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Shredder abundance and leaf breakdown in an Appalachian Mountain stream

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SUMMARY. 1. Breakdown rates of dogwood (*Cornus florida* L.), red maple (*Acer rubrum* L.) and white oak (*Quercus alba* L.) leaves were investigated at two first-order and two second-order sites in an Appalachian Mountain stream.

2. Leaves exposed in mesh bags were sampled on eight occasions over a 207 day period and breakdown rates were compared using an exponential decay model.

3. There was a consistent ranking in leaf breakdown rate within each site, i.e. dogwood > red maple > white oak, and all species broke down faster at second- than at first-order sites.

4. Our data suggest that differences in species-specific leaf breakdown rates were largely a function of shredder abundance on the leaves.

Introduction

Low-order streams in deciduous woodlands are known to be energetically dependent on leaf material from riparian vegetation. Most leaves entering low-order streams travel only short distances before becoming trapped by obstructions and are essentially processed (i.e. reduced to fine particles, dissolved material, or mineralized) in place by a combination of biological and physical factors (e.g. Petersen & Cummins, 1974; Boling *et al.*, 1975; Naiman & Sedell, 1979; Iversen, Thorup & Skriver, 1982). Biological processing of leaf material in most cases has been shown to follow the general sequence of leaching of soluble materials followed by microbial colonization and conditioning and invertebrate feeding (reviewed by Anderson & Sedell, 1979; Cummins & Klug, 1979).

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The quantitative importance of invertebrate (shredder) feeding in the conversion of whole leaves to fine particles is not well known but some estimates are available. Cummins *et al.* (1973), using individual and mixed groups of invertebrates in laboratory experiments, estimated animal processing of leaf material to account for about 20% of total weight loss. In field experiments, Petersen & Cummins (1974) attributed about 24% of the processing of leaf packs to invertebrate feeding. Using an insecticide to exclude macroinvertebrates from a first-order woodland stream, Wallace, Webster & Cuffney (1982) found that leaf pack breakdown rates were reduced by 37% for dogwood, 63% for red maple and white oak, and 78% for *Rhododendron* when compared to a reference stream. Iverson *et al.* (1982) estimated that the annual ingestion by shredders in Danish headwater streams was about one-half of the annual input of leaves. Kirby, Webster & Benfield (1983) compared leaf breakdown in permanent and temporary streams and found that processing was slower in the temporary streams, apparently due to reduced invertebrate abundance. In streams where shredders are numerically unimportant or absent, leaf processing appears to occur as a function of microbial and physical factors alone (Matthews & Kowalczewski, 1969; Benfield, Jones & Patterson, 1977; Reice, 1978; Rounick & Winterbourn, 1983). The demonstration by Suberkropp & Klug (1980) that aquatic hyphomycete fungi are able to macerate leaf tissue enzymatically shows how leaves can be fragmented in the absence of shredder feeding.

The objective of this study was to examine the relationships of shredder abundance and leaf breakdown rate at four sites on an Appalachian Mountain stream.

Study site

The study was conducted in Guys Run, a second-order stream in the James River Basin (79° 39′ W long, 38° 58′ N lat.) located in the Goshen Wildlife Management Area, Rockbridge County, Virginia, U.S.A. Guys Run is about 8 km long and lies in a mountainous catchment (19 km^2) covered by mixed deciduous forest with some pine and hemlock. Geology of the area is mainly lower and middle Devonian shale, sandstone and quartzite with occasional thin layers of limestone (Bick, 1960). Most headwater springs issue acidic water (pH about 5.0) and certain tributaries remain acidic throughout their lengths. Mainstream pH varies between 6.8 and 7.8, apparently due to the presence of limestone in the streambed. In general, streams of the Guys Run system are heavily shaded, low in nutrients, clear and low in autochthonous primary production (Hornick, Webster & Benfield, 1981).

Leaf breakdown rates were investigated at four sites in the Guys Run drainage basin. Two of the sites were on the second-order mainstream: GL and GM, 2.5 and 5.0 km from the mouth, respectively. The other two sites were first order: GU on the mainstream, 7.0 km from the mouth; and PB, a tributary entering the mainstream between GM and GL. Selected abiotic variables for the four sites appear in Table 1.

Materials and Methods

Leaves of dogwood (*Cornus florida* L.), red maple (*Acer rubrum* L.) and white oak (*Quercus alba* L.) were picked from trees in the Guys Run catchment just prior to abscission. Leaves were air dried to constant weight and about 5 g packs were placed in nylon mesh bags (mesh size 1 cm) which were tagged for initial dry weight and species. Cummins *et al.* (1980) reported that leaf breakdown rates measured with small-mesh bags were significantly slower than rates measured with leaf packs tied to bricks and unconfined leaves. However, other studies have shown that as long as reasonably large mesh is used, rates measured with mesh bags and unconfined packs are not significantly different (Benfield, Paul & Webster, 1979; Webster & Waide, 1982). Bags are much easier to handle and, when suitably anchored, are not subject to loss during floods.

Five bags of each species were placed in a

TABLE 1. Selected abiotic variables for the study sites

	GL	GM	GU	PB
Order (Strahler, 1957)	2	2	1	1
Catchment area (km^2)	16.6	8.2	4.2	3.3
Average discharge ($l\ s^{-1}$)	400.0	220.0	70.0	50.0
Mean width at site (m)	4.5	4.5	1.3	1.7
Mean depth at site (m)	0.07	0.16	0.09	0.06
Gradient (%)	2.1	4.5	3.3	5.6
Temperature mean (°C)	11.1	11.0	10.1	10.8
Temperature range (°C)	0.5–20.0	0.5–19.5	0.5–19.0	0.5–19.5
pH mean	7.2	7.1	6.0	5.1
pH range	7.0–7.7	6.8–7.7	5.4–6.5	4.7–6.7

wire mesh 'sandwich' (0.3×0.9 m, 3 cm mesh opening) constituting a sample unit (Paul, Benfield & Cairns, 1978). Eight sample units were secured to the streambed at each site on 21 December 1978, using two parallel lengths of steel chain and steel reinforcing rods. One unit was returned to the laboratory to account for losses due to handling.

One sample unit was retrieved at random from each site after 7, 21, 56, 85, 116, 150, 178 and 207 days. The last unit was removed on 15 July 1979. Bags were removed immediately from the 'sandwiches' and placed individually into plastic containers which were kept on ice and returned to the laboratory. In the laboratory, leaf material was carefully washed of debris and invertebrates and air dried to constant weight. Homogenized sub-samples were ashed at 500°C for 1 h to obtain ash free dry weight (AFDW). Exponential breakdown rates ($-k$) were calculated by regressing log e per cent AFDW remaining against exposure time. The exponential model has been widely used as a means of comparing leaf breakdown rates in streams (e.g. Petersen & Cummins, 1974; Webster & Waide, 1982). Invertebrates were sorted, identified to genus (except Chironomidae), counted, and assigned to functional groups according to Cummins (1973) and Merritt & Cummins (1978). Shredder abundance was expressed as number (number per pack) and density (number per g AFDW leaf material remaining). Only packs containing at least 1 g of leaf material were used in calculating shredder number and density.

Results

Leaf breakdown

Breakdown rates ($-k$) were significantly ($P<0.01$) different from zero for all species at all sites (Table 2), indicating that the exponential model was appropriate for comparing breakdown rates. Breakdown rates followed a consistent rank ordering within each site, dogwood>maple>oak, even though statistical treatment of the data failed to show significant differences for some comparisons (rates for maple and oak were not significantly different at GL and PB, and there were no significant differences among species at GU, Table 2). When breakdown rates were compared between sites, a consistent rank ordering was found for all three species, GL>GM>PB>GU, and all three species broke down significantly faster at second-order than at first-order sites (Table 2).

Shredder abundance on leaf packs

Shredder number and density were analysed for a leaf species effect within each site on each sampling date (ANOVA, Duncans Multiple Range Test, $\alpha=0.05$). There were no

TABLE 2. Mean species-specific breakdown rates ($-k$) of the three species at each study site. Values with the same letter are not significantly different: capital letters represent between site comparisons for each species; lower case letters represent within site comparisons among the three species ($\alpha=0.05$ ANOVA, Fishers Protected Least Significant Difference Procedure; Koopmans, 1981). All values of r (for regression of ln per cent weight remaining against time) are significant ($P<0.01$).

Leaf species	Site	N	Breakdown rate (d^{-1})	95% CL	r
Dogwood	GL	23	0.0486 A a	0.0328–0.0645	0.81
	GM	36	0.0215 B a	0.0153–0.0277	0.77
	PB	45	0.0102 C a	0.0051–0.0153	0.53
	GU	45	0.0055 D a	0.0040–0.0069	0.75
Red maple	GL	35	0.0222 A b	0.0151–0.1292	0.74
	GM	43	0.0141 B b	0.0107–0.0175	0.80
	PB	45	0.0069 C b	0.0058–0.0081	0.87
	GU	45	0.0043 C a	0.0036–0.0050	0.89
White oak	GL	39	0.0182 A b	0.0137–0.0228	0.80
	GM	45	0.0094 B c	0.0072–0.0117	0.80
	PB	45	0.0039 C b	0.0033–0.0045	0.90
	GU	45	0.0021 C a	0.0017–0.0024	0.87

significant differences among species for shredder number on any date at any site; however, there were leaf species differences in shredder density for two dates at GM and one date each at GU and PB. When mean shredder number or density over the 207 day study period were tested for leaf species effects within sites, there were no significant differences among leaf species for any site.

Shredder number and density were also analysed for site differences for each leaf species on each sampling date (ANOVA, Duncans Multiple Range Test, α=0.05). Significant site effects occured on about 70% of the dates for both shredder number and density. Site comparisons of mean shredder number and density over the 207 day study period for each species showed no significant site difference for dogwood. However, both shredder number and density on red maple and white oak were significantly higher at the two second-order sites (GL, GM) than the two first-order (GU, PB) sites (Table 3). When all leaf species were combined at each site, shredder number and shredder density were significantly higher at the two second-order sites (Table 3).

Discussion

Observed patterns of species-specific leaf breakdown rates in the Guys Run system suggest that the absolute rate at which leaves were broken down was primarily a function of their position in the drainage basin. All three species broke down significantly faster at the second-order sites than at first-order sites. In addition, there was strong evidence of a natural ordering of species-specific breakdown rates in which some species broke down faster or slower than others, regardless of their location in the stream system. This finding is consistent with many other studies.

Between site differences in leaf breakdown rates in Guys Run appeared to be related to shredder abundance on the packs; however, shredder abundances did not explain differences in species-specific breakdown rates within sites. There were approximately equal numbers of shredders on each leaf species within each site over the study period, yet species-specific breakdown rates were different within sites. This observation is somewhat surprising because shredders tend to choose fast processing leaves over slower ones (e.g. Kaushik & Hynes, 1971; Petersen & Cummins, 1974; Hart & Howmiller, 1975), and it is thought that the choice is based on differential food quality (e.g. Kaushik & Hynes, 1971; Mackay & Kalff, 1973). At least two explanations can be offered. First, shredder abundance had little or no effect on leaf breakdown rates. Shredders and other aquatic invertebrates are known to

TABLE 3. Between site comparisons of shredder mean number (number per pack) and mean density (number per gram AFDW leaf material)

Species	Site	No. of leaf packs used in analysis	Mean number	Mean density
Dogwood	GL	14	5.1 a*	2.1 a
	GM	14	7.4 a	3.7 a
	PB	35	4.8 a	5.3 a
	GU	35	6.5 a	2.4 a
Red maple	GL	19	26.7 a	33.5 a
	GM	24	26.7 a	26.4 ab
	PB	37	10.0 b	7.2 b
	GU	39	7.0 b	2.4 b
White oak	GL	23	24.1 a	15.4 a
	GM	36	26.1 a	19.6 a
	PB	37	10.5 b	4.2 b
	GU	39	8.8 b	3.1 b
Totals†	GL	56	20.3 a	18.2 a
	GM	74	22.7 a	18.8 a
	PB	109	8.5 b	5.6 b
	GU	113	7.4 b	2.6 b

* Values with the same letter are not significantly different (ANOVA, Duncan's Multiple Range Test, α=0.05).

† Values for all leaf species combined.

use any leaf accumulation as a convenient substrate (Egglishaw, 1964; Fahy, 1975; Benfield *et al.*, 1977; Short, Canton & Ward, 1980; Hawkins & Sedell, 1981), and the mere presence of shredders on leaves does not *a priori* translate to shredder consumption of the leaves. A second explanation is that, although there were approximately equal numbers of shredders on the three leaf species, feeding occurred at a greater rate on the higher quality leaves. It has been demonstrated in the laboratory that the leaf-shredding stonefly, *Petoperla maria* Needham and Smith, tends to prefer dogwood > red maple > white oak (Wallace, Woodall & Sherberger, 1970), and Golladay, Webster & Benfield (1983) demonstrated that ingestion rate by another stonefly, *Pteronarcus proteus* Newman, decreased with these leaf species in the same order. If it is assumed that shredders fed preferentially on dogwood leaves, which broke down faster than the other two species, the second explanation is favoured.

Between-site comparisons provide a more convincing case for a relationship between shredder abundance and leaf breakdown. Leaf packs at the second-order sites had higher numbers of shredders than did those in the first-order sites, and all three species of leaves broke down significantly faster at the second-order than at the first-order sites. The implied relationship between the two data sets is that more shredders means faster breakdown rates, as has been also suggested by a number of other authors (Cummins *et al.*, 1973; Hart & Howmiller, 1975; Iversen, 1975; Petersen & Cummins, 1974; Sedell, Triska & Triska, 1975; Short *et al.*, 1980; Wallace *et al.*, 1982; Kirby *et al.*, 1983; Rounick & Winterbourn, 1983).

While the relationship between shredder abundance and leaf breakdown seems convincing, we are left with the question as to why there were more shredders on leaf packs placed at second- than at first-order sites. A general prediction of the river continuum concept (Vannote *et al.*, 1980) is that shredders should decrease in importance in a downstream direction: a prediction recently tested and largely substantiated in four different drainage basins in North America (Minshall *et al.*, 1983). A study conducted at five sites, including the four sites studied here and a fifth site near the mouth of Guys Run, in the Guys Run catchment in 1977–78 (E. F. Benfield, J. C. Miller and J. R. Webster, unpubl.) showed that mean shredder density on the streambed declined in a downstream direction. Although the site differences were not statistically significant (ANOVA, α=0.05), the trend of declining shredder density downstream in Guys Run tends to follow the predictions of Vannote *et al.* (1980). In contrast, our data for shredder abundance on leaf packs appear to run counter to both theory and actual measurements in the streambed. The key to the unexpected pattern of shredder abundance on leaf packs may be explainable on the basis of differences in litter input and the relative retentiveness for leaf material by first- and second-order sites. Litterfall and blow-in were about equal at the four sites (Hornick *et al.*, 1981), but we estimate that the mass of litter reaching the stream surface to be 2–3 times greater at first- than second-order sites based on differences in stream width. Unfortunately, we have no reliable data for benthic coarse particulate organic matter (CPOM) standing crop at the sites. However, we think the average CPOM standing crop over the study period was higher at first-order sites because they received greater litter input and exhibited slower litter breakdown rates. In addition, first-order reaches in Northeastern (Bilby & Likens, 1980; Bilby, 1981; Naiman, 1983) and Southeastern (Webster, 1977) mountain streams in North America have higher CPOM retention capacities than higher-order reaches. Our leaf packs were placed at sites about 2 months after peak natural litter fall. We hypothesize that shredder abundance on our leaf packs were lower at first-order sites because there was abundant natural litter at the sites and thus little tendency for shredders to move to newly added leaf material. In contrast, there was less natural litter available initially at second-order sites and, at the time our leaf packs were introduced, the natural litter available was probably widely dispersed over the streambed (Petersen & Cummins, 1974). Thus our leaf packs probably served as islands of food and refuge for shredders in the face of declining natural litter. Webster & Waide (1982) offered a similar explanation for differences in leaf breakdown rates associated with logging.

As has been the case in a number of studies (e.g. Petersen & Cummins, 1974; Cummins *et al.*, 1980), we found little direct evidence that physical factors in the stream system significantly affected breakdown rates. In the case of natural leaf accumulations, water currents may well be important in leaf breakdown as leaf packs are continually formed and redistributed in a particular stream reach (Boling *et al.*, 1975). Scouring or burial by sediments may also affect leaf breakdown rates (e.g. Webster & Waide, 1982; Rounick & Winterbourne, 1983). However, we believe that the restraint system employed in the present study largely negated these and other physical effects at the sites.

The one chemical factor that differed substantially between the first-order and second-order sites was pH: the first-order sites were naturally acidic due to geologic factors (Hornick *et al.*, 1981). Field studies have shown that aquatic organisms from various trophic levels are adversely affected by anthropogenic acidity (e.g. Hall *et al.*, 1980; Haines, 1981). In some English headwater streams, Townsend, Hildrew & Francis (1983) found invertebrate species richness and species diversity inversely related to acidic conditions. Total invertebrate diversity and production are somewhat lower in the first-order (acidic) than in second-order (basic) sites in the Guys Run watershed (E. F. Benfield, J. C. Miller and J. R. Webster, unpubl.). However, shredder density and production were higher at first-order sites suggesting that the prevailing low pH did not seriously affect leaf shredding by invertebrates. Hall *et al.* (1980) found that aquatic hyphomycete fungi, a group considered important in the decomposition of CPOM in streams (e.g. Cummins & Klug, 1979), were reduced in number after artificial acidification of Norris Brook. However, Suberkropp & Klug (1980) and Sinsabaugh, Benfield & Linkins (1981) found that cellulases from stream fungi function optimally under acidic conditions suggesting that natural acidic conditions in first-order streams in Guys Run would not seriously affect microbial decomposition.

Our purpose in this study was to investigate the effects of shredder abundance on leaf breakdown in the Guys Run system. The observed 'shredder effect' supports the idea that shredders are important in the processing of leaf litter in Appalachian Mountain streams. The basis for the observed 'order effect' is not clear, in part, due to the timing of our experiment. The results may have differed had our leaf pack placement been synchronous with natural leaf-fall. However, our data suggest that leaf packs formed in late December, e.g. from leaves blown into the stream, would break down faster in the second- than the first-order sites.

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