heath 1967; Wood 1974). In streams, a portion of the polyphenols present are thought to form resistant complexes with proteins and lignin (Suberkropp *et al.* 1976). Leaf palatability has also been shown to be negatively

correlated with gallic and protocatechuic acid content (Anderson 1973) and overall decomposition has been negatively correlated with lignin content (Melin 1930; Triska *et al.* 1975; Meentemeyer 1978). The polyphenol, gallic and protocatechuic acid content of silver maple and cottonwood leaves are unknown.

Summary

1. In 123 day *in situ* cage experiments with cottonwood and silver maple leaves, 20–23% of initial dry weight was lost by leaching and 8–10% by microbial processes.
2. The effects of leaf conditioning was reflected in increased consumption by invertebrates of cottonwood of leaves with time; this pattern was not observed for silver maple leaves.
3. *Tipula abdominalis* and *Pycnopsyche guttifer* consumed more silver maple leaves than cottonwood leaves during the feeding intervals; no significant differences were observed for *Gammarus pseudolimnaeus*.
4. Consumption values generally agreed with known literature values.

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