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Leaf breakdown patterns in a NW Italian stream: Effect of leaf type, environmental conditions and patch size

Stefano Fenoglio, Tiziano Bo, Marco Cucco & Giorgio Malacarne

University of Piemonte Orientale, Di.S.A.V., Via Bellini 25, I–15100 Alessandria, Italy; e-mail: fenoglio@unipmn.it

Abstract: We studied the decomposition process and macroinvertebrate colonisation of leaf packs to determine to what extent leaf consumption and invertebrate abundance depend on the pollution level, season, leaf type and patch size. We exposed 400 leaf packs made of two leaf types, alder and chestnut, at two sites of the Erro River (NW Italy) with different environmental alteration levels. Leaf packs were set out as three patch sizes (alone, or in groups of 6 or 12). A first experiment was carried out in winter and a second in summer. Leaf packs were retrieved after 15, 30, 45 and 60 days of submersion to determine the leaf mass loss and to quantify the associated macroinvertebrates. Natural riverbed invertebrates were collected in the same areas. Patch size, season, leaf type and pollution level significantly affected mass loss. The breakdown process was faster for alder leaves, during summer, at the unpolluted site, and in smaller patches. Leaf type and patch size did not affect macroinvertebrate density and richness, but the highest taxon richness was found in winter and at the unpolluted site. There were more shredders and predators than in the natural riverbed. Our study supports two recent ideas regarding leaf processing in streams: that patch size influences the leaf breakdown rate and that the breakdown rate can be used to evaluate water quality and environmental health.

Key words: Packs, benthic invertebrates, allochthonous inputs, pollution, patch size.

Introduction

Much of the energy input of lotic food webs derives from non-living sources of allochthonous organic matter (Cummins, 1979; Vannote et al., 1980), and the recycling of nutrients during organic matter decomposition is an important component of running water ecosystems (Irons et al., 1988; Cummins et al., 1989; Murphy et al., 1998). Autumn-shed leaves are the most important source of organic material in temperate headwater streams (Wallace et al., 1997; Power & Dietrich, 2002). Leaves falling into the stream are caught by riverbed structures to form masses called leaf packs, which are then degraded by a combination of physical and biological processes (Richardson, 1992; Carlisle & Clements, 2005).

Up to 25% of the initial dry mass can be lost on the first day due to the decrease in soluble constituents (Webster & Benfield, 1986). After a few days, fungi and bacteria colonise the leaves, starting the degradation process by producing enzymes that digest the remaining nutrients. Microbial conditioning (Gessner et al., 1999) leads to changes in the chemistry and structure of the leaves; the importance of this microbial activity was demonstrated long ago by Kaushik & Hynes (1971) and Pattee et al. (1986). After the microbial conditioning period, the leaves represent a good resource for invertebrate shredders (Merritt & Cummins, 1996). The contribution of these shredders to the breakdown is variable but usually substantial (Cuffney et al., 1990; Allan, 1995; Hieber & Gessner, 2002). Through the production of faecal pellets and orts (fine fragments shredded from leaves but not ingested), shredders convert coarse particulate organic matter (CPOM) into fine particulate organic matter (FPOM), which is then distributed downstream and ingested by many other consumers (collector-gatherers and filterers; Mulholland et al., 1985; Pretty et al., 2005).

Leaf breakdown in streams is an important topic in lotic ecology: several studies have investigated leaf breakdown in temperate systems, while others have focused on tropical (Mathuriau & Chauvet, 2002) and Mediterranean streams (Maamri et al., 1998a, b; Casas & Gessner, 1999). Apart from the basic and purely ecological research (reviewed in Allan, 1995), leaf breakdown studies have recently been used to assess the functional integrity of streams at the ecosystem level (Gessner & Chauvet, 2002; Niyogi et al., 2001; Pascoal et al., 2003).

In the present study, we investigated leaf breakdown and macroinvertebrate succession in an Apennine stream (NW Italy) to evaluate the importance of leaf type (alder or chestnut), environmental pollution, season (winter or summer) and patch size on the leaf

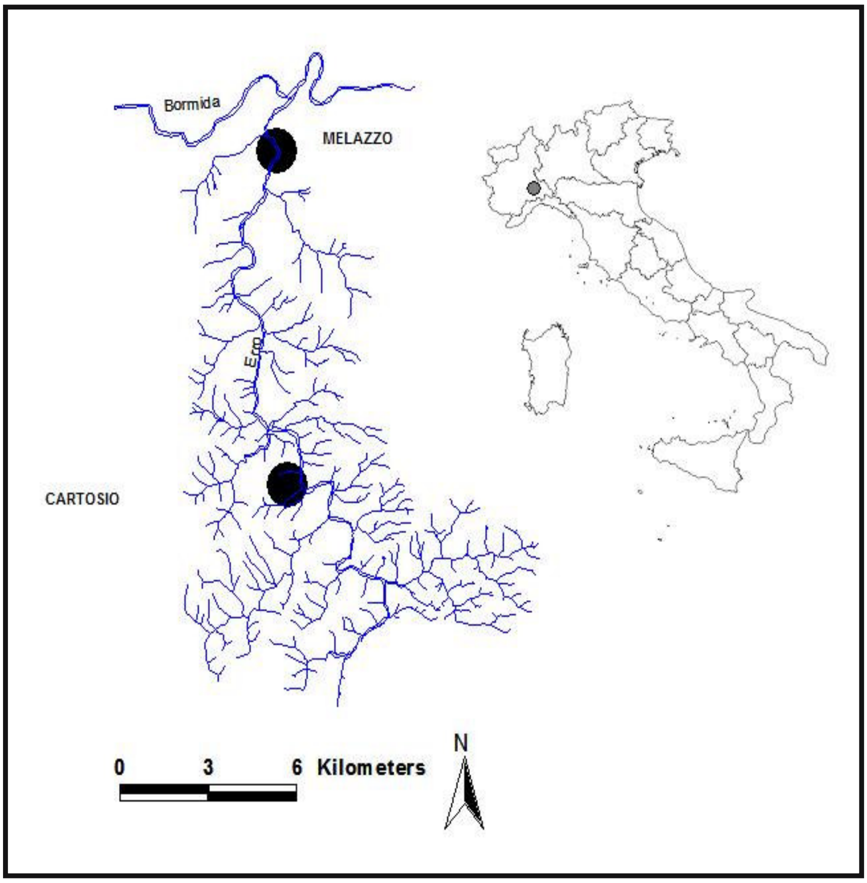

Fig. 1. Location of the two sites in the Erro River (NW Italy).

breakdown rate and the colonising macroinvertebrate assemblages.

Material and methods

Experiments were carried at two sites of the Erro River (Fig. 1), a third-order Apennine stream in NW Italy with a catchment area of 135.33 km^2. At both sites, the channel width was about 8–9 m, with a mean depth of 40–60 cm. The stream substrate consisted mainly of gravel and cobbles. The climate is temperate-Mediterranean, with high autumn rainfall. The stream flows through a large valley in a secondary deciduous forest. The riparian vegetation is dominated by *Robinia pseudoacacia* (L.), *Alnus glutinosa* (L.), *Castanea sativa* (Miller) and *Quercus* spp.

We collected samples at two stations: Cartosio (44°33′ N, 8°26′ E, 261 m a.s.l.) and Melazzo (44°38′ N, 8°25′ E, 160 m a.s.l.). These stations are close to one another (11 km) but have considerably different environmental conditions (Tab. 1): the biological quality of the Erro at the first station is good, reaching the first class of the Extended Biotic Index system (Ghetti, 1997), i.e. an environment without signs of alteration. At Melazzo, the Erro receives organic wastewater from some villages, and the biological quality drops to the third class (environment with evident human-derived alteration). The E.B.I. method includes five classes, from the virtually unaltered first class to the very polluted fifth class. At Melazzo, there are also unpredictable and intermittent increases in suspended sediment transport, due to the proximity of gravel extraction areas.

We placed 200 artificial leaf packs in the riverbed in winter (26.XII.2003) and another 200 in summer (1.VI.2004). Two leaf types were used independently: alder (*Alnus glutinosa*) and chestnut (*Castanea sativa*). Both are common species in the Erro basin, with alder usually present near the river corridor and chestnut diffuse in the nearby woods. Freshly abscised leaves of the two species were collected in autumn 2003 in the Erro basin and were exposed in the stream. In each season, we made 100 packs of alder and 100 of chestnut leaves (dry mass of each pack: 5.03 $\pm$ 0.04 g (mean $\pm$ SD). Packs were prepared with dried leaves tied together with a nylon mesh (2 cm mesh size). To investigate the importance of patch size, we grouped packs in patches, setting the packs one above the other in heaps: 96 packs were grouped into 8 patches of 12 and 48 packs into 8 patches of 6, while 56 packs were placed singly in the water. At each site, we randomly placed four 12-pack patches, four 6-pack patches and 28 single packs. The packs were tied to stones and randomly located in riffle areas: at Cartosio depth 35.0 $\pm$ 6.0 cm (mean $\pm$ SD); current velocity 0.65 $\pm$ 0.22 cm s^{-1}; at Melazzo depth 38.0 $\pm$ 9.0 cm, current velocity 0.61 $\pm$ 0.18 cm s^{-1}. After 15, 30, 45 and 60 days, one 12-pack patch, one 6-pack patch and 7 single packs were removed from each site and placed separately in plastic bags with stream water (in total, 25 packs/station/date). The bags were immediately transported to the laboratory. Leaves were later oven dried at 105 °C until a constant mass was reached in order

Table 1. Main chemical and microbial parameters measured at the two sampling sites.

Parameter	Cartosio	Melazzo
Dissolved oxygen (mg L^{-1})	12.0	8.0
Escherichia coli (CFU)	40	410
BOD_5 (mg L^{-1})	< 2	2.7
COD (mg L^{-1})	< 5	6.6.
NO_3 (mg L^{-1})	< 0.23	1.2
PO_4 (mg L^{-1})	< 0.05	0.06
pH	7.7	7.4

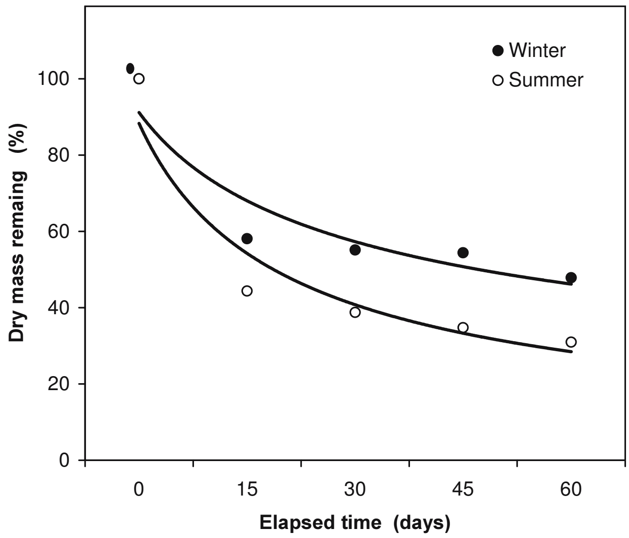

Fig. 2. Mean remaining mass (percentage of initial dry mass) of leaf packs in the two sampling seasons.

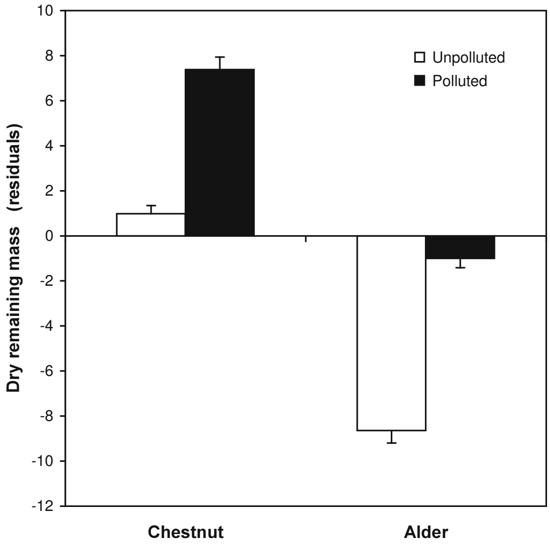

Fig. 3. Mean remaining mass in relation to leaf type and pollution level.

Table 2. Influence of season, leaf type, time elapsed, pollution level and patch size on mass loss.

Parameter	df	*F*-ratio	*P*
Time (days)	1	287.1	0.001 ***
Season (summer, winter	1	1165.0	0.001 ***
Leaf type (chestnut, alder)	1	298.3	0.001 ***
Pollution level (high, low)	1	244.9	0.001 ***
Patch size (1, 6, 12 packs)	2	7.9	0.001 ***

Key: *** $P < 0.001$ (Multivariate ANCOVA, $n = 400$ leaf packs).

to determine the remaining mass. Leaf pack mass loss was quantitatively modelled using percentage remaining mass.

Before the leaves were dried, all macroinvertebrates were collected with tweezers and preserved in 70% ethanol. All organisms counted were identified at the genus level, except for Chironomidae, Simuliidae and early instars of some Trichoptera and Diptera, which were identified at the family level. Each taxon was assigned to a Functional Feeding Group (FFG) according to Merritt & Cummins (1996), (FFG: Sc – Scrapers; Sh – Shredders; Cg – Collector-gatherers; F – Filterers; P – Predators).

At the two sites, we collected 89 Surber samples (0.06 m^2, 500 μm mesh) to compare the abundances of invertebrates colonising the leaf packs with the natural densities of macroinvertebrates in the stream.

Statistical analyses of mass loss, the total number of macroinvertebrates and species richness were performed with multivariate ANCOVAs (Wilkinson, 1992) with leaf type, pollution level and patch size as independent factors, elapsed time as covariate, and abundance or richness as dependent variables. The richness and abundance data were log-transformed, while the percentage data (mass loss) were arcsine square-root transformed (Sokal & Rohlf, 1969). To examine the taxonomic composition in relation to patch size, elapsed time, pollution level and leaf type, we used Canonical Correspondence Analysis (Gauch, 1982) performed with SYNTAX 2000 (Podani, 1997).

Results

Mass loss

Remaining leaf mass was significantly related to elapsed time, season, leaf type, pollution level and patch size (Tab. 2). The decrease was very rapid in the first 15 days in both seasons (Fig. 2), and was significantly higher in summer than in winter on each removal date: after 15 days, the remaining mass was 44.3% in the warm season and 58.1% in the cold season, while the final mean mass was 30.96% and 47.84%, respectively.

Leaf type and pollution level significantly affected mass loss (Fig. 3 shows the residuals of the multivariate analysis after correcting for elapsed time and season). Alder leaves decomposed faster than chestnut leaves, and remaining mass was higher at the polluted site.

Regarding patch size, the packs in the 1-pack and 6-pack patches had a lower remaining mass than those in the 12-pack patches (Fig. 4).

Macroinvertebrate colonisation

Altogether, we collected 16,310 macroinvertebrates be-

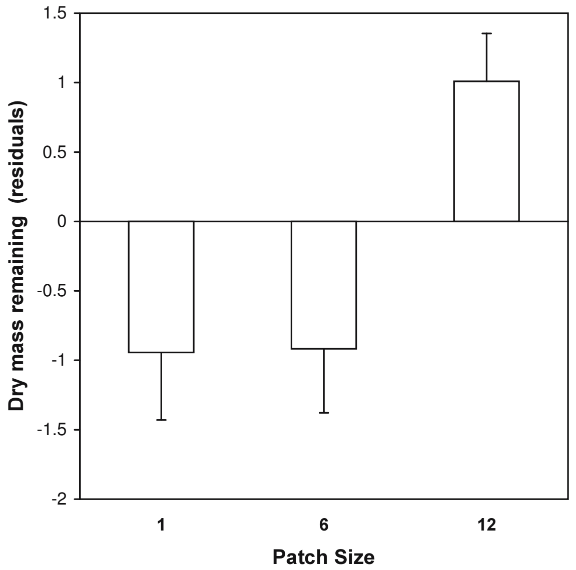

Fig. 4. Mean remaining mass of leaf packs in relation to patch size.

Table 3. Influence of season, leaf type, time elapsed, pollution level and patch size on macroinvertebrate individual abundance and taxon richness.

Parameter	df	*F*-ratio	*P*
Abundance			
Season	1	0.02	0.88
Leaf type	1	0.52	0.47
Time	1	38.6	0.001 ***
Pollution level	1	316.6	0.001 ***
Patch size	2	0.10	0.91
Richness			
Season	1	101.5	0.001 ***
Leaf type	1	0.20	0.65
Time	1	0.34	0.55
Pollution level	1	413.6	0.001 ***
Patch size	2	3.82	0.02 *

Key: * $P < 0.05$, *** $P < 0.001$ (Multivariate ANCOVA, n = 400 leaf packs).

longing to 58 taxa in the leaf packs and 10,312 macroinvertebrates belonging to 53 taxa in the natural riverbed (Appendix 1).

The abundance of colonising macroinvertebrates did not differ between seasons, leaf types and patch sizes, but was significantly affected by the pollution level and elapsed time (Tab. 3). In particular, there were only 25.8 ± 1.50 ind./pack at the polluted site (mean ± SE) *vs.* 95.9 ± 4.94 ind./pack at the unpolluted one. The mean number of individuals decreased from 65.9 ± 6.80 on the first removal date to 32.4 ± 3.27 ind./ pack on the last removal date.

Taxon richness was significantly related to season, patch size and pollution level, while there was no difference in the mean number of taxa in relation to elapsed time or leaf type (Tab. 3). In particular, there were only 4.50 ± 0.15 taxa/pack at the polluted site *vs.* 10.3 ± 0.30 taxa/pack at the unpolluted one, and the mean number of taxa changed from 5.11 ± 0.29 in winter to 8.25 ± 0.29 taxa/pack in summer.

The taxonomic composition of the macroinvertebrate assemblages colonising the leaf packs differed between winter and summer. Therefore, to investigate the relationship between taxa and environmental variables, we performed the Canonical Correspondence Analysis separately for the two seasons (winter: Fig. 5; summer: Fig. 6). In both seasons, the abundance of each taxon was unrelated to leaf type. Moreover, there was no clear tendency for any taxon abundance to vary in relation to elapsed time or patch size, as indicated by the position of the variables near the origin of the axes (Figs 5, 6). These analyses indicate that the communities did not strongly differ in relation to the studied variables.

The density of natural benthic macroinvertebrates was 1,866.6 ind. m^{-2}. There were significant differences in the functional composition of macroinvertebrate assemblages colonizing the natural riverbed and the leaf packs. Collector-gatherers was the most frequent Functional Feeding Group (FFG) in both assemblages (63.8% in the leaves and 59.2% in the substratum), with no significant difference in the percentage composition. Interestingly, there were significant differences in the relative importance of the other four FFG. Both shredders and predators were more frequent in the leaf packs than in the substratum (Sh: 8.5% in the leaves *vs.* 0.9% in the substratum, $F_{1,487} = 53.5$, $P < 0.001$; P: 25.6% in the leaves *vs.* 15.7% in the substratum, $F_{1,487} = 10.2$, $P < 0.005$). In contrast, scrapers and filterers were more abundant in the natural riverbed than in the leaf packs (Sc: 11.2% in the substratum *vs.* 0.89% in the leaves; $F_{1,487} = 255.0$, $P < 0.001$; F: 8.2% in the substratum *vs.* 5.8% in the leaves; $F_{1,487} = 9.90$, $P < 0.005$).

Discussion

In this study, we show that leaf breakdown in an Apennine stream varied significantly in relation to season, pollution level, leaf type and patch size, while the abundance and taxon richness of macroinvertebrates colonising the leaf packs were influenced by pollution level and season but not by patch size and leaf type. The density of natural benthic macroinvertebrates was similar to the values reported in previous studies conducted in this region (FENOGLIO et al., 2002, 2004b, 2005) and in similar temperate areas (GRUBAUGH & WALLACE, 1995; CLARKE & SCRUTON, 1997).

Several studies have examined patterns and aspects of allochthonous CPOM breakdown in streams (MAAMRI et al., 1998a, b; PATTEE et al., 2000; HIEBER & GESSNER, 2002). Hence, the sequence of events occurring during processing and the factors limiting the processing rates are well known (e.g., WEBSTER &

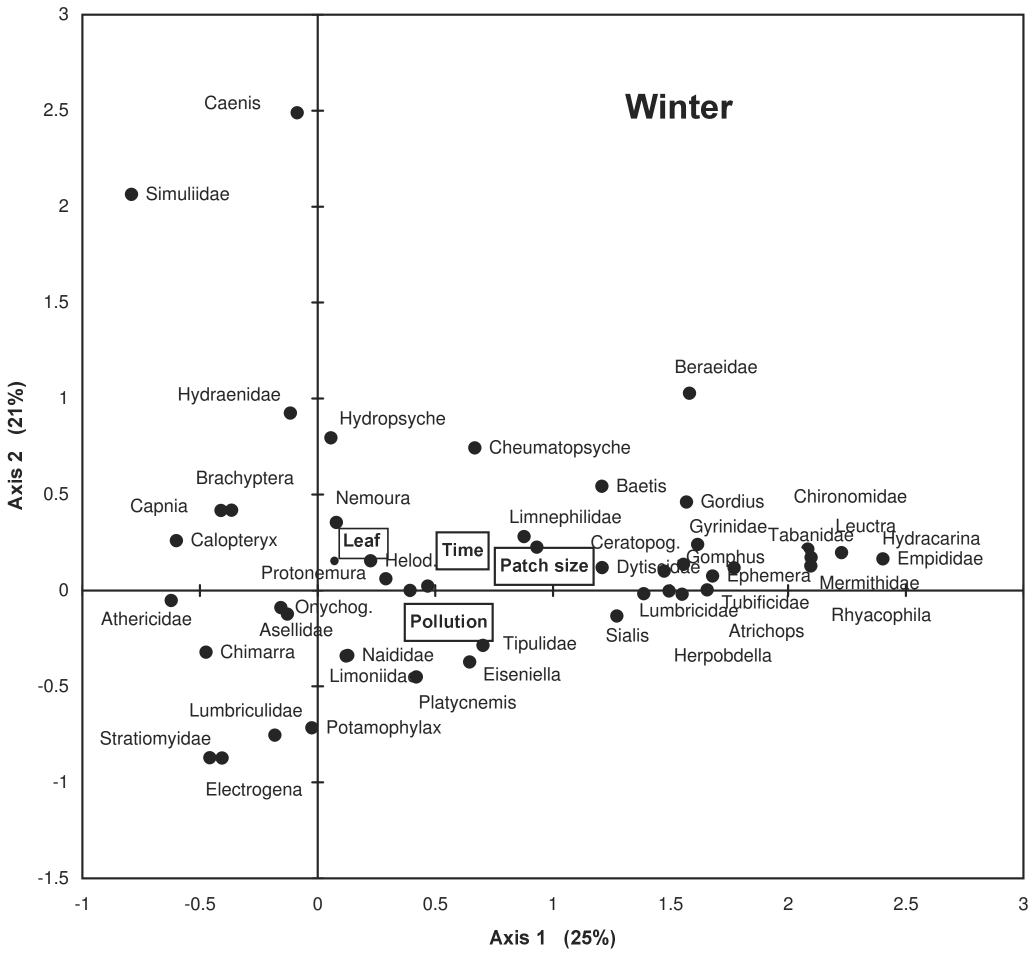

Fig. 5. Canonical Correspondence Analysis: ordination of macroinvertebrates colonising leaf packs in winter.

Benfield, 1986). However, some elements are under-investigated, and we do not fully understand how the numerous interacting variables controlling leaf-processing rates in streams are organized. Recently, it was suggested that hierarchical aspects of the framework of factors controlling leaf processing in streams should be taken into account (Royer & Minshall, 2003).

The pattern of leaf mass loss in our study was within the range reported in the literature (Royer & Minshall, 1997; Giller & Malmqvist, 1998). In temperate streams, the breakdown rates of leaves from different plant species vary; in particular, leaves with better nutritional quality (e.g., lower C:N ratio, higher fungal colonisation, lesser presence of toxic oils and tannins) show the greatest breakdown rate. Shredders show clear preferences for leaf type: for example, Canhoto & Graça (1995) demonstrated that shredders preferred alder over oak and also had a higher growth rate on alder, while chestnut fell in between. Webster & Benfield (1986) reported a 'fast' breakdown rate of alder and a 'slow' breakdown rate of chestnut. Those findings are supported by our results for the Apennine stream, where alder is one of the most common species in the riparian vegetation.

With regard to mass loss in different seasons, it is well known that stream invertebrates in temperate regions are well adapted to the annual input of autumn-shed leaves and have life cycles well timed to the litter fall (Giller & Malmqvist, 1998). Despite the difference in the trophic and structural composition of the benthos, we found that leaf breakdown was faster in summer than in winter at both sites. Our study supports the hypothesis that latitude plays an important role in the decomposition process, probably enhancing bacterial and fungal activity. Recent studies demonstrated that the importance of microbial breakdown decreases with increasing latitude (Irons et al., 1994; Jonsson et al., 2001) and that the importance of macroinvertebrate shredders decreases from tropical to boreal areas (Dobson et al., 2002; Fenoglio et al., 2004a).

Regarding patch size, we found that smaller leaf masses were more rapidly decomposed than larger ones. We presume that the interior of a larger pack becomes more hypoxic, thus decreasing the consumption process, and/or that water has more difficulty removing leaf fragments from larger leaf patches. Patch size did not influence the macroinvertebrate abundance or taxon richness. This demonstrates that macroinverte-

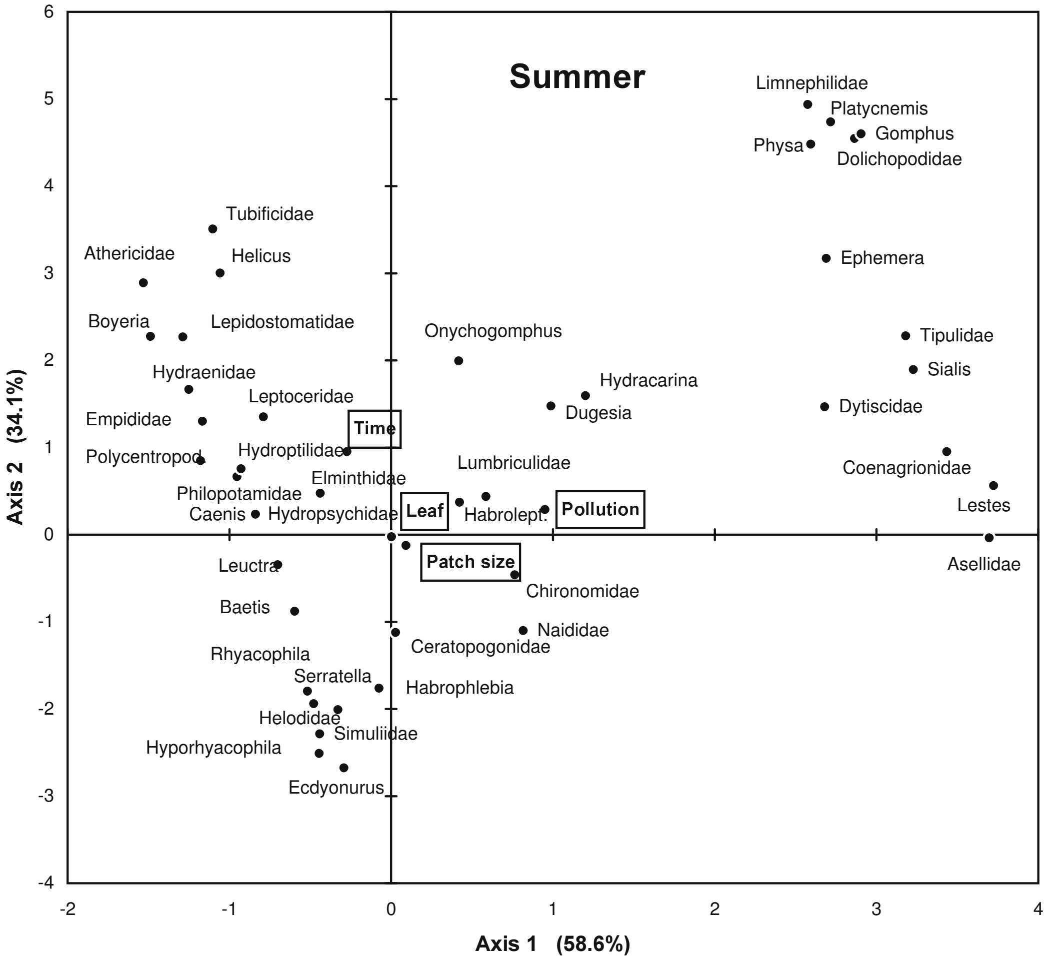

Fig. 6. Canonical Correspondence Analysis: ordination of macroinvertebrates colonising leaf packs in summer.

brates can colonise leaf masses independently of patch size, and suggests that differences in consumption rate largely depend on physical breakdown (running water action) and to a less extent on direct consumption by invertebrates.

Finally, our results support the idea that environmental conditions strongly affect leaf breakdown rates. Interestingly, the faster rate was recorded at the unpolluted site. GESSNER & CHAUVET (2002) proposed that leaf breakdown is a measure of stream integrity. In this regard, we noticed a significant difference between the two sites in the characteristics of the benthic coenosis: at the unpolluted site, the abundance of macroinvertebrates in the leaf packs was four-fold higher and the taxon richness was two-fold greater than at the polluted site. We can hypothesize that the reduced presence of macroinvertebrates (particularly shredders) at the polluted site was a key element in the leaf breakdown rate. Indeed, recent studies demonstrated that mass loss often shows a positive relationship with shredder occurrence, in terms of both organism abundance (FABRE & CHAUVET, 1998) and species richness (JONSSON et al., 2001). Our study agrees with previous results of field (JONSSON et al., 2001) and laboratory experiments (JONSSON & MALMQVIST, 2000) indicating a clear association between species richness and leaf breakdown rate.

In conclusion, the results of the present study support two recent ideas regarding leaf processing in streams: that patch size influences the leaf breakdown rate, i.e., leaves inside larger packs are processed more slowly, and that the breakdown rate can be used to evaluate water quality and environmental health.

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Appendix 1. Taxonomic list and percent relative abundance for macroinvertebrates collected in the natural riverbed and into the leaf packs.

Taxon	FFG	Leaf packs	River bed
Plecoptera			
Capnia bifrons (Newman, 1838)	Sh	1.21	1.12
Brachyptera sp.	Sh	1.47	5.42
Isoperla sp.	P	0.00	0.04
Leuctra sp.	Sh	13.63	6.32
Nemoura sp.	Sh	0.03	0.12
Protonemura sp.	Sh	0.01	0.03
Ephemeroptera			
Baetis sp	Cg	2.77	9.10
Caenis sp.	Cg	0.17	1.04
Electrogena sp.	Sc	0.01	0.01
Ecdyonurus sp.	Sc	0.02	0.24
Heptagenia coerulans Rostock, 1877	Sc	0.00	0.02
Habroleptoides sp.	Cg	0.02	0.49
Habrophlebia sp.	Cg	0.85	1.79
Ephemera danica Müller, 1764	Cg	0.01	0.00
Serratella ignita Poda, 1761	Cg	0.64	0.55
Trichoptera			
Cheumatopsyche lepida (Pictet, 1834)	F	0.04	0.86
Chimarra marginata (L., 1767)	F	14.86	1.84
Hydropsyche sp.	F	13.61	3.22
Hyporhyacophila sp.	P	0.04	0.11
Rhyacophila sp.	P	0.59	0.42
Wormaldia sp.	F	0.00	0.01
Potamophylax cingulatus (Stephens, 1837)	Sh	0.01	0.00
Limnephilidae	Sh	0.00	0.01
Lepidostomatida	Sh	0.18	0.00
Leptoceridae	Cg	1.13	1.89
Hydroptilidae	Sc	0.03	0.24
Beraeidae	Cg	0.01	0.00
Polycentropodidae	F	0.02	0.02
Diptera			
Atherix sp.	P	0.23	0.07
Atrichops crassipes (Meigen, 1820)	P	0.06	0.01
Chironomidae	Cg	24.03	33.64
Ceratopogonidae	P	0.29	0.41
Empididae	P	0.07	0.03
Limoniidae	P	0.01	0.01
Simuliidae	F	1,89	6.51
Stratiomyidae	P	0.01	0.02
Tabanidae	P	0.01	0.00
Tipula sp.	Sh	0.06	0.05
Coleoptera			
Dytiscidae	P	0.06	0.11
Elminthidae	Cg	0.71	8.73
Stenelmis canaliculata (Gyllenhal, 1808)	Cg	0.00	0.03
Gyrinidae	P	0.01	0.00
Helodidae (larvae)	Sh	0.03	0.11
Helichus substriatus (Müller, 1806)	Sc	0.40	0.03
Hydraenidae	Sc	0.06	0.09
Odonata			
Boyeria irene (De Fonscolombe, 1838)	P	0.08	0.00
Calopteryx virgo (L., 1758)	P	0.01	0.00
Lestes sp.	P	0.01	0.00
Gomphus vulgatissimus (L., 1758)	P	0.01	0.01
Onychogomphus forcipatus (L., 1758)	P	0.49	0.60
Platycnemis pennipes (Pallas, 1771)	P	0.05	0.02
Megaloptera			
Sialis fuliginosa (L., 1758)	P	0.04	0.02
Crustacea			
Asellidae	Sh	0.45	0.06
Anellida			
Eiseniella tetraedra (Savigny, 1826)	Cg	0.01	0.12
Lumbricidae	Cg	0.01	0.01
Lumbriculidae	Cg	0.05	0.18
Naidae	Cg	3.74	2.34

Appendix 1. continued.

Taxon	FFG	Leaf packs	River bed
Tubificidae	Cg	0.10	0.55
Tricladida			
Dugesia sp.	P	4.15	0.58
Hirudinea			
Herpobdella sp.	P	0.01	0.00
Nematomorpha			
Gordius sp.	P	0.00	0.01
Gastropoda			
Physa sp.	Sc	0.01	0.00
Arachnida			
Hydracarina	P	4.31	12.39
Nematoda			
Mermithidae	P	0.01	0.09
Total (%)		100	100
Total (N)		16310	10312

Key: FFG – functional feeding groups; Cg – collectors–gatherers; F – filterers; P – predators; Sc – scrapers; Sh – shredders.