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Original Research

The Effect of Stream Bed Morphology on Shredder Abundance and Leaf-Litter Decomposition in Hungarian Midland Streams

Kata Kovács[1]*, Géza B. Selmeczy[1], Tamás Kucserka[1], Nassr-Allah H. Abdel-Hameid[2], Judit Padisák[1]

[1]Department of Limnology, University of Pannonia, Veszprém, Egyetem utca 10. H-8200, Hungary
[2]Department of Zoology, Benha University, Egypt

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Abstract

The aim of this study was to examine the differences between natural and morphologically modified stream bed sections in Hungarian midland streams by means of macroinvertebrate shredder abundance and leaf litter decomposition, and identify the key drivers of poor shredder fauna in modified water bodies. Eight sampling sites on three low order Hungarian watercourses were selected and studied between the springs of 2008 and 2009. Three types of leaf litter were collected and placed into leaf litter bags that were fixed to a metal wire net on the bottom of the river bed. Samples were taken in every four weeks. Leaf litter content and decomposition rate was determined and macroinvertebrates identified. Gammaridae dominated among shredders and their proportion did not differ significantly in bags. The shredders' counts and the leaf litter decay rates were different in the experimental streams. The sampling sites located in modified stream sections, with limited availability of food, exhibited lower shredder densities but higher decomposition rates ($k>0.01\ d^{-1}$) than those observed in sites of undisturbed bed morphology with rich allochtonous organic matter ($k<0.0077\ d^{-1}$). However, no significant differences were obtained in decay rates among the leaf species. Our results suggest that shoreline vegetation and bed morphology are two equally important factors in determining functional properties of streams; and leaf litter decomposition rate is not only a function of shredder density. Thus decomposition rate can be an important functional variable for ecological status assessment of the water.

Keywords: bed morphology, leaf litter, macroinvertebrates, decomposition

Introduction

Leaf litter represents an important allochthonous energy resource in several aquatic environments. Gallery forests and shoreline macrophyte vegetation are the most important sources of allochtonous organic load of river sections, especially in low-order rivers [1-3]. In streams, leaf litter load is processed in three phases:

(1) leaching
(2) microbial colonization
(3) invertebrate feeding and physical abrasion [4, 5].

The use of functional indicators like feeding groups of macroinvertebrates, together with the traditional biomonitoring, has been increasingly accepted [6] in ecological status assessment. The use of functional indicators represents an important step forward in directly measuring certain elements of ecosystem functioning and this makes it possible to further explore aquatic ecosystems [7, 8].

*e-mail: kovacs.kata@almos.uni-pannon.hu

Habitat heterogeneity affects ecological processes at all levels of organization, including behavior, population dynamics, species interactions, community structure and ecosystem functioning [9-11]. The European Union Water Framework Directive [12] claims that streambed modification impoverish flora and fauna, therefore simplifying matter- and energy flow webs, leading to weak ecological condition or potential. In recent years, the ecological impact of bed modification and the importance of restoration were studied in several ways. Waterflow restoration can revert ecosystem variables close to natural state [13] and restoration measures, including re-establishment of proper size riparian forests [14].

Natural streams receive significantly higher leaf litter input. Additionally, their litter retention capacity in accumulation zones can be twice that observed in modified streams [15]. As macroinvertebrate shredders have a key role in decomposition [16], alterations in leaf litter input and retention is expected to influence both their abundance and activity.

The quantitative effect of riverbed modification on biota and their functional performance has been explored only recently. Stenger-Kovács et al. [17] demonstrated alterations in attached diatom communities upstream and downstream of damming. In a Moulton et al. study [18] leaf litter decomposition in urban streams was associated with other macroconsumers such as fish and tadpoles, rather than with shredders. Lorenz et al. [19] examined the impact of restoration of modified water bodies to the macroinvertebrate fauna, highlighting the fact that currently used restoration measures must be carefully used and applied to improve macroinvertebrate diversity. Friberg et al. [20] found relatively weak relations between currently used morphological measures and macroinvertebrate assessments, and urges for systemic biological assessment of bed modifications. Particularly, regarding Hungarian streams, the impact of riverbed modifications to macroinvertebrates were not quantitatively studied by the time of this research.

In this study we aimed to investigate the alteration of natural processes due to bed degradation by using a macroinvertebrate functional group (shredders) in Hungarian midland streams. Our working hypothesis was that modified sites have poor and/or small macro-invertebrate populations because 1) leaf litter input is not sufficient and 2) leaf litter and its fractions are immediately washed away in the modified water bodies. Therefore, such simple processes like leaf litter decomposition are incomplete and any restoration has to take into account both of the above drivers. Thus, the relationship between leaf litter decomposition by shredders and bed morphology were explored using sampling sites that are typical in the geographic region and can be characterized with different degrees of streambed modification. Changes in the composition of the macroinvertebrate shredder population, and in their density, combined with leaf litter decomposition rates were used as indicators.

Site Description

Eight experimental sites in three small watercourses (Cuha, Csigere, and Torna) in a hilly area were selected for the experiments (Fig. 1) and studied between springs of 2008 and 2009. All three streams are located in the area of the hill Bakony, and their lengths vary between 12-63 km (Table 1). Experimental sites were chosen from most characteristic places of the given sections of each stream.

Stream Cuha had two experimental sites. At the first site (C1), (Table 1), the river-bed is a mixture of megalithal (Ø>40 cm, large cobbles, boulders and blocks, bedrock), macrolithal (Ø>20 cm to 40 cm coarse blocks, head-sized cobbles), and mesolithal (Ø>6 cm to 20 cm fist to hand-sized cobbles). The dense forest vegetation along the shores is dominated by *Quercus robur*, *Quercus petraea*, and *Carpinus orientalis*.

At the second site (C2), besides the above three species, *Populus tremula* is also present. The bed is akal (Ø>2 mm

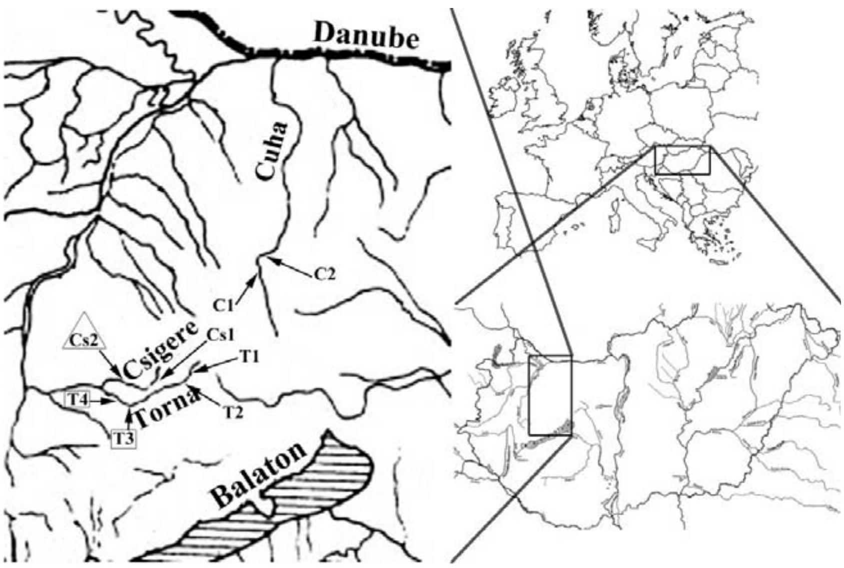

Fig. 1. Location of sampling sites (square: artificial water body, triangle: interim state, all other, not indicated sites: natural water body.

Table 1. The main characteristics of study sites.

	C1	C2	Cs1	Cs2	T1	T2	T3	T4
Bed morphology	Natural		Natural				Strongly modified	
Vegetation	Natural, wooded		deflation forest belt, agricultural area		Natural, wooded		Urbanized environment, agricultural area	
Stream length (km)	63		12		42			
Average water flow	Small/Medium		Small/medium				Large	
Coordinates	47º 12.125'N, 18º37.181'E, 275m a.s.l.	47º22.828'N, 17º50.598'E, 215m a.s.l.	47º8.476'N, 17º34.402'E, 252m a.s.l.	47º7.081'N, 17º25.244'E, 166m a.s.l.	47º12.125'N, 18º37.181'E, 385m a.s.l.	47º10.998'N, 17º40.778'E, 377m a.s.l.	47º5.900'N, 17º28.152'E, 187m a.s.l.	47º6.367'N, 17º26.090'E, 179m a.s.l.
Bed (sead)	mega- macro- mezolithal (cobbles)	akal, psammal, argyllal (sand)	akal, psammal, argyllal (sand)	microlithal, akal (gravel)	microlithal, akal (gravel)	microlithal, akal (gravel)	microlithal, akal (gravel)	microlithal, akal (gravel)
Velocity $ms^{-1}\pm SE$	0.31±0.32	0.38±0.18	0.33±0.15	0.51±0.20	0.28±0.11	0.23±0.17	0.64±0.10	0.71±0.085

to 2 cm, fine to medium-sized gravel), psammal/psammopelal (Ø>6 µm to 2 mm, sand/sand with mud including organic mud and sludge), and in some points argyllal (Ø<6 µm silt, loam, and clay), as a consequence of rather slight slope and large spanning curves.

At the first site of the Csigere-stream (Cs1) the dominant tree species is *P. tremula*, which grows only on the margin of the stream. The bed is appropriately meandering and it is composed of akal (Ø>2 mm to 2 cm fine to medium-sized gravel), psammal/psammopelal (Ø>6 µm to 2 mm, sand/sand with mud, including organic mud und sludge), and at some points argyllal (Ø<6 µm silt, loam, clay (inorganic). There is no natural tree vegetation at the second site of the Csigere-stream (Cs2) except for sporadic specimens of *Salix caprea* and *Populus tremula*. The bed is microlithal (Ø>2 cm to 6 cm, coarse gravel with variable percentages of medium to fine gravel) and akal (Ø>2 mm to 2 cm, fine to medium-sized gravel). The stream is meandering at this site. There is a reservoir located 3 km upstream, and the macrovegetation next to the stream is poor.

From the four sampling sites on stream Torna, two are natural, similarly to the Cuha (C1 and C2) and Csigere (Cs1 and Cs2). There is natural tree vegetation at these two sites (T1 and T2), with *Carpinus orientalis* and Betulaceae. The bed is microlithal (Ø>2 cm to 6 cm coarse gravel) and akal (Ø>2 mm to 2 cm, fine to medium-sized gravel) at both places. The other two Torna sites (T3 and T4) were located on heavily modified sections of the stream, where the bed was strengthened and fortified by trapezoid concrete blocks. The river bed is characterized by microlithal (Ø>2 cm to 6 cm) and akal (Ø>2 mm to 2 cm). There is no natural tree vegetation, because the stream flows through an agricultural area, but some *Populus tremula* and Salicaceae (*Salix viminalis*, *Salix caprea*, *Salix alba*) were present.

Methods

Fresh leaf litter of *Quercus robur*, *Populus tremula*, and *Salix alba* were collected in autumn 2007. The leaf litters were dried at 70ºC until dry mass constancy and 10 g subsamples were filled into bags with sizes 15x15 cm and a mesh size of 5x2 mm.

At each experimental site a 5-6 m^2 homogenous bed plot was chosen. The four corners of leaf litter bags were fixed on a 5-6 m^2 metal wire net (approximately 5x5 cm mesh size), and the wire net was fixed in the river-bed. We used 72 bags at each location (2 types of leaves, 12 sampling days and 3 bags for each sampling). The bags were moistened by water spraying prior to the exposure procedure to avoid fracturing.

From April 2008 until April 2009, litter bags were carefully removed (three bags from each location and from each litter type) from the wire-net on every 28th day during one year. Parameters such as temperature, dissolved oxygen (DO), oxygen saturation, pH, and conductivity were measured *in situ* an with HQ40d (Hach Lange) sensor, and the main chemical variables (NO_2^--N, NH_4^+-N, NO_3^--N, PO_4^{3-}-P, TP, SO_4^{2-}, COD_{PS}) were analyzed in a laboratory [21-22].

Table 2. Averages and standard deviations (StdDev) of some water chemical parameters and the main ions measured across the year per sampling point (N per site=14), Abbreviations: DO – dissolved oxygen, Cond. – conductivity, COD_{PS} – chemical oxygen demand analyzed by permanganate method, TP – total phosphorus.

		DO mg·L^{-1}	DO %	Cond. µS·cm^{-1}	pH	T ºC	NO_2-N mg·L^{-1}	NH_4-N mg·L^{-1}	NO_3-N mg·L^{-1}	COD_{PS} mg·L^{-1} O_2	PO_4^{3-}-P mg·L^{-1}	TP mg·L^{-1}	SO_4^{2-} mg·L^{-1}
Cs1	Avg	9.62	90.82	746.00	7.89	11.52	0.032	0.22	6.79	9.06	0.002	24.42	24.06
	StdDev	0.92	5.34	33.38	0.15	5.80	0.022	0.28	3.43	7.35	0.004	49.47	6.13
Cs2	Avg	9.85	95.24	794.64	7.90	13.42	0.042	3.15	2.40	10.39	101.19	1,089.64	30.96
	StdDev	1.45	8.57	80.36	0.23	7.30	0.039	6.25	2.48	9.18	63.04	1602.36	18.96
C1	Avg	10.01	97.26	977.40	8.26	12.85	0.011	1.34	2.92	13.39	0.034	58.74	43.89
	StdDev	1.13	2.48	144.20	0.11	4.56	0.010	3.37	2.92	7.79	0.051	81.01	19.98
C2	Avg	9.36	90.52	939.44	8.13	13.24	0.013	0.52	2.14	10.89	0.022	121.70	48.22
	StdDev	1.56	7.81	107.10	0.27	4.98	0.007	1.11	2.21	9.25	0.036	158.40	29.60
T1	Avg	9.18	89.57	725.78	7.68	12.40	0.001	0.27	0.34	11.64	0.000	97.83	46.27
	StdDev	0.85	2.59	42.05	0.07	4.50	0.002	0.43	0.24	8.88	0.000	210.97	56.97
T2	Avg	9.8	95.82	713.56	7.92	12.64	0.001	0.06	0.64	10.87	0.000	27.15	37.41
	StdDev	0.83	2.77	13.81	0.08	4.24	0.000	0.16	0.54	7.89	0.000	55.24	29.83
T3	Avg	9.26	96.41	1,496.44	7.95	16.58	0.045	0.93	1.99	11.26	0.001	87.43	150.91
	StdDev	1.42	8.54	349.15	0.10	4.43	0.025	0.73	1.48	9.27	0.004	215.53	94.40
T4	Avg	10.46	99.65	1,455.57	7.90	13.01	0.033	1.41	2.42	6.77	4.944	762.53	152.57
	StdDev	1.71	10.6	345.67	0.16	7.45	0.020	1.30	1.77	6.35	3.714	1,356.57	72.06

Macroinvertebrates were separated from the content of the bags on a tray and preserved in 70% ethanol until identification and counting. After identification, macroinvertebrates were classified into two groups: shredders and non-shredders. This categorization was based on the functional groups of the EU Asterics 3.1.1. (AQEM/STAR Ecological River Classification System) program package [23]. Each species that takes part in shredding to any extent was considered a shredder (e.g. *Limnius volckmari* (Panzer, 1793) is a shredder in only 10%). The number of shredders used and plotted later is the average numbers of the 3 samples taken each time.

Leaf litter content was cleaned from bed material with water, and dried at 70ºC until constant dry mass and then the mass was measured. For each sampling time and each litter type the dry mass of the 3 samples were averaged and the average dry mass (M_t) was plotted. The widely used exponential formula was used to determine the leaf litter decomposition rate [24, 25]:

$$M_t = M_0 \cdot e^{-kt} \tag{1}$$

...where M_t is dry leaf litter mass at time (day) t and M_0 is mass at time 0 (M_0=10 g); k is the exponential decay coefficient and t is time (days). Data were analyzed with the Origin8 program package, and statistical significances were calculated by R 2.7.2. The above exponential decay function was fitted with fixed amplitude (M_0=10 g); the fitted k values, standard error and the determination coefficients (*R2*) values of the fittings were determined.

Based on the daily decay coefficient, leaves were classified as "fast" ($k>0.01$), "medium" ($0.005<k<0.01$), and "slow" ($k<0.005$) decomposing [24]. We also calculated T as $T=\ln 2\ k^{-1}$, which can be explained as the half-life, and represents the time needed for a 50% decrease of the leaf litter mass.

Results

Water Chemistry

The annual average values of the water chemical variables (Table 2) at the eight sampling locations corresponded, on average, to similar values from streams in the Carpathian Basin. High PO_4^{3-}-P and total phosphorus (TP) values were measured at the Cs2 site, and we found high conductivity at T3 and T4 and an above-average temperature at T3. Even with these deviations the sampling points belong to the medium and good classes according to the Hungarian water quality classification.

Shredder Species

Shredders were represented by Gammaridae at all sites. The proportion of shredder species to the other functional groups was 55% and 75% at C1 and C2; 45% and 80% at

Cs1 and Cs2, over 90% at T1 and T2 and 50-80% at T3 and T4. The proportion of shredders did not differ significantly in bags containing leaf litter of different tree species *Quercus robur*, *Populus tremula*, *Salix alba* (Kruskal-Wallis test: χ^2_2=2.946, p=0.229, n=16).

The shredder community was composed of five species in the Cuha-stream: *Asellus aquaticus* (Linnaeus, 1758), *Limnius volckmari* (Panzer, 1793), *Gammarus roeselii* Gervais 1835, *Gammarus fossarum* Koch, 1835, Nemouridae (juvenile individuals). The quantity of shredder species commonly maximized around the 130th day of the experiment (Fig. 2A). Low densities in winter, in most cases, were followed by a very slight increase in the next spring.

At the two points of stream Csigere, six shredder species were identified (*Nemoura sciurus* Aubert, 1949; *Anabolia furcata* Brauer 1857; *Gammarus roeselii*; *Asellus aquaticus*; *Gammarus fossarum*; *Potamophylax rotundipennis* (Brauer, 1857). In this stream, a high density increase of shredders was observed after the winter period. Allochtonous organic matter load was higher at Cs1 than in Cs2, and at the latter site shredders fed rather on the macrophytes growing in the streambed than on allochtonous litter; moreover, the number of shredders was fairly even (Fig. 2B).

At the two natural points of stream Torna (T1, T2), five species (*Gammarus roeselii*, *Gammarus fossarum*, *Anabolia furcata*, *Chaetopteryx fusca* Brauer, 1857, *Potamophylax nigricornis* (Pictet, 1834)) of shredders were identified in the leaf litter bags. Shredder density maximized after the 100th day of exposure and after a decrease in winter it increased considerably next spring (Fig. 2C). These two natural points of Torna-stream offered ideal conditions for macroinvertebrates concerning shelter, flow, and food supply.

At the two heavily modified points of stream Torna (T3, T4) six species (*Gammarus roeselii*, *Gammarus fossarum*, *Anabolia furcata*, *Chaetopteryx fusca*, *Potamophylax nigricornis*, *Physella acuta* (Draparnaud 1805)) of shredders were found and their numbers, though rather low, increased during the experiment. They consumed the leaf litter by the end of autumn (Fig. 2D). The number of shredders was low (Fig. 2D), similar to the upstream part of the Cuha (Fig. 2A).

Leaf Litter Decomposition

In the Cuha-stream, leaf litter decomposed faster at C1 than at C2, i.e. decay rate at C1 is higher than at C2 (Table 3). At site C1, decomposition of *Quercus* was faster than that of *Populus,* while at C2 there was no substantial difference between decomposition rates.

The leaf litter decomposition rate in the stream Csigere (Table 3) was, at both locations, similar to the Cuha-stream, but *Salix* was consumed faster than *Populus*. While the average numbers of shredders per g litter in the bags at Cs1 was similar to C1 and C2, the same measure for Cs2 was significantly higher. The leaf litter decay (*k*) at the two natural points of the Torna-stream (T1, T2) was similar to that in the other examined streams, but the number of shredders per g litter was higher (Table 3, Fig. 3).

Leaf litter decay was considerably faster at the two heavily modified parts of Torna (T3, T4) than at any other natural or close-to-natural experimental sites, even though the average number of shredders in the bags was not particularly high (Table 3). In general, the leaf litter decomposition rate (*k*) depended rather on the sampling location than on the leaf species, there is no significance between *k* values and leaf litter type (Kruskal-Wallis test: χ^2_2=1.869, p=0.393, n=16).

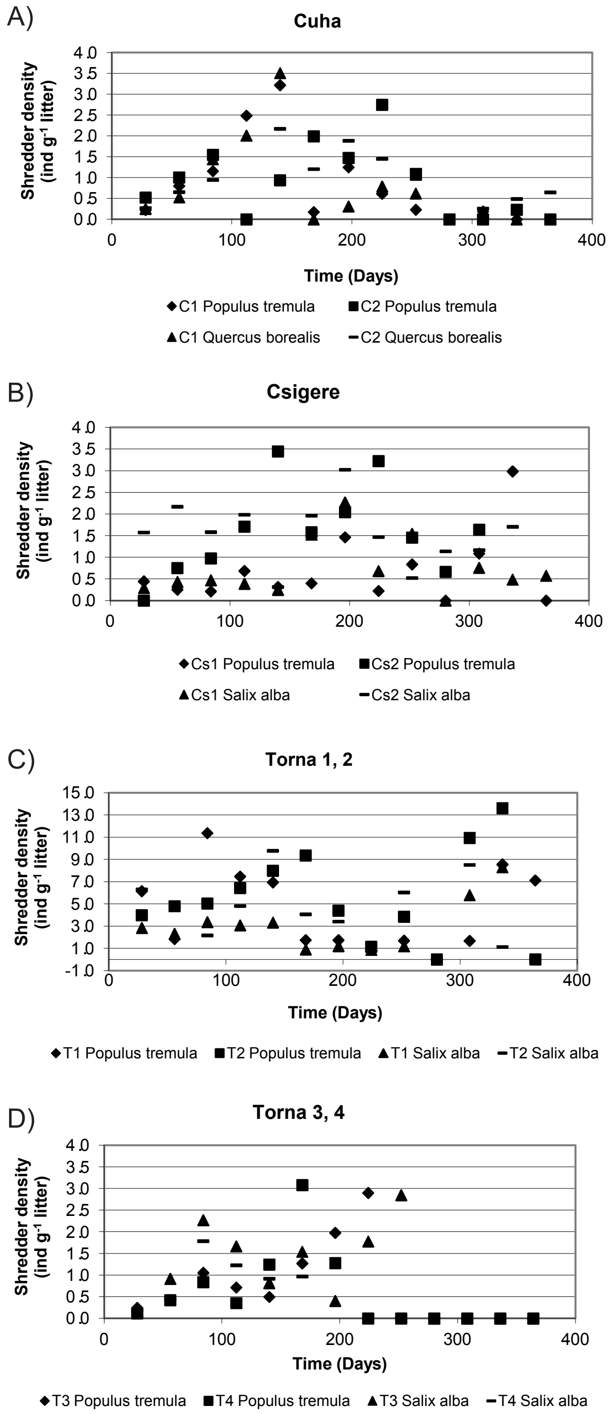

Fig. 2. Relative shredder quantity (specimen per gram of litter) in the two types of litter at the experimental sites (A – Cuha-stream (C1, C2), B – Csigere-stream (Cs1, Cs2), C – Torna-stream two natural points (T1, T2), D – Torna-stream two modified points (T3, T4)).

Table 3. Parameters of leaf litter decay at the 8 sampling locations.

Sampling site	Litter Type	Half-life±SE (days)	*k*±SE (d^{-1})	R^2 of linear fitting	Average Shredder density (Ind. g^{-1} litter)
C1	*Populus tremula*	122.90+22.05	0.0056+0.0012	0.47	0.863
C1	*Quercus borealis*	161.95+9.76	0.0043+0.0003	0.93	0.800
C2	*Populus tremula*	89.22+14.05	0.0078+0.0015	0.72	1.049
C2	*Quercus borealis*	89.50+7.27	0.0077+0.0007	0.94	1.017
Cs1	*Populus tremula*	152.5±13.6	0.0045±0.0004	0.90	0.742
Cs1	*Salix alba*	111.2±6.3	0.0062±0.0004	0.95	0.805
Cs2	*Populus tremula*	130.7±8.7	0.0053±0.0004	0.94	3.074
Cs2	*Salix alba*	127.0±10.8	0.0055±0.0005	0.92	4.011
T1	*Populus tremula*	115.45±7.77	0.0060±0.0004	0.95	4.77
T2	*Populus tremula*	88.31±5.39	0.0078±0.0005	0.96	6.50
T3	*Populus tremula*	63.87±4.21	0.0109±0.0008	0.97	1.93
T4	*Populus tremula*	61.01±4.53	0.0114±0.0009	0.97	1.05
T1	*Salix alba*	105.99±5.48	0.0065±0.0004	0.97	5.52
T2	*Salix alba*	85.04±5.83	0.0082±0.0006	0.95	4.70
T3	*Salix alba*	62.58±3.16	0.0111±0.0006	0.98	1.38
T4	*Salix alba*	52.75±6.56	0.0131±0.0019	0.93	2.01

Comparison of Experimental Sites

The two natural sites of the Torna stream, T1 and T2, had high shredder numbers per g foliar mass, while *k* was medium. The modified sites of this stream, T3 and T4, had a low specimen g^{-1} litter ratio, but high *k*. The sampling sites Cs1, C1, and C2 are between the T1, T2 and T3, T4 with respect to bed morphology (Fig. 3).

Site Cs2 was similar to T1 and T2 natural points according to the variables specimen g^{-1} litter and *k*. With the groups of Fig. 3 (the features described in the sites description) the distinction between Group I. (T3, T4) and Group II. (T1, T2, Cs2) is apparent.

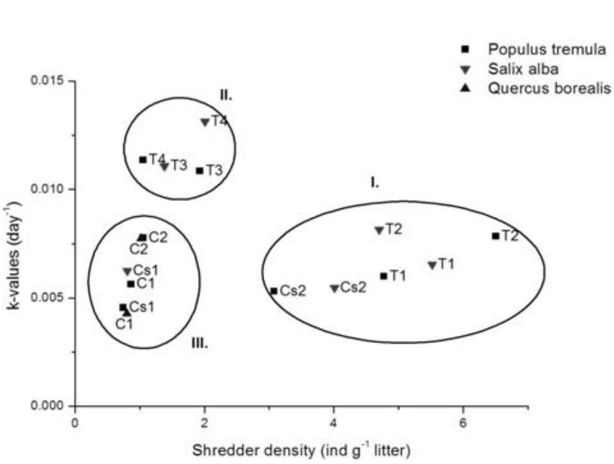

Fig. 3. Grouping of sampling sites based on average shredder quantity and *k*-value.

Group III. is formed by Cs1, C1, and C2. C1 and C2 had a low number shredder species because, having upstream character, there was substantial food accumulation beyond the litter bags. Cs1 has a low number of shredder species because the bed is muddy.

Correlation test of the *k* values and shredder densities did not show significant correlation between the *k* values and the shredder densities (Spearman correlation: r=0.288, p=0.280, n=16), which is demonstrated in Figs. 3 and 4.

At T1 the number of shredders rapidly reached the maximum, which was high (Fig. 4). While Fig. 3 shows T1 and

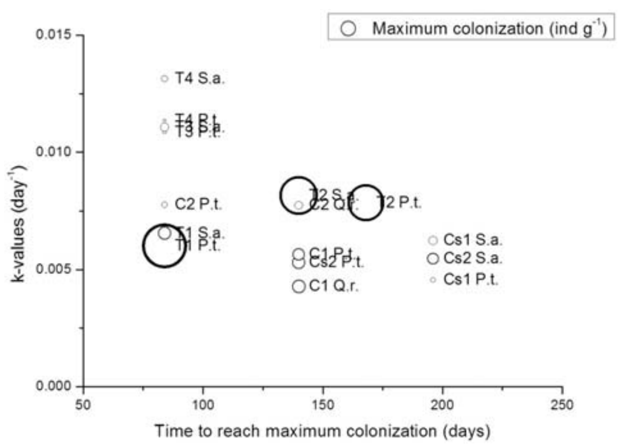

Fig. 4. Relationship between k and the time that was required for maximum colonization. Size of the dots is proportional to density at maximum colonization.

T2 in the same group (i.e. a lot of shredder species and medium *k*), Fig. 4 shows a small difference: while the number of shredders was high at both sites in the bags, to reach the maximum number of shredders took more time at T2 than at T1.

At C1 and C2, the number of shredders was medium and the speed of settling into the bags was also medium. At Cs1 and Cs2, settling into the bags was slow, but shredder quantity was medium. At the two modified sites (T3, T4), colonization of the bags was fast, but the maximum was provided by very few shredders.

Colonization in the bags of Group II (T1, T2, Cs2) was high, which corresponds to the amount of shredders in the stream outside the bag. A similar correspondence can be established for Group I. (T3, T4) where both the size of colonization in the bag and the amount of shredders in the stream was low (Figs. 3, 4). The exception is Group III (C1, C2, Cs1), where size of colonization in the bag is low while the amount of shredders in the stream is high.

Discussion

The water chemical results of the surveyed streams are in line with expectations in Hungary. The TP values (except for point Cs2) correspond to the values found in western Hungary [26], and there also was no significant difference in the main ion contents [27-29]. Deviation can be noticed at Cs2 sites, having higher PO_4^{3-}-P, total phosphorus (TP), and NH_4-N values, which is a result of aquaculture in an upstream fishpond and agricultural activity in the area without any riparian vegetation absorbing nutrients. At the modified water bodies (T3, T4), the higher conductivity values as well as higher temperature are driven by a midsize town with 32,000 inhabitants 9 km upstream from T3 (e.g. the site is impacted by treated sewage). The higher values are not exceptional in the region; even with these parameters we can conclude that the water chemical conditions of the streams were not extremely good and not extremely poor either; therefore, they could not influence substantially the experimental results.

The *k* values of leaf litter species depend on various factors. In studies by Graça et al. [24], *Salix lucida* and *Quercus alba* decomposed at medium rates and for *Quercus faginea* slow *k* was found [30]. In this survey, all leaf litter species fell into the fast decomposing category. In this survey for *Quercus robur* we also found *k* values corresponding to medium and slow decomposition in natural sites (C1 and C2). Langhaus et al. [31] also observed that the decay rate of black poplar (*Populus nigra*) depended on the water body it was placed into. Another paper describes that two poplar species (*Populus alba* and *Populus nigra*) decomposed faster in certain types of rivers, especially in spring and summer [32]. Our results on *Populus tremula* and *Salix alba* also supports the observation that decomposition was influenced not only by shredder quantity, but also by the features of the water body at some sampling sites. Thus our sampling sites, according to our results, could be divided into three groups.

Group 3 shows low shredder density combined with low leaf litter decay, which was found at C1, C2, and Cs1. All these three sites are natural with plenty of available organic matter so that shredders did not prefer the content of the leaf litter bags (c.f. Fig. 2C). A similar phenomenon was studied by Langhaus et al. [31] in NE-Italy, where undisturbed headwater streams were described as having plentiful accumulations of deciduous leaf detritus year-round [34]. Although *Quercus robur*, which was used in the experiment as the natural riparian vegetation of the area, has typically lower decomposition rates, as found in [30] and [31], the above statements are also supported by the results on *Populus tremula*.

Group 2, on the other hand, clusters sites T3 and T4 with low shredder density but high decomposition rates. At these sites the stream is surrounded by agricultural or urbanized areas, so there was no natural allochthonous litter load and the stream bed is heavily modified (trapezoid). This results on one hand in the scarcity in food resources, on the other in higher flow velocities. So the leaf litter fragments cannot remain in the bags for a long time, they drift away quickly. Whiles et al. [33] also observed unusually rapid litter decomposition rates in a disturbed stream, and their results support ours: in disturbed streams *k* value is high despite the low number of shredders, independently from leaf litter species. Statistical correlation between shredder density and *k* values was also insignificant.

In morphologically modified streams, e.g. when the bed is evened, the flow velocity increases and, as a consequence, other species colonize the stream than under natural conditions. Also, leaf litter drifts away fast, as there are no sections of the stream for its accumulation. In this way, even though the quantity of leaf litter decreases quickly, it is not decomposed and utilized locally.

In modified water bodies (varied course and bed material; [31]), there is not only a lack of appropriate macrozoobenthos habitats, but shredder species are starving as well because the little litter they get is washed away rapidly. River beds fortified with concrete have only very thin sediments that are insufficient for the macrophytes to settle, so not even this kind of food is available.

Webster and Waide [35] also described the effect of missing riparian vegetation relevant for points T3 and T4 of our study. According to this study, the decomposition rate of even the most resistant leaf litter species increased due to the lack of an alternative food source of shredders.

Tuchman and King [36] observed higher litter decomposition but lower shredder biomass in litterbags in Michigan headwater stream sections in agricultural areas, compared to streams with an undisturbed forest environment. This holds for both T3 and T4, located in a disturbed area, and C1 and C2, located in an undisturbed area. This implies that not only bed modifications, but also the alteration of riparian zones, differentially influences stream systems [37], because even if it does not directly decrease the number of shredders (it also does at points T3 and T4), it results in taxonomic changes of the fauna [33].

Finally, group 1 shows a transition between the above-described categories in which case high shredder density is combined with low leaf litter decay. T1, T2, and Cs2 sampling points are transitions between natural and heavily modified agricultural areas in terms of riparian belt, meandering of streambed and agricultural impact. T1 and T2 are suitable habitats, having large populations with high shredder diversity. This is combined with abundant organic matter available in multiple locations, which decreases the competition for the additional food in the litter bags and therefore results in low decomposition rates. While Cs2 has the least riparian vegetation out of the three sites, allochthonous organic input can feed the least amount of shredders. The organic matter in the litter bag attracted shredders, which results in relatively higher density of shredders with average decomposition rates, and the mechanical impact of stream velocity is minor.

The quantity of shredder species and the speed of leaf litter decay were different in the experimental streams; however, with no significant differences in the decay rates by various leaf species, as supported by Kruskal-Wallis tests.

Leaf litter decomposition rates can be influenced by several other factors. Leaf litter can drift away from smaller to larger water courses, but it accumulates in the channel-streams of agricultural areas, because they are in many cases not cleaned regularly enough from vegetation and deposits. As a consequence, ditches and streams do not drain off the water at bigger rains, and crop yield decreases due to the damage caused by inland water. Cleaning of stream beds contributes to the avoidance of deposit accumulation and inland water, but it does not contribute to the natural balance and the good ecological potential at these modified water courses [38].

Modified water bodies have low crop of macro-invertebrates due to bed morphology and limited availability of food (lack of or very sparse vegetation at the shores). The chemical composition of leaf litter is also important (nutrient content), and partly explains how shredders can survive in such places [38]. The varied usage of food also contributes to the variety of strategies under inappropriate and limited shelter in modified water bodies [39]. The flexible feeding strategy, which means that shredders are capable of living on other resources than CPOM in case it is needed, explains how the density of shredders can be higher than the resources at certain places [40, 41], and how they can survive under inappropriate circumstances. This mechanism is also working temporarily, when there is a hydrological event, e.g. a flood, which washes away leaf litter [4].

Strongly modified water bodies can often be found in densely inhabited or agricultural areas. The condition of streams running through agricultural areas could be improved with small forest belts in the direct vicinity of the streams [14]. Plants in the catchment area are important for the ecosystem of the stream [3] because leaf litter is balancing the chemical status of the water [42], it decreases the morphological change of the course and it diversifies the microhabitats in the bed [43, 44].

Conclusions

In conclusion, our study supports that leaf litter decomposition is not only the function of the shredder density in the area but also heavily dependent on the flow conditions driven by streambed morphology. Our study also supports that for appropriate leaf litter decomposition: 1) there should be a sufficient amount of leaf litter falling into the streams, and 2) leaf litter should not be immediately washed away. These two conditions are equally important since even if there is a riparian corridor along the stream, it cannot maintain habitat diversity if leaf litter immediately drifts away due to heavy bed modification, as in the cases of the modified water bodies in this study. In such heavily modified water courses the shredder density is low but the existing sparse population, due to starvation, consumes the offered food faster than can be observed in similar, but morphologically unmodified streams. Therefore, even though the fauna is not significantly poorer in such habitats, density of shredders and their food consumption, as functional parameters, clearly reflect the low ecological status of the water course.

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