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Stream Detritus Dynamics: Regulation by Invertebrate Consumers

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Summary. Insecticide treatment of a small, Appalachian forest stream caused massive downstream insect drift and reduced aquatic insect densities to $<10\%$ of an adjacent untreated reference stream. Reduction in breakdown rates of leaf detritus was accompanied by differences in quantity and composition of benthic organic matter between the two streams. Following treatment, transport of particulate organic matter was significantly lower in the treated stream than in the reference stream whereas no significant differences existed prior to treatment. Our results indicate that macroinvertebrate consumers, primarily insects, are important in regulating rates of detritus processing and availability to downstream communities.

Introduction

First and second order streams represent ca. 73% of the total stream length in the United States (Leopold et al. 1964) with those draining forested regions receiving large inputs of autumn shed leaves (e.g., Fisher and Likens 1973; Cummins 1973; Webster and Patten 1979). Factors which affect leaf decomposition processes in these streams may have a vast potential impact on the energy and nutrient budgets of downstream areas due to the unidirectional flow of streams. Studies have suggested that consumers may be important in regulating energy flow and nutrient cycles in ecosystems (Chew 1974; O'Neill 1976); however, in streams this role has never been clearly demonstrated. Of particular significance is the role of macroinvertebrate consumers in regulating the breakdown of autumn shed leaves to provide energy and nutrients to downstream communities.

Stream invertebrates which feed directly on coarse detritus, thus fragmenting this material to smaller particles, are called shredders (Cummins 1973). Typically they have low assimilation efficiencies (e.g., Golladay 1981), which suggest that they are important in the production of fine particulate organic matter (FPOM) used by downstream deposit and filter-feeding organisms (Anderson and Sedell 1979, Short and Maslin 1977; Wallace and Merritt 1980). Actual demonstration and quantification of this role of macroinvertebrates in detrital dynamics of forested headwater streams has been difficult (Anderson and Sedell 1979). Evidence, based primarily on leaf processing studies (e.g., Petersen and Cummins 1974; Short et al. 1980; Grafius and Anderson 1980) supports the suggestion that shredders play an important role in detrital dynamics and stream ecosystem budgets (Fisher and Likens 1973; Webster and Patten 1979).

Our objectives were to assess in small Appalachian streams the influence of macroinvertebrate exclusion on detrital processing, as indicated by leaf litter breakdown rates, concentrations of suspended particulate organic matter (SPOM), and stored organic matter. This was accomplished by treating one of two adjacent streams with a pesticide and comparing the above detrital processing parameters with those of the adjacent untreated reference stream.

Study Site

The study sites were two adjacent streams located at the Coweeta Hydrologic Laboratory (U.S. Forest Service), Macon County, North Carolina, USA. Both streams drain mixed hardwood forests, are heavily shaded by riparian rhododendron, and are equipped with flumes for continuous flow measurements. Physical characteristics of the treated (T) and reference (R) streams are: Watershed areas, R=4.2 ha, T=5.2 ha; elevation (a.s.l.) at each flume, R=841 m, T=829 m; stream gradient, R=33 cm/m, T=27 cm/m. Prior to the severe, 1980, summer-winter drought, base flow in each stream ranged from 1 to 2 l $\sec^{-1}$. Chemical characteristics of the Coweeta Basin streams can be found in Swank and Douglas (1975).

Materials and Methods

Macroinvertebrate exclusion was accomplished by application of the insecticide methoxychlor to one stream. A 24% emulsifiable concentrate of methoxychlor (1,1,1-trichloro-2,2 bis (para-methoxyphenyl) ethane) was diluted and released at a rate based on stream discharge. A stationary 10 h continuous, metered release of 5 ppm methoxychlor was supplemented with a 5 h, 5 ppm hand-sprayer release in leaf packs, seeps, backwater areas, and upstream to the source on 16 February, 1980. Supplementary 10 ppm hand-sprayer releases were conducted on 10 May, 20 August, and 8 November, 1980. Methoxychlor concentration was measured at the discharge flume, using gas chromatography analysis, during the 16 February, 1980, treatment. Prior to and during methoxychlor treatment, animal drift was measured with 230 μm mesh nets placed at each flume to filter total stream flow.

Leaf litter breakdown was measured using plastic mesh (5 × 5 mm) bags filled with ca. 15 g dry wt, equals ca. 12.3 g ash free dry wt (AFDW), of 4 leaf species (rhododendron, *Rhododendron maxima;* white oak, *Quercus alba*; dogwood, *Cornus florida*; and, red maple, *Acer rubrum*). Subunits of 4 leaf bags were placed in each stream and 3 replicate subunits were collected from each stream at 0, 8, 14, 49, 117, 144, 207 and 265 d following introduction on 16 February, 1980. With each collection organisms were removed, identified and counted; and, leaf weight (AFDW) determined. Leaf breakdown rates were calculated using an exponential decay model (e.g., Petersen and Cummins

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Table 1. Comparison of animals collected from stream litter bags containing various leaf species following treatment with methoxychlor (Treatment stream, or T) versus same from an adjacent, untreated (reference, or R) stream at the Coweeta Hydrologic Laboratory between 1 March and 7 November, 1980. Each value is the mean (±95% CL) number of organisms per litter bag

Leaf species	Stream	Insects	Shredders	Predators	Oligochaetes
Rhododendron	R	119.7±46.8	48.7±18.5	20.1±8.6	29.7±17.0
Rhododendron	T	4.8± 3.6	0.6± 0.8	1.1±0.6	80.7±36.1
White oak	R	153.1±53.6	62.5±16.8	19.1±8.4	22.6±10.5
White oak	T	12.7± 5.3	3.6± 1.7	1.4±0.8	93.1±31.9
Red maple	R	151.9±48.5	57.2±13.7	16.5±5.3	30.5±14.1
Red maple	T	9.0±12.4	2.7±10.9	1.4±0.6	92.5±38.0
Dogwood	R	106.3±41.2	37.3± 8.0	8.9±2.1	18.9±8.6
Dogwood	T	14.2± 6.9	2.3± 2.1	1.3±0.6	96.3±44.1

Table 2. Exponential breakdown rates (day^{-1} ±95% CL) of 4 leaf species, calculated by regressing ln (% ash free dry wt remaining) on time, from 16 February, 1980, to 7 November, 1980, at the Coweeta Hydrologic Laboratory. Treated stream received applications of methoxychlor, reference stream received no treatment

Leaf species	Treated stream	Reference stream
Dogwood	0.0106 (±0.0018)	0.0169 (±0.0025)
Red maple	0.0051 (±0.0011)	0.0138 (±0.0020)
White oak	0.0040 (±0.0008)	0.0108 (±0.0010)
Rhododendron	0.0012 (±0.0002)	0.0054 (±0.0012)

1974). Differences in decay coefficients were tested at 95% confidence level using analysis of covariance and Newman-Keuls multiple range test (Zar 1974).

Concentrations of SPOM at each flume (mg AFDW l^{-1}) were determined using the wet-sieving technique described by Gurtz et al. (1980). Dissolved organic carbon (DOC) analysis was performed on prefiltered (Gelman type AE glass fiber filters) water samples on 7 November, 1980, using a Dohrmann Enviro Tech Corp. Organic Carbon Analyzer.

The effect of methoxychlor on microbial respiration was evaluated in the laboratory. Dogwood leaf discs (1.3 cm diam.) were incubated in stream water at 15° C for 2 wks. Replicate (10) respiration rates were measured for 3 h, following equilibration, in Gilson Respirometer flasks (2 leaf discs/flask). One-half of the unused leaf discs were further conditioned for 1 wk in 10 ppm methoxychlor at which time respiration rates were measured. Direct microscopic counts of aquatic hyphomycetes were made using white oak leaf discs from each stream cleared by the procedure of Shipton and Brown (1962). Fungi were enumerated as the mean number of hyphae intersecting reference occular crosshairs in five random fields observed on each leaf disc.

Ten stratified samples (0.10 m^2), were collected at 5 m intervals upstream from the flume to assess organic matter storage on 4 October, 1980. Samples were taken to a depth of 10 cm where possible. Detrital material >1 mm was separated into three fractions: whole leaves, woody litter, and other detritus which was of unknown origin. AFDW was determined for each detrital category.

Results and Discussion

Although methoxychlor concentrations never exceeded 33 ppb at the flume, catastrophic invertebrate drift occurred. Drift densities exceeded 1,000× those of pre-treatment and the untreated stream, with a maximum of 12,188 animals/m^3 during treatment compared to normal drift rates of 4–8 animals/m^3 of discharge. Drift rates of Plecoptera, Ephemeroptera, Trichoptera, Coleoptera and Diptera remained significantly higher in the treated than those of the reference stream one week following application ($P<0.05$). Methoxychlor, applied as a blackfly larvicide, is known to induce similar invertebrate drift in larger streams when applied at lower rates than we used (Flannagan et al. 1979; Wallace and Hynes 1975).

Collections of benthic fauna colonizing leaf bags indicated that total insects, shredders, and predators were significantly lower in the treated than reference stream (Table 1). A shift in community structure also occurred with oligochaetes dominating the community in the treated stream following application. Leaf species breakdown rate relationships, calculated from weight loss of leaves exposed in mesh bags, were similar for both streams (i.e., dogwood > red maple > white oak > rhododendron, Table 2). However, reduction of shredders and other insects in the treated stream significantly retarded leaf breakdown rates when compared to the reference stream (*t*-test, $P<0.05$). The more refractory the leaf species, the greater the effect, which suggests that shredders are proportionally more important on slow-decaying leaves (i.e., rhododendron) than the more rapidly decaying dogwood.

Suspended POM in the treated stream was significantly lower after treatment (*t*-test, $P<0.05$) than that of the reference stream (Fig. 1A). Since summer, 1980, these concentrations have been lower than any other values reported for a natural stream (Webster et al. 1979). Suspended POM concentrations in both streams have been affected by exceptionally low flows caused by severe drought during summer and autumn. Although discharge in the reference stream declined more than discharge in the treated stream (minimum flows of 0.03 and 0.17 l s^{-1}, respectively) SPOM concentrations remained lower in the treated stream. Regressions of SPOM concentration versus flow indicate very different relationships in the two streams (Fig. 1B). No significant difference existed in dissolved organic carbon concentrations between the two streams on 7 November, 1980. DOC concentrations (mg C l^{-1}±95% CL) were: treatment stream = 0.74±0.32; reference stream = 0.68±0.31.

Methoxychlor appears to have no inhibitory effect on microbes at levels we applied. Addition of 10 ppm methoxychlor did not change respiration rates of conditioned leaf discs (*t*-test, $P>0.10$). Furthermore, direct microscopic counts of fungal hyphae from leaves in the treated and reference streams did not suggest any fungal inhibition (*t*-test, $P>0.10$).

Total standing crop of benthic detritus (>1 mm) was not

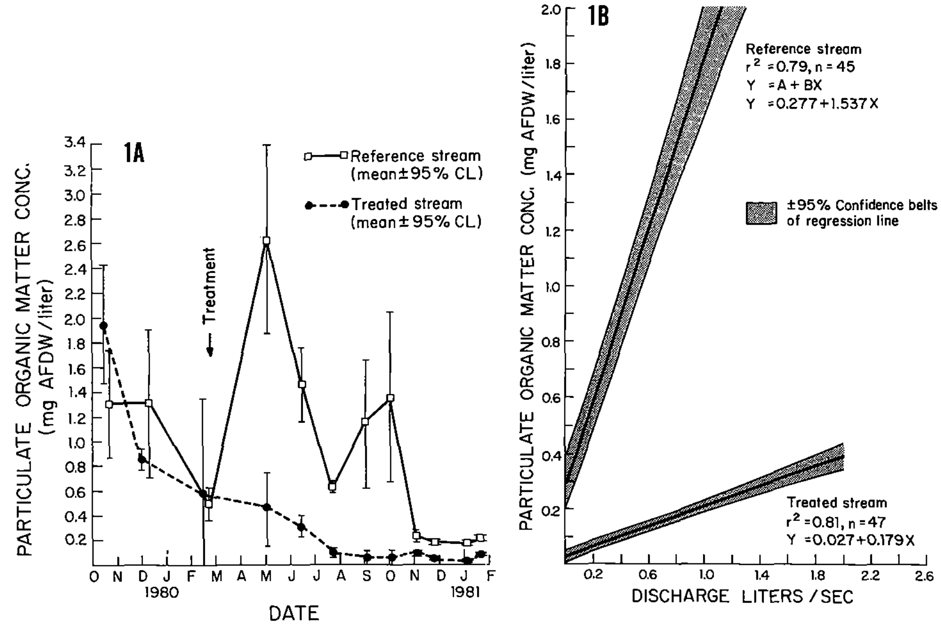

Fig. 1 **A** Suspended particulate organic matter concentrations in the methoxychlor treated and reference streams. **A** Concentrations (±95% CL) between 13 October, 1979, and 18 January, 1981. Insecticide was applied to the treatment 270854,01stream on 16 February, 1980. Data are based on 3–10 samples from each stream on a given date. **B** Regressions of SPOM concentration (±95% Confidence Belts) versus discharge for declining flow during the prolonged drought following methoxychlor application. As flow declined POM concentrations decreased in each steam. But even at lowest flows, concentrations in the reference stream were significantly higher than those of the treated stream

Table 3. Standing crop (g AFDW m^{-2}±95% CL) of benthic detritus >1 mm in early autumn, 1980, in the treated and reference stream (n=10 for each stream)

Category	Treated stream	Reference stream
Woody detritus	904.8±585.0	727.8±573.9
Whole leaves	88.0± 49.8	83.2± 51.4
Other detritus[a]	512.2±273.2	102.9± 96.1
Total detritus (excluding wood)	600.2±315.7	186.1± 96.7
Total detritus (including wood)	1,505.0±803.7	913.9±612.5

[a] Detritus >1 mm and of unknown origin

significantly different in the two streams (Table 3). The categories of woody detritus, which dominated total benthic detritus, and whole leaves were not significantly different between the two streams. However, other detritus (assumed to consist primarily of partially decomposed leaf fragments) was about 5×higher in the treated stream (Table 3).

Conclusions

Headwater streams are known to retain a large portion of their coarse organic inputs and export primarily FPOM (Webster and Patten 1979). It has been suggested that the great abundance of FPOM in transport from headwater streams indicates that FPOM may be generated rapidly and continuously (Naiman and Sedell 1979). We have shown that alteration of the fauna, without accompanying changes in energy inputs to the stream or in the physical characteristics of a stream, influences breakdown, utilization, and subsequent downstream transport of energy inputs. Invertebrate consumption and subsequent egestion appear to produce a significant portion of the FPOM which is transported downstream. This study supports suggestions that consumers are important in regulating energy flow and nutrient cycling in ecosystems (Chew 1974; O'Neill 1976).

The sporadic temporal occurrence of storms may lead to different interpretations of the effect of macroinvertebrates on the utilization of organic material. Within short time frames, i.e., between major storms, macroinvertebrates may contribute to a reduction in overall efficiency (percent of organic carbon reduced to CO_2) by increasing loss of organic material through downstream transport. Conversely, over a longer period they may enhance efficiency by using organic materials that may otherwise be lost through storms before these materials are microbially reduced. Oscillations between inputs and outputs are manifested as changes in storage and transport of organic matter (Vannote et al. 1980). Absence of macroinvertebrates reduces detrital processing rates leading to an accumulation of organic matter. Sporadic storms then become increasingly important in the export of this accumulated material from headwater streams and in the provisioning of downstream reaches with this organic matter. Therefore, the temporal mediation of detrital breakdown, induced by macroinvertebrates, reduces the export variability and lessens the influence of major storms on organic matter transport. Otherwise, a large portion of storm transported material may be pulsed so rapidly through downstream areas that little or no utilization occurs unless a retention device is encountered. Therefore, macroinvertebrate feeding results in a more constant supply of organic matter to downstream areas.

Viewed in the above context, we feel that the action of pesticides on stream ecosystems, e.g., as used in larval black fly control, extends beyond purely toxicological questions. Our data indicate that applications of chemical control measures may potentially affect energy and nutrient flow within stream ecosystems in more subtle and far-reaching manners than previously recognized.

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