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Research Paper

Flow Velocity Effect on Leaf Litter Breakdown in Tufa Depositing System (Plitvice Lakes, Croatia)

key words: decomposition, beech, butterbur, tufa

Abstract

Considerable amount of riparian leaf litter is annually supplied to the cascade Plitvice Lakes and trapped on tufa barriers where it decays together with aquatic macrophytes. These barriers are the sites of heavy calcite precipitation that can widely differ in terms of current velocity. We conducted a leaf-bag experiment at sites differing in flow velocity and tufa deposition rate. Decomposition of *Petasites* spp. and *Fagus sylvatica* was higher under high current (0.80 m/s) and high tufa deposition areas than in low current (< 0.20 m/s) and low tufa deposition areas (k = 0.085 *vs.* 0.021 for *Petasites* spp. and 0.009 *vs.* 0.002 for *Fagus sylvatica*). We concluded that although tufa deposition could interfere with decomposition by obstructing physical abrasion and also restricting microbial conditioning, thin calcite crusts developed on the surface of the leaves made them more fragile and thus accelerated their decomposition. High current velocity probably magnified this effect by supporting higher tufa deposition and coarser type of tufa fabrics.

1. Introduction

Leaf litter processing in aquatic ecosystems involves a sequence of processes, from the dissolution of labile organic compounds (leaching), microbial conditioning to mechanical fragmentation by macroinvertebrates (Webster and Benfield, 1986) and physical abrasion Boulton and Boon (1991), especially by current velocity. The rate of litter breakdown is determined by intrinsic differences among leaves, a number of environmental variables, and the feeding activity of detrivores (*e.g.*, Allan, 1995; Dangles and Chauvet, 2003; Ferreira *et al.*, 2006; LeRoy and Marks, 2006; Carter and Marks, 2007).

Several studies investigated the breakdown of leaf litter in karst systems where tufa precipitates (Casas and Gessner 1999; Vivas and Casas, 2002; Casas *et al.*, 2006; Carter and Marks, 2007). These studies reported contradictory results: Carter and Marks (2007) reported significantly faster breakdown at the tufa site than at the site without tufa precipitation, while Casas and Gessner (1999) found tufa precipitation to impair decomposition.

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With the aim of reconciliation of the different outcomes of the previous studies, learn how super-saturation by calcium carbonates affect litter decomposition and, therefore, nutrient cycling, we included flow velocity into a litter breakdown experiment in a Karst system with tufa precipitation. Our goal was to examine the interaction between current velocity and the intensity of tufa precipitation. For this purpose, we used two leaf species differing in their breakdown rates ("slow" and "fast"). Our hypotheses were that (1) higher current velocity would accelerate leaf breakdown, due to more powerful physical fragmentation and (2) higher tufa deposition would slow down the process of leaf decomposition by creating calcite layer on the surface of the leaves thus impeding physical abrasion.

2. Materials and Methods

2.1. Study Area and Site Description

Plitvice Lakes National Park (Croatia) is a barrage-lake system created by numerous tufa barriers and located in the karst region of north-western Dinarid Mountains. The system is approximately 8.2 km long, located at 636–503 m above sea level and divided into two sections (the upper and the lower lakes). The upper section comprising twelve lakes flows on a dolomite valley, ending with the largest lake (Kozjak Lake 0.83 km^2; 46 m deep). The string of the four lower lakes composing the lower section is located in a limestone canyon and finally joins the Korana River.

The lakes are characterized by specific hydrobiological properties such as low organic matter concentration, super-saturation by calcium carbonates and pH > 8.0 (SRDOČ *et al.*, 1985). According to the KÖPPENS climate classification, this area is influenced by both temperate and continental climates.

Considerable amount of riparian leaf litter is annually supplied to the lakes and trapped on tufa barriers (HORVATINČIĆ *et al.*, 2006), where it decays together with emergent and submerged aquatic macrophytes. These barriers are the sites of heavy calcite precipitation which creates heterogeneous morphological features, *i.e.*, great variety of microhabitats differing in flow velocity (narrow channels, wide plain bottom, small cascades *etc.*). Riparian vegetation, which is the major source of allochtonous organic matter in this system, consists mostly of *Fagus sylvatica* L. Tufa barriers are characterized by well-developed vegetation consisting predominantly of butterbur (*Petasites* sp.), willows (*Salix* sp.) and sawgrass (*Cladium mariscus* (L.) POHL.).

The chosen study sites were on two tufa barriers, one in the upper and other in the lower reach of the lake system (Fig. 1). The barriers of the upper lakes reach are known to have lower tufa deposition rates (LTD) compared to the barriers of the lower lakes, which support high tufa deposition rates (HTD) (GOLUBIĆ, 1969; MATONIČKIN KEPČIJA *et al.*, 2005).

2.2. Litter Decomposition Experiment

Two of the most common plant species in Plitvice lakes area (the herbaceous butterbur, *Petasites* spp. and the riparian woody common beech, *Fagus sylvatica* L.) were chosen for the litter decomposition experiment. Beech and butterbur can be classified as slow and fast decomposing species, respectively, according to the classification scheme by PETERSEN and CUMMINS (1974). Beech leaves were collected in autumn upon natural abscission, while butterbur leaves were cut from the plants while green. Three species of butterbur (*Petasites hybridus*, *P. kablikianus* and *P. albus*) are equally abundant on the barriers and were sampled together, due to inability of species determination in autumn. The leaves were air dried to constant mass. In order to convert a dry mass to ash-free dry mass, five replicated samples (1 g of dry mass each) from each leaf species were weighed on an analytical balance (0.1 mg precision), combusted in a muffle furnace at 500 °C for 5 hours and weighed again. Ten grams (dry mass) of leaf litter were placed into 20 × 30 cm PVC mesh bags with mesh size 2 × 8 mm. Leaf bags were fixed to perforated metal bars (15 per bar) and anchored in streambed on tufa barriers. Two reaches differing in flow velocities (slow < 0.2 m/s and fast 0.7–0.8 m/s) were chosen on each barrier, resulting in four sites abbreviated as LTD-FFV (low tufa deposition-fast flow velocity), LTD-SFV (low tufa deposition-slow flow velocity), HTD-FFV (high tufa deposition-fast flow velocity) and HTD-SFV (high tufa deposition-

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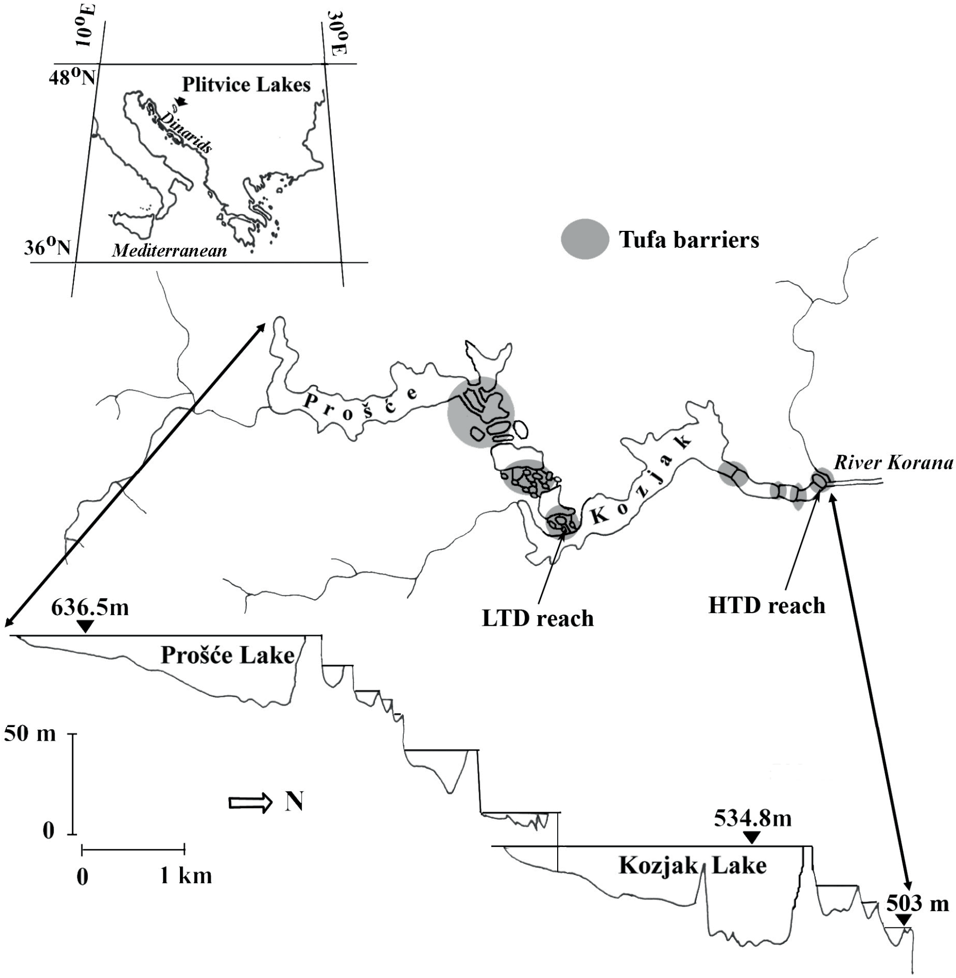

Figure 1. Map of the study area with the position of study reaches. LTD stands for low tufa deposition and HTD for high tufa deposition.

slow flow velocity). Leaf bags were placed in triplicates on each site (4 sites × 12 months × 2 leaf species × 3 = 288 bags). The experiment began in December 2006 and ended in November 2007. Every month during one year 3 bags were retrieved from each site. Upon collection, leaf bags were transported to the laboratory and processed the same day. They were cleaned of debris and invertebrates, air dried to constant mass and weighed. The material was then treated with 15% HCl for 15 seconds and washed with distilled water to remove the deposited tufa, dried and weighed again (the difference provided the mass of deposited tufa). Leaves were then combusted in a muffle furnace at 500 °C for 5 hours and weighed. Ash free dry mass (AFDM), total mass of deposited tufa in a sample and ratio between deposited tufa and AFDW was then calculated.

Measurements of physico-chemical water characteristics were carried out during each retrieval date. Current velocity was measured with current velocity meter SWOFFER 3000 (Swoffer Instruments).

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Dissolved oxygen concentrations, pH, conductivity and temperature were measured *in situ* using a field multi-parameter probe Multi340i (WTW). Water samples were collected from the study sites in 1 L plastic bottles for laboratory analyses, which were done within 3 h after sampling. Chemical oxygen demand (COD) was determined using potassium permanganate acidic method. Orthophosphate concentration was determined using the phosphoantimonylmolybdenum complex method and nitrates using the cadmium reduction method according to APHA (1995) procedures.

2.3. Statistical Analysis

Man-Witney U-test was used to test for difference between water physico-chemical properties of the upper and lower lake sections. Spearman rank correlation coefficient (R_S) was calculated between mass of deposited tufa in a sample and time, as well as between deposited tufa/AFDM ratio and time, to test for significance of increase/decrease with time of exposure.

The negative exponential decay model ($N_t = N_0\, e^{-kt}$) was used to determine leaf litter decomposition rates k (PETERSEN and CUMMINS, 1974). Fitting of the model to data was done by least squares non-linear regression analysis. To test for differences in the rates of decomposition between the treatments we used an ANCOVA procedure with time as a continuous variable, ln(AFDM) as the dependent variable and treatment as a categorical variable. If the ANCOVA results were significant, Tukey test was used for *post-hoc* analyses.

3. Results

Chemical and physical parameters of water were similar between the HTD and LTD reaches, differing only in terms of current velocity (Table 1). Fast decomposition of butterbur compared to beech was evident already after three months of immersion in the HTD-FFV site, as no butterbur leaves was left in the bags. It took six months for butterbur litter to dissapear from leaf bags in the HTD-SFV site, and eight and ten months in the LTD-FFV and the LTD-SFV sites, respectively. Beech leaf litter persisted on all sites during the investigated 12 months, with the exception of the HTD-FFV site in which it dissapeared after 10 months. The difference between beech and butterbur breakdown rates was nearly an order

Table 1. Physical and chemical characteristics (mean ± *SD*) of the two reaches. *P* value shows the result of the Mann-Witney U test for comparisons between reaches. n.s. = not significant ($P > 0.05$). *Data from MATONIČKIN KEPČIJA *et al.* (2005).

Variable		Upper Lakes site (LTD)	Lower Lakes site (HTD)	*P*
Location (GPS)		44°52′45.28″ N 15°36′48.44″ E	44°54′7.45″ N 15°36′40.51″ E	
Altitude (m a.s.l.)		554	534	
Tufa deposition rate (mg/dm^2/d)*		0.31	4.40	
O_2 (mg/l)		10.22 ± 1.87	10.05 ± 1.77	n.s.
pH		8.32 ± 0.11	8.36 ± 0.12	n.s.
Conductivity (μS/cm)		363 ± 19	362 ± 20	n.s.
Temperature (ºC)		13.23 ± 6.49	13.11 ± 6.58	n.s.
$N–NO_3^-$ (mg/l)		0.395 ± 0.140	0.387 ± 0.075	n.s.
$P–PO_4^{3-}$ (mg/l)		0.0033 ± 0.005	0.0042 ± 0.005	n.s.
COD_{KMnO^4} (mg O_2/l)		1.036 ± 0.410	1.091 ± 0.397	n.s.
Mean flow velocity (m/s)	Fast	0.46 ± 0.16	1.06 ± 0.48	< 0.05
	Slow	< 0.20	< 0.20	

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Table 2. Decomposition rates for each leaf species incubated in sites of low and high tufa deposition rate and at fast and slow velocity. r^2 is the variance explained by the negative exponential model.

	Tufa deposition rate	Flow velocity	k (d^{-1})	r^2
Beech	Low	Fast	0.0029	0.783
		Slow	0.0021	0.878
	High	Fast	0.0087	0.878
		Slow	0.0020	0.901
Butterbur	Low	Fast	0.0259	0.960
		Slow	0.0215	0.956
	High	Fast	0.0853	0.998
		Slow	0.0425	0.996

of magnitude (Table 2). For both beech and butterbur, breakdown was significantly faster in fast flow velocity compared to slow flow velocity in the HTD reach (ANCOVA, $P < 0.001$), but not in the LTD reach ($P > 0.05$), despite of an evident trend. Higher tufa deposition supported significantly faster breakdown of butterbur leaves in both flow velocities ($P < 0.01$), with the same proved as significant for beech in fast flow velocity ($P < 0.001$).

The ratio between the mass of deposited tufa and the mass of remaining leaf material increased significantly with time for beech in both flow velocities in HTD reach (slow flow: $R_S = 0.91$, $P < 0.001$, fast flow: $R_S = 0.95$, $P < 0.001$), while no such relation was found in LTD reach. The same pattern was observed for butterbur (HTD, slow flow: $R_S = 1.00$, fast flow: n.a.). This ratio was the highest for beech samples in the HTD reach with a peak of 11.01 g of tufa per g of leaf in fast velocity site. The lowest was recorded for beech in the LTD-SFV site (0.11 g of tufa per g of leaf). Significant differences in those ratios were found for beech between LTD and HTD reaches for both velocities (ANCOVA, $P < 0.001$), and between velocities in HTD reach ($P < 0.001$). No significant differences were detected for butterbur in any combination. In the LTD reach, where butterbur persisted long enough to be compared with beech, this ratio was higher for butterbur leaves (Fig. 2).

4. Discussion

Decomposition of the two leaf species was accelerated in sites with fast flow velocity, suggesting physical fragmentation caused by flowing water as an important breakdown factor. This agrees with findings from CASAS *et al.* (2000); FERREIRA *et al.* (2006) and LEROY and MARKS (2006). FERREIRA *et al.* (2006) discussed that high current velocity in conjuncton with higher amount of transported sediment could affect the breakdown rates of alder leaves through mechanical abrasion. However, fast flow velocity might have also stimulated fungal assemblages as shown by FERREIRA and GRAÇA (2006). This might result in faster breakdown, since aquatic hyphomycetes are known to play a great role in the leaves decomposition process (ALLAN, 1995; GESSNER and CHAUVET, 1997). Shredders, though not analysed in our study, were previously shown to be more abundant in high than in low current stream sections of other studies (*e.g.*, GRAÇA *et al.*, 2004; FERREIRA *et al.* 2006), so we can not rule out their possible importance in the observed pattern. The unexpectedly high variability of flow velocity destabilized our experimental design, as LTD-FFV and HTD-FFV sites did not have equivalent flow velocities throughout the study. Observed differences in flow velocity

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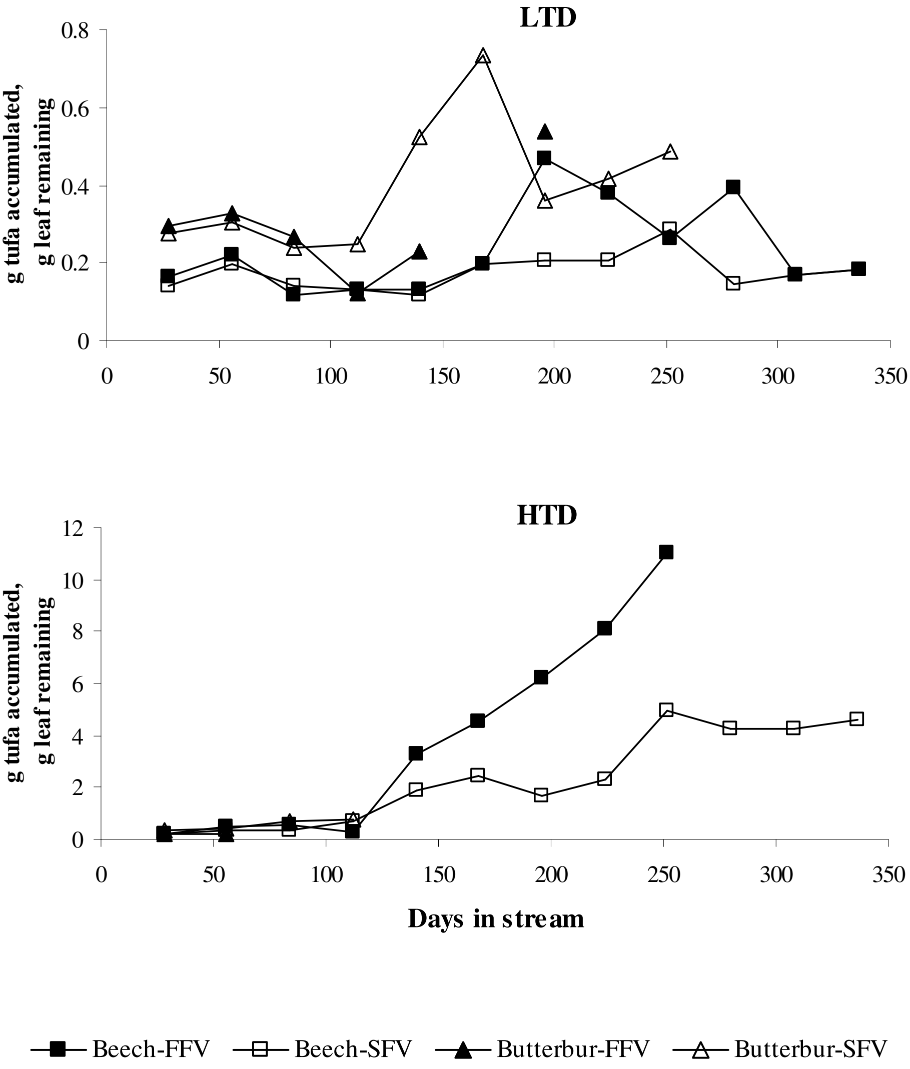

Figure 2. The dynamics of mass of tufa deposited per leaf mass in low tufa deposition (LTD) and high tufa deposition (HTD) reach; FFV = fast flow velocity; SFV = slow flow velocity.

are attributed to specific morphology of tufa barriers and considerable seasonal differences in discharge, combined with the effect of barrage lakes with their retention capacity.

The pattern of high decomposition rate in high tufa deposition sites differed from the reported by CASAS and GESSNER (1999) and CASAS *et al.* (2006). Therefore, we rejected our second hypothesis. However, the sites in the reported studies had considerably higher tufa precipitation compared to ours. Bearing in mind differences in experimental procedures when comparing those studies, it might be possible that only extensive calcite precipitation impedes leaf breakdown, whereas intermediate intensity of tufa deposits accelerate it. Our results are in accordance with the reported by CARTER and MARKS (2007) and MARKS *et al.*

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(2006) who also associated faster breakdown rates with high tufa precipitation, and noted less intensive calcite deposition compared to CASAS and GESSNER (1999).

Current velocity can, however, influence quality and quantity of tufa deposits. Increase in current velocity supports faster calcite precipitation rate (CHEN *et al.*, 2004), which was also observed in our study. Higher water flow leads to spar dominated deposits, characterised by coarse bladed fringes of rhomboid crystals (PEDLEY, 2000). Low current velocity supports loose calcite deposite wheras high current velocity leads to tight crusts (MATONIČKIN KEPČIJA *et al.*, 2005). We postulate that thin calcite crusts, which were well developed on leaves in HTD reach, made them more fragile, and thus more prone to mechanical fragmentation. The type of calcite crystals might have intensified the breakdovn process in our study. We therefore conclude that differences in current velocity affects leaf breakdown directly by (a) physical fragmentation and indirectly by (b) influencing the amount of tufa deposition and (c) influencing the type of tufa fabrics.

Fast decomposing butterbur became more encrusted compared to slow decomposing beech. The reason for this might reside in different surface properties of the butterbur leaves. TURNER and JONES (2005) discussed about the importance of surface properties in the development of calcium carbonate precipitates. Other factor which might cause observed difference is more porous structure of butterbur leaf bags, due to higher specific weight of butterbur in comparison to beech, allowing a higher rate of water exchange over the surface of the leaves.

In our study, summer months supported the highest peaks in tufa deposition as previously reported by ARP *et al.* (2001) and MATONIČKIN KEPČIJA *et al.* (2005). Increased temperature also promotes leaf decomposition (HAUER and LAMBERTI, 2006; MARKS *et al.*, 2006). This, together with mentioned increase in tufa deposition, might influence the dynamics of leaf breakdown, and thereby estimated k's. One way to avoid this problem would have been a simultaneous retrieval design as used by CASAS and GESSNER (1999).

In summary, factors which generally accelerated leaf breakdown were fast current velocity and high tufa deposition. Due to possible effect of current velocity on tufa deposition combined with variability in current velocity in this study, we could not partition their effects on the process of leaf breakdown.

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