

THE EFFECT OF A HEADWATER DAM ON THE USE OF LEAF BAGS BY INVERTEBRATE COMMUNITIES

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ABSTRACT

Breakdown rates and colonisation of leaves from four tree or scrub species differing in quality are studied upstream and downstream of the Canales reservoir, a dam located in the headwater of the River Genil, Sierra Nevada, in southern Spain. This dam, with hypolimnetic release, displays short-term fluctuations of discharge and nutrient enrichment in the tailwater during the study period. Breakdown rates of the four leaf species studied do not differ between sites, despite the higher dissolved nutrient concentration in the tailwater. This lack of differences is attributed to the potentially high physical breakage of leaves during peak flows that are of higher magnitude at the upstream site. The invertebrate density in leaf bags does not differ between sites, and Chironomidae and Ephemeroptera are the numerically dominant taxa at both sites. With regard to functional feeding groups, the scarcity and lack of significant differences between sites for shredders do not match the trend predicted by the Serial Discontinuity Concept in relation to the effect of a headwater dam. Possibly, the discharge fluctuations at both sites causes excessive instability of the natural substrate (leaf litter) for the shredder guild. However, as expected, the biomass of collectors colonising leaf bags is significantly higher at the tailwater, which might be explained not in terms of quantity, but as a consequence of the higher nutritional quality of the fine particulate organic matter (FPOM) accumulated in leaf bags at this site, owing to the eutrophication caused by the dam. Despite the scarcity of functional shredders at both sites, at the community level, the leaf material is significantly more ingested at the upstream site, suggesting the importance of this source of nutrition for the trophic web at this site in contrast with the tailwater, as predicted by the Serial Discontinuity Concept. This also suggests that caution is needed in using functional feeding groups as trophic guilds to infer system-level trophic dynamics in streams, given the prevalence of generalist feeders among benthic macroinvertebrates in these environments. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: functional feeding groups; gut contents; headwater dam; invertebrates; leaf-breakdown; Serial Discontinuity Concept

INTRODUCTION

In headwater streams flowing through forested catchments, a major fraction of the energy sustaining the trophic web is derived from allochthonous inputs in the form of leaf litter (Fisher and Likens, 1973). This observation led to a conceptual model of ecosystem processes (Vannote *et al.*, 1980), in which leaf litter is processed initially by microbial conditioning, and then by particle-size reduction through the activities of invertebrate shredders (Cummins, 1974; Boulton and Boon, 1991). Therefore, microbial and shredder activities may be essential links in the transfer of energy and matter for other primary consumers, such as collectors of fine particles, and also for higher trophic levels (e.g. predators). Consequently, any disturbance affecting the quantity and/or quality of food in a headwater stream would alter leaf litter processing and trigger changes in the trophic structure.

According to Ward and Stanford (1984), regulated streams are suitable systems for examining ecological theory in the context of running waters, particularly for rigorous testing and refinement of continua-based theories such as the River Continuum Concept (Vannote *et al.*, 1980) or the Serial Discontinuity Concept (Ward and Stanford, 1983). Dams located in headwater streams can disturb food

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sources by lowering or suppressing the inputs of leaf litter (CPOM), and possibly increasing the availability of fine particulate organic matter (FPOM) in the tailwater, thereby creating a discontinuity in the gradient of ecological processes (Ward and Stanford, 1983). The processing of leaf litter in streams may be a useful tool in evaluating the effect of disturbance at the ecosystem level (Webster and Benfield, 1986), as used in several studies (e.g. Burton *et al.*, 1985; Stout and Coburn, 1989).

The present study investigates the impact of a headwater dam with hypolimnetic release on the use of leaf litter by invertebrates, and whether this impact disrupts the continuum of the fluvial ecological processes.

MATERIALS AND METHODS

Study sites

The study was conducted in the headwater of the River Genil, a fourth-order stream (scale map 1:25000) of the Sierra Nevada Mountains (Granada province, Andalucía, southern Spain). Two sites located 4 km apart were selected. The first site (upstream site), with abundant riparian vegetation (Table I), is located 1 km upstream of the Canales reservoir and about 5 km downstream of an impoundment for a hydroelectric power station, which caused great peaks and troughs in the normal discharge regime (Figure 1). This power station operates with water impounded from the river by means of direct piping without any dam. The second site (downstream site) was 0.5 km downstream of the hypolimnetic outlet of the Canales reservoir. This reservoir has an area of 156 ha, a capacity of $70.7 \times 10^6 \text{ m}^3$ and was first filled in 1988. According to values of total phosphorus and productivity, it has been catalogued as a eutrophic reservoir (Morales-Baquero *et al.*, 1994). This reservoir regulates the natural discharge of the river, imposing a relatively constant yearly discharge but with short-term fluctuations (Figure 1) depending on water demands of the city of Granada. At this site, the banks are devoid of vegetation (Table I), as this is a concrete-lined canal from the dam.

Table I. Physical and chemical characteristics of the two study sites in the River Genil

	Upstream site	Downstream site
Location	37°9'19"N, 3°26'13"W	37°9'38"N, 3°29'20"W
Altitude (m a.s.l.)	920	800
Slope (%)	5.0	4.5
Canopy (% cover)	50.3	0.0
Temperature (°C)	10.9 (2–19)	11.5 (4–19)
pH	6.7 (6.3–7.1)	7.0 (6.2–7.6)
Conductivity ($\mu\text{S cm}^{-1}$)	118 (140–216)	181 (125–225)
Alkalinity (meq L^{-1})	1.2 (0.9–1.5)	1.2 (0.9–1.9)
Oxygen (mg L^{-1})	10.6 (10.0–0.9)	10.7 (10.5–10.9)
BOD ₅ ($\text{mg O}_2 \text{ L}^{-1}$)	0.9 (0.7–1.1)	2.0 (1.8–2.2)
Nitrate ($\mu\text{g N L}^{-1}$)	122 (85–155)	497 (420–551)
SRP ($\mu\text{g P L}^{-1}$)	8 (4–13)	115 (86–132)
Seston (mg AFDML^{-1})	2.5 (2.0–2.9)	3.9 (3.4–4.4)
CPOM (g AFDM dm^{-2})	0.973 ± 0.154	0.008 ± 0.003
Current velocity (m s^{-1})	0.20 ± 0.02	0.23 ± 0.03

Values of temperature, conductivity, seston and chemical parameters are means with ranges in parentheses.

Values of current velocity and CPOM are means ± 1 S.E.

AFDM is ash-free dry mass.

Data on benthic CPOM (coarse particulate organic matter) were taken from Casas and Descals (1997).

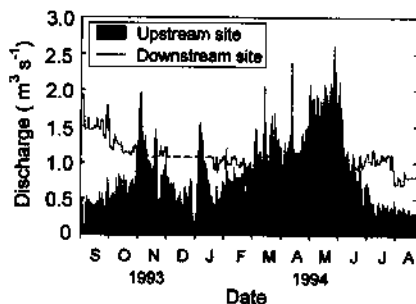


Figure 1. Daily hydrographs at the two sites under study in River Genil, upstream and downstream of Canales reservoir. The study was carried out from November 1993 to July 1994

Field and laboratory physical and chemical measurements

On each sampling date, pH and conductivity were measured *in situ*, and water samples were taken to the laboratory in a cooling box. An aliquot was used to determine alkalinity. An additional aliquot was filtered through an ashed filter (Whatman GF/F) and frozen. The ash-free dry mass of the material retained on the filters was determined at 500°C for 5 h. Later, the filtered water was thawed and analysed for concentrations of nitrate and soluble reactive phosphorus (SRP), following the standard methods described in Wetzel and Likens (1991). Two additional samples of water were taken in biological oxygen demand bottles, one fixed in the field to determine oxygen concentration by Winkler's method, and the other transported to the laboratory to determine biological oxygen demand (BOD₅). Current velocity was measured in front of the leaf bags with a propeller-type current meter (SEBA model M1). Water temperature was recorded on each sampling date with maximum–minimum thermometers.

Field and laboratory procedures to estimate leaf-breakdown and invertebrate colonisation

In autumn 1993, newly fallen leaves were collected, representing four species known to have different qualities: sycamore (*Platanus orientalis* L.), an exotic species in the region; and three indigenous species, black poplar (*Populus nigra* L.), willow (*Salix atrocinerea* Brot.) and blackberry (*Rubus ulmifolius* Schott). Leaves were air-dried at room temperature (about 20°C) and stored for subsequent use. *Platanus* leaves were weighed in 4 g portions, briefly soaked in tap water until pliable, and placed in plastic mesh bags (20 × 20 cm, 5 mm mesh). Leaves of the three indigenous species were used to make mixed-species packs, using 1.35 g of each species, approximating the weight (i.e. 4 g) of the *Platanus* leaf bags.

Six bags containing *Platanus* leaves and six mixed-species bags per site and date were tied to stones and positioned sequentially in riffle areas along 50 m stretches of the two study sites at approximate monthly intervals for 7 months, beginning on 5 December 1993. All leaf bags were simultaneously removed on 8 July 1994, resulting in incubation periods of 215, 175, 141, 112, 76, 49 and 8 days in the stream. Retrieved leaf bags were placed separately in plastic bags on ice and taken to the laboratory for immediately processing. Of the six leaf bags of each type per site and date, three bags were used for gut content analysis of the coloniser invertebrates. The other three bags were carefully rinsed to remove FPOM and invertebrates, which were then frozen for subsequent use. The remaining leaf material was dried (60°C for 48 h) and weighed to calculate the percentage of remaining mass. Breakdown coefficients were calculated for each leaf species at each site using a standard regression of percentage of mass remaining (after ln transformation) over time (Petersen and Cummins, 1974). The invertebrates were thawed, sorted from the FPOM, identified and assigned into functional feeding groups following Merritt and Cummins (1996) and Tachet *et al.* (1991). The invertebrates were oven dried (60°C for 48 h) and weighed to estimate dry biomass. The ash-free dry mass of the remaining FPOM of each replicate was determined after ignition in a muffle furnace at 500°C for 5 h.

Three additional leaf bags of each type were incubated at both sites on 5 December 1993 and removed on 6 March 1994 (91 days of incubation). This was undertaken to improve the temporal representation of the dynamics of the invertebrates colonising leaf bags, given the possible and substantial changes in taxonomic composition over time for the bags removed in July. The leaf material, the invertebrates and the FPOM accumulated in these bags were processed as above.

Comparisons of breakdown rates between sites and leaf species (*Platanus* versus indigenous species) were analysed by analysis of covariance (ANCOVA) with time as the covariate, and site and leaf species as independent factors. Data on total density of invertebrates, total biomass and biomass of each functional feeding group for different sites and leaf bag types were compared using a two-way analysis of variance (ANOVA), after $\ln(x + 1)$ transformation of the data to meet normality and homoscedasticity assumptions. Data on FPOM accumulated in the leaf bags did not meet the ANOVA assumptions, even after logarithmic transformation, and, therefore, were analysed by the Mann-Whitney *U*-test to determine differences between sites and types of leaf bag.

Gut content analysis

When available, six individuals per taxon, replicate leaf bag and date, were analysed. For taxa with hard chitinous cuticle, the gut was dissected, the entire gut being removed and mounted on a microscope slide in Hertwig solution (chloral hydrate + HCl + glycerine + distilled water). The taxa with soft cuticle were not dissected, because the gut contents were easily observed through the cuticle after the treatment with Hertwig solution. After 48–72 h in the oven at 60°C, the guts on the slides were translucent enough to identify the items ingested. The gut contents were quantified at 600× magnification, while the gridded eye-piece covered the central axis of the anterior half of the gut of each specimen. The quantity of each food item identified was estimated from the percentage of the area covered.

Moreover, the gut contents of six nymphs of *Ephemera ignita* colonising the second set of three *Platanus* leaf bags per site and date were examined as above. This species was the most abundant and well-represented leaf-eater at both sites and in both bag types, and was used to compare gut contents of the individuals between bag types, to determine the effect of leaf quality on the ingestion of leaf litter.

For statistical analysis, items in the gut contents with percentages lower than 2% were pooled into the group 'other remains'.

When food consumption was studied by invertebrate community, for a representative sample, the estimation of mean values for each taxon, date and site were weighted by the average number of individuals of each taxon collected in the leaf bags per date and site.

Because variables differed from normal distribution (Kolmogorov-Smirnov, NS), non-parametric tests were used following Siegel and Castellan (1988). Comparisons of gut contents of taxa between sites and leaf species were analysed by Wilcoxon matched pairs tests. Each pair in the analysis was data of packs from different sites and/or types, but from the same date, thereby controlling for variation over time.

RESULTS

Physical and chemical characteristics

Both stream sites had a circumneutral pH, the same mean alkalinity and were well oxygenated (Table I). However, for BOD₅, nitrate-N, SRP and seston, the values were higher at the downstream than at the upstream site (Table I). Differences in nutrient contents between the two sites indicated relative oligotrophic status at the upstream site and eutrophic status at the downstream site. Mean concentration of nitrate-N was circa fourfold, and that of SRP circa 14-fold higher at the downstream than at the upstream site. Current velocity was similar at both sites and mean temperature was slightly higher at the downstream site, possibly owing to the thermal regulation by the reservoir (Table I).

Table II. Leaf-decay coefficients (d^{-1}) for the species assayed at the two sites

Leaf species and site	$-k \pm 1 \text{ S.E.}$	R^2	df	F	p -value
<i>Platanus orientalis</i>					
Upstream site	0.0064 ± 0.0024	0.24	1, 22	7.13	0.0140
Downstream site	0.0109 ± 0.0040	0.22	1, 22	6.06	0.0221
<i>Populus nigra</i>					
Upstream site	0.0151 ± 0.0031	0.45	1, 22	18.34	0.0003
Downstream site	0.0224 ± 0.0037	0.66	1, 19	36.79	0.0000
<i>Rubus ulmifolius</i>					
Upstream site	0.0258 ± 0.0058	0.52	1, 18	19.60	0.0003
Downstream site	0.0305 ± 0.0071	0.57	1, 14	18.55	0.0007
<i>Salix atrocinerea</i>					
Upstream site	0.0113 ± 0.0037	0.30	1, 22	9.43	0.0056
Downstream site	0.0210 ± 0.0057	0.44	1, 17	13.41	0.0019

R^2 is the variance explained by the negative exponential model; df, F and p -value are results of the statistical analysis (ANOVA) of the regression model.

Leaf-breakdown rates and FPOM in the bags

Leaf-breakdown rates (Table II; Figure 2) did not differ significantly between sites (*Platanus*: $F = 2.45$, $p = 0.12$; *Populus*: $F = 0.37$, $p = 0.54$; *Salix*: $F = 1.16$, $p = 0.29$; *Rubus*: $F = 0.00$, $p = 0.98$), though a general trend of faster breakdown rates for the four species assayed appeared at the downstream, compared with the upstream site. The leaves of *Platanus* broke down significantly more slowly at both sites than did those of *Populus* (upstream site: $F = 24.34$, $p < 0.001$; downstream site: $F = 9.56$, $p < 0.01$), *Salix* (upstream site: $F = 17.14$, $p < 0.001$; downstream site: $F = 7.31$, $p < 0.01$) and *Rubus* (upstream site: $F = 26.28$, $p < 0.001$; downstream site: $F = 9.39$, $p < 0.01$).

The amount of FPOM that accumulated in the leaf bags (Figure 3) did not differ significantly between sites, either for the leaf bags removed in July ($U = 627.0$, $p = 0.308$) or for the leaf bags removed in March ($U = 7.0$, $p = 0.078$). However, significantly higher amounts of FPOM per gram of dry mass of leaf litter appeared in mixed-species bags compared with *Platanus* bags removed on July ($U = 406.0$, $p < 0.001$) and,

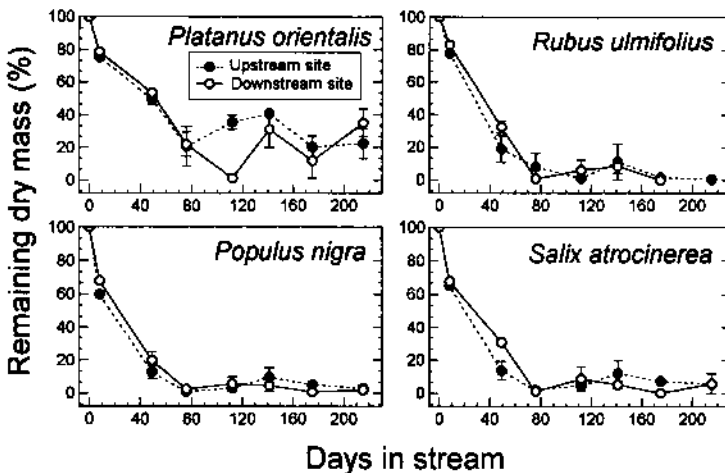


Figure 2. Percentage (mean ± 1 S.E.) of leaf dry mass remaining versus time at the two stream sites for the four leaf species assayed

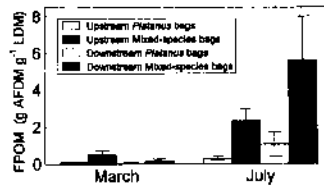


Figure 3. Ash-free dry mass of the fine particulate matter (mean \pm 1 S.E.) accumulated in the two types of leaf bags at both study sites for the two dates of removal; LDM = leaf dry mass

although not statistically significant, the same trend appeared for the leaf bags removed on March ($U = 6.0$, $p = 0.055$).

Invertebrates associated with the leaf bags

The density of invertebrates colonising leaf bags removed in July (Table III) showed no significant differences between sites. However, total biomass of invertebrates and biomass of collector-gatherers and predators (Figure 4) were significantly higher at the downstream than at the upstream site (Table IV). Such differences can be attributed principally to the high abundance of meiobenthic taxa (i.e. Acarina) at the upstream site, and the high abundance of collector-gatherer taxa (e.g. *Baetis* spp.), and the presence of large bodied predators at the downstream site. Differences among sites were not significant for biomass

Table III. Total density of invertebrates (mean number of individuals per gram of leaf dry mass \pm 1 S.E.) and relative abundance (%) of the main taxa colonising each type of litter bag at each site on the two removal dates

Taxon	Upstream site				Downstream site			
	March		July		March		July	
	P.B.	M.S.B.	P.B.	M.S.B.	P.B.	M.S.B.	P.B.	M.S.B.
Naididae	8.7	14.6	0.2	0.1	39.7	33.8	0.0	0.0
Acarina	1.1	1.0	39.3	48.6	0.2	0.1	0.2	0.3
Ostracoda	0.7	0.2	2.4	4.4	30.5	3.9	2.3	14.8
Ephemeroptera small nymphs	2.5	9.5	<0.1	<0.1	0.4	0.0	1.5	0.8
<i>Baetis</i> spp.	0.0	<0.1	0.0	0.0	10.3	8.1	2.4	1.8
<i>Ephemerella</i> <i>ignita</i>	0.0	<0.1	1.6	3.1	0.0	0.0	0.1	0.4
<i>Polycentropus</i> <i>kingi</i>	0.0	0.0	<0.1	<0.1	1.3	1.3	0.2	0.8
<i>Rhyacophila</i> <i>nevada</i>	0.4	<0.1	0.3	<0.1	0.1	0.8	0.2	0.3
Elmidae	0.0	<0.1	1.6	1.4	0.2	0.0	0.1	0.2
Tanyptodinae	0.1	0.8	1.7	2.0	1.8	1.9	0.8	3.3
Orthocladinae	21.6	24.0	21.9	16.6	34.4	43.4	87.6	70.14
<i>Corynoneura</i> spp.	2.2	3.2	0.2	0.2	1.1	1.2	2.2	1.9
Tanytarsini	60.2	45.4	28.4	21.5	3.9	3.2	0.6	1.1
Simuliidae	0.3	0.3	<0.1	0.0	0.0	0.0	0.2	0.5
Total density	1389 \pm 76	2179 \pm 1011	1281 \pm 563	4940 \pm 946	170 \pm 23	850 \pm 354	4975 \pm 2607	6498 \pm 3913

P.B. = *Platanus* bags.

M.S.B. = Mixed-species bags.

Bags removed in March had been in the stream for 91 days and bags removed in July had been in the stream for varying periods of time (see section 'Field and laboratory procedures to estimate leaf-breakdown and invertebrate colonisation').

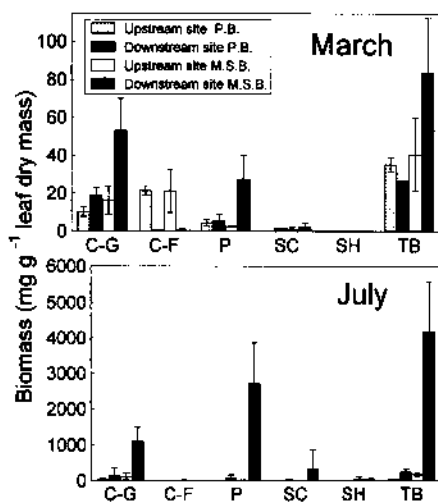


Figure 4. Biomass of functional feeding groups and total invertebrates (mean \pm 1 S.E.) in the two types of leaf bags at both study sites for bags removed in March and July; P.B. = *Platanus* bags; M.S.B. = mixed-species bags; C-G = collectors-gatherers; C-F = collectors-filterers; P = predators; SC = scrapers; SH = shredders; TB = total biomass

of collector-filterers, scrapers and shredders (Table IV). The significantly higher total biomass, and biomass of collector-gatherers at the downstream site, was found also for leaf bags removed in March (Table IV). Again, these differences were related mainly to the high relative abundance of large-sized individuals of *Baetis* spp. (*B. rhodani*, *B. pavidus* and *B. muticus*) at the downstream site, taxa that were almost absent in the bags at the upstream site on this date. In contrast, the total density of invertebrates and biomass of collector-filterers were significantly higher at the upstream than at the downstream site (Table IV). Such differences can be attributed largely to the high densities of larvae of Tanytarsini (Table III; mainly in genus *Rheotanytarsus*), which massively colonised leaf bags, attaching their tubes to the leaf litter or to the bag itself at the upstream site in March. This taxon was scarcely represented at the downstream site on this date (Table III). For leaf bags removed in March, no significant differences between sites appeared either for biomass of predators or for scrapers and shredders (Table IV).

The analysis of data for colonising invertebrates in July showed significantly higher density of invertebrates, total biomass and biomass of collector-gatherers and predators in the mixed-species bags

Table IV. Results of Mann-Whitney *U*-tests (March, *U*-values) and two-way ANOVAs (July, *F*-values) comparing total density and biomass, and biomass of functional feeding groups between sites and leaf bag types

	March		July	
	Site	Bag type	Site	Bag type
Total density	5*	12 NS	0.38 NS	15.04***
Total biomass	6*	14 NS	10.51**	8.34**
Collector-gatherers biomass	5*	11 NS	11.12**	8.93**
Collector-filterers biomass	0**	15 NS	0.98 NS	0.40 NS
Predators biomass	7 NS	16 NS	6.88*	4.27*
Scrapers biomass	9 NS	17 NS	2.77 NS	2.01 NS
Shredders biomass	12 NS	17 NS	1.66 NS	3.23 NS

Levels of significance: NS = not significant, * = $p < 0.05$, ** = $p < 0.001$, *** = $p < 0.001$.

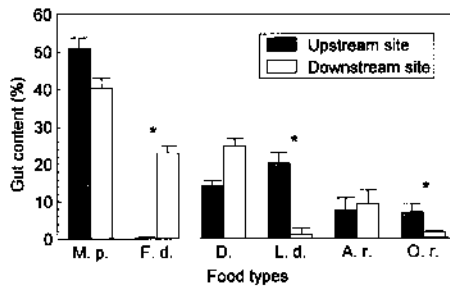


Figure 5. Percentages (mean \pm 1 S.E.) estimated for each of the food types identified in the gut of all invertebrates colonising mixed-species bags removed in July at the two stream sites; *indicates significant differences between sites taking into account the variation of the data over time within each site (Wilcoxon matched pairs test; $p < 0.05$); M.p. = mineral particles; F.d. = fine detritus; D. = diatoms; L.d. = leaf debris; A.r. = animal remains; O.r. = other remains. Means were weighted by the average number of individuals of each taxon collected per date and site, to make the data representative of the invertebrate community of each site. S.E.s were not weighted.

than in *Platanus* bags, but no significant differences between leaf bag types appeared for biomass of collector-filterers, scrapers or shredders (Table IV). No significant differences were found in the comparison between leaf bag types for any one of the variables studied on leaf bags removed in March (Table IV).

Gut contents

Eleven types of ingested items were distinguished: mineral particles, fine amorphous organic detritus, diatoms, remains of leaf debris, animal remains, fungal hyphae, non-diatom filamentous algae, non-diatom unicellular algae, pollen, moss and other remains (of unidentified origin). As some items were rare (less than 2%), they were pooled with the group 'other remains', which included remains of unidentified origin plus fungal hyphae, non-diatom unicellular algae, non-diatom filamentous algae, pollen and moss. The animal fraction was consistently underestimated because the soft parts of the ingested prey either disappeared or became discoloured; most frequently, the chitinous parts, setae and chaetae of the animals were the only remains observed under the microscope.

The analysis of gut contents of all taxa colonising mixed-species leaf bags revealed significant differences between sites for most food types (Figure 5). The percentage of leaf debris and other remains in gut contents were significantly higher at the upstream site than at the downstream site (Table V). In contrast, percentage of fine detritus was significantly higher at the downstream than at the upstream site (Table V). Separate dietary analyses for the main invertebrate taxa common at both sites revealed a similar trend of differences between sites (Figure 6). The percentages of leaf debris ingested at the upstream site were higher than at the downstream site (although were only significant for *E. ignita* and

Table V. Pair-wise comparisons (Wilcoxon matched pairs test, Z-values) of the means of percentages estimated for different food types in the gut of all invertebrates and the main invertebrates taxa (except *E. ignita*), common at both sites, colonising mixed-species leaf bags removed in July between the two stream sites

	All invertebrates	<i>R. nevada</i>	Orthocladinae	Tanyodinae	Tanytarsini
Mineral particles	1.69 NS	1.07 NS	1.83 NS	0.68 NS	1.83NS
Fine detritus	2.37*	-	1.83 NS	1.75 NS	1.83NS
Diatoms	1.52 NS	0 NS	0 NS	1.89 NS	0.73NS
Leaf debris	2.37*	1.60 NS	1.83 NS	2.37*	1.83NS
Animal remains	0.51 NS	1.07 NS	1.60 NS	1.01 NS	0.73NS
Other remains	2.20*	1.60 NS	1.83 NS	2.20*	1.83NS

Levels of significance: NS = not significant; * = $p < 0.05$.

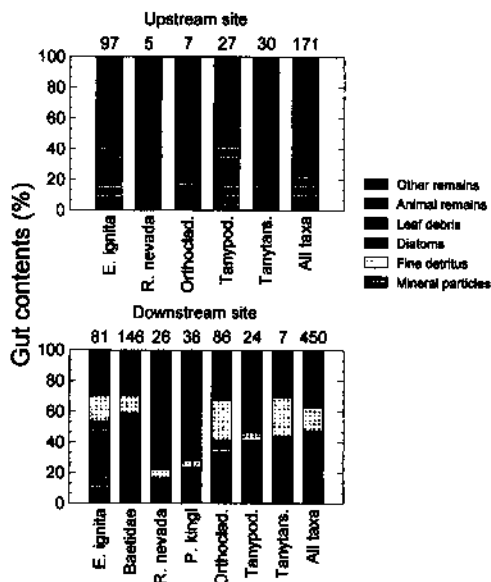


Figure 6. Means of percentages estimated for each of the food types identified in the gut of the main invertebrate taxa colonising mixed-species bags removed in July. Sample size of each taxa is indicated at the top of each graph

Tanypodinae; Tables V and VI). On the other hand, higher percentages of fine detritus were found in the gut of all main taxa at the downstream site (although the values were only significant for *E. ignita*; Table VI).

The analysis of gut contents of *E. ignita* colonising *Platanus* leaf bags (Figure 7) showed differences between sites similar to those for mixed-species bags, with significantly higher percentages of leaf debris ingested at the upstream site (Table VI), and significantly higher percentages of fine detritus at the downstream site (Table VI). The type of leaf bag considered was not a major factor affecting the percentage of food items ingested by *E. ignita*. Percentages of leaf debris ingested by this species did not significantly differ between leaf bags types, either at the upstream or at the downstream sites (Table VI), the same being true for the rest of food types, except for mineral particles and fine detritus (Table VI; Figure 7). Significantly higher percentages of fine detritus ingested were obtained in *Platanus* bags at both sites (Figure 7).

Table VI. Pair-wise comparisons (Wilcoxon matched pairs test; Z-values) of the mean of the percentage estimated for different food types in the gut of *E. ignita*

	Between sites comparisons		Between bag types comparisons	
	Mixed-species leaf bags	<i>Platanus</i> leaf bags	Upstream site	Downstream site
Mineral particles	2.37*	2.20*	2.37*	2.20*
Fine detritus	2.37*	2.20*	2.20*	2.20*
Diatoms	1.69 NS	1.99 NS	0.68 NS	0.11 NS
Leaf debris	2.37*	2.20*	1.69 NS	0.73 NS
Animal remains	0.51 NS	0.73 NS	1.01 NS	0.73 NS
Other remains	2.37*	0.94 NS	1.52 NS	1.78 NS

Levels of significance: NS = not significant; * = $p < 0.05$.

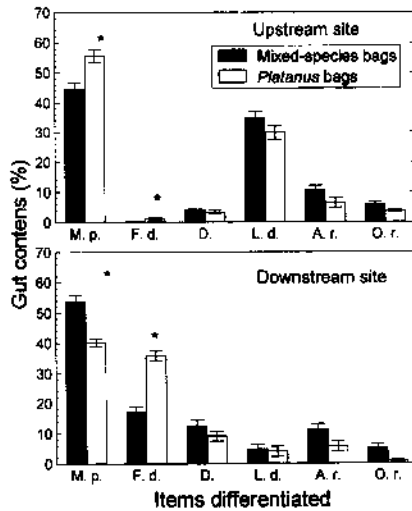


Figure 7. Means of percentages estimated for each of the food types (mean \pm 1 S.E.) identified in the gut of *E. ignita* colonising *Platanus* bags and mixed-species bags removed in July at the two stream sites; *indicates significant differences between leaf bag types, taking into account the variation of the data over time within each site (Wilcoxon matched pairs test; $p < 0.05$); M.p. = mineral particles; F.d. = fine detritus; D. = diatoms; L.d. = leaf debris; A.r. = animal remains; O.r. = other remains

DISCUSSION

Leaf-breakdown rates

Leaf-breakdown rates are usually faster in nutrient-rich environments and/or in those where invertebrate shredders constitute a conspicuous guild of the aquatic community (see reviews: Webster and Benfield, 1986; Maltby, 1992). Both variables are potentially, directly and/or indirectly, affected by dam regulation (Ward and Stanford, 1979). Nutrient enrichment is expected to occur, especially in tailwaters below dams with deep-release (Ward and Stanford, 1984), as found by Bello (1997), and in the present study, where nitrate and SRP were noticeably higher downstream than upstream of the reservoir. Several studies have documented the increase of breakdown rates in streams with high nitrate concentration (e.g. Meyer and Johnson, 1983) or high phosphorus concentrations (e.g. Elwood *et al.*, 1981). Other studies have attributed high breakdown rates to greater fungal activity on leaves decomposing in high-nutrient streams (Suberkropp and Chauvet, 1995; Weyers and Suberkropp, 1996). Indeed, the key role of stream microfungi in controlling breakdown rates of leaf litter in streams and rivers has been recently demonstrated (Gessner and Chauvet, 1994; Baldy *et al.*, 1995). Using the same study sites as in this study, Casas and Descals (1997) reported higher fungal reproductive activity (sporulation rates) on leaves of *Platanus orientalis*, *Populus nigra* and *Salix atrocinerea* at the downstream, compared with the upstream of the reservoir. Sporulation rates are often positively correlated with the amount of fungal biomass in the leaf litter (Gessner and Chauvet, 1994). Despite expectations, we did not find differences in the breakdown rates of the four leaf species above and below the reservoir.

Physical abrasion is considered to be one of the main factors in leaf-breakdown in lotic environments (Webster and Benfield, 1986). For instance, Paul and Meyer (1996) attributed the higher breakdown rates of leaves in a fourth-, compared with a first-order stream to the more pronounced effect of a flood on physical abrasion of the leaves in the fourth-order stream. Chauvet (1997), in a review of the factors responsible for the frequently observed higher breakdown rates in a low-order stream compared with a large river in the network of the River Garonne, concluded that biotic factors seem to be of minor

importance compared with the potentially higher physical abrasion in headwater mountain streams. There is, however, little empirical evidence of this, at least at the scale of drainage network (Chauvet, 1997). In the present study, physical breakage may have played an important role in controlling breakdown rates, given that the two sites were subjected to short-term peaking flow, which possibly lead to greater stream power and potential boundary shear stress during increasing discharge. This, together with the possible transport of sand during discharge peaks, might have produced great physical abrasion of the leaves. In fact, at both sites, many bags contained sand and gravel when removed from the stream. Accordingly, breakdown rates calculated in the present study for the four species assayed at both sites were among the higher values for congeneric species, and were the highest within species (see review by Casas and Gessner, 1999). This, together with the lack of predictable differences in breakdown rates according to the quality of leaf litter (see Webster and Benfield, 1986) among three of the species assayed, reinforces the opinion that physical abrasion may have acted as the overriding factor in the process of leaf-breakdown at both sites under study. However, we should not overlook the role of decomposers, as annual and short-term fluctuations of discharge were of greater magnitude at the upstream site, and even breakdown rates, though without statistical significance, were slightly higher for the four leaf species at the downstream site. The higher fungal activity on leaves incubated in the tailwater (see Casas and Descals, 1997) might have caused greater softening of the leaf tissue, possibly resulting in stronger physical abrasion induced by the peaking flow, despite the lower magnitude of flow fluctuations compared with the upstream site.

Invertebrates

The invertebrate assemblages colonising leaf bags at the two sites under study were dominated numerically by chironomid larvae. Several studies have reported an increase in the relative abundance of Chironomidae under peaking flow conditions below dams or downstream of hydroelectric facilities (Bretschko and Moog, 1990; Valentin *et al.*, 1995). In any case, the dominance of chironomid larvae in leaf bags in the present study is not surprising, as this taxon is often one of the most, if not the most, numerically abundant macroinvertebrate group associated with leaf detritus in streams (e.g. Benfield *et al.*, 1977; Grubbs *et al.*, 1995), regardless of the discharge regime of the stream.

Other macroinvertebrate taxa typically colonising and/or shredding in leaf bags, at least in cool water streams, Plecoptera and Trichoptera, were scarcely represented in the present study at the two sites. Plecoptera taxa in particular may be strongly affected by peaking flow (Moog, 1993; Valentin *et al.*, 1995). Only Ephemeroptera were relatively abundant at both sites, this order being one of the less affected by dam regulation or downstream hydroelectric facilities, at least in terms of overall biomass or number of individuals (Brittain and Salveit, 1989). *E. ignita*, a species notably abundant at the upstream site in July, has been documented to have considerable success in regulated European rivers in part because of the long period of egg development and hatching, coupled with a short period of late spring and summer nymphal growth (Bohle, 1972; Bournaud *et al.*, 1987; Alba-Tercedor, 1990)—thus the nymph is exposed to flow fluctuations for only a short time (Brittain and Salveit, 1989). Additionally, species in the genus *Baetis* (mainly *B. rhodani*) were remarkably abundant, at least in terms of biomass, at the tailwater. This genus has often been found to be especially dominant in regulated rivers, thanks to their life cycle plasticity or the great abundance of algae in deep-release tailwater (see review in Brittain and Salveit, 1989), as noted by Bello (1997) in the same study area.

According to Ward and Stanford (1984), a headwater dam with hypolimnetic release can in theory alter the ratio CPOM:FPOM in the benthos of a river, with a concomitant biotic response on the trophic structure of the invertebrate community. In fact, Bello (1997) recorded higher values of FPOM downstream of the Canales reservoir compared with the upstream site. Consequently, a decrease in the relative abundance of shredders, and a higher relative abundance of collectors might be expected at the site below the dam, as a result of the decrease of the CPOM:FPOM ratio determined by the dam. However, the expected higher abundance of shredders in the leaf bags at the upstream site was not shown in this study for both dates of removal. Bello (1997) also pointed out a low relative abundance of shredders in benthic samples upstream and downstream of this reservoir. Although the upstream site had

a great canopy and the amount of benthic CPOM was clearly higher than at the downstream site, the peaking discharge at this site possibly caused too much instability of the substrate (leaf litter) to allow the maintenance of a considerable shredder guild. For instance, Schade and Fisher (1997), in a desert stream (Sycamore Creek), ascribed the lack of leaf-shredder macroinvertebrates in leaf packs to disturbance, particularly flash floods, which lowered the leaf availability to benthic communities; consequently, leaves were not a reliable food source, and, therefore, no group of macroinvertebrates specialised on them.

Otherwise, our results match the trend expected for collector-gatherers, which were significantly more abundant in biomass and were the main contributors to the higher total biomass at the downstream, compared with the upstream site. Collector-gatherers frequently form a substantial component of the invertebrates colonising leaf packs, often the most abundant guild (Cummins, 1974); in fact, this group also showed the higher relative abundance in the leaf bags incubated in the upstream site. The abundance of collector-gatherers in leaf packs incubated in woodland streams often correlates with the amount of FPOM accumulated in the leaf packs (e.g. Dobson *et al.*, 1992; Richardson, 1992). However, in the present study, the quantity of this variable is not helpful in explaining differences in biomass of collector-gatherers between sites, as at both sites the amount of FPOM accumulated in the bags did not differ significantly. An explanation for the higher biomass of this group in leaf bags at the downstream site appears simply to be their higher abundance in the benthic community at this site (Bello, 1997). Nevertheless, we suggest another explanation, not necessarily exclusive, related to the dietary quality of the fine particles for the invertebrates, as the sites differ primarily in the biomass per individual more than in the number of individuals in this group. Eutrophication is a problem in certain tailwaters with deep-release, owing to the high nutrient concentration of the hypolimnetic water, which tends to increase productivity in the receiving stream (e.g. Ward and Stanford, 1979), possibly producing large amounts of high quality food in the form of fine algae-derived detritus (Armitage, 1977; Fisher and Gray, 1981). This would be the case in the tailwater studied here, in agreement with the relatively high nitrate and phosphorus concentrations measured over the study period. Moreover, in the same study site, Bello (1997) found that a high quality fine detritus (phytoplankton and zooplankton) was derived from the Canales reservoir itself. In contrast, the upstream site was poorer in nutrient and consequently, the diatoms were not present year round (Bello, 1997). Further, the fine material accumulated in the leaf bags removed in July was composed mostly of visually recognisable fragments of the algae *Hydrurus foetidus*, which is commonly considered to be resistant to grazers by virtue of its tough mucilaginous sheaths (e.g. Malej and Harris, 1993). Another argument supporting the above hypothesis is that fine amorphous detritus constituted a higher proportion of the gut content of the invertebrates colonising leaf bags in the tailwater compared with those at the upstream site. This suggests differential quality of this type of food between sites.

The proportion of leaf litter, unlike the pattern for the fine particles, was significantly higher in the gut content of the invertebrates colonising leaf bags incubated at the upstream site. The palatability of leaf litter for invertebrates is frequently correlated with the degree of its colonisation by aquatic microfungi (e.g. Maltby, 1992). These fungi showed higher reproductive activity on leaves at the tailwater site, with similar specific assemblages at both sites (Casas and Descals, 1997). Therefore, it seems convincing that the higher intake of leaf litter at the upstream site could not be related to its higher fungal conditioning; more likely, it is related to the possibly low nutritional quality of the fine material accumulated in the leaf bags at this site.

Platanus leaf litter has been demonstrated to be among the foods least accepted by invertebrate shredders, and reportedly results in weak survival rates in laboratory tests (Malicky, 1990). Therefore, the higher densities and biomass of total invertebrates and collector-gatherers registered in mixed-species, compared with *Platanus* bags could be interpreted as an effect of the quality of the leaf litter on the colonisation by invertebrates. However, these results are somewhat surprising and must be treated with caution because of the limited amount of shredders at both sites, together with the limited or null use of leaf litter in mixed-species bags by the invertebrates at the tailwater (where there was also higher density in mixed-species compared with *Platanus* bags). Moreover, the gut content for *E. ignita* revealed a significant effect of site, but not of the type of leaf bag, suggesting that the quality of leaf litter was not

a major factor in food selection, at least for this species. We conjecture that differences in density between leaf bag types need not be taken as a preference of mixed-species bags over *Platanus* leaf bags by the invertebrates, but rather as a consequence of the way of representing the data of density, as per leaf dry mass remaining. This might have resulted from the smaller amount of leaf litter remaining in mixed-species bags removed in July, compared with that in *Platanus* bags, and from the evidence that the bag itself also served as substrate for colonisation.

Implications for the Serial Discontinuity Concept and the functional feeding groups approach

Ward and Stanford (1984) considered the ratio of CPOM:FPOM to be one of the main variables potentially affected by a headwater dam with hypolimnetic release. These authors predicted a downstream shift of this variable, determined by a decrease of the amount of CPOM, with a concomitant increase of the amount of FPOM below the dam. The results of the present work, and those reported by Bello (1997) from the same study sites, are consistent with the above prediction. Moreover, it is hypothesised that this change in resource availability would alter the trophic structure of the invertebrate communities, involving a predicted higher relative abundance of shredders upstream, compared with downstream of the reservoir (Vannote *et al.*, 1980; Ward and Stanford, 1984). However, the change in the type of resource availability in the tailwater compared with the upstream site was not followed by the predicted change in the relative abundance of shredders. Nevertheless, the leaf material constituted a substantial part of the diet for invertebrates at the upstream site in contrast with the downstream site, where this material was seldom ingested. This finding emphasises the value of this food source for the invertebrate community at the upstream site, unlike that at the tailwater, despite the scarcity of functional shredders, and revealed a downstream shift of the process, as was implicit in Ward and Stanford (1984).

Mihuc and Minshall (1995) drew attention to the danger of using functional feeding groups as trophic guilds to infer systems-level trophic dynamics in streams, owing to the prevalence of generalist trophic function among benthic macroinvertebrates in these environments. These trophic generalists are frequently more important to stream communities under disturbed conditions, as in the present study. Trophic generalists may display important shifts in resource utilisation in space and time, depending on the type of food available (e.g. Short, 1983). A spatial shift in resource utilisation (ingestion) was clearly observed in the downstream direction at the community level, but also at the level of species (*E. ignita*), despite the prediction given by the functional feeding groups approach. However, for a stronger evaluation of the proportional contribution of CPOM to the food web at both sites, the examination of gut content might be coupled with stable isotope analysis ($^{13}\text{C}/^{12}\text{C}$ ratios; Rau, 1980) aimed at identifying with certainty the sources of nutrition utilised for tissue growth.

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