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Nutrient addition accelerates leaf breakdown in an alpine springbrook

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Abstract This study assessed the effect of nutrient enrichment on organic matter breakdown in an alpine springbrook, using alder leaf packs to which phosphorus and nitrogen were added in the form of slow-release fertilizer briquettes. The breakdown of leaf packs with nutrients added (k=0.0284 day^{-1}) was significantly faster than that of unfertilized packs (k=0.0137 day^{-1}), resulting in a 30% higher mass loss after 42 days. Unfertilized leaves enclosed in fine-mesh bags broke down at an even slower rate (k=0.0062 day^{-1}). Phosphorus and nitrogen concentrations were initially higher in leaf packs with nutrients added, but this difference disappeared within 3 weeks. Fungal biomass developing in decomposing leaves was substantial (*c*. 55 mg dry mass per 1 g leaf dry mass) although similar between fertilized and unfertilized packs, as was the sporulation activity of aquatic hyphomycetes. There was a significantly greater number and higher biomass of macroinvertebrates (shredding nemourid stoneflies in particular) on the fertilized packs, suggesting that the increased leaf mass loss was brought about by shredder feeding.

Key words Alpine springbrook · Leaf breakdown · Nutrient addition · Aquatic hyphomycetes · Macroinvertebrates

Introduction

Streams in alpine areas appear resource-limited in terms of both nutrients, such as nitrogen and phosphorus, and organic matter as a source of carbon. This is inferred from the relatively harsh environmental conditions in alpine catchments and their resulting influence on stream ecosystems (Ward 1994). Streams in alpine areas have low temperatures (typically <10°C), and both temperature and flow regimes typically display high seasonal and diel variation (Milner and Petts 1994). Low rates of rock weathering imply minimal edaphic inputs of nutrients, phosphorus in particular, although there are significant atmospheric inputs of nitrogen to Swiss alpine streams (Malard et al. 1999). Sparse woody vegetation results in low inputs of terrestrially derived particulate organic matter (i.e., leaf litter and wood) which plays a critical role in stream functioning at lower elevations. Concomitantly, autotrophic production of organic matter may be limited, particularly when scour and water turbidity increase during high flow (Milner and Petts 1994; Uehlinger et al. 1998).

Notwithstanding these general trends, streams in alpine glacial flood plains can display a wide variety of types, ranging from channels fed by glacial meltwater to groundwater-fed springbrooks (Ward 1994). Springbrooks are considered a relatively benign flowing-water environment in alpine flood plains (Klein and Tockner 1999); however, they still may be severely limited by resource availability, and this may influence resident populations of both invertebrate detritivores, as demonstrated for some low elevation streams (Dobson and Hildrew 1992), and other organisms such as aquatic hyphomycetes. When resources such as nutrients and/or organic matter are scarce, ecosystem-level processes also may be constrained. For example, primary production has been shown to be nutrient-limited in arctic tundra and temperate woodland streams (e.g., Arscott et al. 1998). Evidence from woodland streams also suggests that heterotrophic processes such as leaf litter breakdown can be restrained by nutrient limitation (Elwood et al. 1981; Meyer and Johnson 1983; Suberkropp and Chauvet 1995).

Litter breakdown in streams is an ecosystem process that both detritivorous macroinvertebrates ("shredders") and microorganisms contribute (Webster and Benfield 1986; Gessner et al. 1999). Fungi, aquatic hyphomycetes in particular, play an important role among the latter

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(Gessner et al. 1997; Suberkropp 1998a). Because aquatic hyphomycetes growing on leaves take up nutrients from the surrounding water (Suberkropp 1998b), and because rates of leaf breakdown in streams are correlated with nutrient concentrations, microbial (mostly fungal) biomass, and fungal sporulation activity associated with leaves, it has been suggested that nutrient control of litter breakdown in streams is mediated by fungal activity (Gessner et al. 1997). The mechanism of this mediation may be direct or indirect because aquatic hyphomycetes also can promote leaf breakdown by enhancing leaf palatability to shredding invertebrates (Cummins and Klug 1979; Suberkropp 1992).

The main objective of this study was to ascertain whether nutrient availability may limit heterotrophic processes in an alpine springbrook, and if so, whether the effect is mediated by macroinvertebrate shredders, fungi, or both types of organisms. Even though allochthonous litter inputs to alpine streams are generally sparse or absent, leaf breakdown does occur in alpine streams when this resource becomes available (Gessner et al. 1998; Robinson et al. 1998). Therefore, leaf breakdown may serve as a surrogate to assess whether heterotrophic processes, in general, may be nutrient-limited in alpine streams.

Materials and methods

Site description

The study was conducted in an alpine (2080 m above sea level, a.s.l.) springbrook in the 49.5-km^2 Val Roseg catchment of the Swiss Alps (9°53'57"E, 46°29'28"N). A detailed description of the catchment can be found in Tockner et al. (1997). The catchment is covered mostly by glaciers and bare rock (75%), with an additional 18% covered by grassland. In the catchment, the predominant woody vegetation is restricted mostly to valley sideslopes and consists of larch (*Larix decidua* Mill.) and arve pine (*Pinus cembra* L.). Alder (*Alnus viridis* Chaix, Dc.) grows mostly at lower altitudes, although both alder and larch occur in the riparian area of the springbrook. Width of the wet channel ranged from 0.5 to 1 m, and water depth was 10–30 cm. The springbrook had clear water 1.7 NTU (nephelometric turbidity units), 0.55 mg l^{-1} dissolved organic carbon (DOC), a circumneutral pH (6.8), specific conductance of 81 µS cm^{-1}, ortho-phosphate concentrations of <1 µg P l^{-1}, and nitrogen concentrations of 0.4 mg l^{-1} (as NO_2^-+NO_3). Water temperature ranged between 3.5 and 6.1°C during the study period, as monitored continuously with a StowAway XTI datalogger (Onset Computer Corp., N. Falmouth, Mass., USA).

Methods

Leaf packs were made of alder (*A. viridis*) leaves picked from shrubs *c*. 1 km downstream of the study area on 29 September 1997. Care was taken to include only leaves that were easily detached from branches. Following overnight storage in plastic bags at outdoor temperatures, 7.0 g fresh mass of leaves (corresponding to a mean dry mass of 2.3 g) were placed into fine (0.5-mm mesh) and coarse (5-mm mesh) mesh nylon bags (following Robinson et al. 1998). Nutrients were added to half of the coarse-mesh packs in the form of a slow-release fertilizer briquette containing magnesium ammonium phosphate ($MgNH_4PO_4\,H_2O$; IMC Vigoro Corp., Winter Haven, Fla., USA). Analyses indicated that briquettes initially contained 6.7% N and about 17.6% P, decreasing to 5.1% N and 14.5% P after placement in water for several weeks (K. Ashley, University of British Columbia, personal communication). Bags with and without fertilizer briquettes were tethered to individual steel rods anchored into the stream bottom on 30 September 1997. Ten randomly chosen leaf packs were returned to the laboratory the same day, dried and weighed to determine the average moisture content of leaves. This information was used together with the initial fresh mass of individual leaf packs to calculate initial dry mass. Four replicate leaf packs of each treatment were retrieved 1, 9, 22, 42, and 77 days after immersion or until no more leaf material remained. Immediately following retrieval, leaves were removed from individual mesh bags, placed in Whirl-Pac bags with stream water added, stored in a cooler with ice, and returned to the laboratory. Fertilizer briquettes were reduced to about half their size on the last sampling date.

Following the removal of macroinvertebrates and extraneous sediments, halves of three individual leaves (about 0.2 g dry mass) were placed in 50 ml of deionized water and incubated on a shaker for 5 days at 4°C to facilitate sporulation of aquatic hyphomycetes (Gessner et al. 1998). Following incubation, each sample was gently agitated and the fungal slurry preserved with 2% formalin for later identification and quantification of fungal spores. For that purpose, samples were treated with dilute Triton X-405 solution, vortexed, 1–20 ml of the suspension filtered through a membrane filter (5 µm pore size), and the trapped conidia were stained with 0.02% Trypan blue in lactic acid, identified and counted at 200× (Gessner et al. 1998). The leaf material from each sample was dried at 60°C (several days) and weighed.

The remaining leaf material from each pack was stored at –20°C until analysed for ergosterol, a measure of fungal biomass (Gessner and Newell 1997). The leaf material was freeze-dried, weighed, and crushed, and lipids were extracted from 50-mg subsamples with hot alkaline methanol. The lipid extract was cleaned by solid-phase extraction (SPE), and purified and quantified by high performance liquid chromatography (HPLC) (Gessner and Schmitt 1996). Ergosterol concentrations were converted to fungal biomass using the ratio of 5.5 µg ergosterol per 1 mg fungal dry mass (Gessner and Chauvet 1993; Gessner and Newell 1997). Additional subsamples (50–100 mg) were removed from each leaf pack for determination of leaf nitrogen and phosphorus concentrations as described previously (Gessner et al. 1998; Robinson et al. 1998).

Exponential breakdown rates of leaves were estimated using non-linear regression analysis with the initial leaf mass (intercept) fixed at 100%. Linear regressions on ln(x+1) transformed data produced very similar results. Analysis of covariance (ANCOVA) followed by Tukey's test was used to test for differences in breakdown rates among treatments (Boulton and Boon 1991). Differences in ergosterol concentrations were also assessed by ANCOVA, whereas ordinary and/or repeated-measures analysis of variance (ANOVA) were used to test for differences in nutrient concentrations, sporulation rate (log-transformed data) and species richness of aquatic hyphomycetes, macroinvertebrate numbers and biomass, and shredder numbers.

Results

Leaf breakdown was significantly faster in coarse-mesh packs with nutrients added than in coarse-mesh control packs without added nutrients (Table 1; P<0.01). After 6 weeks, only 28% of the initial leaf mass remained in the fertilized packs, whereas 54% remained in the unfertilized coarse-mesh packs (Fig. 1). It took 11 weeks for coarse-mesh control packs to reach 30% leaf mass remaining (data not shown). Fine-mesh packs showed an even slower breakdown in the absence of nutrients (Table 1), with 73% of leaf mass remaining after 7 weeks (Fig. 1) and 68% remaining after 11 weeks.

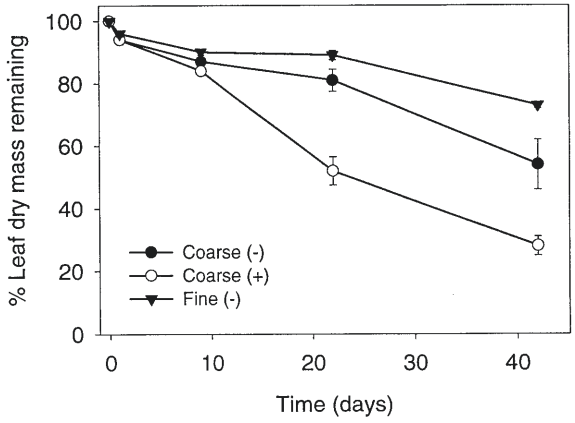

Fig. 1 Mean (±1 SE, *n*=4) percent leaf dry mass remaining of alder leaves decomposing in an alpine springbrook in coarse-mesh control packs (–), coarse-mesh packs with nutrients added (+), and fine-mesh packs with no nutrients added (–)

Table 1 Breakdown rates (*k*) of fertilized and unfertilized alder leaf packs placed in coarse (5-mm) and fine (0.5-mm) mesh bags in an alpine springbrook. Breakdown rates were estimated by nonlinear regression analyses (*c.l.* 95% confidence limit; r^2 corrected coefficient of determination). Rates with different *superscript letters* are significantly different

Mesh size	Enrichment	*k*±c.l. (day^{-1})	r^2	*n*
Coarse	Yes	–0.0284±0.0036^a	0.947	16
Coarse	No	–0.0137±0.0029^b	0.817	18
Fine	No	–0.0062±0.0010^c	0.791	18

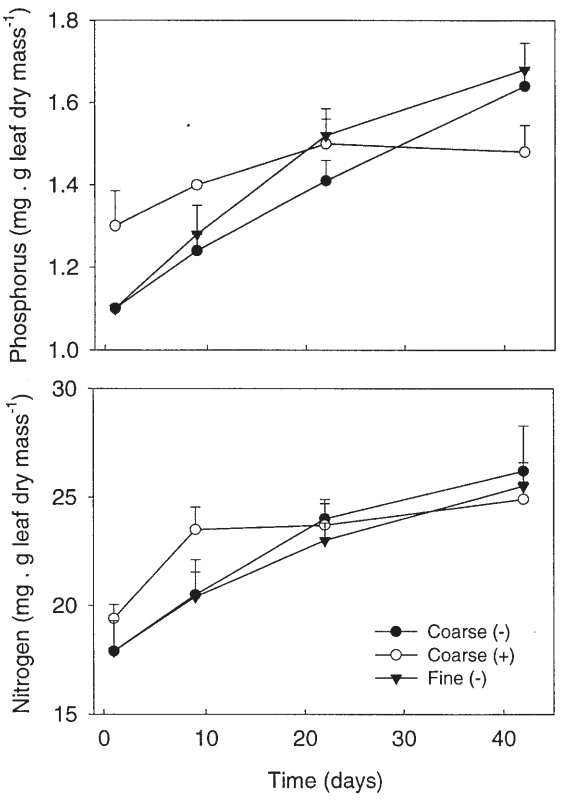

Fig. 2 Mean (± 1 SE, *n*=4) **A** phosphorus and **B** nitrogen concentrations of leaves decomposing in an alpine springbrook in coarse-mesh control packs (–), coarse-mesh packs with nutrients added (+), and fine-mesh packs with no nutrients added (–)

Increases in phosphorus concentrations for the decomposing leaves and associated microflora were more substantial, relative to the initial concentration, than increases in nitrogen concentrations (Fig. 2). Average phosphorus concentrations were initially higher in fertilized packs than in packs without added nutrients (P<0.05). Nitrogen concentrations also were initially higher in fertilized packs, but this difference was not significant (P>0.13). No differences in nutrient concentrations were found among treatments by day 22, and repeated-measures ANOVA likewise showed no significant effect across all sampling dates (P>0.38). Phosphorus concentrations began to decrease in the fertilized packs by day 42, but continued to increase in unfertilized packs during the whole experiment.

Fungal biomass of leaf packs increased over time regardless of treatment, attaining levels of *c*. 55 mg dry mass/g leaf dry mass in 7 weeks (Fig. 3A). There were no significant differences in fungal biomass among treatments (P>0.26). After 11 weeks, fungal biomass had increased to around 90 mg g^{-1} leaf dry mass in both coarse- and fine-mesh packs to which no nutrients were added (data not shown; leaves had disappeared from packs with nutrients by this time).

There were no significant differences in the total number of conidia produced by aquatic hyphomycetes among pack types collected on either day 22 or 42 (Fig. 3B). Mean sporulation rates were 2155 conidia per 1 mg leaf dry mass per day on day 22 and 1686 conidia on day 42. Of the 14 species recorded, *Flagellospora curvula* typically made up >95% of the released conidia, and was the only species found sporulating on fertilized leaves on day 22 (Table 2). Other common taxa consisted of *Lemonniera aquatica*, *Clavatospora longibrachiata*, and *Heliscus lugdunensis*. Species richness was significantly higher on day 42 than day 22 (P<0.0001) and more species sporulated on leaves in coarse-mesh control packs (mean=6.5) than in fertilized coarse-mesh (mean=3) or fine-mesh (mean=3.8) packs.

Macroinvertebrates were effectively prevented from entering fine-mesh packs (Fig. 4). By day 9, significantly more macroinvertebrates were associated with leaves in fertilized coarse-mesh packs than in packs without added nutrients (numbers: P<0.0001; biomass: P<0.05). Fertilized packs collected on day 22 had, on average, 400 specimens associated with the leaves, whereas only about 100 animals per pack were collected from the unfertilized control packs. The biomass of macroinvertebrates exhibited a similar pattern as numbers, with the fertilized packs containing twice as much as the control packs. Both the numbers (P<0.001) and biomass (P<0.005) of shredding nemourids (*Nemoura* sp. and *Protonemura* sp.) were 3 times higher in the fertilized

Table 2 The mean relative abundance (%) of aquatic hyphomycetes associated with alder leaves after 22 and 42 days of immersion in an alpine springbrook (n=3 or 4 for each treatment and day)

Fungal species	Coarse mesh (no nutrient)		Coarse mesh (nutrients added)		Fine mesh (no nutrients)	
	22 days	42 days	22 days	42 days	22 days	42 days
Alatospaora acuminata Ingold		0.03				
Clavariopsis aquatica de Wild.		0.1				
Clavatospora longibrachiata (Ingold) Marvanová et Nilsson		3.0				1
Flagellospora curvula Ingold	99.6	91.3	100	98.4	99.6	97
Heliscus lugdunensis Sacc. et Thérry	0.1	2.2		1.2	0.2	1.4
Heliscella stellata (Ingold et Cox) Marvanová et Nilsson		0.03				
Lemonniera aquatica de Wild.	0.3	0.6		0.2	0.2	0.6
L. terrestris Tubaki		0.03				
Tetrachaetum elegans Ingold		2.5				
Tricladium curvisporum Descals		0.1				
T. patulum Marvanová et Marvan		0.03				
Tumularia aquatica Descals et Marvanová				0.2		

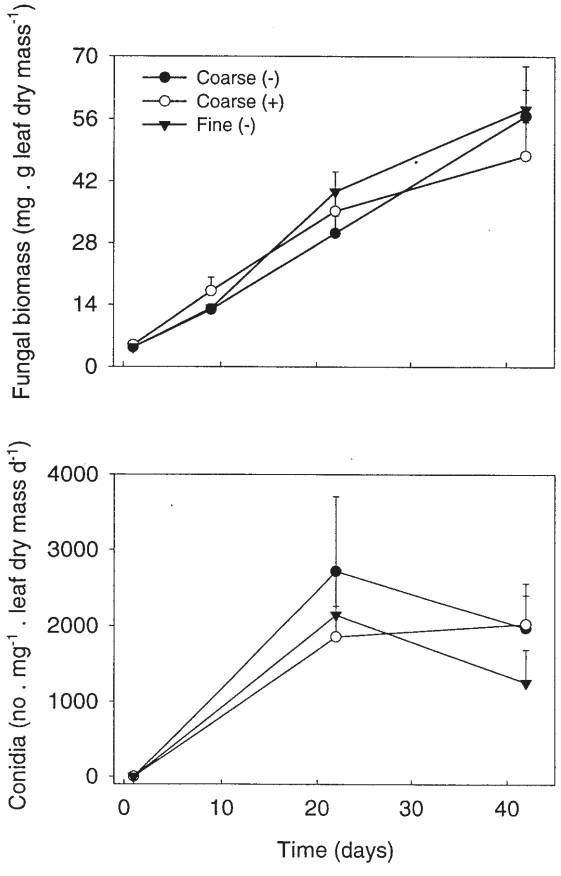

Fig. 3 Mean (±1 SE, n=4) **A** fungal biomass and **B** sporulation rates of aquatic hyphomycetes associated with leaves decomposing in an alpine springbrook in coarse-mesh control packs (–), coarse-mesh packs with nutrients added (+), and fine-mesh packs with no nutrients added (–)

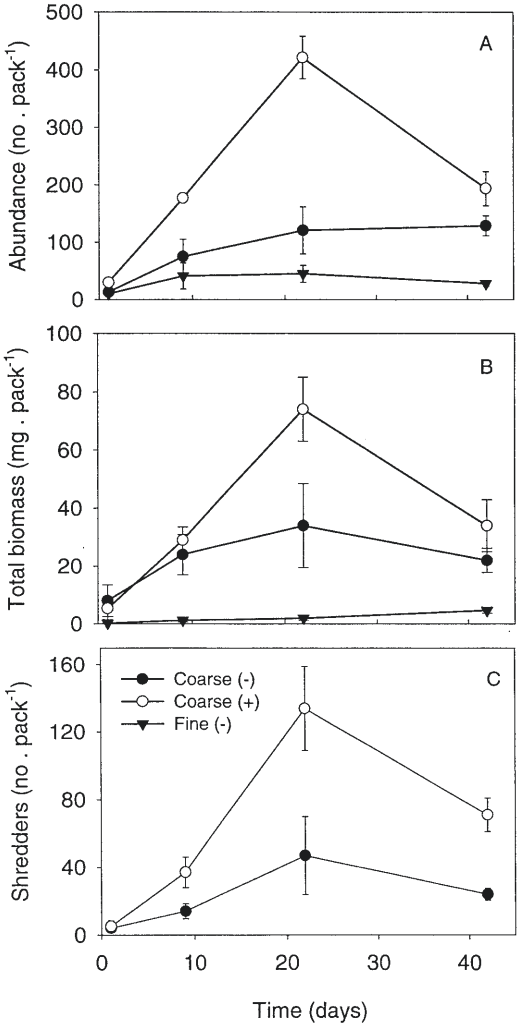

Fig. 4 Mean **A** (±1 SE, n=4) number and **B** biomass of macroinvertebrates, and **C** number of shredders associated with leaves decomposing in an alpine springbrook in coarse-mesh control packs (–), coarse-mesh packs with nutrients added (+), and fine-mesh packs with no nutrients added (–). Values expressed per gram leaf mass remaining showed similar patterns

packs by day 9. On day 22, when more than 100 nemourids were counted in some of the fertilized packs, the difference was especially pronounced. The other dominant taxon was the chironomids, making up 58–70% of the numbers in coarse-mesh packs, although they ac-

counted for less than 33% of the macroinvertebrate biomass in control packs and less than 6% in fertilized packs.

Discussion

The markedly faster breakdown rate of experimentally fertilized leaf packs suggests strong nutrient limitation of organic matter breakdown in our alpine study stream. This finding is different from data obtained in a whole-stream nutrient enrichment study, where no evidence was found for accelerated breakdown of fresh green *Carex* leaves placed in litter bags in an arctic tundra stream (Peterson et al. 1993). However, Elwood et al. (1981) found an increase in breakdown rates of leaf packs placed in a woodland stream supplied with excess phosphorus, although ammonium addition to the same stream did not produce the same effect (Newbold et al. 1983). Circumstantial (Meyer and Johnson 1983) and correlational (Suberkropp and Chauvet 1995) evidence from studies in woodland streams further indicate that nutrient limitation of leaf breakdown may not be an uncommon phenomenon in running waters. This idea is in line with the observation that the degradative activity of aquatic hyphomycetes, the predominant fungi colonizing and degrading leaf-litter in streams (Gessner et al. 1997), is stimulated by increased nutrient availability (Suberkropp 1998b). Additional studies are needed to assess how general the occurrence of nutrient limitation of organic matter breakdown is in streams, or whether the dramatic response seen in this study simply reflects the special case of severely resource-limited alpine streams.

The significantly higher abundance and biomass of macroinvertebrates (especially shredders) on fertilized leaf packs suggest that nutrient addition resulted in higher-quality resource patches, which these animals rapidly exploited. Conceivably, the greater abundance of shredders and/or an increase in their feeding intensity on leaf packs with added nutrients accelerated leaf breakdown rates. Why the enriched leaf packs were more attractive to shredders than the controls is not clear from the present results. Although phosphorus and nitrogen concentrations were initially higher for enriched leaves, significant differences in leaf mass remaining (Fig. 1) and macroinvertebrate abundances and biomass (Fig. 4) were observed only by day 22 when nutrient concentrations of leaves were similar among treatments (Fig. 2). Consequently, higher nutrient concentrations *per se* are unlikely to be the critical cause. Likewise, fungal biomass and sporulation rates of aquatic hyphomycetes did not differ among treatments, implying that the quantity of fungal mass present, or fungal activity, did not account for the observed shredder preference. Shredders do show distinct feeding preferences, discriminating even between different fungal species that colonize the same leaf (Suberkropp 1992). However, fungal species composition did not differ greatly among types of leaf packs in the present study; *Flagellospora curvula* was by far the dominant species sporulating on leaves in all treatments, contributing >90% of all fungal spores. It must be noted, however, that the measured rates and concentrations (sporulation, ergosterol, N, P) are the net result of several simultaneous processes that may offset one another when gains and losses are of the same magnitude. For example, nutrient enrichment may have stimulated fungal growth and activity, but this stimulation would not result in a higher fungal biomass if the increase was immediately removed by higher feeding activity. Unfortunately, the experimental design did not include a nutrient treatment of leaves in fine-mesh bags, which would have allowed a test of this hypothesis.

In the absence of added nutrients, macroinvertebrates and micro-organisms (fungi and bacteria) both had a significant effect on leaf breakdown in the alpine springbrook examined in this study. Fine- and coarse-mesh packs without nutrients added exhibited similar breakdown rates during the first 3 weeks, but by the end of the experiment (7 weeks) unfertilized coarse-mesh packs had 20% less leaf mass remaining than the fine-mesh packs. Thus, although leaves without nutrients added had a significantly lower breakdown rate than fertilized packs, the former packs also were shredded and consumed by macroinvertebrates. If one assumes that only microbial breakdown occurred in fine-mesh bags, whereas mass loss was due to shredders and micro-organisms in coarse-mesh packs, then both types of organisms would have contributed about equally to mass loss of the unfertilized leaves.

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