DOE/EV/10004-02

THERMAL-NUTRITIONAL REGULATION OF FUNCTIONAL GROUPS IN RUNNING WATER ECOSYSTEMS

Technical Progress Report

for period Oct. 1, 1978 - Nov. 1, 1980

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Nov. 1, 1980

Prepared for
THE U.S. DEPARTMENT OF ENERGY
UNDER CONTRACT NO. DE AT06 79EV 10004

DISCLAIMER

1.0 ABSTRACT

Thermal-Nutritional Regulation of Functional Groups
in Running Water Ecosystems

The research encompassed three general areas:

1) Characterization of stream macroinvertebrate functional feeding groups (shredders, collectors, scrapers, and predators) based on morphological and behavioral adaptations and food-source-specific growth responses of selected species.
2) Demonstration of the relative importance of temperature and food quality (in which maximum quality is defined as that producing the most growth) in controlling growth rate and survivorship of stream functional groups.
3) Derivation and refinement of conceptual and quantitative models of stream ecosystem structure and function, with particular emphasis on detrital processing.

Verification of the functional group concept (which was developed with DOE funding) as a tool for assessing and predicting are reflected in alterations of the relative dominance of various functional groups. Food quality can strongly influence the growth rates of shredders, collectors and scrapers and override the effects of temperature in a number of cases. Gathering collectors may select food particles by size (or at least be restricted to a limited portion of the total range available) but representative species do not appear to select for quality.

2.0 SUMMARY OF PROGRESS

Oct. 1, 1978 - Nov. 1, 1980

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In addition to the attached reprints and preprints acknowledging DOE support, the Progress Report consists of short statements on the status of a range of experiments and field analyses in various stages of analyses and

evaluation prior to preparation of research papers. The two broad areas of research have involved: 1) characterization of macroinvertebrate functional feeding groups and documentation that such groupings can be utilized as an environmental assessment tool; and 2) determination of the relative importance of temperature and food quality in controlling the growth and survival of representatives of each functional group.

The major goals of the stream macroinvertebrate functional feeding group analytical methods have been to: 1) maximize the ecological information obtained per unit taxonomic effort; 2) provide a method of community assessment highly reflective of the nutritional resource base of a given aquatic system; and 3) emphasize modes of food acquisition rather than diet (trophic analyses) because although essentially all species are omnivorous, they have very different morphological and behavioral adaptions for harvesting the nutritional resources. The most recent evaluation of functional groups appeared in Merritt and Cummins (1978, An Introduction to the Aquatic Insects of North America) in 16 tables (67 pp) organized by taxonomic group.

Data generated with DOE support have demonstrated that temperature controls of growth of stream macroinvertebrates can be overridden by food quality - at least for some species under some conditions. This "override" has been documented for shredders (Tipula, Pycnopsyche, Clistoronia); collectors (Stichtochironomus, Partendepes, and probably Ptychoptera, Paraleptophlebia and Optioservus); and scrapers (Glossosoma and probably Dicosmecus). Such compensatory responses by selected species in the major functional groups suggest that: 1) representative forms can be used as indicators of the food quality base of a given stream system; and 2) general management procedures are possible in which the nutritional base would be manipulated to compensate for temperature effects. In as much as the nutritional resources for microorganisms and macroinvertebrates in headwater streams is strongly influenced by particulate (and dissolved) organic matter

derived from the riparian zone, the management of the streamside vegetation corridor could be a major tool influencing community structure and production. Thus, manipulation of composition and density of riparian plant species could have a major effect on the turnover rates of organic matter in recipient stream ecosystems.

3.2. Food quality and temperature effects on feeding, growth, and biochemistry of *Clistoronia magnifica* in laboratory feeding experiments.

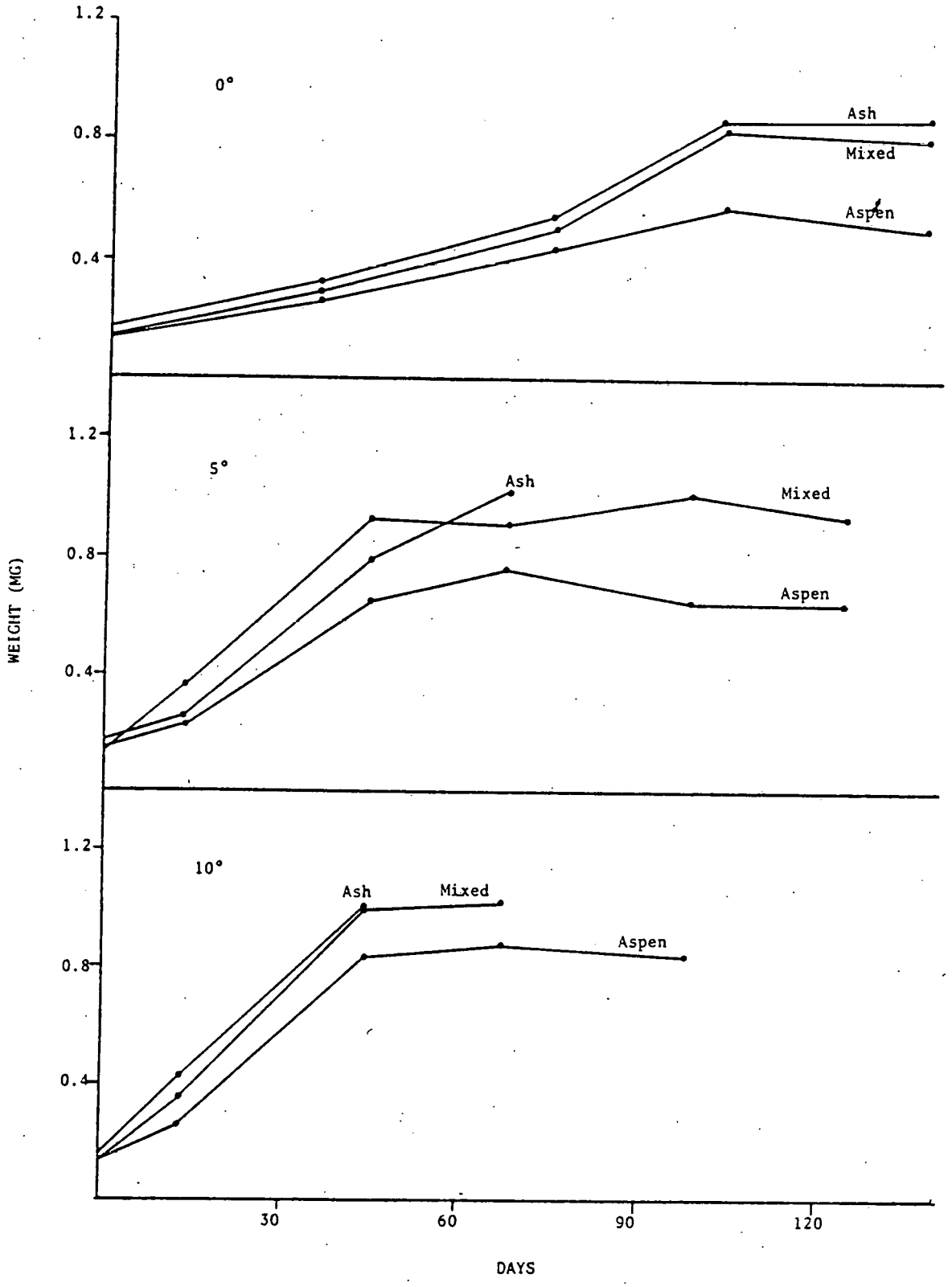
The interactive effect of food quality and temperature on feeding, growth, and biochemistry of a limnephilid caddisfly, *Clistoronia magnifica* was examined. Late instar larvae from a laboratory culture were randomly assigned to one of four food quality treatments (wheat, unconditioned alder leaves, laboratory-conditioned alder leaves, HCl-hydroloyzed alder leaves) at one of two temperatures (8.5°C, 17°C). In a second experiment two additional food quality treatments (unhydrolyzed filter paper, HCl-hydrolyzed filter paper) were used at the lower temperature. Food was changed every second day to minimize microbial colonization of the unconditioned substrates, and weight loss of the food during the two day period was determined and used to calculate consumption. Food quality and temperature effects on the insects are reflected by relative growth rate, consumption index, relative nitrogen change, and relative lipid change (Table 1). Insects eating wheat (a high quality food) did well at both temperatures. Insects fed the alder diets (medium quality, but high in nitrogen) lost weight, primarily in the form of lipids at the higher temperature; while insects on the same diets gained weight at the lower temperature. Insects on the poor quality, low nitrogen filter paper diet lost weight, nitrogen, and lipids; all at similar rates.

3.0 Influence of Food Quality and Temperature on the Growth of Selected Shredders

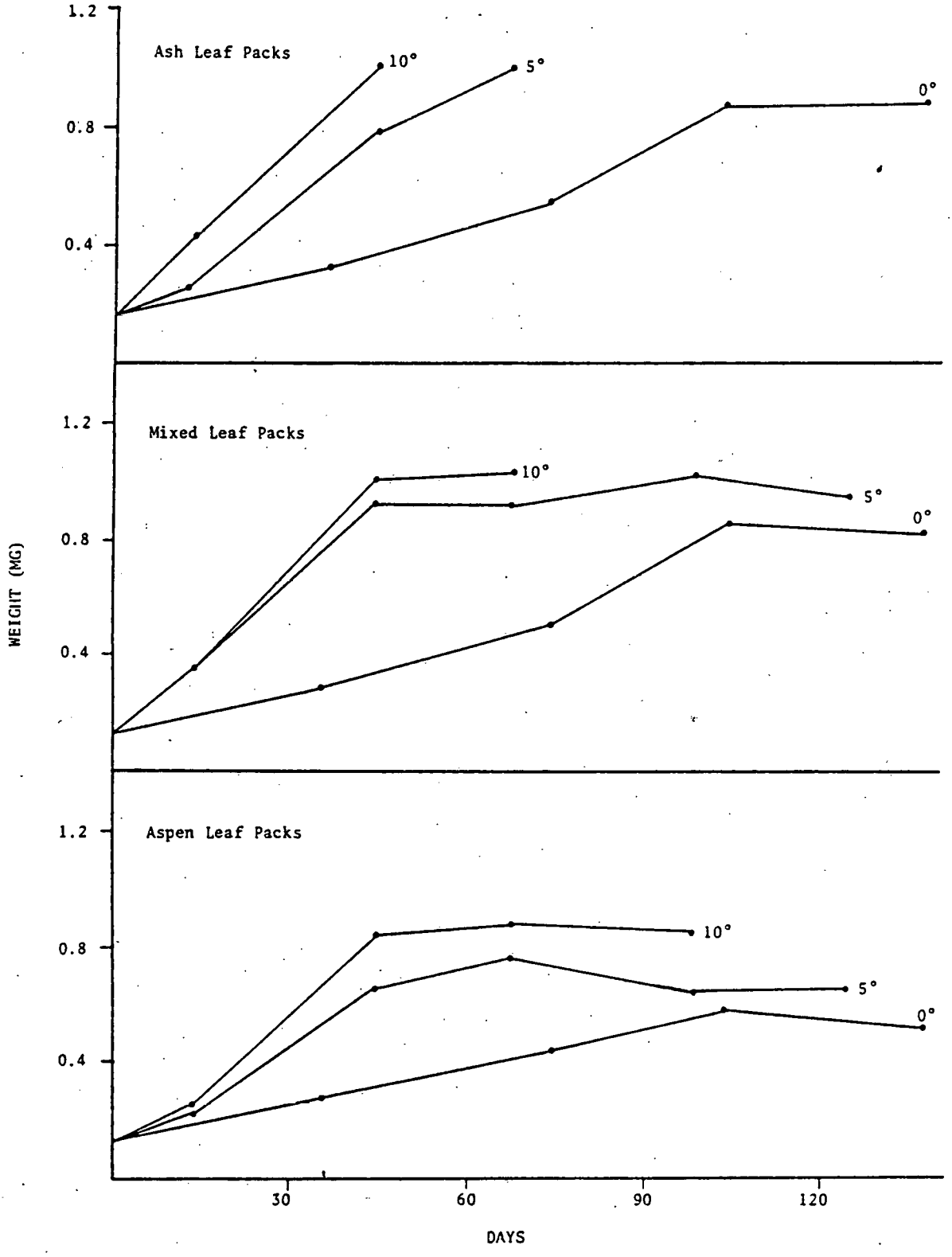
3.1 Mean and maximum relative growth rates of Brillia spp. in Augusta Cr. and the experimental stream channels on four kinds of leaf packs at different temperatures. Mixed leaf packs contained ash and aspen leaves.

Leaf Pack Type	Temp. (°C)	Relative Growth Rate	Maximum Relative Growth Rate
Ash	1.0	1.30	1.68
Mixed	1.0	1.26	1.76
Aspen	1.0	1.34	1.99
Total	1.0	1.31	1.85
Ash	5	3.28	3.28
Mixed	5	2.83	2.83
Aspen	5	3.18	3.18
Total	5	2.99	2.99
Ash	10	3.23	3.23
Mixed	10	3.41	3.41
Aspen	10	3.22	3.22
Total	10	3.33	3.33
Hickory	2.3	0.97	1.12
Hickory	2.0	0.86	1.19
Hickory	1.9	0.85	1.48
Hickory	1.6	1.17	2.06
Hickory	2.0	1.38	1.79

Although the growth rate (RGR) on the leaf types (ash, aspen, and ash-aspen randomly mixed), Brillia larvae attained a larger final weight on ash leaves. Since the same final weight was observed on both ash and mixed packs, Brillia larvae probably selectively fed on ash. Similar growth at 5° and 10°C on the high quality ash leaves provides additional evidence for the override of temperature effects by food quality.



Growth of Brillia spp. in Augusta Cr. and the experimental channels.



Growth of Brillia spp. in Augusta Cr. and the experimental channels.

TABLE 1

(Expressed as $mg \cdot mg^{-1} \cdot day^{-1}$ X 100)

Temperature	Food	Relative Growth Rate	Consumptive Index	Relative Nitrogen Change	Relative Lipid Change
8.5°C	Wheat	2.53	13.53	2.3	4.6
	Unconditioned Alder	0.69	14.15	1.4	-2.9
	Conditioned Alder	1.76	15.22	1.7	1.1
	Hydrolyzed Alder	0.63	4.75	0.7	2.1
	Unhydrolyzed Filter Paper	-1.64	5.33	-2.0	-1.0
	Hydrolyzed Filter Paper	-1.59	11.98	-1.7	-1.4
17.0°C	Wheat	2.90	31.79	2.7	4.8
	Unconditioned Alder	-1.34	1.56	-0.1	-6.4
	Conditioned Alder	-0.15	9.85	-0.1	-3.5
	Hydrolyzed Alder	-0.95	6.18	-0.6	-1.9

3.3 Field introduction of *Clistoronia magnifica* into Old Growth Coniferous and Second Growth Alder watersheds.

Late instar larvae of a leaf shredding caddisfly, *Clistoronia magnifica* were introduced into streams in an old growth coniferous watershed and a second growth alder watershed to assess food quality differences of detritus in the two streams. Some larvae from the same group were also maintained in standard laboratory conditions and others in laboratory conditions with food from the second growth alder site. Insects were removed from food and starved for 24 hrs to clear guts before weights were measured. Total lipids were extracted and weighed from a subsample of the insects, and fatty acids were analyzed (Table 2). Insects not used for lipid extraction were dried, but dry weight measurements are not yet available. The sources of the differences in fatty acids and total lipids between food treatments is the subject of continuing research. Linoleic and linolenic acid are of special interest since they have been shown to be essential in some insects and may occur in high quantities in alder leaves. The high nutritive value of alder leaves, which has been assumed to result from high nitrogen content, may also have been related to high levels of essential fatty acids.

TABLE 2

Fatty Acids (expressed as a percentage of total fatty acids)

Fatty Acid	Initial Unstarved	Control Starved	Lab-Conditioned Alder & Wheat	Field-Conditioned Alder	Old Growth	Second Growth Alder
Myristic 14:0	1.80	1.93	1.19	2.14	2.28	3.48
Myristoleic 14:1	0.28	0.28	0.88	1.58	0.20	.80
Palmitic 16:0	20.71	18.32	25.83	21.39	15.02	12.82
Palmitoleic 16:1	4.59	4.59	7.68	5.02	3.55	1.93
Unknown A	4.03	3.64	3.79	3.31	----	1.67
Stearic 18:0	2.93	3.27	2.51	3.48	4.27	4.47
Oleic 18:1	21.35	20.87	20.03	21.47	39.47	36.05
Linoleic 18:2	26.12	24.96	22.13	18.72	18.93	13.52
Linolenic 18:3	14.39	17.63	14.21	21.85	10.58	22.01

Total Lipids (expressed as a percentage of wet body weight)

Initial Unstarved	Control Starved	Lab-conditioned Alder & Wheat	Field-conditioned Alder	Old Growth	Second Growth Alder
2.49	1.76	2.80	1.89	1.42	0.52

3.4. Field collections of caddisflies as an index of Old-Growth Clearcut food quality differences

The effects of clearcutting on growth and biochemistry of two caddisflies; a shredder, Lepidostoma quercina and a grazer, Allocosmoecus sp. was examined by field collection and lipid analysis of insects collected from upstream, old growth and downstream, clearcut sections of a third-order stream (Table 3). Fatty acid patterns did not differ substantially between old growth Lepidostoma and those collected in the clearcut, although the lipid content was higher in the more nautral old growth. Total lipid levels also differed in Allocosmoecus, which also had fatty acid differences between the two sites. The fatty acid differences in the insects may be due to fatty acid differences in the algal communities between the two sites.

TABLE 3

Fatty Acids (expressed as a percentage of total fatty acids)

Location	Fatty Acid	Lepidostoma sp. Prepupae	Lepidostoma sp. Pupae Female	Lepidostoma sp. Pupae Male	Allocosmoecus sp. Prepupae
Old Growth	Myristic 14:0	5.73	2.01	2.65	1.35
	Myristoleic 14:1	1.59	1.61	1.69	trace
	Palmitic 16:0	26.78	26.94	24.12	23.17
	Palmitoleic 16:1	7.28	12.69	8.74	7.90
	Unknown A	4.83	2.27	4.26	4.32
	Stearic 18:0	3.44	2.41	3.58	2.91
	Oleic 18:1	18.03	15.41	19.49	27.02
	Linoleic 18:2	7.34	7.77	8.13	10.32
	Linolenic 18:3	16.48	17.91	14.71	16.16
	Unknown A	1.44	4.18	1.90	2.11
Clear Cut	Myristic 14:0	3.88	2.36	-----	2.69
	Myristoleic 14:1	1.08	0.62	-----	1.00
	Palmitic 16:0	28.48	24.37	-----	18.23
	Palmitoleic 16:1	4.85	13.28	-----	14.48
	Unknown A	4.13	4.27	-----	1.29
	Stearic 18:0	3.11	1.76	-----	3.01
	Oleic 18:1	21.41	17.24	-----	17.69
	Linoleic 18:2	8.26	13.93	-----	6.47
	Linolenic 18:3	17.05	15.28	-----	14.86
		2.60	3.06	-----	7.29

Total Lipids (expressed as a percent of dry body weight)

Location	Lepidostoma sp. Prepupae	Lepidostoma sp. Pupae Female	Lepidostoma sp. Pupae Male	Allocosmoecus sp. Prepupae
Old Growth	23.7	21.3	18.0	34.7
Clear Cut	17.9	19.4	----	23.8

3.5 Taxonomic-Functional Group Differences in Fatty Acid Patterns

Fatty acid patterns of terrestrial insect orders show taxonomic differences which override seasonal, life history, and ecological differences within orders. Fatty acid patterns of aquatic insects have received little attention except for pest species which are atypical. Fatty acid patterns may be indicators not only of taxonomic grouping but also of feeding habits and functional group position. Field collections of insect nymphs and larvae for examination of fatty acids have recently commenced. In addition to the data previously given for caddisflies (Trichoptera) from various laboratory and field conditions, we have also obtained analyses of a caddisfly (Heteroplectron sp.) and a beetle larvae (Dryopidae) from an older growth coniferous watershed, and a caddisfly (Pseudostenophylax sp.) and a stonefly (Acroneuria sp.) from a second growth alder site (Table 4). We are currently collecting and examining other insects from a classification-functional group matrix.

TABLE 4

Fatty Acids (expressed as a percentage of Total Fatty Acids)

Fatty Acid		Heteroplectron sp.	Dryopidae	Pseudosteno-phylax sp.	Acroneuria sp.
Myristic	14:0	1.39	1.06	4.75	1.99
Myristoleic	14:1	1.78	1.41	0.34	0.45
Palmitic	16:0	23.62	13.76	14.40	13.90
Palmitoleic	16:1	4.58	11.99	2.18	5.46
Unknown B		----	8.61	----	----
Unknown A		----	----	3.42	----
Stearic	18:0	3.58	3.59	5.30	5.14
Oleic	18:1	21.98	24.26	25.47	22.48
Linoleic	18:2	16.33	12.60	9.30	16.34
Linolenic	18:3	22.35	3.90	27.21	11.75

Total Lipids (expressed as a percent of wet body weight)

Heteroplectron sp.	Dryopidae	Pseudosteno-phylax sp.	Acroneuria sp.
4.10	3.17	1.28	2.83

4.0 Influence of Food Quality on Growth and Survival of Selected Collector Gatherers

As part of the continuing collector feeding studies, questions of particular interest are selection for food quality vs. particle size, e.g. by % organic or nitrogen content, microbial biomass and/or activity. Gathering collectors (FPOM-feeders) belonging to large, widely distributed genera were chosen for study, particularly the mayflies, Ameletus sp. (Siphlonuridae), Ephemerella spp. (Ephemerellidae), Paraleptophlebia sp. (Leptophlebiidae), and the false crane fly larva, Ptychoptera sp. (= Liriope sp.; Ptychopteridae).

4.1 Growth of Ameletus sp. on Mixtures of Natural Detritus and Sand

Ameletus sp. nymphs were collected from backwaters (alcoves) of the West Fork of the Clark's Fork of the Yellowstone River (Park Co., Montana) and sorted into small, medium, and large size categories. Total length of approximately one-third of these animals was measured - i.e. length from the occiput of the head to the base of the cerci with the head in its normal, hypognathus position. An initial length-weight regression (dry wt, 50°C) was derived for these experimental animals to represent the group introduced into flasks containing substrates of varying organic content (Table 1). Nymphs surviving in each flask after 7.5 days were dried and weighed to determine treatment-specific final weights.

Food substrates were prepared from red alder (Alnus rubra) leaves ground and sieved to particles ranging in size from 63 µm to 177 µm. This particulate detritus was conditioned in aerated water for two days and wet mixed with ashed (550°C) silica sand of the same size range to produce the treatments of varying relative organic content. Relative proportions of alder detritus and sand by treatment were as follows: A, 80/20; B, 50/50; C, 20/80; and D, 100% detritus. Treatment E consisted primarily of detritus > 1 mm collected along with the animals.

Approximately 15 ml total wet volume of substrate were added with stream water, filtered through 53 µm mesh sieve, to each 250 ml flask; there were five flasks per treatment. Flasks were aerated with capillary tubing held in position by foam rubber stoppers and inserted into tygon tubing clamped at one end and attached to an aeration pump at the other. The flasks were maintained in the laboratory at an average temperature of 5°C. Five pre-measured Ameletus sp. nymphs were placed in each flask for the 7.5 day growth period.

Table 1. Initial and final (after 7.5 days) average organic content of food substrate mixtures of ashed sand plus detritus used in Ameletus sp. growth experiment.

	% Organic Content	
Treatment	Initial	Final
A	15.0	15.7
B	4.5	5.4
C	1.8	1.5
D	88.4	89.0
E (no sand)	70.2	68.6

Length-weight regression coefficients for equations derived for the initial subsample of Ameletus sp. and for animals recovered from each of the treatments at the conclusion of the experiment are presented in Table 2. Survival (n) was generally inversely correlated with the rate of growth of animals on each of the treatments, A, B, C, and D. One explanation for this is that animals on substrates with relatively high organic content grew at relatively faster rates, reached their final instar, but were unable to emerge. For example, animals on Treatment C survived better because they grew at the slowest rate, possibly because they were not able to select for particles of higher organic content, and did not, in the time frame of this experiment, reach their final instar. Survival was best, but growth was only moderate on Treatment E, probably because this substrate contained far fewer particles within the size range Ameletus sp. are able to ingest. Final lengths averaged for each treatment vs.

respective initial lengths (Table 3) also suggest that Ameletus sp. were unable to emerge under the given experimental conditions - i.e. that the larger animals died. The average change in length observed over the experimental period generally is greater when dead animals, in reasonably good condition, are included in the measurement. The value in Table 3 for the change in length in Treatment E animals does not vary because there was no mortality. Similarly, average change in animal dry weight follows no obvious pattern, but generally indicates animals lost weight, possibly because only relatively small animals survived and were weighed.

A test for the equality of slopes of several regression lines (Sokal and Rohlf 1969, p. 450) revealed that there were significant differences ($p < .005$) in growth rates between initial animals and those on all treatments (A-E). A posteriori tests for differences among a set of regression coefficients by the Simultaneous Test Procedure (Ibid., p. 457), however, indicated that Treatments A, B, and E were not significantly different from the initial animals, whereas Treatments D and C were. Inability to differentiate between treatments is probably the result of small n values (Table 2). Nonetheless, both the regression coefficients and the total change in length (Table 3) indicate a trend of growth on Treatments A, B, C, and D which corresponds directly with percentage organic matter in the substrate (Table 1). These results justify further experiments of longer duration with earlier instar Ameletus nymphs.

Table 2. Regression (y=a+bx) of weight (y) onto length (x) of Ameletus sp. presented substrates of varying organic content.

Treatment	n	a	b	r^2
Initial	69	-4.5257	.0940	.8869
A	9	-4.5495	.0853	.7150
B	13	-3.4217	.0688	.4129
C	17	-1.7324	.0469	.6036
D	6	-5.5983	.1038	.9385
E	20	-2.8786	.0652	.8270

Table 3. Average change in length of live (1) and live plus dead (but in good condition) (2) and average change in day weight of Ameletus sp. nymphs recovered from each of five food treatments (Table 1).

Treatment	Change in length (mm)		Change in dry weight (mg)
	(1)	(2)	
A	0.250	0.829	-0.500
B	0.217	0.455	-0.684
C	-0.025	0.194	-0.644
D	-0.011	0.828	0.213
E	-0.075	-0.075	-0.573

4. 2. Growth of Ephemerella delantala and E. infrequens on Detritus: Sand Mixtures

Ephemerella delantala and E. infrequens nymphs were collected from the South Fork of Rock Creek (Mary's Peak Watershed, Benton County, Oregon) and sorted into small, medium, and large size categories. Subsamples of about 10% of the animals to be used in the growth experiment, and representing the three size classes, were dried and weighed after total lengths (to base of cerci) and head widths were measured.

Nine or ten nymphs of a given size category and species were placed in each section of three (one per treatment) eight-section, flow-through feeding chambers. Treatments A, B, and C were the same as described above for the Ameletus experiment; the relative organic contents are given in Table 4. Approximately 10 ml wet volume of substrate were added to each section of the chambers. Water temperatures were maintained at 13°C, similar to the temperature of Rock Creek from which the animals were collected. After the 14 day growth period, live nymphs recovered from each section were measured and dry weights, determined.

Table 4. Initial and final (after 14 days) average organic content of food substrate mixtures of ashed sand and detritus used in Ephemerella delantala (1) and E. infrequens (2) growth experiment.

	% Organic Content		
Treatment	Initial	Final(1)	Final (2)
A	15.0	21.9	20.6
B	5.2	8.7	4.7
C	2.8	2.3	2.1

Low survival of Ephemerella spp. on experimental substrates, possibly because of wide variations in chamber temperature, resulted in data too ambiguous for interpretation. The feeding chamber set-up has been modified to stabilize flow, and therefore insure temperature control. Additional experiments will be conducted with Ephemerella delantala and E. infrequens.

4.3. Growth of Mayflies on Three Size Fractions of Ground Leached Alder

Ephemerella veruca and Ameletus sp. were collected from Parker Creek, (Mary's Peak, Benton County, Oregon), and Polypedilum sp. from Berry Creek (Benton County, Oregon). Animals were placed in individually aerated three dram vials (six each treatment) containing ground leached alder 53-125 µm, 125-250 µm, and 250-500 µm in diameter. Mean % organic matter of each of these size fractions for each animal and a control (vials set up and treated similarly, but without the introduction of animals) are given in Table 5.

Table 5. Percentage organic matter of ground leached alder.

Treatment	Particle Size Range (µm)			
	53-125	125-250	250-500	$\bar{x}$ ± SE
AA (Ephemerella veruca)	93.2	93.8	93.8	93.6 ±.4
DD (Ameletus sp.)	94.3	95.0	95.0	94.8 ±.4
EE (Control)	95.3	95.2	95.4	95.3 ±.1

4.4. Ptychoptera sp. and Paraleptophlebia sp. Growth on Freshly-Produced and Stored (frozen) Feces

Alder (Alnus rubra) leaves were collected from Oak Creek (Benton County, Oregon) for use as a food substrate for the shredders Lepidostoma sp. and Zapada sp. These animals produced fresh feces of an appropriate size range for feeding by the gathering collectors Ptychoptera sp. and Paraleptophlebia sp.

In addition, Lepidostoma sp. and Holorusia sp. were fed alder leaves, and resultant feces of particle size ranging from 53 to 500 µm were sieved from the material and stored in a freezer prior to use. Specific treatments and average organic contents are reported in Table 6. The experiment continued for 34 days in flow-through chambers using water from a temperature-controlled recirculating channel. Tap water was conditioned, i.e. allowed to stand 48 hr, prior to use. Initial dry weights of animals were estimated from wet/dry weight regressions, and final dry weights were measured on a Cahn electrobalance.

Table 6. Specific treatments and average organic content of food substrates provided for Ptychoptera sp. and Paraleptophlebia sp.

Treatment	Animal(s)	Substrate	% Organic
A_{1-4}	Paraleptophlebia sp.	Feces	78.1(±3.6)
A_{5-8}	Ptychoptera sp.	Feces	79.3(±2.8)
C_{1-4}	Paraleptophlebia sp., Zapada sp., Lepidostoma sp.	Leaves	76.9(±6.2)
C_{5-8}	Ptychoptera sp., Zapada sp., Lepidostoma sp.	Leaves	78.7(±3.6)
D_{1-4}	Paraleptophlebia sp.	Leaves	71.0(±2.0)
D_{5-8}	Ptychoptera sp.	Leaves	86.7(±7.5)
F_{1-4}	Zapada sp., Lepidostoma sp.	Leaves	84.6(±2.9)
F_{5-8}	Zapada sp., Lepidostoma sp.	Feces	78.2(±1.7)

Wet weight/Dry weight conversions were as follows:

Ptychoptera sp., $y = -0.7476x + 149.0860$ ($r^2 = .95$)
Paraleptophlebia sp., $y = -0.0575x + 275.7205$ ($r^2 = .86$)
Zapada sp., $y = 0.1697x + 167.7246$ ($r^2 = .83$)
Lepidostoma sp., $7 = -0.7295x + 356.1197$ ($r^2 = .86$)

Mean relative growth rates of Ptychoptera sp. and Paraleptophlebia sp. on feces, leaves with shredders, and leaves, and of Zapada sp. and Lepidostoma sp. on leaves and feces are presented in Table 7. Ptychoptera sp. appears to have grown most rapidly on feces that were stored (frozen) for a period of time prior to use, and less rapidly on leaf material. The amount of material produced from leaves with shredders present was substantially less than the amount of stored feces, and may have been growth-limiting. This factor negates an attempt to compare growth on fresh vs. stored feces at this time.

Table 7. Mean relative growth rates (mg/mg/day) of Ptychoptera sp. and Paraleptophlebia sp. on feces (A), leaves with shredders, Zapada sp. and Lepidostoma sp. (C), and leaves (D), and of Zapada sp. and Lepidostoma sp. on leaves (E) and on feces (F).

Species	A	C	D	E	F
Ptychoptera sp.	.0046	-.0011	-.0059		
	.0036				
Paraleptophlebia sp.	.0054	.0143	.0192		
		.0080	.0104		
Zapada sp.				-.0102	.0025
Lepidostoma sp.				-.0127	.0055
				-.0076	

Ptychoptera sp. lost a relatively large portion of weight when fed leaves alone. This was expected because these animals are believed to be obligate FPOM-feeders.

Paraleptophlebia sp., however, responded differently. These animals were seen to gain progressively larger amounts of weight on feces, leaves with shredders (part leaf, part fecal material), and leaves, suggesting an ability to shred as well as to collect. A plot of relative growth rates Ptychoptera sp. and Paraleptophlebia sp. vs. mean initial weight produced no obvious pattern.

Contrary to what was expected, Zapada sp. and Lepidostoma sp. appeared to lose weight on leaves and to gain weight on feces. Leaves were conditioned

when collected from the stream, but laboratory conditions might not have been correct for promoting or sustaining growth of microbes essential for adequate nutrition. Both shredders consumed large amounts of leaves throughout the experiment. These results suggest some ability of both these animals to consume and to gain weight on fine particulates.

Except for the emergence of one Zapada sp. on leaves (E), emergence and pupation of shredders were limited to those feeding on leaves with collectors. Five Zapada sp. (mean adult dry weight + cast skin = 1.247 mg + .209 mg) emerged, and four Lepidostoma sp. (mean pupal dry weight = 3.029 mg) pupated on Treatment C during the course of the experiment.

4.5. Growth of Ptychoptera sp. on Wood, Alder, and Natural Detritus

Substrates (see Table 8 for initial and final mean % organic content) were placed in individually aerated clear plastic box chambers for a period of 24 hr prior to introduction of pre-weighed Ptychoptera sp. Chambers were maintained at approximately 10°C for 19 days (190 degree days) in refridgerators with daylight control approximating that of the environment. Water was collected from Oak Creek, Oregon, and poured through a 53 µm sieve before being added to the chambers. Alder, sawdust and maple were pre-leached for about 1 week before they were sieved to the desired particle size range. All alder treatments contained 1.5 g dry weight of alder fines. One 3 X 9 cm strip of Nitex was placed in each chamber to provide a tactile substrate for the animals. Water was not changed during the experiment.

Table 8. Food substrates and respective organic contents provided for Ptychoptera sp.

Treatment	Substrate (Dilution)	Particle Size Range (μm)	$\bar{x}$% Organic Content	
			Initial	Final
A	Alder	53-125	94.4	92.7
B	Alder:Sand (4:1)	53-125	46.1	32.1
C	Alder:Sand (1:1)	53-125	46.1	14.6
D	Alder:Sand (1:4)	53-125	2.8	5.9
E	Alder:Wood (4:1)	53-125	---	94.1
F	Alder:Wood (1:1)	53-125	95.2	95.4
G	Alder:Wood (1:4)	53-125	97.0	97.5
H	Wood	53-125	97.0	96.4
I	Detritus	53-125	13.9	14.7
K	Maple	53-125	86.3	88.9
L	Sand	53-125	1.3	3.8
M	Detritus	53-125	13.9	14.2
N	Detritus	125-250	12.8	14.1
O	Detritus	250-500	13.4	15.5
P	Alder	53-125		92.9
R	Alder	125-250		92.6
S	Alder	250-500		94.4

Relative growth rates measured for animals in treatments with 100% survival were generally highest on natural detritus, and lowest on mixtures of alder and wood. No aminals survived on wood alone (Treatment H). Conversely, larvae survived on sand, and did not lose as much weight on alder/sand mixtures. This suggests the possibility of the presence of a toxin in the wood, even though it was well leached, or a physiological change in response to, for instance, sand, which does not occur on wood, possibly due to the nature of the material.

Ground alder often produces rates of growth which are faster than those obtained on natural detritus. Increased growth rates on alder were not found in this experiment, in part due to wide variations in the quality of detritus. There were no obvious trends in growth on different particle size fractions, except that animals on the 125-250 µm portion consistently grew least.

6. Growth of *Ptychoptera* sp. on Three Size Fractions of Ground Conditioned Alder

Ptychoptera sp. were placed in individually aerated vials containing alder (*Alnus rubra*) of three size fractions: 53-125 µm, 125-250 µm, and 250-500 µm. Final mean percentage organic contents of substrates were similar and are presented in Table 9. Treatments A, B, and C were maintained at 10°C, and Treatments D, E, and F, at 15°C to test for temperature as well as particle size effects.

Table 9. Organic content of three size fractions of alder fines presented to *Ptychoptera* sp.

Treatment	Size Fraction (µm)	$\bar{x}$% Organic Content
A_1	53-125	91.6
A_2	53-125	91.2
B_1	125-250	91.8
B_2	125-250	91.1
C_1	250-500	92.3
C_2	250-500	90.6
D	53-125	89.5
E	125-250	90.0
F	250-500	91.4

Growth rates obtained on all treatments indicate that *Ptychoptera* sp. grows best on the 53-125 µm particle size fraction, at an intermediate rate on the 125-250 µm fraction, and least on particles ranging from 250 to 500 µm in diameter. Growth rates on respective treatments were generally higher at 10°C

than at 15°C. Changes in animal wet weight exhibited the same pattern of increasing rate of growth on decreasing particle size.

4.7. Growth and Survival of *Ptychoptera* sp., *Paraleptophlebia* sp. and *Polypedilum* sp.

Growth and survival of *Ptychoptera* sp., *Paraleptophlebia* sp. and *Polypedilum* sp. from Berry Creek, Oregon were measured on various substrates (Table 10) in individually aerated vials maintained in refridgerators at 10°C. Initial wet weight of the larvae and total length of the nymphs were measured, and initial dry weights were estimated from regressions for subsamples. Final dry weights were measured on a Cahn electrobalance.

Table 10. Initial and final percentage organic matter of food substrates presented to *Ptychoptera* sp., *Paraleptophlebia* sp., and *Polypedilum* sp.

Treatment	Substrate	Particle Size Range (µm)	Dilution Ratio	Initial % Organic	Final % Organic $\bar{x}$1-6	$\bar{x}$7-12	$\bar{x}$13-18
AA	Natural detritus	53-125	----	32.90	19.46	33.21	38.26
BB	Natural detritus	125-250	----	53.73	32.78	37.45	31.49
CC	Natural detritus	250-500	----	63.10	50.68	58.06	45.41
DD	Leached alder	53-125	----	90.96	92.13	92.77	93.68
EE	Leached alder	125-250	----	88.94	89.72	91.92	91.86
FF	Leached alder	250-500	----	89.74	92.91	93.56	94.29
GG	Alder leaves		----	79.06	81.24	85.78	82.17
HH	Alder + leachate	53-125	----	93.70	93.68	94.95	94.64
II	Leached alder:Sand	53-125	1:1	8.42	9.01	9.25	9.98
JJ	Sand	53-125	----	0.11	0.51	0.51	0.49
KK	Leached alder:Leached sawdust	53-125	1:1	96.09	96.31	96.97	96.59
LL	Leached sawdust	53-125	----	97.99	94.79	97.34	98.50
MM	Leached alder:sand	53-125	1:4	3.58	2.87	3.05	3.12
NN	Leached alder:Leached sawdust	53-125	1:4	97.68	96.79	97.73	97.76
OO	Natural detritus:Sand	53-125	1:1	6.63	6.12	5.37	5.60
PP	Natural detritus:Leached sawdust	53-125	1:1	62.61	42.54	46.36	40.94
RR	Natural detritus:Sand	53-125	1:4	2.08	2.81	2.45	2.17
SS	Natural detritus:Leached sawdust	53-125	1:4	75.55	66.45	72.42	70.28
TT	Shredder feces	53-250	----	86.98	83.15	84.50	86.87

4.8. Growth of Ptychoptera sp. and Paraleptophlebia sp. on Alder Leaves, Holorusia sp. Feces and Natural Stream Sediment

Ptychoptera sp. maintained in the lab for 16 days prior to the beginning of the experiment (Treatment I) and introduced immediately from the field (Treatment III), and Paraleptophlebia sp. (Treatment II) were placed on substrates indicated in Table 11 (four replicates per treatment). Natural detritus and animals were collected from Berry Creek, Oregon. Conditions were maintained at 10°C and a light period comparable to coincident daylight for 22 days (approximately 22 degree-days).

Table 11. Substrates and respective organic contents presented to Ptychoptera sp. and Paraleptophlebia sp.

Treatment	Substrate	Particle Size Range (μm)	Initial % Organic	Final % Organic
A - I	Alder leaves + shredders		80.66	83.91
A - II	Alder leaves + shredders		80.66	84.71
A - III	Alder leaves + shredders		80.66	82.47
B - I	Alder leaves		80.66	86.29
B - II	Alder leaves		80.66	87.60
B - III	Alder leaves		80.66	85.19
C - I	Holorusia feces	53-250	72.77	86.76
C - II	Holorusia feces	53-250	72.77	87.65
C - III	Holorusia feces	53-250	72.77	86.91
D - I	Stream sediment		47.79	45.77
D - II	Stream sediment		47.79	52.32
D - III	Stream sediment		47.79	56.88

Plexiglass cylinders with mesh of an appropriate size at either end were attached to bricks and placed in Berry Creek. Substrates and animals were introduced into the chambers and changes in dry wt, measured in order to obtain growth rates under more natural conditions of temperature and light. Modifications have since been made.

4.9. Growth and Survival of Paraleptophlebia sp.

Paraleptophlebia sp. nymphs were collected from Oak Creek, Oregon, and carefully measured for total length. Eight animals, all of the same initial

length, were introduced into 1ℓ flasks. Substrates and other conditions are given in Table 12. Pre-measured Papaleptophlebia sp. (each set of the same intitial total length) were also placed in chambers containing substrates listed in Table 13 and in individually aerated vials containing substrates listed in Table 14 in order to compare growth rates obtained in flasks with those in flow-through chambers and in vials. This procedure was adopted to minimize effects of natural variation and mortality on experimental results.

4.10. Growth of Collectors and Grazers in a Fire - Affected Basin

Ephemerella doddsi and Optioservus sp. were collected from Connection Creek (Mary's Peak, Benton Co., Oregon) and Ptychoptera sp. from Berry Creek, Oregon, and microscope-sorted into size categories. Three animals of a given size were placed in individually numbered 3 dram vials with mesh attached to either end to allow water to flow through. They were transferred in an aerated cooler to the drainage of the Middle Fork of the Salmon River, Idaho. Sediment from Little Creek, an area that burned approximately one year before, and from the East Fork of Indian Creek, an unburned stream of similar temperature and size were sorted into 53-125 µm, 125-250 µm and 1-4 mm size classes and introduced into the vials with animals. Subsamples for initial dry weight estimates were taken at the time the sediments were introduced. Final dry weights were measured after 21 days.

Ephemerella coloradensis, E. tibialis, Cinygma sp., Baetis bicaudata, and Simulium sp. were collected from the West Fork of Little Loon Creek, affected by the burn, and White Creek, a control stream of the same approximate size and thermal regime, in order to compare total length: dry weight regressions. Neothrema sp. pupae and Neophylax sp. prepupae were also collected in order to compare pupal dry weights.

Table 12. Substrates and relative conditions for Paraleptophlebia sp. in flasks.

Treatment	Substrate	Conditions	% Organic Matter Initial	Final
Set I				
1	Alder, equal amounts of 53-125, 125-250, 250-500 µm	Aerated, in distilled water.	96.4	96.5
2	Maple, equal amounts of 53-125, 125-250, 250-500 µm		91.5	94.4
3	Fern, equal amounts of 53-125, 125-250, 250-500 µm		95.9	98.1
4	Sawdust, equal amounts of 53-125, 125-250, 250-500 µm		99.9	100.0
5	Alder:Sand (4:1), 53-125 µm		23.6	18.7
6	Alder:Sand (1:4), 53-125 µm		11.6	3.4
Set II				
1	Alder, equal amounts of 53-125, 125-250, 250-500 µm	Aerated, in filtered stream water	96.3	95.4
2	Maple, equal amounts of 53-125, 125-250, 250-500 µm		94.0	91.8
3	Fern, equal amounts of 53-125, 125-250, 250-500 µm		95.0	96.5
4	Sawdust, equal amounts of 53-125, 125-250, 250-500 µm		99.8	93.4
5	Alder:Sand (4:1), 53-125 µm		30.8	23.8
6	Alder:Sand (1:4), 53-125 µm		18.4	5.5
Set III				
1	Alder, equal amounts of 53-125, 125-250, 250-500 µm	Not aerated, in filtered stream water	96.7	96.7
2	Maple, equal amounts of 53-125, 125-250, 250-500 µm		90.8	93.4
3	Fern, equal amounts of 53-125, 125-250, 250-500 µm		95.7	97.1
4	Sawdust, equal amounts of 53-125, 125-250, 250-500 µm		99.0	99.5
5	Alder:Sand (4:1), 53-125 µm		28.6	26.0
6	Alder:Sand (1:4), 53-125 µm		6.1	2.1
Set IV				
1	Alder, 53-125 µm	Aerated, in filtered stream water	93.7	95.7
2	Alder, 125-250 µm		95.0	87.5
3	Alder, 250-500 µm		95.7	96.1
4	Alder, 500 µm - 1 mm		96.6	95.8
5	Maple, 53-125 µm		89.5	93.0
6	Fern, 53-125 µm		98.1	99.3
Set V				
1	Stream sediment, 53-125 µm	Aerated, in filtered stream water	9.3	9.0
2	Stream sediment, 125-250 µm		10.7	11.9
3	Stream sediment, 250-500 µm		9.8	3.6
4	Stream sediment, 500 µm - 1 mm		9.0	5.6
5	Stream sediment, 1 - 4 mm		17.6	33.7
6	Stream sediment, unsieved		52.3	57.8

Table 13. Substrates presented to Paraleptophlebia sp. in flow-through chambers.

Treatment	Substrate	$\bar{x}$ % Organic Initial	Final
A	Alder, equal amounts, 53-125, 125-250, 250-500 µm	95.7	95.8
B	Maple, equal amounts, 53-125, 125-250, 250-500 µm	92.3	92.0
C	Fern, equal amounts, 53-125, 125-250, 250-500 µm	92.6	95.4
D	Sawdust, equal amounts, 53-125, 125-250,250-500 µm	93.5	98.6
E	Alder:Sand (4:1), 53-125 µm	12.7	19.0
F	Alder:Sand (1:4), 53-125 µm	4.3	2.8
G	Alder, 53-125 µm	96.1	92.5
H	Alder, 125-250 µm	88.8	93.0
I	Alder, 250-500 µm	92.5	93.5
J	Alder, 500 µm - 1 mm	94.1	94.6
K	Maple, 53-125 µm	87.0	85.5
L	Fern, 53-125 µm	92.2	94.1
M	Stream sediment, 53-125 µm	16.9	13.9
N	Stream sediment, 125-250 µm	5.1	4.1
O	Stream sediment, 250-500 µm	4.5	3.6
P	Stream sediment, 1-4 mm	25.0	32.9

Table 14. Substrates provided for Paraleptophlebia sp. in individually aerated vials.

Treatment	Substrate	$\bar{x}$ % Organic Initial	Final
AA	Alder, 53-125 µm	91.3	94.1
BB	Alder, 125-250 µm	92.9	93.9
CC	Alder, 250-500 µm	97.0	93.0
DD	Alder, 500 µm - 1 mm	92.0	92.8
EE	Stream sediment, 53-125 µm	10.7	6.8
FF	Stream sediment, 125-250 µm	16.1	4.3
GG	Stream sediment, 250-500 µm	6.5	3.8
HH	Stream sediment, 1-4 mm	---	4.8

4.11. Ptychoptera sp. Growth on Mt. St. Helens Ash

Sediments were collected from progressively more heavily impacted sites on Mt. St. Helens: Elk Creek, Upper and Middle Clearwater, Muddy River and Ape Canyon, and sorted into 53-125 µm and 125-250 µm particle size categories. Ptychoptera sp. from Berry Creek, Oregon were size-classed and allowed to feed on these substrates in aerated flasks with filtered stream water. Initial dry weights were estimated from subsamples taken from each size class.

5.0 A Review of Feeding Strategies and Effects of Food Quality on Growth and Survival of Selected Stream Macroinvertebrates

R.L. Mattingly

The following review of selective feeding and its ramifications is provided in an attempt to bridge recent and proposed studies of stream macroinvertebrates, particularly those animals that collect fine particulate organic matter (FPOM), e.g. collector-gatherers (Merritt & Cummins 1978) such as Ptychoptera sp. and Ameletus sp. Collectors have been defined as a functional group of stream macroinvertebrates feeding on particles ranging from 0.45 μm to 1 mm in diameter (Cummins 1973). These particles are derived from, or consist of: both shredder and collector feces; organic and inorganic particles (and associated microbes and adsorbed organics); fragments of algae, macrophytes and animals; particles formed by flocculation of dissolved organic matter (DOM); and microbes. Food quality of each of these categories may vary greatly depending on such things as age of the animal, species of, for example plant or animal from which the food particles are derived, light period, and growth phase. Food quality also depends on the relative contribution of each of these categories to the total food resource, and the relative composition of the resource changes on a seasonal basis.

Although its significance as an input both from the surrounding watershed and from upstream areas has been established (Hynes 1963; Minshall 1967; Fisher & Likens 1973), the role of allochthonous organic matter and its associated microflora in the nutrition of stream macroinvertebrates has received less attention (Hynes 1970; Cummins & Klug 1979). Events in the riparian ecosystem in large part determine the quantity and the quality of organic material that enters the stream (Nelson 1969; Cummins 1974; Hynes 1975).

Minshall (1978) recently emphasized the potential significance of stream autotrophy, both as a direct food source and as a part of the detrital food chain. Many invertebrates ingest both FPOM and algal material scraped from surfaces, depending on such parameters as particle size (e.g. Wieser 1956; Lopez and Levinton 1978). In addition, seasonal variation in consumption of algae and detritus frequently occurs (e.g. Chapman & Demory 1963; Cummins 1964).

Activities which lead to, for example, increased sedimentation and changes in flow and temperature regimes may affect the benthos by physically, chemically, and microbiologically altering the food resource and habitat (e.g. Paerl & Goldman 1972; Moring 1975; Ringler & Hall 1975; Malmqvist et al. 1978; Lehmkuhl 1979). Animals which are able to selectively ingest preferred substrates are probably less vulnerable, at least initially, to such alterations than are those which feed indiscriminantly on available substrates. However, both spatial and temporal distribution, and growth of animals which do not select may be more amenable to experimental manipulations of size distribution, quality, and total amount of fine particulate organic matter inputs (Rabeni & Minshall 1977; McLachlan et al. 1978; Cummins et al. 1979). Some invertebrates, e.g. shredders, have been proposed to select for detritus maximally colonized by microbes (Kostalos 1971; Barlocher & Kendrick 1973). However, others, e.g. collectors, have been proposed to select particles on the basis of size, independent of food quality (Cummins 1974; Cummins & Spengler 1978; Cummins & Klug 1979).

References to both selection and food quality are frequently ambiguous, in large part because selection may be made on a variety of bases. Among these are: 1) particle size, the diameter of particles ingested vs. that available (Chance 1970; Wallace 1975), 2) food quality, e.g. organic, nitrogen or caloric content of gut material and feces vs. that of the available

substrate (Brinkhurst et al. 1972; Davies 1975; Hylleberg & Gallucci 1975; Zimmerman et al. 1975; Bolton & Phillipson 1976), 3) habitat and behavior, e.g. a midge which changes the shape of its tube seasonally and thereby utilizes a different food resource (Wieser 1956; Egglishaw 1964; Eriksen 1964; Jonasson 1972; McLachlan 1977), 4) digestive capability, e.g. ability to digest and assimilate a given species or type of bacteria (Fredeen 1964; Chua and Brinkhurst 1973; Baker and Bradnam 1976), and 5) combinations of the above, e.g. ingestion and assimilation, and particle size and behavior (Chua & Brinkhurst 1973; Wallace 1975; McLachlan 1977). In a similar way, food quality may vary greatly (also see Appendix I), and has been described as: 1) microbial biomass, e.g. as measured by ATP (Suberkropp & Klug 1976; Geesey et al. 1978; Perkins & Kaplan 1978; Ward & Cummins 1979) or by direct count, 2) microbial activity, e.g. respiration (Gilson 1963; Ward & Cummins 1979) and organic substrate uptake, 3) presence/absence of various biochemical constituents, 4) total content of organic matter (King 1978; Mattingly et al. 1980), nitrogen (McMahon et al. 1974), or protein (Lowry et al. 1951; Kaushik & Hynes 1971), or amino acid composition, 5) texture, 6) presence of an organic film (e.g. Meadows 1964; Lopez and Levinton 1978), and 7) ability to produce animal growth (Cummins & Klug 1979).

Arguments against selection for food quality by collectors generally have been based on studies with suspension feeders (e.g. Simuliidae and Hydropsychidae) which filter particles of an ingestible size range from the water column (see review by Wallace & Merritt 1980). Ingestion of non-nutritious particles (such as charcoal or sand), as demonstrated by Ladle et al. (1972) and Mulla and Lacey (1976), cannot be taken as evidence against selection (Becker 1958; Cummins 1973).

Arguments for selection on the basis of food quality are generally grounded on studies in which, for example, organic, nitrogen, or caloric

content of gut material and/or feces of deposit feeders is compared with that of the ingested sediments. None of the food quality measures are adequate. For example, direct count may not give the proportion of live to dead cells or adequately account for the biomass of fungal hyphae. Respiration is generally measured in chambers which alter flow and possibly temperature, and add surface area for colonization. Organic content may not indicate the amount of material that is useful to the animal, and, likewise, nitrogen may not indicate the amount that is available. Thus, even if food quality is chosen as the particular basis for selective feeding, the question of what this means to the animal remains. An attempt to construct a generalized nitrogen budget for a stream collector (Fig. 1, Appendix II) indicates the need for a more sophisticated approach to the question of selective feeding by these animals.

Many studies suggest that deposit feeders depend for their nutrition on microbes, directly (microbial biomass) or indirectly (microbial alteration of the substrate), associated with the particles they ingest (Newell 1965; Fenchel 1970; Wavre & Brinkhurst 1971; Hylleberg Kristensen 1972; Berrie 1976; Yingst 1976; Lopez et al. 1977; Rossi & Fano 1979). In addition, although epilithic detritus is richer in organic matter, protein and total potential energy than other sediments, it is probably utilized by animals indirectly through associated bacteria (Madsen 1972; Calow 1975), and microbes attached to algae may in some cases support invertebrate growth (Smyly & Collins 1975). Food quality may vary depending on particle size (Hargrave 1972a; Dale 1974; Brennan et al. 1978), temperature and the relative contribution of each food source, all of which vary seasonally (e.g. Perkins & Kaplan 1978). In some cases, food quality may be relatively more important than temperature in controlling the growth rates of stream invertebrates,

e.g. Paratendipes albimanus (Ward & Cummins 1979) and Stictochironomus annulicrus (King 1978), and also may have a stronger influence on assimilation efficiencies, as shown for slugs (Davidson 1976).

Any consideration of invertebrate feeding and food quality must recognize that nutritional requirements, feeding mode, and habitat of invertebrates may vary with life stage (Brown 1961; Anderson & Cummins 1979), season (Chapman & Demory 1963; Mason & Bryant 1975), and environmental conditions (Kajak & Warda 1968; Izvekova 1971; McLachlan 1977). Ingestion, egestion, and gut passage rates and assimilation efficiencies may vary with food quality (McCullough et al. 1979a; Rossi & Fano 1979) and quantity (Kajak & Warda 1968), life stage (Mulla & Lacey 1976), and temperature (Armitage 1968; Hargrave 1972b; Zimmerman & Wissing 1978). Food quality may change animal growth rates during a particular phase, but have little effect over the entire life cycle, or it may enable animals to emerge at different times or to reach different weights at maturity. Life cycles may be keyed into seasonal availability of required substrates (Vannote & Sweeney 1979), and seasonal change in rates of processing may be important in the exchange of dissolved material with the water column (Nichols 1974).

Evidence that diatoms grow at an exponential rate (Fenchel & Kofoed 1976) and microbial biomass associated with particles increases (Lopez et al. 1977) when animals graze on them, and also that particle size distributions may be modified (e.g. O'Connors et al. 1976) indicate that animal feeding may alter the food resource. Invertebrate feces are a potential food resource (Newell 1965; Ladle et al. 1972; Cummins et al. 1973; Hargrave 1976), and deposit feeders in general probably both enhance their food supply and stimulate sedimentary organic matter decomposition by reworking the substrate, thereby increasing space for microbes (Hargrave 1976). Cop rophagy may accelerate the breakdown of feces and also play a role in the cycling

of elements (Boothe & Knauer 1972). Similarly, soil fauna may stimulate decomposition because of increased microbial activity (Standen 1978). Invertebrates also excrete dissolved organic compounds which may increase the rate of recolonization of fecal material (Hargrave 1970).

Differential selection and/or assimilation of food materials could in part determine the effect of an invertebrate on co-occurring species, particularly those closely related in function (e.g. Rossi & Fano 1979). In addition, the feces of one animal may be the preferred substrate of another (Chua & Brinkhurst 1973). Interactions probably occur, both within and between functional groups; for example, collector growth may be enhanced when shredders are present (Cummins et al. 1973; Short & Maslin 1977). The role of the intestinal flora of aquatic invertebrates in modifying feces and in promoting growth is undoubtedly important, but remains to be thoroughly investigated (Whitley & Seng 1976; Meitz 1977; Cummins & Klug 1979; Klug & Kotarski 1980). Food partitioning by particle size has been demonstrated for both filter feeders (Wallace 1975) and deposit feeders (Fenchel et al. 1975; Fenchel & Kofoed 1976). At least for filter feeders, this is thought to impede energy and nutrient losses downstream (Wallace et al. 1977; McCullough et al. 1979b).

Functional group designations are based on feeding mode, but functional groups have been separated to date on the basis of gut content analyses which only indicate food ingested (Cummins & Klug 1979). Because the majority of macroinvertebrates are opportunistic in their ingestion, the ways in which functional designations may facilitate understanding of stream ecosystem processes need to be verified and refined (e.g. Anderson 1978; Anderson & Sedell 1979). In addition, the meaning and use of the terms "selective feeding" and "food quality" obviously need to be clarified before the relative impact of alterations in the FPOM resource, particularly on gathering collectors,

and the impact of these animals, both on the resource and on co-occurring species can be assessed. Any solutions will require, at the very least, a combination of techniques, careful attention to experimental design, very careful observation, and knowledge and understanding of the animal's natural history.

ACKNOWLEDGEMENTS

Preparation of this paper was funded by Department of Energy Contract DE-AT06-79EV 10004, Environmental Programs, Division of Biomedical and Environmental Research.

Portions of this review were presented as:

Mattingly, R.L. & Cummins, K.W. Effects of food quality on growth and survival of selected collector-gatherers. Twenty-eighth Annual Meeting, North American Benthological Society. March 26-28, 1980. Savannah, Georgia.

Fine particulate organic matter (FPOM) was collected during autumn from the South Fork of Rock Creek (Mary's Peak, Benton County, Oregon). Samples were fixed in 5% formaldehyde solution, freeze-dried with liquid N_2, and mounted on stubs and vacuum-coated with a gold-palladium alloy.

These scanning electron micrographs provide an indication of the variable nature of this food resource. A particle may appear as an amorphous mass of material comprised of (probably) largely refractory compounds (Fig. 1) with associated microbes and other particles (Fig. 2), diatoms (Figs. 3 and 4), and fragments (Figs. 5 and 6). Measurements of the quality of FPOM currently requires a range of techniques, none of which adequately estimate the value of specific components to animals which feed on this resource.

Sediments collected during the summer from the South Fork of Rock Creek and from Berry Creek, Oregon were sieved to size fractions of 53-125 µm, 125-250 µm, 250-500 µm, 500 µm - 1 mm, and total, and analyzed for total organic content (Table 1). Wide variations were found among sites, but relatively less, and with larger standard deviations, among particle classes for each stream. Freshly deposited samples taken from the South Fork of Rock Creek contained, on the average, a higher organic content, and those from Berry Creek, approximately the same organic content as those reported in Table 1.

Table 1. Mean percent organic content (± standard deviation) of sediment samples collected from the South Fork of Rock Creek (A) and from Berry Creek (B), Oregon.

SITE (All Particle Sizes)	Mean % Organic A	B
1	5.89 ± 1.48	10.45 ± 1.35
2	3.53 ± 1.09	26.03 ± 17.18
3	4.99 ± 1.72	7.32 ± 3.91
4	38.14 ± 19.55	29.11 ± 13.13
5	5.09 ± 2.40	12.71 ± 2.23
6	8.47 ± 4.51	9.44 ± 3.27
7	4.40 ± 0.93	73.94 ± 7.13
8	14.06 ± 8.81	47.63 ± 11.97
9	9.10 ± 4.39	31.90 ± 10.59
10	4.77 ± 1.65	31.86 ± 14.52
Particle Size Range		
53-125 µm	10.29 ± 5.45	21.84 ± 15.10
125-250 µm	9.58 ± 8.11	26.33 ± 21.08
250-500 µm	9.27 ± 11.04	28.75 ± 23.51
500 µm - 1 mm	10.03 ± 16.21	37.53 ± 26.19
TOTAL	10.05 ± 17.07	26.24 ± 22.52

APPENDIX II. Elements of a Nitrogen Budget for a Stream Collector

The framework for a simplified nitrogen budget for a generalized stream collector-gatherer may serve to point up the state of knowledge about nitrogen, the forms it assumes and interconversions, and the relative availability of these forms to the invertebrate. It also indicates the sparsity of information about the microbiology of insects in general and its potentially critical role in insect processing of food material and overall function. The problems which may be encountered in conducting feeding experiments of short duration, e.g. secretion of nitrogen compounds under stress or mobilization of storage material, may interfere with data interpretation; likewise, the unknown fate of nitrogen once it enters the animal may affect analyses of studies which compare the content of food available for ingestion with material in the gut (or egested) assuming the difference was assimilated by the animal. Involved processes must be elucidated before the impact of individual organisms on the function of associated species and on the function of the system of which they are a part of may be understood.

A simple diagram of a preliminary nitrogen budget for a generalized collector-gatherer is presented in Fig. 1. The internal anatomy of Chironomus sp. (Fig. 2; modified from Wesenberg-Lund 1943) indicates its potential for fairly complex physiological processes. The system is divided into six "compartments": foregut-midgut, animal tissue, fat-body, hindgut, lumen bacteria, and attached microflora. One prerequisite in constructing a budget of this type is that a time period be carefully delimited. This is especially important seasonally, particularly with multivoltine species, and because food requirements and growth rates may vary with life stage. In addition, the length of a larval instar will vary depending on the temperature regime of a given year.

Such times as the prepupal period, which occurs at the end of the terminal instar in some species, and during which the animal does not feed, must also be considered.

Ingestion (I) includes nitrogen in both material on which a collector feeds, and water ingested with the food. The origin of the food substrate, along with the relative contribution of each source to the total food resource, largely defines the amount (and form) of nitrogen taken in by the animal. The relative contribution of each source to the total may vary seasonally in a given stream environment. Nutritional requirements (Anderson & Cummins 1979), feeding mode (Jonasson 1972; McLachlan 1977), and habitat of invertebrates may vary with life stage, season, and under different environmental conditions. Ingestion (and egestion), growth rate, and assimilation efficiency vary, depending on food quality (Davies 1975; Ward 1977; King 1978), amount of food available, animal life stage (Hargrave 1970), and temperature (Zimmerman & Wissing 1978). Consumption indices may be used to estimate the amount of food consumed over a given period. Gut analyses to determine the various sources of this food, however, are subject to error introduced by differential digestion of material ingested.

Ward (1977) and King (1978) found a poor relationship between the nitrogen contents of food and larval growth. The bulk of material ingested by deposit-feeders is probably indigestable, being comprised of relatively refractory nitrogen compounds. Rapid passage of this material along the gut allows little time for digestion. Thus, the major portion of the deposit-feeding organism's diet may consist of microbes (Bjarnov 1972). The availability of nitrogen both to the microbes and to invertebrates is a key question. Nitrogen ingested with the food is associated with the interconversions of nitrogen in the guts of animals, and the multiplication of bacteria in gut contents retained for more than a few hours. Short retention times, however, may help

minimize problems associated with this. For example, in the lab Chironomus thummi retains food for less than two hours (Baker and Bradnam 1976). In addition, organic matter may leak from food material during its ingestion (Conover 1966).

Along with nitrogen ingested as food is that taken in from water accompanying the food material. The amount of water may be estimated from determinations of water content of detritus, algae, and animal fragment food. The nitrogen content of salivary gland enzymes secreted into the foregut and digestive enzymes secreted into the midgut is not known.

Outputs from the foregut-midgut compartment include nitrogen in material assimilated (A) by the animal, and that which is passed on (D) to the hindgut. Material then is assimilated (A) taken across the gut wall to be incorporated into animal tissue, respired (R), lost as exuviae (cast skins; X), stored (S) in or mobilized (M) from the fat body, excreted by the Malpighian tubules (P) or actively transported as amino acids (T) from the rectum. As already mentioned, assimilation efficiency and animal growth vary with food type, animal age, and temperature. Monakov (1972) in a review of invertebrate feeding reports that, whereas indices of assimilation vary widely for most invertebrates, they rarely exceed 50%. Hargrave (1970) reports a wide range of assimilation efficiencies for Hyalella azteca, a deposit-feeding amphipod, when fed various organic substrates. Assimilation (A) includes nitrogen from detrital food, including bacteria, and dissolved organic nitrogen (DON, < 0.5 μm) released as bacterial extracellular products or resulting from lysing of cells in the midgut and the hindgut. These include lumen bacteria and the attached microflora, which Meitz (1975) has described as dense mats of bacterial filaments associated with the gut wall. This material is assimilated directly by bacteria and/or their enzyme systems. Animals may vary in organic nitrogen content; for example, Trama (1957) found organic N values of 11.0, 10.6, 10.3 and 8.9%

of dry weight for 4, 5, 6, and 7 mm Stenonema pulchellum nymphs, respectively. Exuviae probably differ in organic (Wilhm 1970), and therefore nitrogen, content from the rest of the animal tissue.

An undetermined quantity of nitrogen may be stored primarily as urate in the fat body of insects, a tissue which may be of considerable size. Nitrogen thus stored is generally thought to be destined for excretion, but Cochran (1975) reports mechanisms by which it may be mobilized in times of need, e.g. by symbionts or protein-bound physiological processes.

Other transfers include excretion loss through the Malpighian tubules (including diffusion of amino acids from the haemolymph - see Cochran 1975, and possible secretion of nitrogenous substances under stress - see Davies 1975) and active transport of amino acids from the rectum. Imms (1964) cites references alluding to great variations in chemical composition of urine excreted by the Malpighian tubules, depending on the nature and the amount of food taken, and, in aquatic forms, on the ionic composition of the external medium. Baldwin (1970) reports percentages of total nitrogen excreted in various forms by invertebrates; these data were obtained by averaging analyses of excreta of seven aquatic species, and are reported as percent of total nitrogen: ammonia, 52.2; urea, 6.1, uric acid, 1.3; amino acids, 14.0; and 26.5% undetermined. These values, which are presumably fairly typical of aquatic invertebrates, indicate that ammonia is the major nitrogenous end-product. Trama (1957) found that ammonia comprised 80-100% of the total nitrogenous excretion of Stenonema pulchellum nymphs, a loss of 10% of body nitrogen daily (a value he believed to be ten times too large). Johannes and Satomi (1966) demonstrated that Palaemonetes pugio lost 33% of carbon ingested as soluble excretory products. These findings indicate that, though excretory losses are generally assumed to be negligible in calculating energy budgets (Cummins 1975), they may be significant in constructing nitrogen budgets.

Potential volatilization of ammonia as demonstrated for terrestrial isopods and for Helix may also be a consideration.

Bacteria in the midgut may be those ingested with the food, whereas hindgut bacteria are probably residents. Estimations of hindgut volume, and of bacterial biomass and nitrogen content are required in order to calculate a total nitrogen budget. Microbial transfer and turnover of nutrients is rapid, but rates must be quantified before nitrogen uptake from the hindgut (U_1 and U_2) can be estimated. The microbes probably convert nitrogen in a form utilizable by the animal to an even more assimilable form, which may be essential to the function of the system. An estimate of nitrogen released by microbes as extracellular products and other substances, which may be directly assimilated by the animal, would be informative. Outputs (O_1 and O_2) to the hindgut are in the form of amino acids, which can be taken up by the rectum, and lysed cell products, which can be similarly utilized. Mechanical sloughing and death of attached microflora (L), which then become part of the lumen bacterial system, may provide additional output.

The amount of nitrogen passed on to the hindgut (D) must also be determined. Baker and Bradnam (1976) report that Chironomus thummi digests at least half the bacteria it ingests in situ, and that it does not appear to select for bacterial type (Gram negative vs. Gram positive). This contrasts with Fredeen's (1964) finding that a filter-feeding collector has reduced survival on Gram positive bacteria, presumably because of their thicker cell walls. Refined data on the amounts of bacteria and other components ingested, their assimilability, and the transfers which can occur in transit (microbially-mediated or otherwise) are required for such an estimate. Net movement of ammonia out of the midgut, and net movement into the hindgut against a concentration gradient (Cochran 1975) also must be considered. Deamination of amino acids is known to occur in the hindgut, and there is some question as

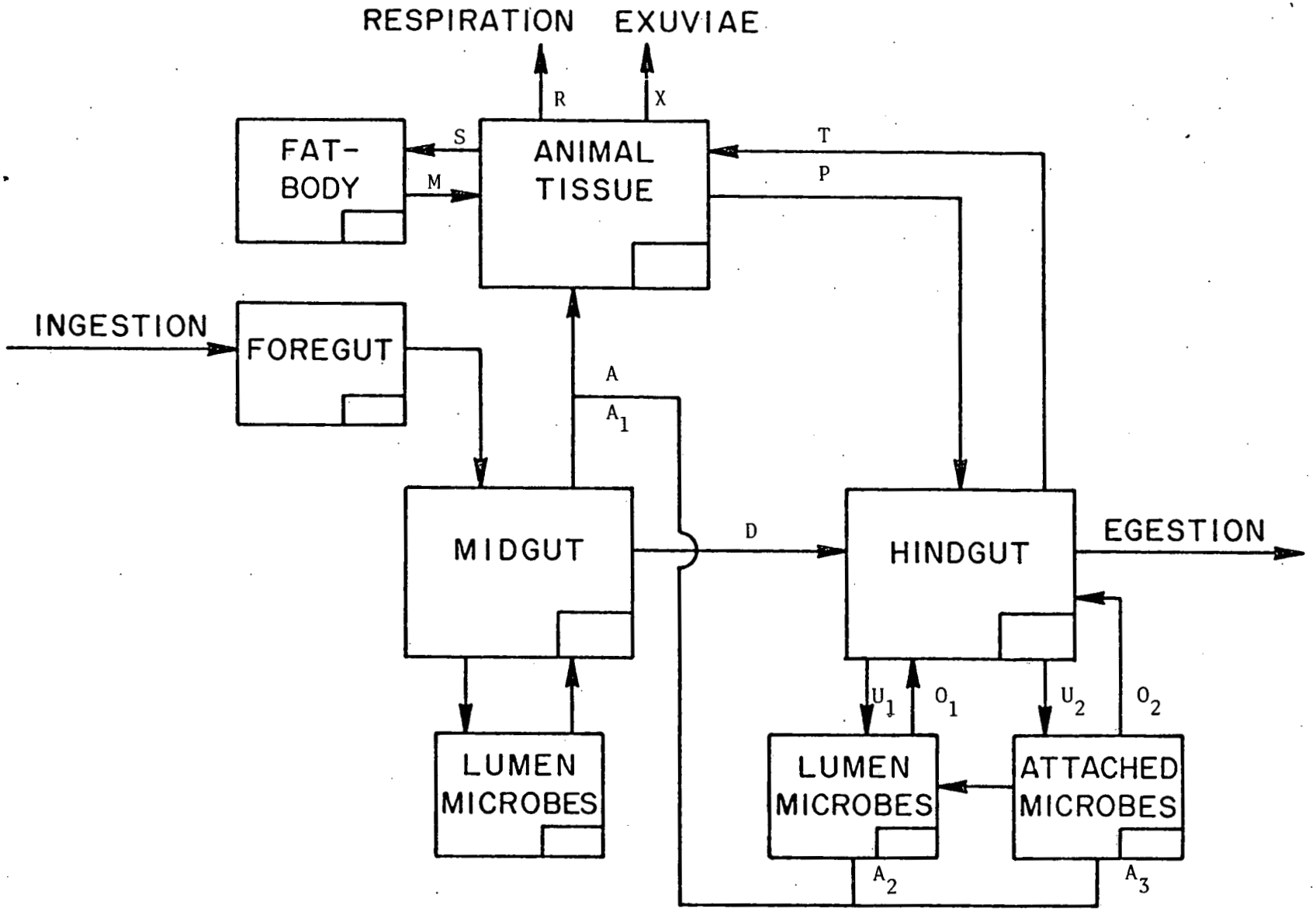


Figure 1. *COMPARTMENTS and TRANSFERS of a HYPOTHETICAL NITROGEN BUDGET for a GENERALIZED STREAM DETRITIVORE*

to whether or not nitrogen fixation occurs there as well (Cochran 1975). Loss of nitrogen through secretions such as those involved in tube-building by midges must also be taken into account before an estimate of total nitrogen egested (E) can be made. Baldwin (1970) suggests that high levels of amino acid secretion (up to 30% in some cases) may be due to deficient metabolic machinery or "leakage" across the permeable body surface. Egested material (E) and cast skins (X) may be reingested. The role of feces in enhancing food supply, nutrient uptake and growth has been suggested (Cummins et al. 1973; Hargrave 1976; Short & Maslin 1977; Ward 1977), and requires further investigation.

The status of information on components necessary to calculate even a short-term nitrogen budget for a stream collector-type macroinvertebrate is poor. Interpretations of feeding strategies for such animals from simple, short-term input-output assessments are premature.

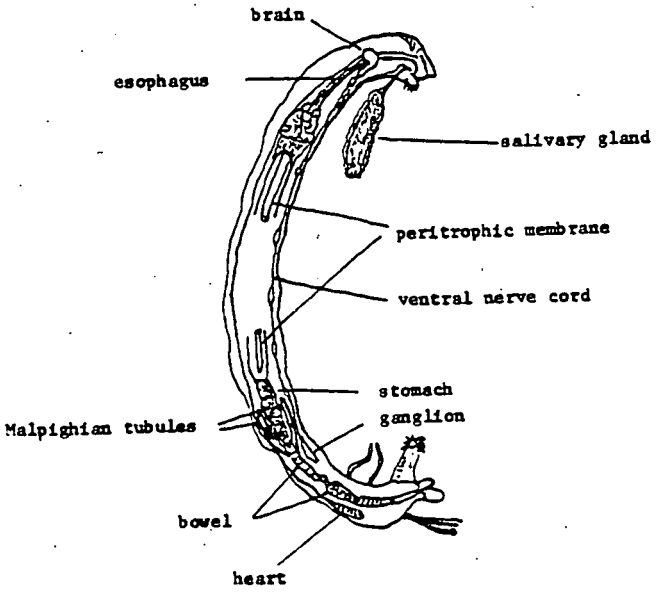


Figure 2. Schematic representation of the internal anatomy of Chironomus sp. (modified from Wesenberg - Lund 1943).

INTRODUCTION

In forested headwater streams a major source of allochthonous CPOM is autumn-shed leaves (Hynes 1963; Fisher and Likens 1972). Microorganisms, particularly aquatic hyphomycete fungi, and macroinvertebrates play an important role in the conversion of large particles such as leaves to fine particles, animal and microbial biomass and CO_2. In addition, microbial colonization increases the palatability and protein content of the leaves (Barlocher and Kendrick 1975a; Suberkropp and Klug 1980) increasing the potential for consumption by macroinvertebrates. In turn, conditioning and palatability has an important effect on macroinvertebrate consumption rates, growth rates, and survival (Barlocher and Kendrick 1975b; Kostalos and Seymour 1976). The contribution of large particle shredders to overall leaf processing has been estimated at less than 25% (Winterbourn and Davis 1976) to 32% (Cummins 1972). Many studies have shown that consumption rates will vary considerably, from 0% to well over 100% of the animals body weight being consumed per day, depending on life stage of the animal, leaf type, in stream conditioning time and temperature (Anderson and Grafius 1975; Nilsson 1974). These differences in consumption rates will have a significant impact on the amount of leaf litter processed if the contribution of shredders to total processing is high.

Both temperature and leaf type have been documented as important variables affecting community level processing rates (Suberkropp et al. 1975; Petersen and Cummins 1974). While leaf processing is faster at higher temperatures, leaf type, through food quality regulation of microbial and invertebrate activity, and the composition of the macroinvertebrate shredder community can moderate these differences (Anderson and Cummins 1979). Various investigators (Cummins et al. 1973; Sedell and Anderson 1979; Short and Maslin 1977) have

estimated the relative contribution of the microbial and shredder communities to leaf processing but there have been no attempts to directly measure the effect of temperature and leaf type on these processes.

In this experiment we have separated the microbial and macroinvertebrate contributions to leaf weight loss and have attempted to factor in the effects of temperature, over a range commonly encountered during peak leaf standing crop periods in Michigan. The weight loss of a rapidly processed leaf, basswood (Tilia americana), and one processed at an intermediate rate, pignut hickory (Carya glabra) was followed in the presence and absence of large particle shredders. Since macroinvertebrate shredders are known to play an important role in leaf processing, an additional objective of this work was to examine the effects of in stream conditioning time, food quality and temperature on the growth, consumption and gross growth efficiency of a common large particle shredder in our study area, Tipula abdominalis.

METHODS

Two experiments were carried out between December 1977 and April 1978 in two approximately 6000ℓ (11 m X 1.2 m X 0.6 m) artificial stream channels (Cummins 1972). Each channel contained 60% riffle and 40% depositional pool zones. Riffle sections had a sand and gravel substrate while depositional areas predominantly contained fine particulate organic matter (FPOM < 1 mm). These channels are excellent for studies of this kind because the size and discharge closely approximate that of many first-order streams. One channel was held at 5°C and the other at 10°C during the course of the experiments. Leaves of basswood and pignut hickory were collected just prior to abscission in October, 1977 and dried to a constant weight at 45°C.

In the first experiment (Fig. 1) 100 hickory and 100 basswood 6 gram leaf packs (Petersen and Cummins 1974) were attached to bricks and placed in the riffle sections (120 g/m^2). These type of packs have been shown to closely simulate leaf processing under natural conditions (Cummins et al. 1980). Fungal and bacterial innoculation was accomplished by adding foam, leaves, sticks, and other detritus from a first-order stream (Augusta Creek; Mahan and Cummins 1978), to each channel. After 2 weeks, epiflorescent microscopic examination of leaves demonstrated significant microbial colonization and visual observations showed that 585 Pycnopsyche spp. (instars II - V; mean dry weight = 7.80 mg) and 195 Tipula abdominalis (instars II and III; mean dry weight = 36.93 mg) were evenly distributed in sections of the channels that contained leaf packs. The Pycnopsyche used included P. lepida, P. guttifer, and P. scabripennis. Pycnopsyche spp. and Tipula sp. are known to feed readily on conditioned basswood and hickory leaves. The initial numbers and biomass added correspond to densities found on leaf packs in Augusta Creek. Leaf pack weight loss and shredder growth were measured by periodically removing several packs and the associated animals (Fig. 1). After all leaf packs had been removed, sediment from most of the riffle sections and some of the pool sections was removed and searched for animals.

In the second experiment, after all Pycnopsyche spp. and Tipula sp. had been removed from the channels, fifteen 6 gram basswood and hickory leaf packs were placed in each channel (Fig. 2). Weight loss of these packs, in the absence of shredders, was measured by the periodic removal of packs. In addition the consumption and growth of T. abdominalis was measured as outlined in Figure 2. Prior to use in the feeding experiment mid to late third instar Tipula sp. were kept in loose accumulations of basswood or hickory leaves at 2°C. Test organisms were isolated at 5°C without food for

Figure 1.

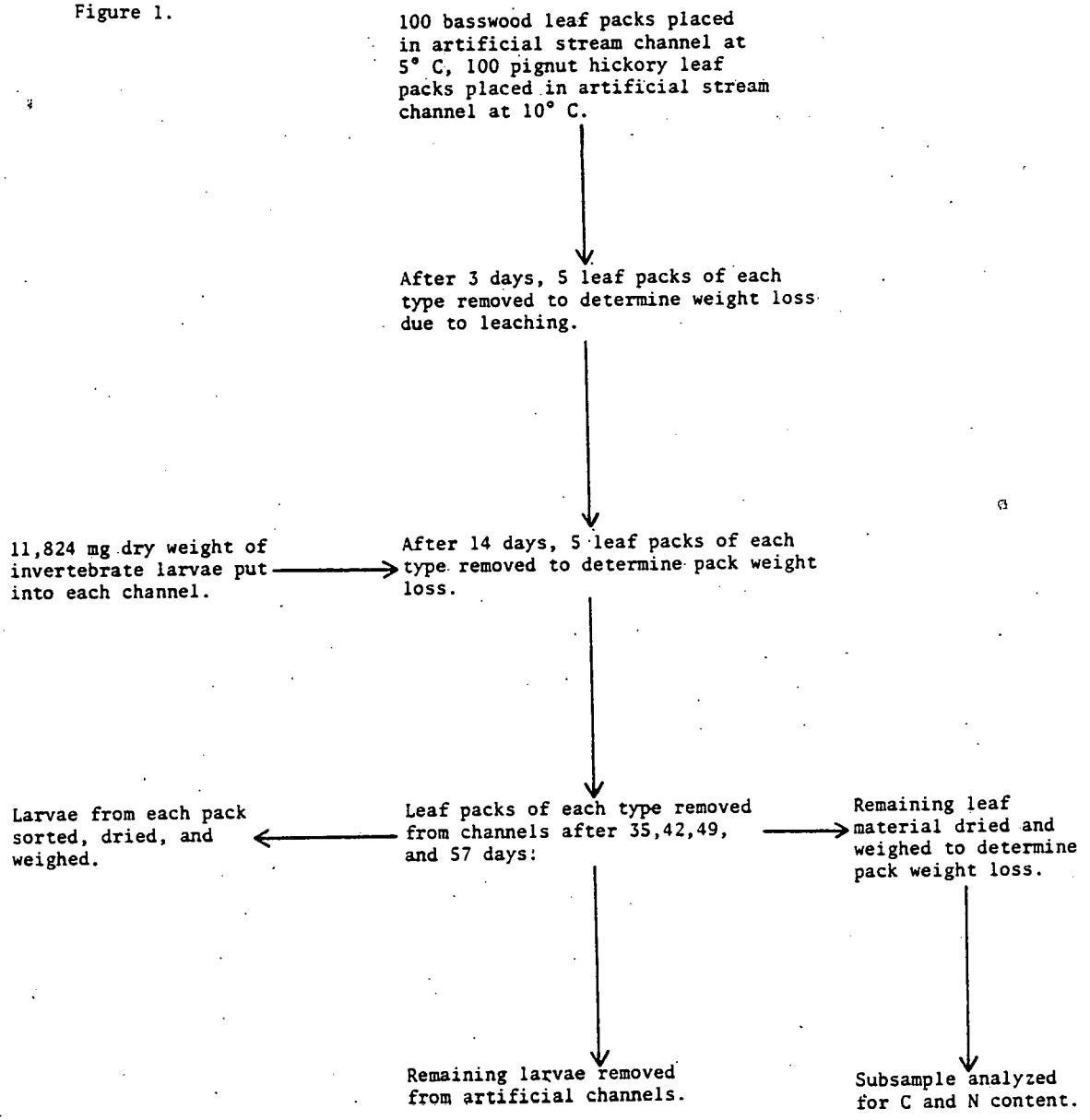
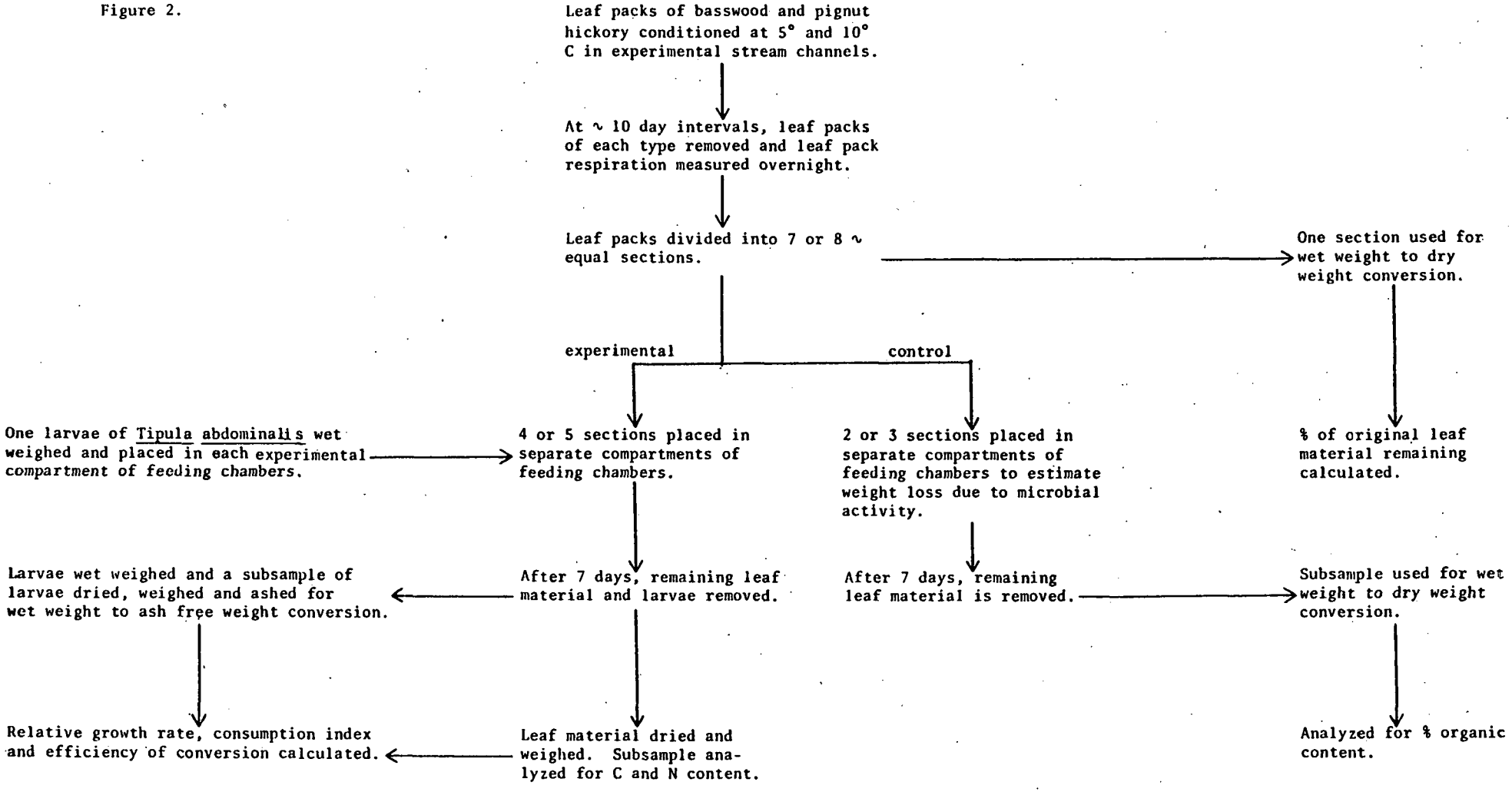

100 basswood leaf packs placed in artificial stream channel at 5° C, 100 pignut hickory leaf packs placed in artificial stream channel at 10° C.
After 3 days, 5 leaf packs of each type removed to determine weight loss due to leaching.
11,824 mg dry weight of invertebrate larvae put into each channel.
After 14 days, 5 leaf packs of each type removed to determine pack weight loss.
Larvae from each pack sorted, dried, and weighed.
Leaf packs of each type removed from channels after 35,42,49, and 57 days:
Remaining leaf material dried and weighed to determine pack weight loss.
Remaining larvae removed from artificial channels.
Subsample analyzed for C and N content.

Figure 2.


Leaf packs of basswood and pignut hickory conditioned at 5° and 10° C in experimental stream channels.
At ∿ 10 day intervals, leaf packs of each type removed and leaf pack respiration measured overnight.
Leaf packs divided into 7 or 8 ∿ equal sections.
One section used for wet weight to dry weight conversion.
experimental
control
One larvae of Tipula abdominalis wet weighed and placed in each experimental compartment of feeding chambers.
4 or 5 sections placed in separate compartments of feeding chambers.
2 or 3 sections placed in separate compartments of feeding chambers to estimate weight loss due to microbial activity.
% of original leaf material remaining calculated.
Larvae wet weighed and a subsample of larvae dried, weighed and ashed for wet weight to ash free weight conversion.
After 7 days, remaining leaf material and larvae removed.
After 7 days, remaining leaf material is removed.
Subsample used for wet weight to dry weight conversion.
Relative growth rate, consumption index and efficiency of conversion calculated.
Leaf material dried and weighed. Subsample analyzed for C and N content.
Analyzed for % organic content.

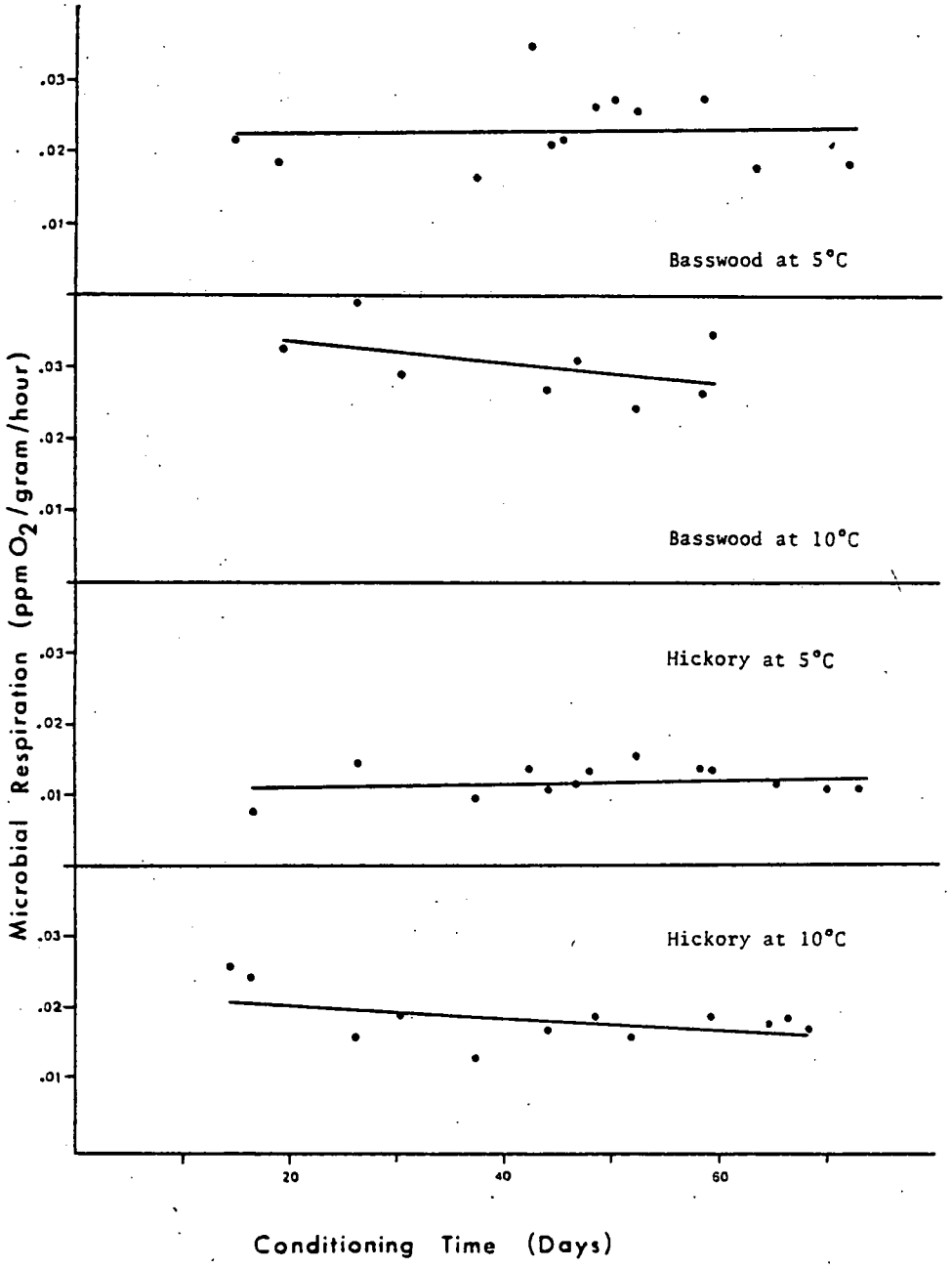


Figure 3.

Microbial respiration on basswood and hickory leaf packs.

Leaf Type	Temperature (°C)	CONDITIONING TIME (DAYS) 19	31	42	52	63	80	Mean RGR
Basswood	5	-1.0	1.3	1.2	1.4	2.0	2.0	1.6
Basswood	10	----	1.8	2.7	2.0	3.8	----	2.6
Hickory	5	----	0.9	1.5	1.5	2.0	1.1	1.4
Hickory	10	1.5	2.3	2.2	1.6	3.2	2.6	2.4

TABLE 1. The relative growth rates of T. abdominalis feeding on basswood and hickory leaves at two temperatures. Leaves were conditioned in artificial stream channels for the time indicated. Growth rates are depressed at the time of the first feeding experiment in most treatments. Mean values include rates after the initial conditioning has increased the food quality of the leaf to a level sufficient for near maximum growth. Each point is the mean of 4 or 5 individuals.

Leaf Type	Temperature (°C)	CONDITIONING TIME (DAYS) 19	31	42	52	63	80	Mean RGR
Basswood	5	13.8	11.7	15.6	12.0	18.3	19.1	15.1
Basswood	10	----	39.4	22.8	25.4	29.7	----	29.3
Hickory	5	----	24.6	24.8	23.4	18.3	36.0	25.4
Hickory	10	37.9	43.7	30.1	36.2	50.0	37.3	39.2

TABLE 2. The consumption indices of T. abdominalis feeding on basswood and hickory leaves at two temperatures. Leaves were conditioned in artificial stream channels for the time indicated. Each point is the mean of 4 or 5 individuals.

Leaf Type	Temp. (°C)	% Nitrogen	Microbial Respiration Rate	Gross Growth Efficiency
Basswood	5	3.1 - 3.9	0.023	11.1
Basswood	10	3.1 - 3.8	0.28-0.34	9.6
Hickory	5	1.2 - 2.2	0.012	7.2
Hickory	10	1.2 - 2.5	0.018	5.8

TABLE 3. The food quality, expressed as % Nitrogen and Microbial Respiration Rate (in ppm O_2/gram/hour) of basswood and hickory leaves and the gross growth efficiency of T. abdominalis. Microbial Respiration Rates are means over the experimental period except for basswood leaves at 10°C (the range is shown) which showed a declining respiration rate through time.

Leaf Pack Type	Temp. (°C)	Leaching (3day)	Microbial Utilization and Fragmentation	Macroinvertebrate Utilization	Total Weight Loss
Basswood	5	25.5	25.3	34.4	85.2
Hickory	10	18.4	18.8	56.0	93.2

TABLE 4. Partitioning of leaf pack weight loss based on processing rates with and without macroinvertebrate shredders present. Basswood packs were processed in 57 days (43 days with shredders) and hickory packs were processed in 49 days (35 days with shredders).

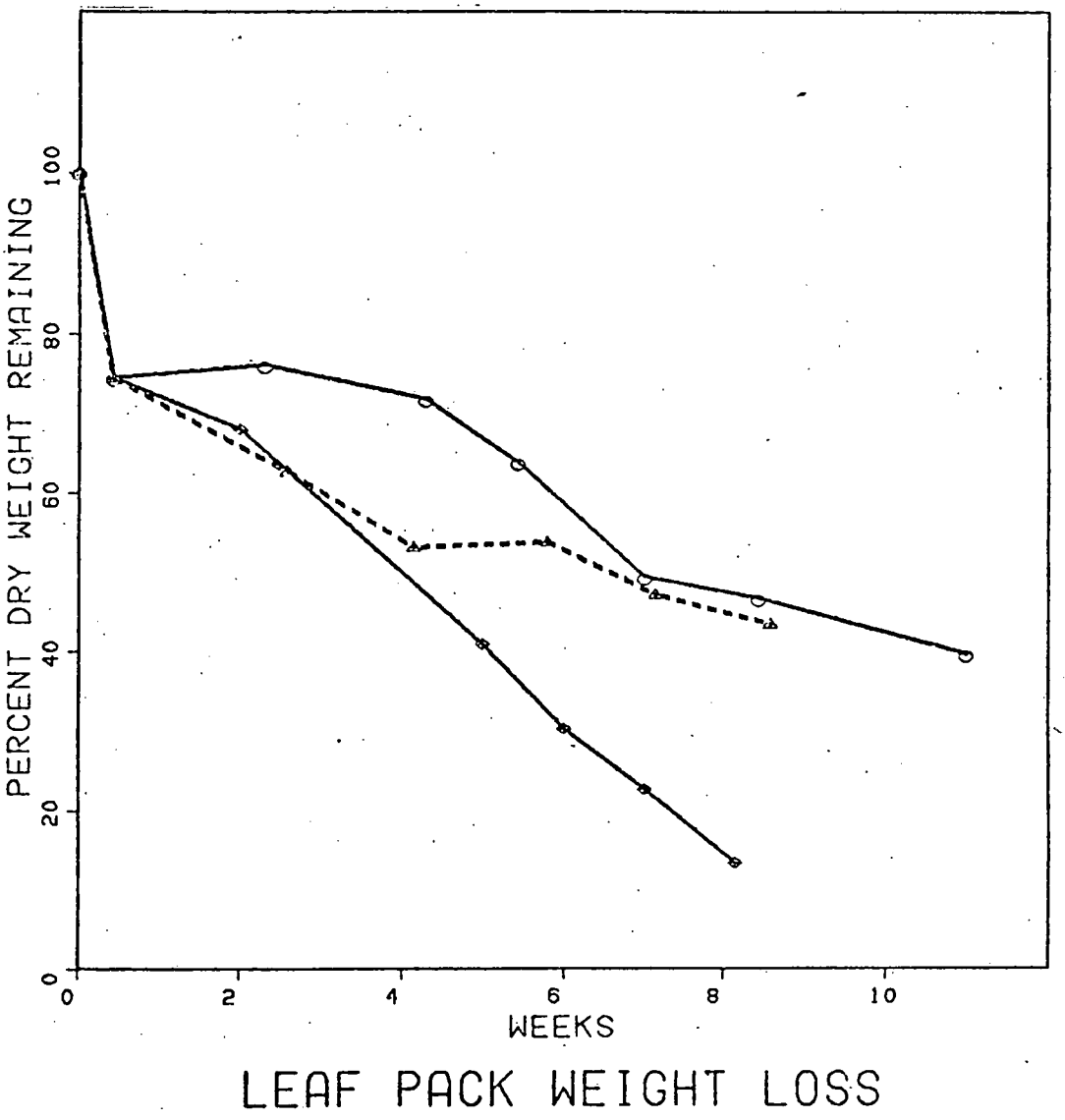


Figure 4.

◆- Basswood packs at 5°C with shredders - % loss/day = 1.87
o- Basswood packs at 5°C without shredders - % loss/day = 0.63
▲- Basswood packs at 10°C without shredders - % loss/day = 0.73

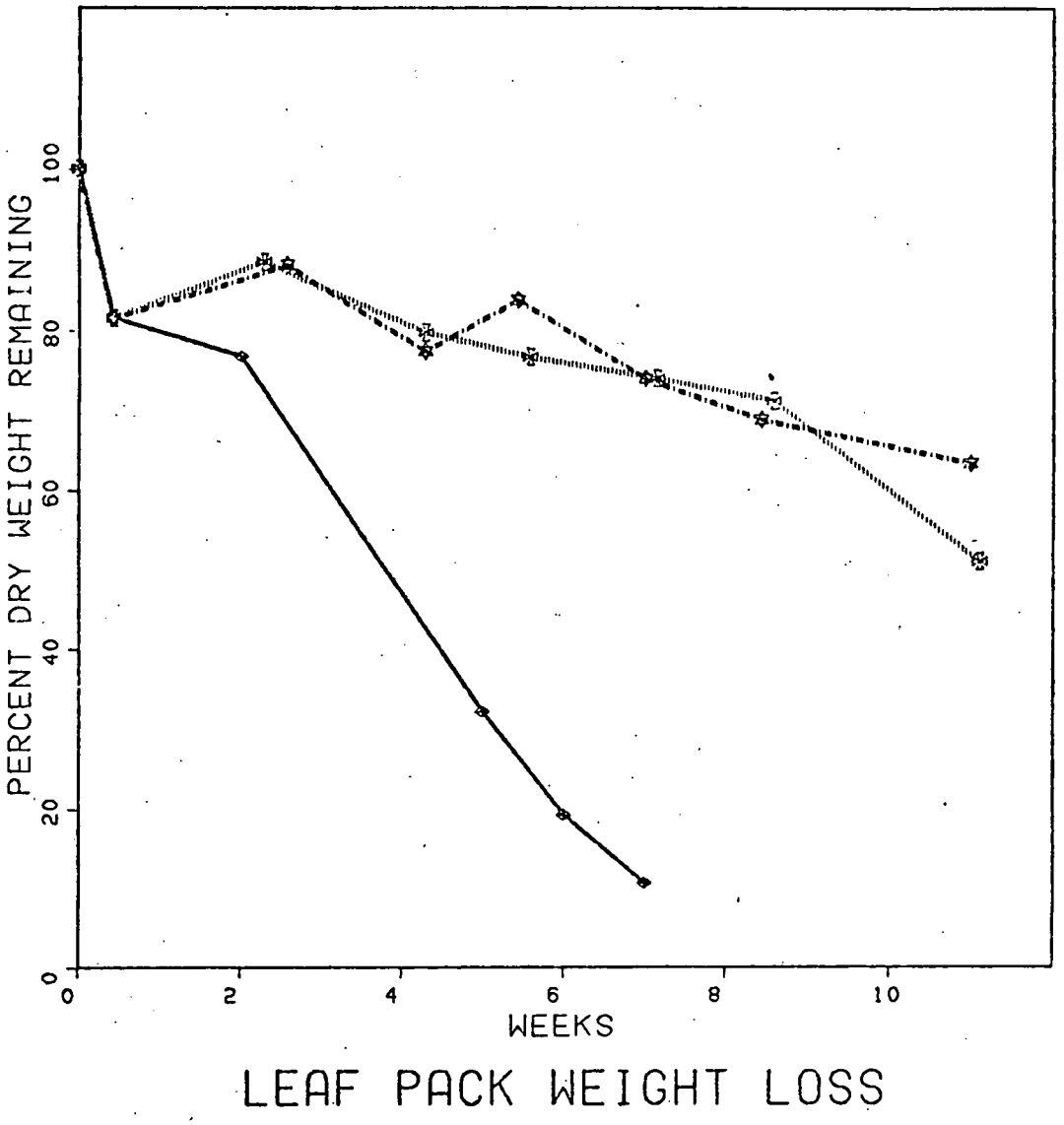


Figure 5.

◆- Hickory packs at 10°C with shredders - % loss/day = 2.46
✡- Hickory packs at 5°C without shredders - % loss/day = 0.30
✱- Hickory packs at 10°C without shredders - % loss/day = 0.50

five hours to allow evacuation of gut contents before and after the feeding period. Leaf material provided for feeding was always greater than twice the amount consumed.

Microbial respiration on leaf packs were measured every few days by placing two randomly selected packs in a closed, 12ℓ chamber with circulating stream water and measuring oxygen changes overnight (Bott et al. 1978). Carbon and nitrogen levels were determined from subsamples of leaf packs throughout both experiments on a Carlo-Erba C:H:N Analyzer.

RESULTS

Microbial respiration rate, leaf nitrogen content, and the growth and consumption of shredder larvae were used as indicators of the nutritive value or food quality of the leaf material.

Respiration rates reached a high level very quickly (Fig. 1). The first measurement, at 16 days, was near the maximum level reached over 10 weeks. In another study (Ward, unpublished data), hickory leaves in 80ℓ of recirculating stream water at 10°C showed microbial respiration rates near the 12 week maximum within 7 days. There were significant differences in respiration rates between all treatments. Respiration rates were influenced more by leaf type than by temperature, the progression being: basswood at 10°C > basswood at 5°C > hickory at 10°C > hickory at 5°C. Absolute rates of microbial respiration in the experimental channels were comparable in the two experiments but were considerably lower than rates on leaf discs from Augusta Creek determined using a Gilson respirometer (Dr. K.W. Cummins, Oregon State Univ., unpublished data). A large part of these differences could be due to higher rates on leaf surfaces that are exposed to the current and reduced rates on leaves nearer the center of a leaf pack.

Basswood leaves had a much higher nitrogen concentration than hickory leaves inititally, 3.1% to 1.2%, and at the end of the experiment, 3.8% to 2.3%. A gradual increase nitrogen content was observed for both leaf types throughout the experiment. Temperature differences had no effect on the %N of either leaf type (Table 3).

CONSUMPTION AND GROWTH RATES

Relative growth rates (Waldbauer 1968) of Tipula were low or even negative during the early stages of conditioning. At 10°C the leaf matrix required four weeks of conditioning while six was required at 5°C, to support growth rates that approached the maxima for a given leaf type and temperature. After the initial conditioning period growth rates remained relatively constant through time. Temperature-related differences in growth rate were greater than differences due to leaf type (Table 1). While growth rates increased between 5° and 10°C, there was no difference in the growth of T. abdominalis feeding on basswood or hickory leaves at the same temperature.

Consumption rates (% of body weight consumed/day) remained constant throughout the experiment. Even during the early stages of conditioning when growth rates were low, consumption was near the highest level reached in all the treatments. Mean consumption rates (Table 2) increased significantly with increasing temperature and food quality.

Since hickory leaves were consumed much more rapidly than basswood while the rate of growth of Tipula was the same on both leaf types, gross growth efficiency was higher on basswood leaves (Table 3). The effect of restricted feeding on lower quality hickory leaves was to increase feeding rate in order to achieve an equal growth rate resulting in a lower gross growth efficiency.

LEAF PACK PROCESSING

Leaf pack weight loss is a result of leaching of soluble components, fragmentation of large particles, sloughing of fine particles and microbial and macroinvertebrate utilization. In the absence of macroinvertebrate shredders, the post leaching processing rates of basswood and hickory leaf packs at 5° and 10°C were not significantly different. Even though there were differences in microbial respiration on the packs (Fig. 1), these differences did not result in differential weight loss (Figs. 2,3). The differences in absolute weight loss of the packs was caused by differences in leaching during the first three days in the stream.

When shredders were present in densities comparable to those found in first-order sites on Augusta Creek (Dr. K.W. Cummins, unpublished data), leaf packs were processed three to five times faster than when shredders were absent, with hickory packs at 10°C being processed faster than basswood packs at 5°C. The processing rates observed in this experiment correspond well with previously reported values for basswood (1.41% per day; Cummins et al. 1980) and hickory (1.83-3.16% per day, Suberkropp et al. 1975).

The relative contribution by the microbial and macroinvertebrate communities to the processing of the leaf packs was calculated from differences in rates of weight loss with and without shredders present (Table 4). The lack of difference in the slopes of regression lines describing the weight loss of leaf packs without shredders despite differences in microbial activity suggests: 1) variance associated with leaf pack weight loss blurred any real difference in the processing rates, 2) differential losses due to measured differences in microbial respiration were below the sensitivity of our weight loss analysis technique, 3) effects of microbial activity on particulate losses are similar for each leaf type and temperature, while

differences in activity do exist, much of the carbon utilization may have been from dissolved organic carbon. Combined microbial utilizaton and mechanical breakage accounted for 18.8 to 25.3% of the observed weight loss involved in the processing of 90% of either leaf type. Invertebrate activity, through feeding and physical abrasion of particles accounted for 34.4 to 56.0% of leaf processing. The accelerated feeding activity of Tipula and Pycnopsyche on hickory because of the increased temperature and lower food quality (Table 2) resulted in faster processing of leaf material and a much greater contribution to processing by the invertebrate component. The combined effect of increasing temperature 5°C and decreasing food quality was 22% greater processing by macroinvertebrates and 19% faster overall processing rate.

DISCUSSION

Previous studies have shown that the rate of decomposition of leaf litter in streams and the degree of utilization of this litter by microorganisms and macroinvertebrates are a function of chemical properties of the stream, the timing of the inputs, the shredder community, the type of leaf and the temperature. Reported processing rates range from very slow for resistant leaf species or in areas with relatively poor shredder communities (Benfield et al. 1977; Mathews and Kowalczewski 1969; Reice 1978; Davis and Winterbourn 1977) to very fast for exceptionally palatable leaves or in areas where shredders are abundant (Petersen and Cummins 1974; Cummins et al. 1980). The processing rates of pignut hickory leaf packs at different sites during fall and winter are directly related to shredder densities (Dr. K.W. Cummins, unpublished data). Thus in locations with well developed macroinvertebrate shredder communities these organisms may contribute significantly to leaf litter processing. In the absence of shredders, microbial

processing and physical degradation proceed at a much slower rate. In this study there was no detectable difference in the weight loss of basswood and hickory leaves over ten weeks in the absence of shredders.

We have demonstrated that under the conditions of our experiment, hickory leaves were processed faster than basswood. This may at first to be contrary to other published reports (i.e. Petersen and Cummins 1974). Temperature, however, can override differences in processing rates between leaf types, as observed here (Suberkropp et al. 1975). This override was a result of increased shredder activity as shown by the three to five fold increase in processing rates with shredders in the system. This mechanism is supported by the results of the T. abdominalis feeding experiment (Table 2) where consumption was greater on hickory at both temperatures with consumption of hickory leaves at 10°C being nearly three times greater than consumption of basswood leaves at 5°C. These results indicate that hickory should be processed more rapidly than basswood at the same temperature based on differences in consumption. Although no significant amounts of physical breakage were measured here it is possible that the softer basswood leaves are more susceptible to fragmentation in the stream. Selective consumption of prepared leaves, such as basswood, was not possible in this study, but may contribute to the observed differences in field processing rates (Wallace et al. 1970; Barlocher and Kendrick 1973).

The adjustment of consumption rate to maintain a constant growth rate with changing food quality has been documented for the shredder Sericostoma personatum (Iversen 1974) and for various terrestrial phytophagus Lepidoptera (House 1965; Slansky and Feeny 1977). These studies indicate that once food quality has reached a certain level further increases will not result in higher growth rate for the organism and conumption is adjusted to the

lowest level that will support optimum growth. Slansky and Feeny (1977) observed adjustment of feeding rates to bring about maximum nitrogen accumluation. Since growth rates are the same on basswood and hickory leaves it is possible that much of the leaf litter entering Augusta Creek is of high enough quality to support comparable growth rates. Natural CPOM accumulations from Augusta Creek contained 2% nitrogen (Cummins et al. 1980). This is near the nitrogen concentration of conditioned hickory leaves and about the point at which Iversen (1974) observed levelling off of growth in S. personatum. Changes in food quality will affect the shredder community by regulating growth rate when food quality is low (Anderson and Grafius 1975; Otto 1974) and through the rate of consumption when food quality is high (Iversen 1974). A reduction in consumption rate on higher quality food should result in a larger standing crop of shredders being supported by the system due to a greater efficiency of conversion of ingested material to body weight.

In stream conditioning affects that palatability and nutritional value of leaves through microbial production and microbial catalysis (Barlocher and Kendrick 1975a). Both basswood and hickory leaves are conditioned to a point that permits consumption relatively rapidly (in less than 3 weeks). Further conditioning did not result in increased consumption as was seen for Lepidostoma quercina feeding on alder leaves (Grafius 1977). Grafius hypothesized that the increase in consumption was a result of declining food quality of the alder, a rapidly degraded leaf. Basswood and hickory were apparently of relatively uniform nutritive value from six to eleven weeks of conditioning. The chemical composition of the leaf material and the length of time necessary for sufficient conditioning are major factors in determining the extent of macroinvertebrate utilization. The toughness of the leaf matrix and/or the presence of secondary compounds that inhibit

microbial and shredder utilization, and the long preliminary conditioning periods of leaves such as oak and beech may result in reduced shredder processing.

While the contribution of shredders to leaf processing found here is substantially higher than the estimates of some other investigators (Cummins et al. 1973; Petersen and Cummins 1974; Winterbourn and Davis 1976) evidence that shredders may play a larger role at times (Sedell et al. 1975). A high level of shredder utilization is dependent on retention of the leaf material in the system until sufficient conditioning has occurred and the availability of the leaves to shredders, as well as the existence of a well developed shredder community. A large majority of the leaf material entering upper Augusta Creek is rapidly conditioned and the major leaf inputs occur during base flow. Under these conditions it may be possible for shredder utilization to approach the level estimated in this study.

7.09 A Preliminary Experiment on Field Introductions of a Stream Leaf Shredder (Clistoronia magnifica: Insecta: Trichoptera).

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Stream macroinvertebrate growth rates have been used in laboratory experiments as bioassays to evaluate both food quality and the effects of temperature (e.g. Anderson and Cummins 1979; Cummins and Klug 1979). Because laboratory conditions may not adequately represent the natural stream conditions of the test species and to evaluate the feasibility of large scale introductions of non-perpetuating introductions in the field, pilot studies using the leaf shredder Clistoronia magnifica were initiated.

The experimental species, Clistoronia magnifica (Trichoptera: Limniphilidae), is a litter shredding caddisfly which is found in alpine lakes of western North America. Clistoronia meets two primary requisites for field introduction experiments: Incapability to perpetuate in the natural stream system and ease of mass culture. Laboratory culture also permits the production of more than the normal one generation per year. In addition, an intermittent stream which normally flows less than 6 months per year would further insure avoidance of a permanent introduction.

The study area was divided into 4 sections. The lower two sections (3 and 4) received introductions of 40 5 g alder (Alnus rubra) leafpacks (Merritt et al. 1979), while the food supply of the upper two sections remained unchanged. Leafpacks were placed in the stream one week prior to the introduction of Clistoronia larvae to allow for a period of microbial colonization of the packs. As a control, insects were also placed in a laboratory stream stocked with field conditioned alder. The insects were collected after 32 days (285 degree days) in the stream, and after 47 days (282 degree days) in the laboratory channel. Although numbers recovered were small, due to

unusual meteorological conditions during the study, Clistoronia pupae recovered from the alder enriched section were significantly heavier than those found in the control section ($p < .025$) and grown the laboratory stream ($p < .005$) (Table 1). In addition, pupal weights from the experimental section of the intermittent stream, were similar to those reported by Anderson (1977) for "normal" laboratory reared individuals.

Therefore, despite the far from optimal field conditions, the results of this experiment indicate that laboratory-reared shredders introduced into natural stream environments can be recovered and that they do respond to food enhancement (in this case alder leaves) in a predictable fashion.

Additional experiments are planned involving the release of Clistoronia larvae in first and second order streams with and without associated food supplements. The experiments will be conducted in the Oregon Cascades where streams exposed to a variety of land use practices are readily available, including a variety of temperature, sediment, terrestrial organic input and fish population regimes that would be associated with energy projects such as low head hydro dams.

Table 1. Summary of weights (mg) of Clistoronia magnifica, at start and conclusion of experiment, and elapsed days and degree days for each treatment, and related temperature data.

	Average Weights (Std. Dev.)			Degree	Temperature		
	Larvae	Pupae	Days	Days	$\bar{x}$	Max	Min
Initial	18.95 (7.69) n = 45	-	-	-	-	-	-
Laboratory Stream with Alder	27.21 (9.92) n = 40	18.35 (2.70) n = 4	47	282	6.0	5.0	7.0
Intermittent Stream without Alder	30.66 n = 1	19.07 (13.61) n = 2	32	285	8.9	6.0	18.0
with Alder	-	46.00 (13.97) n = 8					

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