THE ROLE OF SHREDDERS IN DETRITAL DYNAMICS OF PERMANENT AND TEMPORARY STREAMS

by

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INTRODUCTION

The importance of leaves from riparian vegetation to stream ecosystem energy dynamics is a tenet of stream ecology (e.g., Cummins, 1974; Cummins, 1977; Vannote et al., 1980). Leaves, or coarse particulate organic matter (CPOM), are major components of the detrital energy base of small headwater streams draining forested watersheds in the eastern deciduous forest of North America. Leaf detritus in both terrestrial and aquatic systems is broken down by a combination of physical, chemical, and biological factors including mechanical breakage, leaching of water soluble compounds, microbial decomposition, and invertebrate feeding (Cummins, 1974; Anderson and MacFadyen, 1975).

There are many instances where the heterotrophic organisms of an ecosystem modify or regulate the flow of energy within and between trophic levels. Chew (1974) reviewed the importance of detritivores and herbivores in regulating terrestrial decomposition processes and in influencing plant production and diversity. He concluded that regulatory properties of consumers were more important to ecosystem functioning than simply the ability to move energy through the system. Lee and Inman (1975) indicated that consumers may not provide stability to the ecosystem, but may dampen deviations from equilibrium and help maintain system homeostasis. Based on various ecosystem models, O'Neill (1976) suggested that small changes in heterotroph biomass could re-establish ecosystem equilibrium and reduce effects of perturbation.

In terrestrial ecosystems consumer regulation often increases the primary production of the ecosystem. For example, phytophagous insects are important regulators of forest primary production (Mattson and Addy, 1975). Wildebeest grazing in the Serengeti Plains increase net primary productivity of the grassland by preventing plant senescence (McNaughton, 1976). The leaf cutter ant, *Atta colombica*, of a tropical forest accelerates net primary production by cropping leaves for use in nest construction (Lugo et al., 1973).

Certain aspects of nutrient cycling can also be regulated, in part, by consumers. Kitchell et al. (1979) reviewed consumer regulation of nutrient cycling and concluded that nutrient cycling rates may be altered by translocation (movement of nutrients across subsystem boundaries) or transformation (change in the surface/volume relationship of a prey organism or other food substrate) of nutrients by consumer consumption or behavior patterns.

In aquatic ecosystems grazing zooplankters affected algal productivity, growth, community structure, and succession, all of which can influence energy flow in an aquatic ecosystem (Porter, 1976 and 1977). Wallace et al. (1977) and Merritt and Wallace (1981) stressed the importance of stream invertebrates that filter particulate organic matter from suspension in retarding the loss of energy from a given stretch of stream.

Stream insects that feed directly on vascular plant detritus are designated as shredders (Cummins, 1973). Terrestrial invertebrates with similar feeding habits significantly affect the breakdown rates of leaves on forest floors (reviewed by Crossley, 1977). The role of shredders in streams has been more difficult to define (Anderson and

Sedell, 1979) and has been evaluated by two general techniques: comparisons of breakdown rates in streams with different shredder abundances, and calculations of detritus utilization budgets from shredder ingestion or production data. Hart and Howmiller (1975), Iversen (1975), and Sedell et al. (1975) compared leaf breakdown in two or more streams and, in each case, suggested that differences in breakdown rates were due to differences in the invertebrate fauna. Petersen and Cummins (1974) found slower leaf breakdown rates in artificial channels where shredders were excluded than in channels where shredders were present. Fisher and Likens (1973) found that macroconsumers accounted for only a small portion of the energy flow in Bear Brook. However, Cummins (1971) estimated that detritivores in a woodland stream ingested almost 32% of gross LPOM (large particulate organic matter) input on a daily basis, and Webster and Patton (1979) calculated that annual detritivore ingestion in a small stream at Coweeta Hydrologic Laboratory was approximately 80% of leaf fall.

Since detritivores have relatively low assimilation efficiencies (e.g., Berrie, 1976; Golladay, 1981), much of the leaf matter ingested by detritivores is returned to the stream greatly reduced in size. This fine particulate organic matter (FPOM) provides an energy source for other consumers that feed on deposits of FPOM or filter FPOM from suspension (Short and Maslin, 1977; Wallace et al., 1977). Grafius and Anderson (1979) found that though _Lepidostoma quercina_ production was only a small portion of the total secondary production in Berry Creek, this shredder produced sufficient FPOM to support 1/4 to 1/2 of the simuliid production in the stream. Based on laboratory experiments, Cummins et al. (1973) concluded that shredders have an important influence on energy flow in detritus dominated stream ecosystems.

One way to investigate the influence of feeding activities of leaf shredding insects on detrital dynamics is to compare detrital processing parameters among streams with different levels of shredder abundance. In this study I have compared rates of leaf breakdown and POM transport in three temporary and three permanent streams draining small forested watersheds. It was postulated that temporary streams, due to their seasonal dry periods, would have fewer species of shredders and/or fewer numbers of individuals per species than permanent streams (Williams and Hynes, 1977). This has been demonstrated in several studies (Clifford, 1966; Williams and Hynes, 1976; Iversen et al., 1978). I further postulated that reductions in shredder populations in the temporary streams would result in concomitant changes of various detrital parameters.

SITE DESCRIPTION

This study was conducted in six first-order tributaries of Guy's Run, a tributary of the Calfpasture River (James River Basin, Rockbridge County, Virginia; 79 39' W longitude, 38 58' N latitude). Most of the 19 km^2 watershed of Guy's Run is located within the Goshen Wildlife Management Area.

The six tributaries of Guy's Run used in this study are typical of the low order, low nutrient streams of the southern Appalachian Mountains. Glade Brook, Beckney Hollow, and Three Dwarf Run are permanent streams. Highest flows occur in winter and lowest flows in summer. Dry Branch, Tower Branch, and Grave Branch are temporary streams with no channel flow during late summer and early autumn. The six streams varied in length, width, gradient, and watershed area (Table 1). Average stream velocity and temperature were similar among the six streams (Table 2). Overstory vegetation of the six watersheds is dominated by several oak species, hemlock, red maple, hickory, and several other deciduous species (Table 3).

Table 1. Stream lengths, widths, gradients, and watershed areas for three permanent streams and three temporary streams in the Guy's Run watershed.

	Stream Length (m)	Stream Width (m)	Stream Gradient (m/m)	Watershed Areas (km^2)
		Permanent Streams		
Grale Brook	400	2.30	0.22	1.13
Beckney Hollow	1350	1.75	0.08	0.83
Three Dwarf Run	550	1.98	0.06	0.38
		Temporary Streams		
Dry Branch	549	1.20	0.15	0.33
Tower Branch	555	1.60	0.13	0.94
Grave Branch	1173	1.20	0.05	0.36

Table 2. Mean (± 95% CI) and ranges of stream velocities (m/sec) and water temperatures (c) recorded from the six study streams.

	Glade Brook	Beckney Hollow	Three Dwarf Run	Dry Branch	Tower Branch	Grave Branch
Stream Velocities	0.29± .06	0.36± .08	0.24± .06	0.20± .06	0.28± .09	0.28± .11
Stream Temperatures	8.58± 2.24	8.93± 2.61	9.06± 2.42	7.96± 2.40	8.33± 2.47	8.87± 2.44

Table 3. Percent composition of overstory vegetation of the six study watersheds. Percents based on basal area (m^2/h) as determined by the Bitterlich Method.

	Glade Brook	Beckney Hollow	Three Dwarf Run	Dry Branch	Tower Branch	Grave Branch
White Oak	10	5	11	6	6	40
Chestnut Oak	6	14	26	23	25	2
Red/Black Oak	14	34	28	18	17	10
Scarlet/Pin Oak	4	9	5	17	2	5
Red Maple	4	10	8	4	12	13
Yellow Birch	3	1	5	5	4	
Dogwood	2	1	1		3	9
Witch Hazel	1	1	1		1	
Tulip Tree	8	3	5	3	2	4
Black Locust	1	1	2			2
Sassafras	1					
Cucumber Magnolia	4	1	1			
Pignut Hickory	8	11	8	6	10	10
Sycamore	2	1			4	
Sugar Maple	1			2	1	1
Hemlock	26	6	4	6	1	
White Pine	4	2		3	6	3
Pitch Pine		1		4	1	1

METHODS

Leaf Breakdown Rates

Leaf breakdown rates were measured in the six study streams using nylon mesh bags (10 x 10 cm, 1 cm^2 openings) filled with approximately five grams of dried and weighed red maple (*Acer rubrum*) leaves. Thirty bags were placed in each stream on 20 January 1979, and five bags were recovered from each site on six dates (approximately 30 day sampling intervals) beginning 10 February 1979 and ending 5 July 1979 before the temporary streams became dry. The same sampling regime was used to measure leaf breakdown for a second year. Thirty bags were placed in each stream on 8 December 1979 and the final five bags were removed from each site on 5 July 1980.

Retrieved leaf bags were put into individual plastic bags, placed on ice, and transported to the laboratory where invertebrates were sorted and preserved for identification. The leaf material was air-dried to constant weight. Subsamples (1 g) from each bag were ashed (500 C, 15 min) to determine ash free dry weight (AFDW) of the remaining leaf matter. Breakdown rates were calculated by regressing log transformed remaining weight against exposure time (Jenny et al., 1949; Olson, 1963). Breakdown rates were compared using the Least Significant Difference test for comparisons of two or more slopes (Sokal and Rohlf, 1969).

Microbial respiration was measured on red maple leaves using a Gilson Respirometer. Two replicate discs were punched from the leaves collected from a stream on a given pickup date. The leaf discs were then placed in respirometry flasks containing filtered stream water.

The flasks were attached to the Gilson apparatus and allowed to equilibrate at 21 C for 4 - 5 hours. Two flasks, which contained only filtered streams water, were used as reference flasks. Microbial respiration was measured in ul O_2/mg leaf tissue/hour.

Particulate Organic Matter

Suspended particulate organic matter (seston) was collected from the six study streams on 10 dates beginning in August 1978 and ending in June 1980. Larger POM size fractions were collected by pouring measured volumes of stream water through a 20 um plankton net. Water was also collected in carboys to obtain samples of smaller particles. All POM samples were collected during periods of base flow. Samples were analyzed using a wet filtration system (Gurtz et al., 1980). Measured volumes of stream water or resuspended net samples were filtered with suction through a series of stainless steel screens into the following size classes: 234 um, 105 - 234 um, 43 - 105 um, 25 - 43 um. Material collected on the screens was resuspended and collected on pre-ashed, pre-weighed Gelman A/E glass fiber filters. An aliquot of material passing through the 25 um screen was filtered through a glass fiber filter to obtain a 0.5 - 25 um size fraction. All samples were oven-dried (50 C, 24 h), desiccated (24 h), weighed, ashed (500 C, 15 min), rewetted (to restore water of hydration; Weber, 1973), redried, desiccated, and weighed. From these weights POM was determined as ash-free dry weight (AFDW). POM concentrations (mg/l), median POM particle sizes (um), and transport load (g/d) were calculated based on weight. Flow measurements used in the analysis of the POM data were determined either by capturing the total discharge per unit of time in a bucket (liters of water) or by measuring stream velocity, width, and depth and computing discharge from these measurements.

Leaf Pack Shredders

Benthic organisms were placed into the shredder functional group based on life history and feeding behavior studies from the literature and based on preliminary feeding studies by this author.

Shredders were sorted live from leaf packs in the laboratory and preserved in 4% formalin and later transferred to 70% ETOH. Shredders were identified (to genus and when possible to species), enumerated, and measured (length and head capsule width in mm). Mean shredder densities were calculated as numbers of organisms/g AFDW of leaf matter. Biomass (mg DW shredders/g AFDW leaf matter) was estimated using length (mm) measurements and oven-dried weights (60 C, 24 h) of freshly killed (exposure to carbonated water for 15 min) organisms. These data were then regressed to obtain length-dry weight relationships for each shredder genus or species (Table 4). The lengths (mm) of preserved shredders, collected from leaf packs or natural substrates, were then used in these regression formulas to obtain dry weight biomass for each genus or species.

Shredders and CPOM in the Substrate

A Surber square-foot sampler (220 um mesh size) was used to quantitatively sample shredders from substrates of the six streams on 16 dates between 27 January 1979 and 5 July 1980. Three Surber samples

Table 4. Regression statistics for length (mm) and dry weight (mg) data used to determine shredder biomass estimates.

	N	Slope	Intercept	R^2	Mean Length	Mean Dry Weight
Allonarcys	37	.00388	-.04079	.88	19.0	0.0330
Peltoperla	40	.00094	-.00205	.98	5.5	0.0031
Leuctra	45	.00009	-.00017	.98	6.1	0.0004
Lepidostoma	31	.00003	-.00001	.98	4.7	0.0013
Pycnopsyche	30	.00204	-.01494	.90	13.0	0.0116
Tipula	40	.00084	-.01246	.94	25.0	0.0085

were collected from each stream on a given sampling date. The substrate was sampled to a depth of 10 cm when possible. Samples were collected from riffles using stratified random sampling. The samples were pooled and the organisms preserved in 4% formalin for analysis in the laboratory. Shredders were identified, enumerated, and measured as above. The biomass of each shredder was estimated using the regression equations discussed above.

Benthic CPOM was also collected from the Surber samples. Identifiable leaves were separated to species and air-dried, and weighed. Annual dry weight production of shredders was estimated using the size frequency method described by Hynes and Coleman (1968) and as modified by Hamilton (1969). This method does not require species identification, but treats the average size frequency distribution of populations over the year as an "average cohort". The production estimate was then corrected to actual development period, or cohort production interval (CPI), of the nymph or larvae using the method proposed by Benke (1979) and Benke and Wallace (1980). The CPI for each species was estimated from size distributions of individuals collected from monthly substrate samples and from literature data on voltinism and development periods. Leuctra spp. were found to be univoltine (Hynes, 1970; Merritt and Cummins, 1978) and I used an estimated CPI of 270 days. Peltoperla is thought to have a two year cycle (Merritt and Cummins, 1978) and I estimated a CPI of 660 days. Allonarcys has a 2-4 year life cycle (Hynes, 1970; Merritt and Cummins, 1978) and I used a conservative CPI of 780 days. All Trichoptera were considered univoltine (Wiggins, 1977; Merritt and Cummins, 1978) and I used a CPI of 270 days for all genera. *Tipula* was considered univoltine and to have a CPI of 270 days based on benthic substrate samples. Length classes were constructed from measurements of preserved material. Dry weights used in estimating production were obtained from the length/dry weight regression formulae. The production estimates of all genera were combined to obtain shredder annual production.

RESULTS

Maple Leaf Breakdown

Breakdown of red maple leaf packs in the six study streams for two sampling seasons is shown in Figures 1 and 2. Generally, permanent streams had faster breakdown rates than temporary streams (Table 5). First-year breakdown rates for Glade Brook and Beckney Hollow, both permanent streams, were significantly faster ($P < 0.05$) than the other four streams. Second-year breakdown rates for all streams, except Grave Branch, were not significantly different. However, the order of breakdown rates for both seasons is nearly identical suggesting a relatively consistent trend in CPOM processing among streams.

Microbial respiration measured on second season red maple leaf packs suggested that most of the streams had similar microbial activities (Table 6). The only stream with significantly different respiration ($P < 0.05$, two-way anova) and multirange test was Dry Branch, a temporary stream. Dry Branch red maple leaves had the highest average microbial respiration and Glade Brook, a permanent stream, the lowest. Microbial respiration did not correlate well with leaf breakdown rates ($r = 0.04$, $N = 6$).

Density and Biomass of Shredders on Leaf Packs

The dominant shredders found on the leaf packs were two trichopteran genera, *Lepidostoma* sp. and *Pycnopsyche* sp., four plecopteran genera, *Leuctra* sp., *Peltoperla maria*, *Allonarcys proteus*, *Taeniopteryx* sp., and one dipteran, *Tipula* sp. Other invertebrates

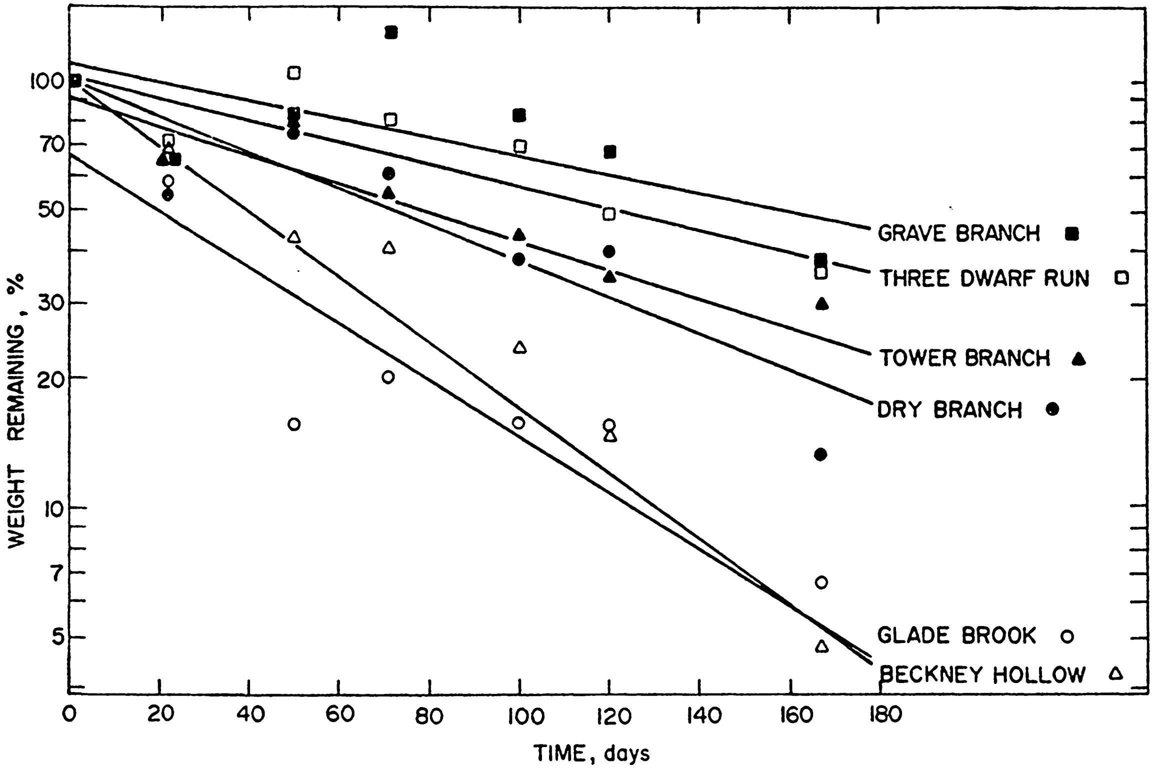

Figure 1. First year breakdown of red maple leaves from the six study streams. Open symbols represent permanent streams and closed symbols represent temporary streams.

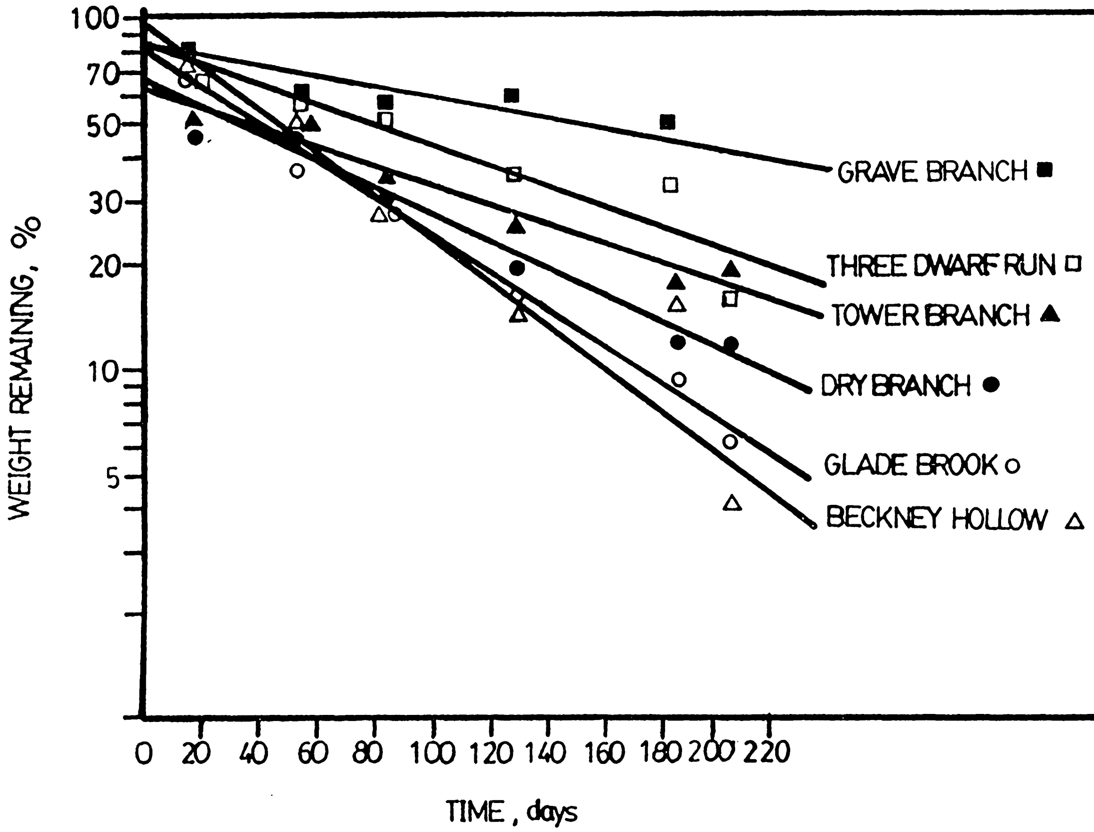

Figure 2. Second year breakdown of red maple leaves from the six study streams. Open symbols represent permanent streams and closed symbols represent temporary streams.

Table 5. Red maple leaf breakdown rates in the six study streams for two seasons.

Stream	Breakdown Rate (d^{-1})	95% CI	r^2	N	Least Significant Difference[1]
<u>Season 1</u>					
Beckney Hollow	0.0175	±0.0078	0.72	35	╻
Glade Brook	0.0149	±0.0075	0.66	35	╹
Dry Branch	0.0098	±0.0050	0.65	35	╻
Tower Branch	0.0077	±0.0051	0.53	35	┃
Three Dwarf Run	0.0059	±0.0045	0.46	35	┃
Grave Branch	0.0045	±0.0047	0.33	34	╹
<u>Season 2</u>					
Beckney Hollow	0.0127	±0.0018	0.86	35	╻
Glade Brook	0.0109	±0.0014	0.88	35	┃
Dry Branch	0.0080	±0.0018	0.69	35	┃
Three Dwarf Run	0.0064	±0.0011	0.79	35	┃
Tower Branch	0.0061	±0.0015	0.66	35	╹
Grave Branch	0.0029	±0.0015	0.34	34	❙

[1] Vertical bars indicate rates that were not significantly different (= 0.05).

Table 6. Mean (± standard error) respiration (ul O_2/g DW leaf matter/hr) of microbes colonizing red maple leaf packs from the six study streams. Respiration rates were determined using a Gilson respirometer with a water bath temperature of 21 C.

	Glade Brook	Beckney Hollow	Three Dwarf Run	Dry Branch	Tower Branch	Grave Branch
10 Dec 1979	387 ± 68	393 ± 81	295 ± 88	579 ± 102	325 ± 54	432 ± 77
10 Jan 1980	280 ± 30	410 ± 60	272 ± 29	262 ± 36	304 ± 27	224 ± 24
11 Feb 1980	378 ± 31	229 ± 23	451 ± 34	440 ± 62	249 ± 36	307 ± 22
27 Mar 1980	280 ± 24	213 ± 59	349 ± 60	122 ± 60	204 ± 41	245 ± 31
16 May 1980	219 ± 48	258 ± 56	202 ± 40	489 ± 137	467 ± 120	453 ± 120
5 Jul 1980	202 ± 60	457 ± 255	477 ± 162	718 ± 193	455 ± 106	---

categorized as shredders were rarely found in the leaf packs. Shredder density on first season leaf packs increased with time, especially after about 70 days, as the leaves became conditioned by microbes (Figure 3). Densities from the second season were generally higher than first season, especially for the two permanent streams, Glade Brook and Beckney Hollow which were significantly different from the other streams ($P < 0.05$, two-way anova and multirange test) (Figure 4). However, Tower Branch, a temporary stream, had a decrease in second season shredder numbers, particularly during late spring and early summer. For both seasons densities of shredders in the permanent streams increased during early summer.

Average biomass of shredders colonizing leaf packs in the second season was significantly ($P < 0.05$, two-way anova and multirange test) larger than during the first season, except for Tower Branch (Table 7). The trend for shredder biomass in the first season was a general increase through time, however, in second season there were two packs of shredder biomass, winter and early spring.

Total shredder biomass on maple leaves from two permanent streams, Beckney Hollow and Glade Brook, was significantly ($P < 0.05$, two-way anova and multirange test) larger than for the other four streams for both sampling seasons. Three Dwarf Run and Dry Branch had intermediate biomass for both seasons, while the two remaining temporary streams, Tower Branch and Grave Branch, had the smallest biomass.

The species composition of shredders was more varied in permanent streams than in temporary streams. <u>Allonarcys proteus</u>, <u>Pycnopsyche</u>

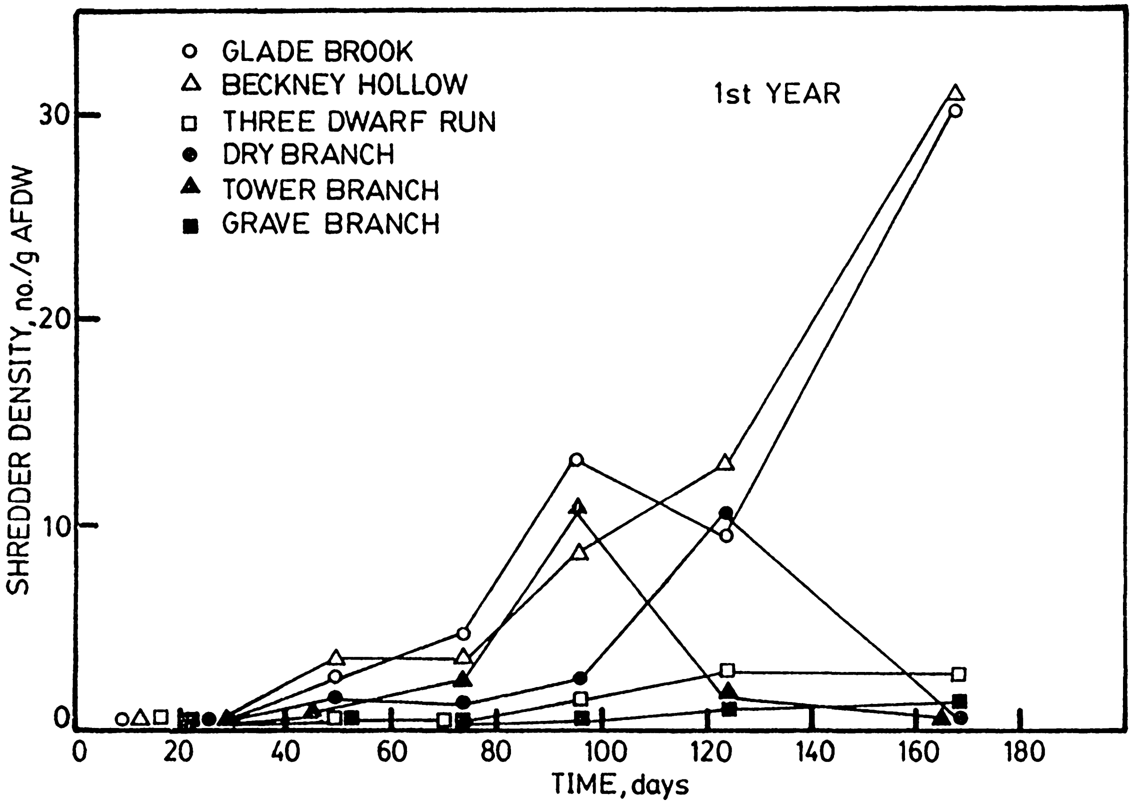

Figure 3. Total shredder density on first season red maple leaves from the six study streams for six sampling dates. Open symbols represent permanent streams and closed symbols represent temporary streams.

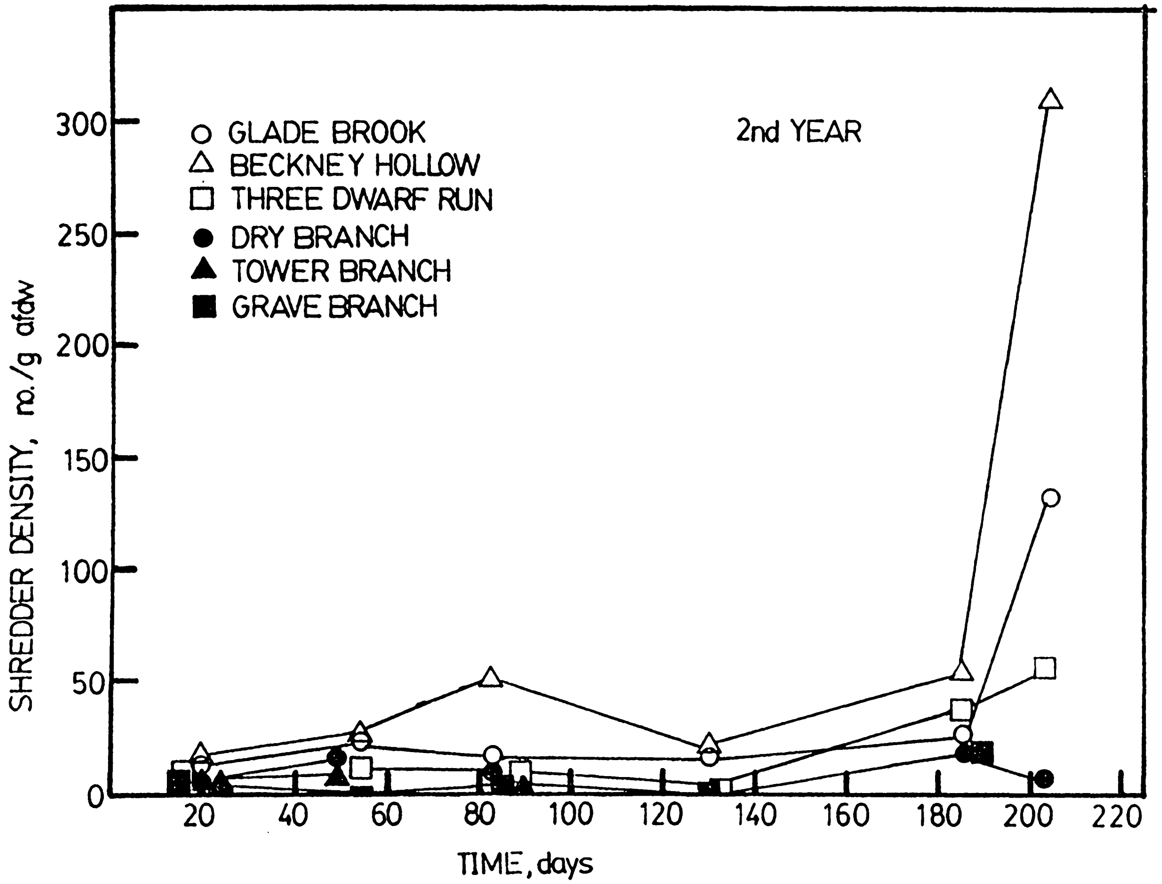

Figure 4. Total shredder density on second season red maple leaves collected from the six study streams on six sampling dates. Open symbols represent permanent streams and closed symbols represent temporary streams.

Table 7. Total shredder biomass (mg dry weight shredders/g AFDW red maple leaf matter) on leaf packs from the six streams for two sampling seasons.

	Glade Brook	Beckney Hollow	Three Dwarf Run	Dry Branch	Tower Branch	Grave Branch
Season 1						
10 Feb 1979	0.39	6.54	0.0	0.74	0.0	0.36
10 Mar 1979	0.57	4.78	1.85	0.40	0.37	0.29
31 Mar 1979	8.42	3.18	1.72	0.30	0.66	0.0
28 Apr 1979	8.40	3.23	1.03	1.64	2.83	0.55
19 May 1979	10.30	6.62	2.00	6.38	2.84	1.12
5 Jul 1979	19.14	34.75	0.78	3.25	1.28	1.87
$\bar{X}$	= 7.87	= 9.85	= 1.23	= 2.11	= 1.33	= 0.69
Season 2						
8 Dec 1979	4.21	15.23	2.36	3.05	0.41	0.94
10 Jan 1980	20.97	21.77	3.16	5.13	2.91	2.83
11 Feb 1980	29.96	15.71	2.31	18.70	4.64	4.65
27 Mar 1980	19.46	20.07	10.97	0.0	0.71	3.95
16 May 1980	5.22	66.61	7.64	6.33	0.0	14.96
5 Jul 1980	23.22	210.60	6.71	1.18	0.0	---
$\bar{X}$	= 17.17	= 58.33	= 5.52	= 5.73	= 1.35	= 5.46

sp., and Peltoperla maria were the primary organisms colonizing leaf bags in the permanent streams. The dominant shredders on leaf packs from all six streams for both seasons were Leuctra spp. and Lepidostoma sp. (Table 8). The plecopterans Allonarcys proteus and Peltoperla maria constituted a small percentage of total shredder densities on leaf packs. Tipula spp., a common dipteran shredder, was found predominantly on permanent stream leaf bags during the second season. Pycnopsyche and Taeniopteryx were found in very low densities on leaf packs from all streams.

The main contributors to shredder biomass on leaf packs were Peltoperla maria, Leuctra spp., and a few Allonarcys proteus and Tipula spp. (Table 9). The relatively high Leuctra biomass was due to their large numbers on the leaf packs during the spring and early summer, while moderate biomass of shredders such as Allonarcys and Tipula were due to a few large individuals. Generally, individual shredder biomass was greatest in two permanent streams, Glade Brook and Beckney Hollow, intermediate in Three Dwarf Run and Dry Branch, and low in the temporary streams Grave and Tower Branches.

Shredder and CPOM Composition in the Substrate

Seasonal trends in shredder densities based on benthos collections fluctuated more widely than shredder densities noted from leaf bags (Table 10). However, differences in densities of shredders among streams followed the same trend for both benthic and leaf bag samples. Mean densities of shredders in two permanent streams, Glade Brook and

Table 8. Mean numbers (no. shredders/g AFDW red maple leaf matter) and percent composition of individual shredder genera from each stream for two sampling seasons.

	Glade Brook		Beckney Hollow		Three Dwarf Run		Dry Branch		Tower Branch		Grave Branch	
	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%
					Season 1							
Allonarcys	1.78	10	0.70	2	-	-	0.04	1	-	-	-	-
Peltoperla	-	-	4.86	17	0.17	4	0.09	1	-	-	-	-
Leuctra	10.39	58	12.42	44	3.44	74	6.04	67	6.65	72	2.29	82
Lepidostoma	5.46	30	10.02	37	0.86	19	2.85	32	2.50	27	0.52	19
Pycnopsyche	0.33	2	0.07	1	0.17	4	-	-	-	-	-	-
					Season 2							
Allonarcys	0.62	2	1.90	2	-	-	-	-	-	-	-	-
Peltoperla	1.36	4	22.83	29	0.19	1	0.43	4	0.21	9	-	-
Taeniopteryx	-	-	0.12	1	0.30	2	0.20	2	-	-	-	-
Leuctra	26.01	75	28.03	36	14.86	74	5.98	49	0.13	5	6.98	96
Lepidostoma	5.88	17	15.97	20	2.70	14	5.18	43	2.11	86	0.05	1
Pycnopsyche	0.49	1	0.55	1	0.28	1	0.30	2	-	-	-	-
Tipula	0.51	1	8.87	11	1.67	8	0.09	1	-	-	0.22	3

Table 9. Mean biomass (mg shredders/g AFDW red maple leaf matter) and percent composition of individual shredder genera from each stream for two sampling seasons.

	Glade Brook		Beckney Hollow		Three Dwarf Run		Dry Branch		Tower Branch		Grave Branch	
	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%
					Season 1							
Allonarcys	1.53	17	1.20	12	-	-	0.03	1	-	-	-	-
Peltoperla	-	-	3.85	39	0.39	32	0.13	6	-	-	-	-
Leuctra	4.63	59	3.14	32	0.54	44	1.48	70	0.96	72	0.63	91
Lepidostoma	0.90	11	1.57	16	0.13	11	0.46	22	0.36	27	0.06	9
Pycnopsyche	0.97	12	0.06	1	0.16	13	-	-	-	-	-	-
					Season 2							
Allonarcys	2.57	15	2.82	5	-	-	-	-	-	-	-	-
Peltoperla	5.94	35	23.85	41	0.90	12	1.57	30	1.04	78	-	-
Leuctra	5.35	31	15.77	27	2.58	33	1.39	24	0.04	3	3.30	61
Taeniopteryx	-	-	0.01	1	0.05	1	0.04	1	-	-	-	-
Lepidostoma	1.00	6	2.54	4	0.42	5	1.02	18	0.26	19	0.01	1
Pycnopsyche	0.86	5	0.74	1	0.32	4	0.70	12	-	-	-	-
Tipula	1.43	8	12.54	22	3.51	45	0.98	17	-	-	2.15	39

Table 10. Monthly standing stocks (shredders/m^2) of shredders collected from the substrate of the six streams by Surber sampler.

	Glade Brook	Beckney Hollow	Three Dwarf Run	Dry Branch	Tower Branch	Grave Branch
27 Jan 1979	57	50	11	43	75	0
3 Mar	68	46	14	7	61	25
31 Mar	223	104	50	39	18	32
21 Apr	43	54	75	36	0	0
12 May	75	93	39	36	36	72
5 Jul	82	65	29	14	29	11
19 Jul	61	115	22	dry	dry	dry
21 Sep	82	18	4	4	0	7
6 Oct	36	50	39	18	0	7
3 Nov	104	115	129	179	36	32
1 Dec	140	194	136	136	75	90
19 Jan 1980	124	197	147	75	47	11
11 Feb	115	82	47	18	57	46
27 Mar	158	125	82	39	47	32
16 May	100	93	43	129	11	39
5 Jul	176	68	25	25	0	---

Beckney Hollow, were significantly ($P < 0.05$, one-way anova and multirange test) higher than for the other four streams (Table 11). Three Dwarf Run, a permanent stream, and Dry Branch, a temporary stream, had intermediate shredder densities. Tower Branch and Grave Branch, both temporary streams, had the lowest benthic shredder densities. Based on mean standing stocks, *Leuctra* spp., *Lepidostoma* sp., and *Peltoperla maria* were the most abundant shredders in the substrate of the six streams (Table 12).

Differences in biomass were even more pronounced than differences in shredder densities between the two stream types (Table 11). The permanent streams had larger mean biomass values than did temporary streams. This was especially true for Glade Brook and Beckney Hollow which had significantly ($P < 0.05$, one-way anova and multirange test) larger biomass than the other four streams. Dry Branch, a temporary stream, and Three Dwarf Run, a permanent stream, were intermediate. The two remaining temporary streams had very low biomass. On a monthly basis the permanent streams usually had larger shredder biomass than the temporary streams (Table 13). All three permanent streams generally had much larger biomass for individual shredder species than the temporary streams (Table 14). *Allonarcys proteus* and *Peltoperla maria* were the two main contributors to shredder biomass in the permanent streams, while *Leuctra* spp., *Peltoperla maria*, and a few *Tipula* and *Pycnopsyche* were the most important in temporary streams. For all seasons the permanent streams had larger shredder densities and much larger biomass in the substrate than temporary streams (Figure 5).

Table 11. Mean (± 95% CI) and ranges of shredder standing stocks and biomass for shredders collected from the benthic substrates of the six streams by Surber sampler.

	Standing Stocks (no./m^2)	Biomass (mg DW/m^2)
	Permanent Streams	
Glade Brook	103 ± 26 (36 - 233)	350 ± 228 (13 - 1452)
Beckney Hollow	92 ± 25 (18 - 197)	486 ± 353 (15 - 2522)
Three Dwarf Run	56 ± 22 (4 - 147)	176 ± 144 (2 - 1216)
	Temporary Streams	
Dry Branch	53 ± 27 (4 - 179)	66 ± 52 (2 - 399)
Tower Branch	33 ± 14 (0 - 75)	20 ± 16 (0 - 121)
Grave Branch	29 ± 14 (0 - 90)	31 ± 22 (0 - 145)

Table 12. Mean standing stocks (no. shredders/m^2) and percent composition of shredder genera collected from the substrate of the six streams by Surber sampler.

	Glade Brook		Beckney Hollow		Three Dwarf Run		Dry Branch		Tower Branch		Grave Branch	
	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%
Allonarcys	15	19	15	14	15	5	5	8	1	2	-	-
Peltoperla	10	13	5	5	32	32	12	18	2	5	1	1
Leuctra	28	35	74	70	33	33	23	35	16	48	16	36
Taeniopteryx	11	13	-	-	6	6	12	18	4	11	11	24
Lepidostoma	11	13	6	6	9	8	10	15	11	33	9	19
Pycnopsyche	4	5	4	3	4	4	5	8	-	-	7	16
Tipula	2	2	2	2	2	2	3	5	-	-	2	5

Table 13. Monthly biomass (mg shredders/m^2) of shredders collected from the substrate of the six streams by Surber sampler.

	Glade Brook	Beckney Hollow	Three Dwarf Run	Dry Branch	Tower Branch	Grave Branch
27 Jan 1979	21	476	2	8	20	0
3 Mar	196	37	25	2	23	10
31 Mar	889	244	185	15	6	6
21 Apr	65	42	82	7	0	0
12 May	18	18	27	4	7	13
5 Jul	13	16	11	11	11	1
19 Jul	60	159	88	dry	dry	dry
21 Sep	34	214	39	13	0	14
6 Oct	302	85	24	7	0	89
3 Nov	63	1534	75	103	31	8
1 Dec	1453	2523	271	76	121	69
19 Jan 1980	403	1470	1217	166	52	2
11 Feb	114	174	27	28	10	145
27 Mar	1285	395	224	88	19	38
16 May	585	375	321	399	2	36
5 Jul	104	24	205	57	0	---
$\bar{X}$	350	487	176	72	19	31

Table 14. Mean biomass (mg shredders/m^2) and percent composition of shredder genera collected from the substrate of the six streams by Surber sampler.

	Glade Brook		Beckney Hollow		Three Dwarf Run		Dry Branch		Tower Branch		Grave Branch	
	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%
Allonarcys	312	89	402	80	111	63	-	-	13	51	-	-
Peltoperla	14	4	81	16	42	24	39	59	6	23	3	9
Leuctra	17	5	8	1	5	3	7	10	5	20	4	13
Taeniopteryx	-	-	1	1	1	1	1	1	1	1	1	1
Lepidostoma	1	1	1	1	1	1	1	2	1	5	1	4
Pycnopsyche	1	1	5	1	2	1	7	11	-	-	11	35
Tipula	6	2	10	2	16	9	12	18	-	-	12	38

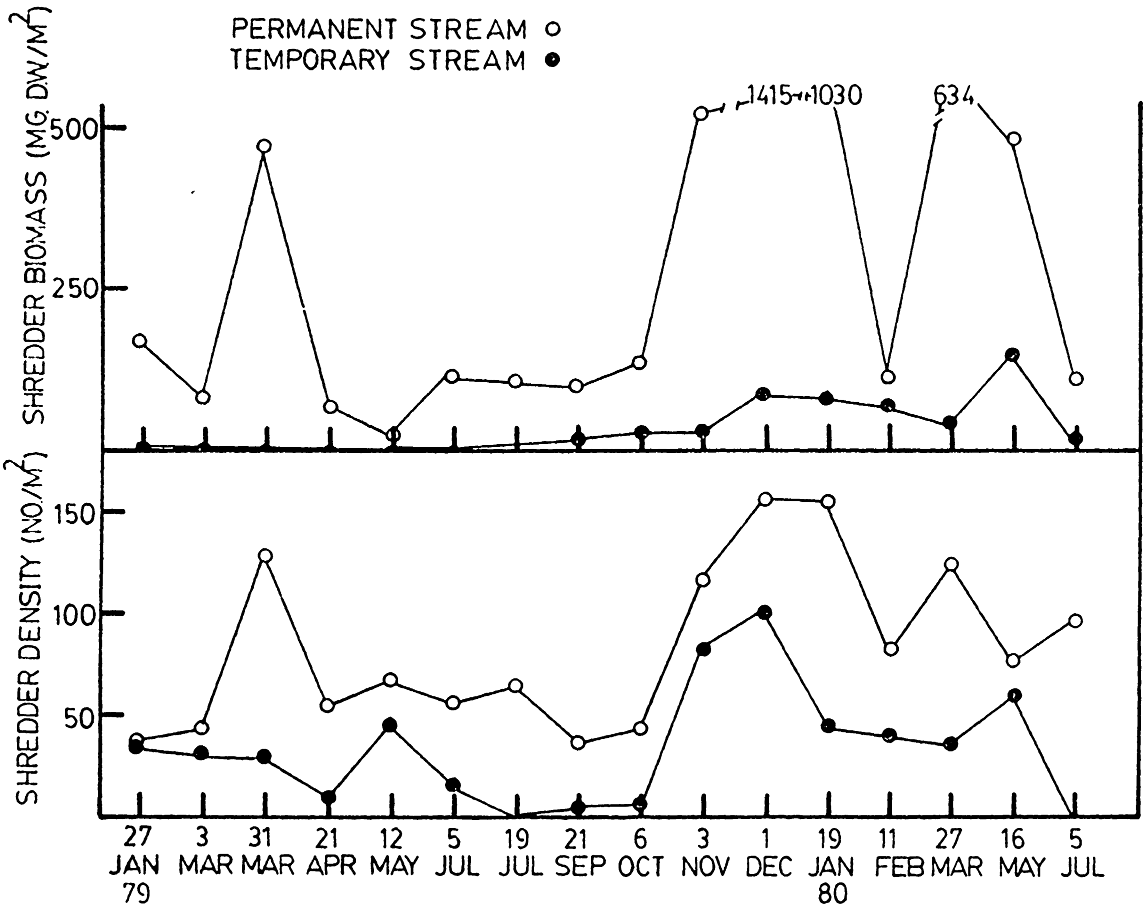

Figure 5. Combined densities and biomass estimates of shredders collected from the substrates of the permanent and temporary streams on 16 sampling dates.

Seasonal trends were generally similar for both stream types, though attenuated in the temporary streams.

Total shredder production was higher in the permanent streams than in the temporary streams (Table 15). Beckney Hollow, a permanent stream, had highest production (6.11 g DW/m^2/y) while Tower Branch, a temporary stream, had lowest production (0.26 g DW/m^2/y). Shredder production in the six streams was greatly influenced by the larger shredder species. In permanent streams *Allonarcys proteus* and *Tipula* spp. had the greatest production. The production of *Allonarcys proteus* was greatest in Beckney Hollow, but the turnover ratios were similar for this species in all permanent streams. *Tipula* spp. had a lower production rate in Glade Brook than in Beckney Hollow, but the turnover rate for this dipteran in Glade Brook was higher. *Lepidostoma* sp., *Leuctra* spp., and *Peltoperla maria* had higher production in Beckney Hollow than in the other two permanent streams, but the turnover ratios for these shredders fluctuated widely among streams. *Tipula* spp. were the most important component of shredder production in the temporary streams. Dry Branch and Grave Branch had similar production and turnover ratios for *Tipula*. This species, as indicated by earlier data, was not found in Tower Branch. Production by the remaining shredders was generally higher in Dry Branch than in the other two temporary streams.

There were no apparent differences in mean standing crop of benthic CPOM among the six study streams ($P > 0.05$, two-way anova and multirange test) (Table 16). There were significant differences

Table 15. Annual dry weight production (P), biomass (B), and turnover ratios (P/B) of the dominant shredders found in the six study streams.

	Lepidostoma			Leuctra			Peltoperla			Allonarcys			Tipula		
	P	B	P/B	P	B	P/B	P	B	P/B	P	B	P/B	P	B	P/B
							Permanent Streams								
Glade Brook	9	2	5	61	14	4	280	37	8	995	211	5	2430	459	5
Beckney Hollow	7	1	7	45	9	5	470	82	6	1650	257	6	3942	480	8
Three Dwarf Run	11	2	6	22	5	4	304	47	7	828	113	7	2200	400	8
							Temporary Streams								
Dry Branch	11	2	6	30	8	4	350	64	5				1910	532	4
Tower Branch	13	2	7	32	7	5	200	23	9						
Grave Branch	9	2	5	13	5	3	31	7	4				1640	412	4

P = mg DW shredder/m^2/y

B = mg DW shredder/m^2

Table 16. Benthic CPOM standing crops (g DW/m^2) of deciduous leaves collected by Surber sampler from the six study streams.

	Glade Brook	Beckney Hollow	Three Dwarf Run	Dry Branch	Tower Branch	Grave Branch
6 Oct 1979	31	14	25	23	46	17
3 Nov 1979	124	137	79	52	47	92
1 Dec 1979	66	107	56	47	48	83
19 Jan 1980	78	168	44	214	94	91
11 Feb 1980	99	145	99	153	112	110
27 Mar 1980	120	122	142	163	107	130
16 May 1980	19	40	41	93	32	37
5 Jul 1980	0	0	5	0	6	6

among CPOM standing crops among dates ($P < 0.05$, two-way anova and multirange test). October, May, and July standing crops were significantly different from each other and the remaining dates. CPOM standing stocks, in all streams, increased in the autumn, peaked during midwinter, and declined in late spring and early summer. The leaf species composition of the benthic CPOM from the six streams was similar to the overstory composition of these watersheds. Several oak species dominated the benthic CPOM, while red maple, yellow birch, and a few other deciduous species were also common in the samples.

POM Transport

POM concentrations were generally higher in the permanent streams than in the temporary streams (Table 17). Concentrations in the permanent streams were highest in summer, lowest in winter, and intermediate in spring and autumn. POM concentrations in the temporary streams declined in early summer, and then the midsummer to midautumn dry period halted further POM transport. Through the peak period (May-Sept.), POM concentrations were consistently highest in Beckney Hollow, lowest in Three Dwarf Run, and intermediate in Glade Brook. Among the temporary streams, Dry Branch generally had the highest POM concentrations. Trends in average POM particle sizes were not as clear, but followed the same general pattern (Table 18). The average particle size was usually largest in Beckney Hollow and Glade Brook, both permanent streams, and smallest in Tower and Grave Branches, both temporary streams. Three Dwarf Run and Dry Branch were intermediate. Transport of POM (g/day) was greater in the permanent streams than in

Table 17. Means and standard errors of POM concentrations (mg/l) for each stream on nine sampling dates. Horizontal lines indicate streams with significantly different concentrations (P 0.05, one-way anova and multirange test). GB = Glade Brook, BH = Beckney Hollow, 3D = Three Dwarf Run, DB = Dry Branch, TB = Tower Branch, GV = Grave Branch. Asterisks indicate permanent streams.

7 Aug 78

BH*	GB*	TB
1.50 ± .03	1.31 ± .31	.30 ± .02

1 Feb 79

BH*	3D*	GB*	TB	GV	DB
.15 ± .01	.15 ± .01	.12 ± .01	.12 ± .01	.10 ± .01	.07 ± .01

17 May 79

BH*	GB*	3D*	GV	DB	TB
.91 ± .07	.74 ± .05	.71 ± .07	.38 ± .04	.35 ± .02	.29 ± .03

Table 17 Continued.

11 Jul 79

BH*	GB*	3D*	(temporary streams dry)
1.52 ± .13	1.41 ± .15	.91 ± .06	

2 Sep 79

BH*	GB*	3D*	(temporary streams dry)
1.31 ± .08	.79 ± .09	.49 ± .18	

9 Nov 79

BH*	3D*	DB	GB*	TB	(GV dry)
.74 ± .02	.73 ± .02	.61 ± .03	.46 ± .01	.37 ± .01	

Table 17 Continued.

29 Jan 80

GB*	BH*	DB	TB	3D*	GV
.68 ± .09	.41 ± .01	.41 ± .01	.20 ± .03	.15 ± .01	.13 ± .01

19 Apr 80

GB*	BH*	DB	GV	3D*	TB
.68 ± .10	.67 ± .03	.44 ± .12	.33 ± .02	.24 ± .03	.12 ± .02

24 Jun 80

BH*	3D*	GB*	(temporary streams dry)
2.18 ± .15	1.51 ± .01	.75 ± .01	

Table 18. Means and standard errors of median PCM sizes (um) for each stream on nine sampling dates. Horizontal lines indicate streams with significantly different median particle sizes (P 0.05, one-way anova and multirange test). GB = Glade Brook, BH = Beckney Hollow, 3D = Three Dwarf Run, DB = Dry Branch, TB = Tower Branch, GV = Grave Branch. Asterisks indicate permanent streams.

7 Aug 78

BH*	GB*	TB
31 ± 2	21 ± 2	15 ± 1

1 Feb 79

BH*	GB*	TB	3D*	DB	GV
28 ± 2	19 ± 2	17 ± 1	16 ± 1	16 ± 1	15 ± 1

17 May 79

BH*	3D*	DB	GB*	TB	GV
33 ± 3	32 ± 5	30 ± 3	28 ± 3	20 ± 1	19 ± 1

Table 18 Continued.

11 Jul 79

BH*	3D*	GB*
45 ± 5	43 ± 1	39 ± 1

(temporary streams dry)

2 Sep 79

BH*	3D*	GB*
22 ± 1	21 ± 1	19 ± 1

(temporary streams dry)

9 Nov 79

GB*	DB	BH*	3D*	TB
32 ± 4	23 ± 1	22 ± 1	16 ± 1	16 ± 1

(GV dry)

Table 18 Continued.

29 Jan 80

BH*	3D*	DB	GB*	GV	TB
26 ± 3	24 ± 4	21 ± 1	20 ± 1	19 ± 1	17 ± 1

19 Apr 80

3D*	GV	BH*	GB*	DB	TB
69 ± 3	56 ± 12	42 ± 5	33 ± 7	24 ± 1	23 ± 1

24 Jun 80

BH*	3D*	GB*	(temporary streams dry)
64 ± 10	59 ± 12	35 ± 12	

the temporary streams (Table 19). Winter POM transport in the permanent streams, at higher base stream discharges, was lower than summer transport values at lower stream discharges. This trend was modified by rain storms which would temporarily increase POM transport. However, even during a rising hydrograph, summer transport was generally higher than winter transport. A typical seasonal hydrograph of a Guy's Run first-order stream is represented by Piney Branch (Figure 6).

Table 19. Means and ranges of POM transport (g/day) and means and ranges of stream discharge (l/sec) for each study stream. N = sample size.

	Mean Transport (g/d)	Mean Discharge (l/s)	N
	Permanent Streams		
Glade Brook	557 (80 - 1627)	8.37 (1.60 - 16.78)	8
Beckney Hollow	733 (71 - 1797)	9.55 (1.64 - 23.81)	8
Three Dwarf Run	237 (16 - 703)	6.65 (0.38 - 16.66)	8
	Temporary Streams		
Dry Branch	116 (2 - 342)	3.00 (0.02 - 8.75)	6
Tower Branch	153 (48 - 255)	8.21 (4.28 - 16.50)	5
Grave Branch	93 (1 - 260)	3.55 (0.11 - 8.80)	5

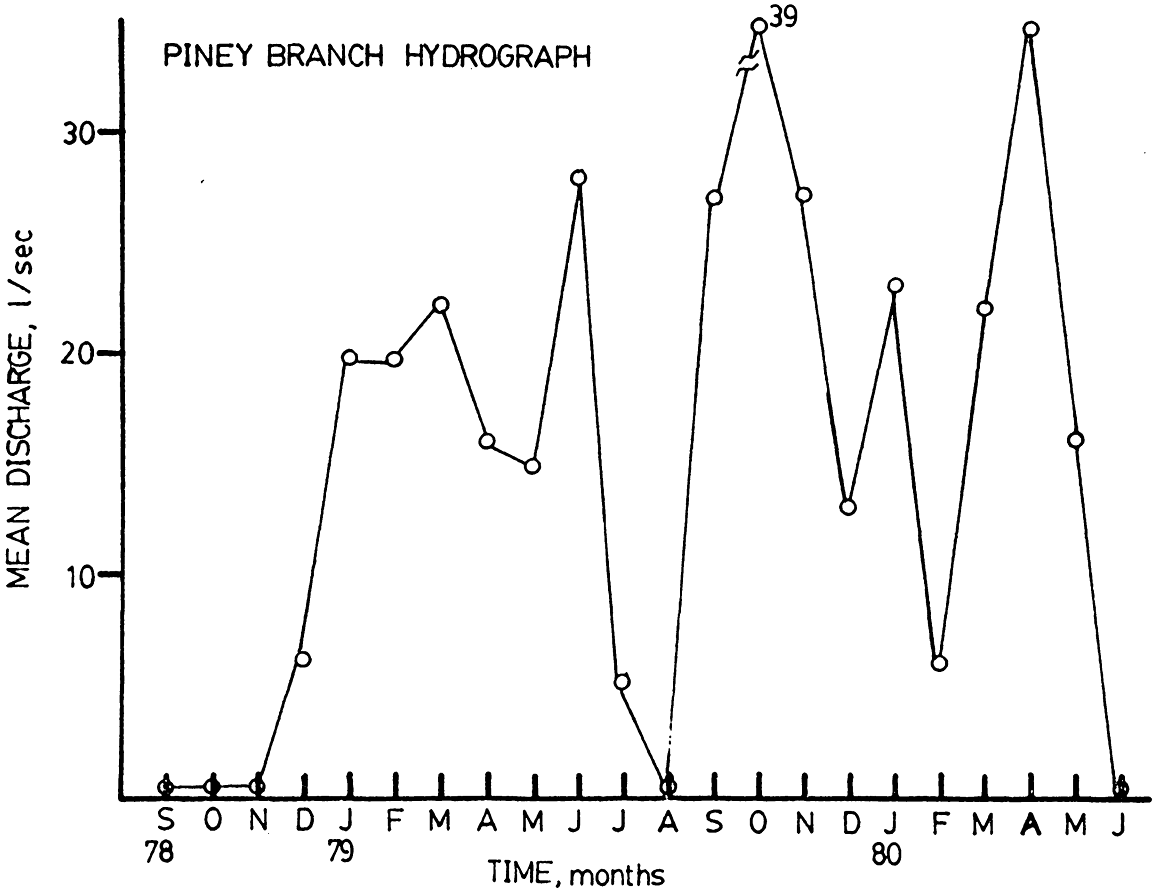

Figure 6. Average monthly discharge of Piney Branch, a first-order tributary of Guy's Run, over a 22 month period.

DISCUSSION

Leaf Breakdown

Red maple leaf breakdown rates were generally faster in the permanent streams than in the temporary streams. However, Three Dwarf Run, a permanent stream, and Dry Branch, a temporary stream, did not fit as expected into the permanent and temporary stream groups. In general, the permanent-temporary stream condition in a continuum. In this case, Three Dwarf Run and Dry Branch had characteristics which placed them near the middle of the continuum. Three Dwarf Run, even though a permanent stream, had very low flow during summer and conditions in this stream seemed to approach that of a temporary stream. Dry Branch, on the other hand, took longer to dry up during summer and regained its channel flow earlier than the other two temporary streams. Dry Branch, therefore, approached the permanent stream condition. The intermediate nature of these two streams along the permanent-temporary continuum was reflected in leaf breakdown rates, and other factors discussed below.

Red maple leaf breakdown rates measured in this study were all slower than the rate of 0.0298 d^{-1} found by Thomas (1970) for a small stream in Tennessee, but similar to the 0.0062 d^{-1} breakdown rate measured in Augusta Creek by Petersen and Cummins (1974). Reed (1979) reported breakdown rates of red maple leaves in a eutrophic lake in Ohio of 0.0300 d^{-1} at a depth of 1 m and 0.0150 d^{-1} at depths of 4 m and 12 m.

Red maple leaves have generally been considered an intermediate species in terms of leaf processing or breakdown rates (Petersen and Cummins, 1974; Reice, 1978). Other species of maple leaves have been found to vary widely in their breakdown rates. Sedell et al. (1975) found that *Acer circinatum* (vine maple) had a breakdown rate of 0.0068 d^{-1} and *Acer macrophyllum* (bigleaf maple) a rate of 0.0024 d^{-1}. In a later study, Triska and Sedell (1976) found similar rate for vine and bigleaf maples in response to nitrate manipulation. Both of these leaves had relatively slow breakdown rates similar to the rates of red maple leaf breakdown in the temporary streams of this study. Petersen and Cummins (1974) reported a breakdown rate for *Acer saccharum* (sugar maple) of 0.0107 d^{-1}, which was similar to breakdown rates of red maple in two permanent streams of this study, but faster than the temporary streams. Finally, Mathews and Kowalczewski (1968) found an intermediate breakdown rate of 0.0110 d^{-1} for *Acer pseudoplatanus* in the River Thames, which was similar to the breakdown rate for red maple in Glade Brook for both years.

Leaf Pack Shredder Composition, Density, and Biomass

Shredders were a relatively important component of the assemblage of insects collected from leaf packs and in the substrate from the six study streams (Table 20). Shredder and total aquatic insect composition on enclosed red maple leaf packs and in natural leaf and substrate samples from these six streams were similar in composition to the aquatic insect faunas found in other eastern and midwestern woodland streams (e.g., Woodall and Wallace, 1972; Petersen and Cummins, 1974).

Table 20. Percent compositions of functional groups of aquatic insects collected from red maple leaf packs from the six streams. CG = collector/gatherers, CF = collector/filterers, P = predators, Sc = scrapers, Sh = shredders.

	CG	CF	P	Sc	Sh
			Permanent Streams		
Glade Brook	31	3	7	0	59
Beckney Hollow	24	2	11	0	63
Three Dwarf Run	40	1	17	2	40
			Temporary Streams		
Dry Branch	33	6	6	1	54
Tower Branch	20	2	16	0	62
Grave Branch	31	3	13	0	53

Various seasonal factors influence shredder densities on red maple leaf packs. Moderate densities and biomass of shredders in permanent streams during winter and spring were a result of fewer individuals of a larger size (later instars), while larger numbers of early instars in midsummer increased density and sometimes biomass. Hynes (1970) noted similar seasonal trends in stream insect biomass and density. Emergence of various shredders also changes density, biomass, and composition of the shredder populations. Two events which often occur in the late summer decrease densities of shredders in permanent and temporary streams. Moderate cohort attrition (i.e., death) of early instars in the late summer and early autumn may act to initially decrease aquatic insect populations (Hynes, 1970). Cohort attrition is certainly a factor influencing shredder population structure in both types of streams at all times of year. Cessation of channel flow in temporary streams in summer and often well into autumn either decreases shredder populations by death or initiates diapause in some species. All of the above factors may have contributed to decreased colonization of leaf packs, particularly in temporary streams. A factor which might increase the numbers of aquatic invertebrates on enclosed leaf packs is the nylon mesh bag which may act as a substrate for attachment by various species (Winterbourn, 1978). The presence of the bag may have increased the surface area for colonization, however bags recovered with little or no leaf material remaining generally lacked invertebrates.

POM Transport

POM concentrations measured in this study were generally lower than the concentrations measured in other small North American streams. Gurtz et al. (1980) measured POM concentrations in Hugh White Creek, which drains in undisturbed watershed at Coweeta Hydrologic Station, and found average concentrations ranging from 0.31 mg/l in December to 3.01 mg/l in July, compared to a range of 0.07 mg/l in February to 2.18 mg/l in July in the six tributaries of Guy's Run. Higher POM concentrations than those found in the tributaries of Guy's Run were found in small streams in Pennsylvania (Sedell et al., 1978), Michigan (Wetzel and Manny, 1977), and Mississippi (de la Cruz and Post, 1979). POM concentrations more similar to the six study streams (annual average 1 mg/l) have been reported from Hubbard Brook streams (Bormann et al., 1969; Fisher and Likens, 1973; Bilby and Likens, 1979) and streams in western United States (Maciolek, 1966; Maciolek and Tunzi, 1968; Sedell et al., 1978; Naiman and Sedell, 1979).

The average POM particle size in the six study streams was generally smaller than the 37-65 um found in Hugh White Creek (Gurtz et al., 1980), but larger than the average particle size (5-12 um) reported by Naiman and Sedell (1979) for first and second order streams in Oregon. In a comparison of four streams from differing geographical-hydrological regions in the United States, Sedell et al. (1978) found that POM between 0.45-53 um made up to 70% of total transported seston for all stream sites, at all locations in all seasons. This was the predominant size range of POM collected from the six tributaries of Guy's Run.

Seasonal trends in POM concentrations and average POM particle sizes were evident. During the winter, when stream flows were highest, POM concentrations were lowest, and the average particle size was smallest. During summer when stream flows were lowest, POM concentrations were highest and the particle sizes were largest. These trends were particularly evident for the permanent streams. Similar seasonal trends in POM concentrations have been reported from other small streams. POM concentrations in Hugh White Creek were generally highest in summer and lowest in winter (Gurtz et al., 1980). In another study, de la Cruz and Post (1979) noted general increases in summer POM concentrations over winter values. Two peak POM concentration periods were noted from Augusta Creek (Wetzel and Manny, 1977): 1) a summer maximum associated with maximum riparian vegetation growth rates and reduced stream flow; 2) increasing concentrations in early winter during periods of high precipitation prior to ground freezing.

Shredders and Detrital Dynamics

Leaf breakdown rates were a direct reflection of shredder density, biomass, and production in the six study streams. Glade Brook and Beckney Hollow, with fastest breakdown rates, had highest shredder densities and biomass, and Tower and Grave Branches, both temporary streams with slow breakdown rates, had low shredder density and biomass (Table 21). Three Dwarf Run, a permanent stream, and Dry Branch, a temporary stream, had intermediate breakdown rates and intermediate shredder densities. Significant correlations were found between red maple leaf breakdown rate and shredder density for both sampling seasons

Table 21. Means (± 95% CI) and ranges of shredder standing stocks (no. shredders/g AFDW leaf matter) and biomass (mg shredders/g AFDW leaf matter) for shredders collected from red maple leaf packs.

	First Year Red Maple Leaf Packs		Second Year Red Maple Leaf Packs	
	Standing Stocks	Biomass	Standing Stocks	Biomass
		Permanent Streams		
Glade Brook	32 ± 28	8 ± 5	35 ± 38	17 ± 8
	3 - 103	1 - 19	10 - 130	4 - 30
Beckney Hollow	29 ± 31	10 ± 9	78 ± 92	58 ± 56
	2 - 113	3 - 35	12 - 310	15 - 210
Three Dwarf Run	5 ± 3	1 ± 1	19 ± 17	6 ± 3
	0 - 13	0 - 2	4 - 54	2 - 11
		Temporary Streams		
Dry Branch	9 ± 9	2 ± 2	12 ± 10	6 ± 5
	1 - 32	1 - 6	0 - 34	0 - 19
Tower Branch	9 ± 7	1 ± 1	3 ± 2	1 ± 1
	0 - 27	0 - 3	0 - 5	0 - 5
Grave Branch	3 ± 2	1 ± 1	7 ± 8	5 ± 4
	0 - 7	0 - 2	1 - 24	1 - 15

(Table 22). As noted earlier, other researchers have found similar associations between the presence (or absence) of shredder organisms and the rate of leaf breakdown in small streams (Petersen and Cummins, 1974; Hart and Howmiller, 1975; Iversen, 1975; and Sedell et al., 1975). Other factors which might affect breakdown rate, such as stream gradient, water velocity, stream temperature, and microbial activity, were not significantly correlated with red maple breakdown rates.

There was also a strong association between shredder density, biomass, and production and POM characteristics of the six study streams. The two permanent streams, Beckney Hollow and Glade Brook, with the largest shredder density, also had the highest POM concentration and largest average particle size. Three Dwarf Run, a permanent stream, and Dry Branch, a temporary stream, had intermediate shredder densities, intermediate POM concentrations, and intermediate average POM particle sizes. The two remaining temporary streams had the lowest shredder densities, lowest POM concentrations, and smallest POM sizes. Transport of POM (g/day) followed the same general pattern: streams with high, intermediate, or low transport had large, intermediate or small shredder density.

The correlations and associations described above suggest that shredders may be important in regulating POM transport. However, the argument can be made that shredders are not a primary factor regulating POM dynamics, but rather such physical characteristics as stream gradient, velocity, and stream power control POM transport (Sedell et al., 1978). In general, increasing stream power (e.g., during storms)

Table 22. Correlation (r) values comparing leaf breakdown rates for two sampling seasons and several possible leaf breakdown factors.

	Shredder Densities	Microbial Respiration	Stream Velocities	Stream Gradient	Stream Temperatures
First Season Breakdown Rates	0.90*	---	0.36	0.22	0.10
Second Season Breakdown Rates	0.72*	0.04	0.23	0.21	0.06

* r values significantly different from zero at the = .01 level.

results in increased POM concentrations and theoretically larger average particle sizes being transported in the water column. However, in this study with all samples taken during non-storm periods, I found no relationships between stream gradient, discharge, or watershed area and increased POM concentration or size. There was, however, an apparent association between shredder density and transported POM characteristics in the streams of Guy's Run watershed. POM concentrations were greatest and average particle size largest during late spring and early summer when shredder densities were the greatest. Higher shredder densities should result in high fecal production, thus greatly influencing both POM concentrations and particle size. The predominant particle sizes collected fell well within the range of invertebrate fecal pellet sizes (Joe O'Hop, personal communication, University of Georgia).

Several studies have documented that rising hydrographs increase the transported loads of POM (Lush and Hynes, 1978; Sedell et al., 1978; Bilby and Likens, 1979; Dance et al., 1979; Paustian and Beschta, 1979; de la Cruz and Post, 1980; Gurtz et al., 1980). However, Sedell et al. (1978) found only a weak relationship between POM transport rate and unit stream power, under normal flow conditions, in four streams from widely varying physiographic regions of the United States. The findings of the present study support the data of Sedell et al. and suggest that in headwater streams leaf shredding aquatic invertebrates play an important role in POM transport at least during non-storm periods.

The direct impact of shredders on leaf breakdown and POM production was estimated using the back-calculation technique of Benke and Wallace (1980). I used an assimilation efficiency of 17% based on estimates by Vannote (1969), McDiffett (1970), and Golladay (1981) and a production efficiency (production as a percent of assimilation) of 75% (Vannote, 1969; McDiffett, 1970). The potential ingestion was then computed using estimates of leaf fall and blow-in at Guy's Run (Hornick, 1978). Permanent streams, with highest shredder production rates, were most efficient in processing CPOM (Table 23). A significant portion (17-31%) of leaf breakdown in the permanent streams can be attributed to shredder activities. Temporary stream shredder populations were less efficient (1-12%) in processing CPOM entering these streams. These comparisons corroborate the relationship noted earlier between leaf breakdown rate and shredder population size.

By subtracting assimilation from ingestion, I estimated the amount of egesta or POM generated by shredders for the six streams (Table 23). From this manipulation it is evident that the permanent stream shredders, especially those inhabiting Beckney Hollow and Glade Brook, contribute a greater proportion of POM to the seston entering the main channel of Guy's Run than shredder populations in temporary streams. The amount of shredder generated POM per stream per day (calculated using the stream length and width measurements of Table 1 and egestion of Table 23) often exceeded the amount of daily POM transport (Table 24). Even when transport was high for both permanent and temporary streams, shredders generated POM was usually no lower than 10% of the transport value. Since egestion often exceeded transport it is obvious that not

Table 23. Shredder CPOM processing efficiency (SPE) based on shredder production (g DW shredders/m^{2}y, 75% assimilation to respiration), total assimilation (g DW leaf matter/g shredder/y), total ingestion (based on 17% assimilation efficiency), and leaf fall into the six streams (g/m^2/y).

	Shredder Production	Assimilation	Ingestion	Egestion	Leaf Fall	SPE
			Permanent Streams			
Glade Brook	3.80	15.20	89.35	74.10	460	19%
Beckney Hollow	6.10	24.45	143.40	119.0	460	31%
Three Dwarf Run	3.45	13.60	80.0	66.35	460	17%
			Temporary Streams			
Dry Branch	2.30	9.20	54.10	44.95	460	12%
Tower Branch	0.25	1.0	5.85	4.85	460	1%
Grave Branch	1.70	6.80	40.0	33.5	460	9%

Table 24. Transport (T, g/day) of POM on 10 sampling dates compared to total shredder egestion (E, g egesta/total stream area/day) for each stream.

	Glade Brook		Beckney Hollow		Three Dwarf Run		Dry Branch		Tower Branch		Grave Branch	
	T	E	T	E	T	E	T	E	T	E	T	E
2 Jan 79	80	184	71	770	136	196	5	81	48	12	1	127
18 May 79	479	184	1360	770	410	196	103	81	255	12	141	127
10 Jul 79	184	184	436	770	37	196	2	81	dry		dry	
12 Aug 79	1627	184	1797	770			dry		dry		dry	
9 Sep 79	99	184	186	770	16	196	dry		dry		dry	
11 Nov 79					703	196	182	81	147	12	dry	
8 Dec 79											18	127
29 Jan 80	870	184	864	770	108	196	62	81	107	12	43	127
19 Apr 80	1000	184	773	770	356	196	342	81	204	12	260	127
24 Jun 80	118	184	378	770	131	196	dry		dry		dry	

all shredder egesta enters the seston at once. Much of the egesta may remain as benthic organic matter until entering the water column during a rising hydrograph. Also, egestion is not constant through the year, but undoubtedly shows some seasonal variation. However, these comparisons suggest that shredder generated POM is a significant component of daily stream transport.

The findings of this study suggest that leaf shredding aquatic insects may be important in the regulation of detrital dynamics in headwater stream ecosystems. A regulatory role of detrital processes by shredders is not a new concept in stream ecology (Cummins, 1971 and 1973; Webster and Patton, 1979; Grafius and Anderson, 1979) but is a concept which has not been sufficiently tested. In this study I have integrated several major detrital processes with shredder population dynamics to elucidate the shredder-detrital relationship in six headwater streams. Even though there was a great deal of variation between streams, shredder population structure was strongly associated with various detrital processes. In addition, this research further illuminated some of the differences in faunal structure and detrital processes between permanent and temporary streams of a watershed. The use of the temporary stream environment was a convenient and useful tool in examining the role of shredders in detrital dynamics and had the added advantages of being a naturally occurring perturbation which recurs on a predictable, seasonal basis.

SUMMARY

This study elucidated the role of one group of aquatic invertebrates, leaf shredding aquatic insects (shredders), in regulating certain aspects of detrital dynamics in headwater streams. Shredder population dynamics were associated with several stream detrital parameters: CPOM breakdown rates, POM concentrations, average POM particle sizes, and POM transport. The shredder-detrital relationships were examined in two stream types: permanent and temporary. The temporary stream environment was found to depress species numbers, density, biomass, and production of benthic invertebrates, particularly shredders, inhabiting this type of stream. Associated with the reduction in invertebrate population densities in temporary streams was a reduction in leaf breakdown rates and transported POM. Populations of shredders inhabiting the permanent streams had greater densities, biomass, and production than temporary stream populations. Associated with the larger shredder populations in the permanent streams were increased rates of leaf breakdown and increased transported POM concentrations and particle sizes. Generally, two permanent streams, Glade Brook and Beckney Hollow, with the largest shredders populations had increased detrital parameters. Two of the temporary streams, Tower and Grave Branches, which had smaller shredder populations, had decreased detrital characteristics. Three Dwarf Run, a permanent stream, and Dry Branch, a temporary stream, had intermediate shredder population levels and generally intermediate detrital characteristics. These factors are summarized in Table 25.

Table 25. General comparisons of CPOM breakdown rates, shredder populations, and transported POM characteristics for the six study streams.

	Leaf Processing Rates	Total Shredder Density, Biomass, and Production	POM Concentrations	POM Particle Sizes
		Permanent Streams		
Glade Brook	Fast	High	High	Large
Beckney Hollow	Fast	High	High	Large
Three Dwarf Run	Slow	Intermediate	Intermediate	Large
		Temporary Streams		
Dry Branch	Intermediate	Intermediate	Intermediate	Intermediate
Tower Branch	Slow	Low	Low	Small
Grave Branch	Slow	Low	Low	Small

The relationships stressed in this study further support the hypothesis that leaf shredding aquatic insects play important roles in regulating detrital dynamics in headwater streams.

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THE ROLE OF SHREDDERS IN DETRITAL DYNAMICS OF PERMANENT AND TEMPORARY STREAMS

by

John Michael Kirby

(ABSTRACT)

The goals of this study were 1) to integrate several aspects of detrital dynamics with the composition and production of shredder populations and 2) to present evidence of a shredder regulatory role in headwater stream detrital dynamics. The importance of leaf shredding aquatic insects (shredders) in the breakdown of leaf detritus and production of particulate organic matter (POM) was evaluated in three permanent and three temporary southern Appalachian headwater streams. Shredder population dynamics were compared to several stream detrital parameters: CPOM breakdown rates, POM concentrations, average POM particle sizes, and POM transport. In general, permanent streams with the greatest shredder densities, biomass, and annual production rates had the fastest leaf breakdown rates, highest low-flow POM concentrations, largest average POM particle sizes and greatest POM transport estimates.

Temporary stream environments depressed shredder populations resulting in a reduction of detrital processing and POM transport. Microbial activity, stream velocity, base-flow discharge, and water temperature did not correlate with detrital parameters for comparisons between permanent and temporary streams. Shredder contribution to total benthic CPOM breakdown in the six study streams ranged from 31% in a permanent stream to 1% in a temporary stream.